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Ecological Drivers of Carnivoran Body Shape Evolution

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ABSTRACT: Morphological diversity is often attributed as adaptations to distinct ecologies. Although biologists have long hypothesized that distinct ecologies drive the evolution of body shape, these relationships are rarely tested across macroevolutionary scales in mammals. Here, I tested hypotheses that locomotor, hunting, and dietary ecologies influenced body shape evolution in carnivorans, a morphologically and ecologically diverse clade of mammals. I found that adaptive models with ecological trait regimes were poor predictors of carnivoran body shape and the underlying morphological components that contribute to body shape variation. Instead, the best-supported model exhibited clade-based evolutionary shifts, indicating that the complexity and variation of body shape landscape cannot be effectively captured by a priori ecological regimes. However, ecological adaptations of body shapes cannot be ruled out, as aquatic and terrestrial carnivorans exhibited opposite allometric patterns of body shape that may be driven by different gravitational constraints associated with these different environments. Similar to body size, body shape is a prominent feature of vertebrate morphology that may transcend one-to-one mapping relationships between morphology and ecological traits, enabling species with distinct body shapes to exploit similar resources and exhibit similar ecologies. Together, these results demonstrate that the multidimensionality of both body shape morphology and ecology makes it difficult to disentangle the complex relationship among morphological evolution, ecological diversity, and phylogeny across macroevolutionary scales.

Keywords: axial skeleton, body elongation, ecomorphology, macroevolution, phylogenetic comparative methods, thoracolumbar vertebrae.

Introduction

Biologists have striven to investigate the selective forces that drive and maintain phenotypic diversity across the tree of life. Advances in phylogenetic comparative methods have provided evidence for adaptive evolution of morphologies with respect to different ecological traits. Perhaps the most commonly examined morphological trait is body size because it is easier to obtain from the literature and, more importantly, many ecological, physiological, and morphological traits scale with size (Schmidt-Nielsen 1984; LaBarbera 1989). Therefore, body size is often used as a proxy for functionally relevant morphologies (e.g., jaws, limbs, vertebrae) to test macroevolutionary relationships with ecological traits (Price and Hopkins 2015; Gearty and Payne 2019; Burns and Bloom 2020; Grossnickle 2020; Velasco et al. 2020). However, using body size as a proxy may conceal macroevolutionary patterns that otherwise would have been uncovered when using functionally relevant traits (Slater and Friscia 2019; Grossnickle 2020). Unsurprisingly, many researchers have revealed strong relationships between dietary ecologies and craniomandibular morphology (Janis 1990; Olsen 2017; Law et al. 2018*a*; Arbour et al. 2019; Grossnickle 2020; Paluh et al. 2020) as well as between locomotor and hunting behaviors and the limbs (Van Valkenburgh 1985; Taylor 1989; Higham et al. 2015; Citadini et al. 2018; Baeckens et al. 2020) and vertebrae (Buchholtz 1998; Randau et al. 2016; Jones et al. 2018; Gillet et al. 2019; Luger et al. 2019).

Although the adaptive evolution of functionally relevant morphologies such as skulls, limbs, and vertebrae are well studied, whether ecological traits such as locomotion, hunting behavior, and diet also influence overall body shape remains unclear across macroevolutionary scales. Body shape is a prominent feature of the body plan with important effects on the physiology, performance, and ecology of organisms (Brown and Lasiewski 1972; Sharpe et al. 2015; Ward et al. 2015; Law et al. 2019; Morinaga and Bergmann 2020). The continuum from body elongation to body robustness is the primary axis of body shape variation within many vertebrate clades (Ward and Mehta 2010; Bergmann and Irschick 2012; Price et al. 2019). Variation in body shape facilitates morphological, functional, and ecological innovations that can lead to increased diversification and/or niche specialization (Wiens et al. 2006; Collar et al. 2016; Law 2019; Morinaga and Bergmann 2020). For example,

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extreme body elongation in Australian *Lerista* lizards enhances fossorial locomotion by enabling elongate species to penetrate sand substrates faster than more robust bodied species (Morinaga and Bergmann 2020). Similarly, evolutionary shifts toward more elongate bodies is hypothesized to enable mustelid weasels to hunt prey in crevices, burrows, and other small constricted spaces (Law et al. 2018*b*, 2019). However, empirical studies testing whether distinct locomotor ecologies drives adaptive evolution of different body shapes have produced conflicting results in fishes, salamanders, and reptiles (Blankers et al. 2012; Friedman et al. 2016; Baken and Adams 2019; Grinham and Norman 2020), and these relationships are completely unknown in mammals. In mammals, hunting behavior—and subsequently dietary differences—can also influence the evolution of different parts of the body plan (Van Valkenburgh 1985; Polly 2007; Santana et al. 2010; Slater 2015), but how they relate to overall body shape is also unknown. Furthermore, body shape variation is driven through multiple pathways, including the reduction of body depth, elongation of the head, and lengthening of the body axis by increasing individual vertebral lengths or adding additional vertebrae to the body across evolutionary time (Parra-Olea and Wake 2001; Head and Polly 2007; Ward and Mehta 2010; Collar et al. 2016). Despite these studies, investigation of how locomotion, hunting behavior, and diet influence the adaptive evolution of these underlying morphological components remains largely untested using phylogenetic evolutionary modeling approaches.

In this study, I tested the hypothesis that distinct ecologies influenced the evolution of body size and shape in carnivoran mammals. Carnivora is an ideal clade to test this because of its high species richness (>280 species; fourth-largest mammalian order) and diverse ecologies in locomotion (aquatic to semifossorial to arboreal lifestyles), hunting behaviors (rapid cursorial pursuits to digging), and diets (carnivory to omnivory to herbivory; Wilson and Mittermeier 2009). These diverse ecologies enable carnivorans to survive in all biomes across the planet from deserts and tropical forests to aquatic waterways and the ocean. In addition, carnivorans range in body sizes and shapes from large robust bears to small elongate weasels. Although recent work revealed that smaller carnivorans exhibited more elongate bodies, body size explained only 42% of body shape variation (Law 2021*a*). This suggests that additional independent factors may influence body size and body shape separately across carnivoran evolution. Furthermore, multiple morphological components contribute to carnivoran body shape variation (Law 2021*a*); therefore, I also test whether locomotor, hunting, and dietary ecologies influenced the evolution of these underlying morphological components. Because of the different mechanical demands of moving through diverse environments (Kardong 2014), I predict that locomotion and hunting behavior will have the greatest influence on the evolution of carnivoran body size and shape as well as on the thoracolumbar region underlying body shape variation.

Methods

Body Shape and Size and Ecological Data

I quantified carnivoran body shape and size using osteological specimens held at 10 natural history museum collections. My data set consisted of 205 carnivoran species (~74% of total species diversity), sampling between one and 10 individuals per species ($N = 685$ individuals; median $= 3$ individuals per species; data have been deposited in the Dryad Digital Repository [https://doi.org/10.5061/dryad.pg4f4qrpm; Law 2021*b*]). All specimens were fully mature, determined by the closure of exoccipital-basioccipital and basisphenoid-basioccipital sutures on the cranium and ossification of all vertebrae and limb bones. I used a combination of females, males, and unknown sexes because I was unable to use just one sex without compromising sample sizes, in terms of both the number of species and the number of individuals per species used. Carnivoran body shapes were quantified as the head-body elongation ratio (hbER), which was calculated as the sum of head length (L_H) and body length (L_B) divided by the body depth (L_R): $\text{hbER} = (L_H + L_B)/L_R$. I measured head length as the condylobasal length of the cranium. I estimated body length by summing the centrum lengths (measured along the ventral surface of the vertebral centrum) of each cervical, thoracic, lumbar, and sacral vertebrae, and I estimated body depth as the average length of the four longest ribs. Each rib was measured as a curve from the end of the capitulum to the point of articulation with the costal cartilage. I omitted measurements of the caudal region in calculations of body length because the number of caudal vertebrae in most species is unknown and there was no way to determine whether the osteological specimens that we used contained all caudal vertebrae.

I also obtained the underlying morphological components that contribute to body shape variation. I quantified head elongation ratio (head ER) by dividing cranial length (L_H) by cranial height (H_H). I then used a modified version of the axial elongation index (AEI; Ward and Brainerd 2007; Law et al. 2019) to examine how each vertebral region (i.e., cervical, thoracic, lumbar, and sacral) contributes to elongation. For each vertebral region (V), I calculated AEI_V as the total sum of vertebral lengths (L_V measured along the ventral surface of the vertebral centrum) divided by the average vertebral height (H_V measured from the ventral surface of the centrum to the tip of the neural spine): $\text{AEI}_V = \Sigma L_V/\text{mean}(H_V)$.

Last, body size was quantified as the geometric mean of linear measurements taken from the cranium, vertebrae, and ribs (i.e., cranial length and height, curved rib length, and length and height of each vertebrae). The geometric mean was derived from the *N*th root of the product of *N* ($N = 11$) linear measurements, which is widely used as a predictor of the size of an individual (Mosimann 1970; Jungers et al. 1995). All measurements were taken to the nearest 0.01 mm with digital calipers. Species means were calculated prior to statistical analyses.

I classified the 205 carnivoran species into one of six locomotor categories: arboreal (species that primarily live in trees and rarely come down to the ground), semiarboreal (species that spend equal time in trees and on the ground), aquatic (species that primarily live in the ocean), semiaquatic (species that regularly swim for dispersal and/or foraging), semifossorial (species that regularly dig for shelter and/or foraging), and terrestrial (species that primarily live on the ground). Similarly, I classified the 205 species into one of six hunting behavior categories: ambush (species that stalk and kill prey within a short distance), pounce (species that conduct a moving search ending with a pounce or short chase), pursuit (species that chase prey over long distances), occasional (species that rarely hunt), semifossorial (species that dig for prey), and aquatic (species that hunt in the aquatic/marine system). I classified the 205 species into six dietary categories: carnivory (diets consist of >70% terrestrial vertebrates), omnivory (diets consist of 50%–70% terrestrial vertebrates), insectivory (diets consist of >70% nonplants and nonvertebrates), aquatic carnivory (diets consist of >90% aquatic prey), and herbivory (diets consist of >90% plant material). Definitions of locomotor and hunting behaviors were largely derived from Van Valkenhurgh (1985) and Samuels et al. (2013), and dietary ecologies were obtained from the *Handbook of the Mammals of the World* (Wilson and Mittermeier 2009). Although aquatic carnivorans also exhibit diverse locomotor and feeding ecologies (Kienle et al. 2017), I did not separate these ecologies further for three reasons: (1) underwater locomotion and feeding are not well defined and quantified, (2) differences in hunting behavior are often analyzed with respect to the morphology and function of the skull but rarely examined with respect to the body, and (3) there are too few aquatic species and separating them into distinct categories may lead to inaccurate estimations of trait optima.

Phylogenetic Comparative Methods

I performed all analyses under a phylogenetic framework using the most recent phylogeny of mammals pruned to include just carnivorans (Upham et al. 2019). All analyses were performed in R version 3.5.1 (R Core Team 2017).

I first tested whether locomotor, hunting, and dietary ecologies influenced the relationship between hbER and body size using three phylogenetic generalized least squares (PGLS) with an ANCOVA design. I evaluated the statistical significance of the slope vector angles of each regime using the random residual permutation procedure (RRPP; Adams and Collyer 2018) with 1,000 iterations in the R package RRPP (ver. 0.3.0; Collyer and Adams 2018).

I then tested the hypothesis that locomotor, hunting, and dietary ecologies influenced the evolution of body shape (hbER) and body size (size) using generalized evolutionary models (Hansen 1997; Butler and King 2004). I fit five models independently to my hbER and size data sets: a single-rate Brownian motion model (BM1), a single-optimum Ornstein-Uhlenbeck model (OU1), and three multipeak Ornstein-Uhlenbeck models (OUMs) that allowed locomotor ($\mathrm{OUM}_{\mathrm{locomotion}}$), hunting ($\mathrm{OUM}_{\mathrm{hunting}}$), and dietary ($\mathrm{OUM}_{\mathrm{diet}}$) regimes to exhibit different adaptive optima. All models were fit using the R package OUwie (Beaulieu et al. 2012) across 500 stochastically mapped trees to take into account uncertainty in phylogenetic topology and the ancestral character states. I inferred the evolution of locomotory, hunting, and dietary regimes by performing stochastic character mapping with symmetric transition rates between regimes (Nielsen 2002; Huelsenbeck et al. 2003; Bollback 2006) using the make.simmap function in the phytools R package (Revell 2011). I simulated 10 stochastic character maps across 1,000 tree topologies randomly drawn from the posterior distribution of trees (Upham et al. 2019), resulting in 10,000 character maps for each set of locomotory, hunting, and dietary regimes. I randomly sampled 500 trees for subsequent analyses. Additionally, I accounted for trait measurement error by incorporating the standard errors of species means to each model and used the mean standard error of all species for species with only one specimen. Relative support for each of the five models was assessed through computation of small sample–corrected Akaike information criterion weights (AICcW). All models with ΔAICc below 2 were considered to be supported by the data (Burnham and Anderson 2002). I then generated 95% confidence intervals for all model parameters of the best-fit model using parametric bootstrapping with the OUwie.boot function in the R package OUwie (Beaulieu et al. 2012). Because of computational limits, I used a random sample of just 100 character maps and performed 10 bootstrap replicates per stochastic character map sampled. To determine whether I had significant power to accurately distinguish complex OU models from Brownian motion, I performed 1,000 OUwie simulations for hbER and size using the parameter estimates of the best-fit model in the empirical data set. These simulated data sets were generated using OUwie.sim (Beaulieu et al. 2012). I then ran the simulated data through all five models in OUwie to determine whether the simulated model could be accurately recovered (Boettiger et al. 2012). A potential caveat to my evolutionary modeling analyses is that hbER is a ratio. The use of ratios may violate the normal assumptions of processes like Brownian motion where the ratio may not necessarily evolve under the same rate as the two variables. A worst-case scenario is that the evolutionary rate of the ratio will exponentially increase, whereas the constituent variables evolve at a constant rate if the denominator is much smaller than the numerator (D. Polly, personal communication). This caveat is unlikely to affect the outcome of these results because I am primarily focused on examining the optima rather than the evolutionary rates. Nevertheless, additional work is needed to investigate best practices to address these issues with the use of ratios.

Additional factors aside from my locomotory, hunting, and dietary ecologies may also influence the evolution of carnivoran body shape and size. Model selection approaches may unintentionally hide patterns of phylogenetic natural history that are biologically relevant (Uyeda et al. 2018). Therefore, I also quantified evolutionary shifts of carnivoran body shape and size without a priori groupings of locomotor, hunting, and dietary ecologies with the R package bayou (ver. 2.1.1; Uyeda and Harmon 2014). Bayou uses a reversible-jump Markov chain Monte Carlo (MCMC) to fit multipeak OU models to estimate the placement and magnitude of regime shifts. I placed a Poisson prior with $\lambda = 16$ on the number of shifts between adaptive regimes and allowed only one shift per branch with equal probability that each branch has a shift. I ran two independent MCMC chains with 3 million generations each sampled every 10,000 and examined whether the two chains converged using Gelman and Rubin's R statistic. All effective sample sizes were >200 after discarding the first 30% of samples as burn-in. I reported only evolutionary shifts with a posterior probability (pp) above 0.5; parameters were averaged from the two chains. I then converted the bayou model into the OUwie format to compare ecology-based OUMs with this clade-based model using the bayou2OUwie R function (Uyeda and Harmon 2014). I also generated 95% confidence intervals for all model parameters of the bayou model using parametric bootstrapping with the OUwie.boot function in the R package OUwie. Relative support for each of the six models was assessed through computation of AICcW, as described above. Because body shape is driven by strong allometric effects of body size (Law 2021*a*), I also performed OUwie and bayou analyses on size-corrected hbER. I size-corrected hbER by obtaining residuals from a PGLS regression of ln hbER against ln body size (geometric mean) using the R function phyl.resid (Revell 2009). I also performed OUwie and bayou analyses without pinnipeds because these aquatic carnivorans are vastly different and could potentially influence model selection.

Last, multiple morphological pathways contribute to carnivoran body shape variation, including elongation/shortening of the head (head ER), elongation/shortening of vertebral regions (cervical AEI, thoracic AEI, lumbar AEI, sacral AEI), and reduction/widening of body depth (size-corrected rib length; Law 2021*a*). Therefore, I also tested how locomotor, hunting, and dietary ecologies influenced the evolution of these morphological components using the methods described above.

Results

Ecological Effects on Body Shape–Body Size Relationships

Carnivorans exhibit a relationship between body size and hbER where larger carnivorans exhibited more robust bodies and smaller carnivorans exhibited more elongate bodies (Law 2021*a*). Here, further investigation revealed that locomotor ($Z = 3.88$, $P = .001$), hunting behavior ($Z = 3.66$, $P = .001$), and diet ($Z = 3.13$, $P = .001$) all influenced the relationship between body size and hbER. However, statistical testing of the slope vectors revealed that this was driven by carnivorans with aquatic regimes (fig. 1). Carnivorans with aquatic locomotion, aquatic hunting behavior, and aquatic dietary ecology exhibited positive slope vectors that were significantly different from most carnivoran regimes ($P = .001$–$.047$; table S1; tables S1–S4 are available online). In contrast, post hoc pairwise comparison tests revealed that terrestrial carnivorans with different ecological regimes did not statistically differ from one another ($P > .296$; table S1).

Ecological Effects on Body Shape Evolution

When excluding the data-driven approach of bayou, the multipeak $\text{OUM}_{\text{hunting}}$ model was the best-fitting model for hbER (mAICcW $= 0.49$; mAICcW is the mean AICcW across all 500 replications), whereas $\text{OUM}_{\text{locomotion}}$ and OUM_{diet} models received poor support (AICcW < 0.08). However, parametric bootstrapping of the $\text{OUM}_{\text{hunting}}$ model revealed that the 95% confidence intervals (in brackets) of Θ values overlapped between hunting regimes ($\Theta_{\text{ambush}} = 5.1$ [4.1 to 7.5], $\Theta_{\text{aquatic}} = 4.8$ [3.9 to 7.1], $\Theta_{\text{occasional}} = 4.9$ [4.5 to 6.2], $\Theta_{\text{pounce}} = 6.0$ [4.9 to 6.8], $\Theta_{\text{semifossorial}} = 4.9$ [3.6 to 7.8]; Θ values reverted from ln transformed values), indicating that optimal values of hbER do not significantly differ between hunting behaviors. The Θ value associated with the pursuit regime exhibited an unrealistic optimum potentially driven by the low number of pursuit species ($n = 5$; see "Discussion"). Nevertheless, simulations under the best-fitting model ($\text{OUM}_{\text{hunting}}$) confirm that there was substantial statistical power to distinguish

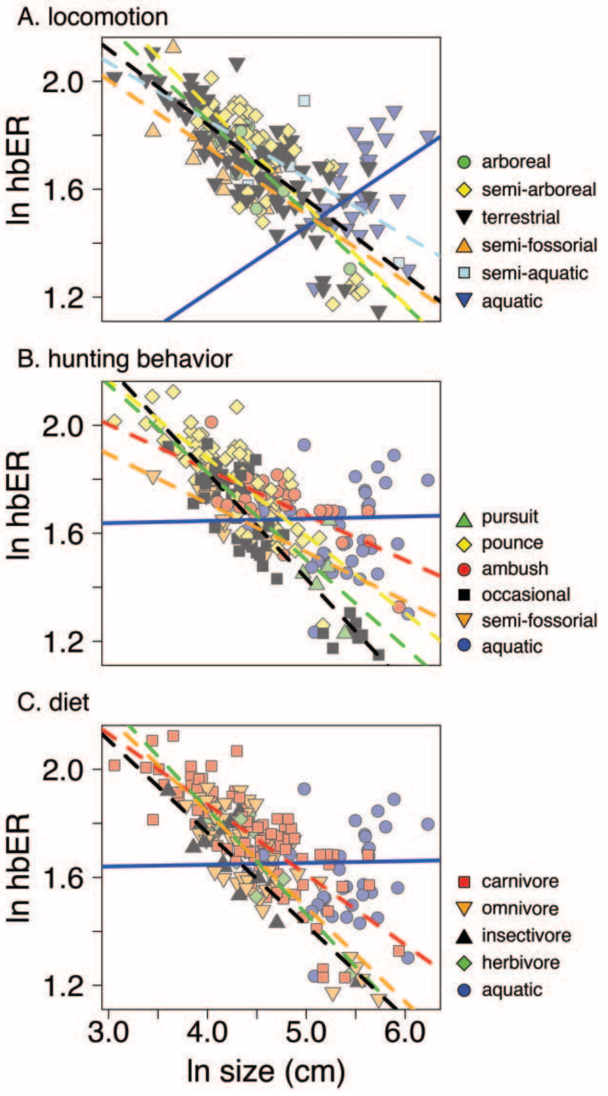

Figure 1: Plots of ln body size and ln head-body elongation ratio (hbER) subsetted by locomotion (*A*), hunting behavior (*B*), and dietary ecology (*C*). Dashed lines indicate that regimes did not significantly differ from each other.

complex OUMs from the BM1 and OU1 models. AICc estimates indicate that the $\mathrm{OUM_{hunting}}$ model was unequivocally the best-fitting model for the simulated data ($\mathrm{OUM_{hunting}}$ sim, AICcW = 1.00).

However, the bayou model exhibited greater support than a priori ecology-based OUMs (mAICcW = 0.75; table 1, pt. A). The data-driven approach of bayou revealed 13 evolutionary shifts in hbER ($\Theta_{\mathrm{ancestral}} = 5.1$ [4.8 to 5.5], $\mathrm{pp} > 0.5$; fig. 2*A*). Shifts toward increased body elongation occurred in feliforms ($\Theta = 5.9$ [5.4 to 6.3], pp = 0.66), followed by a secondary increase in genets (*Genetta* species; $\Theta = 6.8$ [3.9 to 11.4], pp = 0.77), southern seals (Monachinae; $\Theta = 6.0$ [2.9 to 6.5], pp = 0.76), ringtails (*Bassariscus* species; $\Theta = 6.3$ [not applicable; single species], pp = 0.65), olingos (*Bassaricyon* species; $\Theta = 6.0$ [3.2 to infinity], pp = 0.70), and mustelids ($\Theta = 6.0$ [3.0 to 15.1], pp = 0.51); this was followed by a secondary increase in musteline weasels (*Mustela* species; $\Theta = 8.9$ [4.2 to 13.6], pp = 0.63) and the African striped weasel (*Poecilogale albinucha*, Ictonychinae; $\Theta = 8.0$ [not applicable; single species], pp = 0.55). Shifts toward robust body shapes occurred in hyenas (Hyaenidae; $\Theta = 3.3$ [2.3 to 4.4], pp = 0.94), bears (Ursidae; $\Theta = 3.5$ [1.8 to 5.5], pp = 0.93), the wolverine (*Gulo gulo*; $\Theta = 4.6$ [not applicable; single species], pp = 0.68), and otters (Lutrinae excluding the giant otter; $\Theta = 5.5$ [2.1 to 11.0], pp = 0.5), followed by a secondary shift to more robust bodies in the sea otter (*Enhydra lutris*; $\Theta = 3.6$ [not applicable; single species], pp = 0.94). A few of these shifts exhibited wide 95% confidence intervals and unrealistic optima as a result of the large number of shifts (see "Discussion"). Analyses with OUwie and bayou without pinnipeds revealed the same patterns (fig. S1, available online; table S2).

Analyses with size-corrected hbER led to slight differences. The multipeak $\mathrm{OUM_{hunting}}$ (mAICcW = 0.38) and OU1 (mAICcW = 0.34) models were also the best-fitting models for size-corrected hbER. Parametric bootstrapping of the $\mathrm{OUM_{hunting}}$ model revealed that the 95% confidence intervals of Θ values overlapped between ambush ($\Theta_{\mathrm{ambush}} = 0.10$ [−0.02 to 0.22]), aquatic ($\Theta_{\mathrm{aquatic}} = 0.10$ [0.03 to 0.19]), and pounce ($\Theta_{\mathrm{pounce}} = 0.08$ [0.02 to 0.14]) hunting regimes. In contrast, occasional ($\Theta_{\mathrm{occasional}} = -0.03$ [−0.09 to 0.02]) and semifossorial ($\Theta_{\mathrm{semifossorial}} = -0.08$ [−0.19 to 0.04]) hunting regimes exhibited relatively more robust bodies than the remaining hunting behaviors. Similarly, the pursuit regime exhibited an unrealistic optimum (see "Discussion"). The data-driven approach of bayou revealed seven evolutionary shifts in size-corrected hbER ($\mathrm{pp} > 0.5$; fig. 2*B*), all of which were represented in analyses with hbER (fig. 2*A*). Last, comparisons of this bayou model with ecology-based OUMs also revealed overwhelming support for the bayou model ($\mathrm{mAICcW} > 0.77$; table 1, pt. B).

Ecological Effects on Body Size Evolution

The multipeak $\mathrm{OUM_{hunting}}$ model was the best-fitting model for body size (AICcW = 0.49). Parametric bootstrapping revealed that carnivorans with aquatic hunting behaviors are larger than all other carnivorans with different hunting behaviors ($\Theta_{\mathrm{ambush}} = 105$ cm [53 to 178], $\Theta_{\mathrm{aquatic}} = 307$ cm [137 to 452], $\Theta_{\mathrm{occasional}} = 99$ cm [74 to 173], $\Theta_{\mathrm{pounce}} = 79$ cm [61 to 148], $\Theta_{\mathrm{semifossorial}} = 62$ cm [30 to 127]). Similar to hbER, the body size Θ value associated with the pursuit regime exhibited an unrealistic high optimum. Simulations

Table 1: Comparisons of the best-fitting evolutionary models in head-body elongation ratio (pt. A), size-corrected head-body elongation ratio (pt. B), and body size (pt. C)

Model	k	AICc	ΔAICc	mAICcW	%
A. Head-body elongation ratio:					
BM1	2	−307.92	11.48	.06	.05
OU1	3	−308.63	10.76	.04	.00
$\mathrm{OUM}_{\mathrm{locomotion}}$	8	−300.75	18.64	.01	.00
$\mathrm{OUM}_{\mathrm{hunting}}$	8	−310.74	8.66	.14	.13
$\mathrm{OUM}_{\mathrm{diet}}$	7	−301.98	17.41	.00	.00
$\mathbf{OUM}_{\mathbf{bayou}}$	**16**	**−319.40**	**.00**	**.75**	**.81**
B. Size-corrected head-body elongation ratio:					
BM1	2	−277.97	52.60	.00	.00
OU1	3	−310.94	19.63	.08	.07
$\mathrm{OUM}_{\mathrm{locomotion}}$	8	−302.27	28.29	.02	.01
$\mathrm{OUM}_{\mathrm{hunting}}$	8	−313.46	17.11	.12	.12
$\mathrm{OUM}_{\mathrm{diet}}$	7	−307.21	23.36	.01	.00
$\mathbf{OUM}_{\mathbf{bayou}}$	**16**	**−330.57**	**.00**	**.77**	**.80**
C. Body size:					
BM1	2	98.86	5.38	.08	.10
OU1	3	99.05	5.58	.05	.00
$\mathrm{OUM}_{\mathrm{locomotion}}$	8	101.73	8.25	.07	.07
$\mathbf{OUM}_{\mathbf{hunting}}$	**7**	**94.05**	**.57**	**.33**	**.35**
$\mathrm{OUM}_{\mathrm{diet}}$	8	97.80	4.32	.08	.07
$\mathbf{OUM}_{\mathbf{bayou}}$	**5**	**93.48**	**.00**	**.38**	**.40**

Note: Small sample–corrected Akaike information criterion weights (AICcW) were calculated for each of the 500 replications to account for uncertainty in phylogenetic topology and the ancestral character states. Rows in boldface type represent the best-fit model as indicated by the lowest ΔAICc score. The final column shows the percentage of 500 phylogenetic and stochastic reconstructions in which each model was favored. ΔAICc = the mean of AICc minus the minimum AICc between models; mAICcW = mean AICcW across all 500 replications.

under the best-fitting model ($\mathrm{OUM}_{\mathrm{hunting}}$) confirm that there was substantial statistical power to distinguish complex OUMs from the BM1 and OU1 models ($\mathrm{OUM}_{\mathrm{hunting}}$ sim, AICcW = 1.00).

The data-driven approach of bayou revealed two evolutionary shifts in body size ($\Theta_{\mathrm{ancestral}} = 132$ cm [93 to 192]), both within Musteloidea. The first shift occurred at the base of Musteloidea toward smaller body sizes ($\Theta = 42$ cm [37 to 124], pp = 0.52), followed by a reversal back toward larger body sizes within otters ($\Theta = 131$ cm [28 to 890], pp = 0.75). Comparisons of this bayou model with ecology-based OUMs revealed nearly equal support for the bayou model (mAICcW = 0.38) and the $\mathrm{OUM}_{\mathrm{hunting}}$ model (mAICcW = 0.33; table 1, pt. C).

Ecological Effects on Morphological Components Underlying Body Shape Evolution

When excluding the data-driven approach of bayou, the multipeak $\mathrm{OUM}_{\mathrm{hunting}}$ model was the best-fitting model for head ER (mAICcW = 0.49), cervical AEI (mAICcW = 0.69), and lumbar AEI (mAICcW = 0.45). The single-peak OU1 model (mAICcW = 0.34; ΔAICc = 1.36) and $\mathrm{OUM}_{\mathrm{locomotion}}$ model (mAICcW = 0.26; ΔAICc = 1.71) were also comparable fits for head ER and lumbar AEI, respectively. Support for multiple models in head ER and lumbar AEI is consistent with parametric bootstrapping that revealed overlapping 95% confidence intervals of most Θ values. Similar to hbER, Θ values associated with the pursuit regime exhibited unrealistic optima for all components with $\mathrm{OUM}_{\mathrm{hunting}}$ as the best model. Ignoring the pursuit regime revealed that semifossorial carnivorans exhibit shorter, more robust necks (cervical AEI $\Theta_{\mathrm{semifossorial}} = 3.2$ [2.9 to 3.4]) and pouncing carnivorans exhibit more elongate necks (cervical AEI $\Theta_{\mathrm{pouncing}} = 4.5$ [4.3 to 4.6]) than other carnivorans with different hunting behaviors (cervical AEI $\Theta_{\mathrm{average}} = 3.8$ [3.6 to 4.0]; table S3). In contrast, the $\mathrm{OUM}_{\mathrm{locomotion}}$ model (mAICcW = 0.71) was the best-fitting model for sacral AEI; however, parametric bootstrapping revealed overlapping 95% confidence intervals of sacral AEI Θ values (table S3). Last, the BM1/OU1 model (combined mAICcW = 0.55) and OU1 model (mAICcW = 0.45) were the best-fitting models for thoracic AEI and size-corrected rib length, respectively. Simulations under all of the best-fitting models confirm that there was substantial statistical power to distinguish complex OUMs from the BM1 and OU1 models (all AICcW > 0.99).

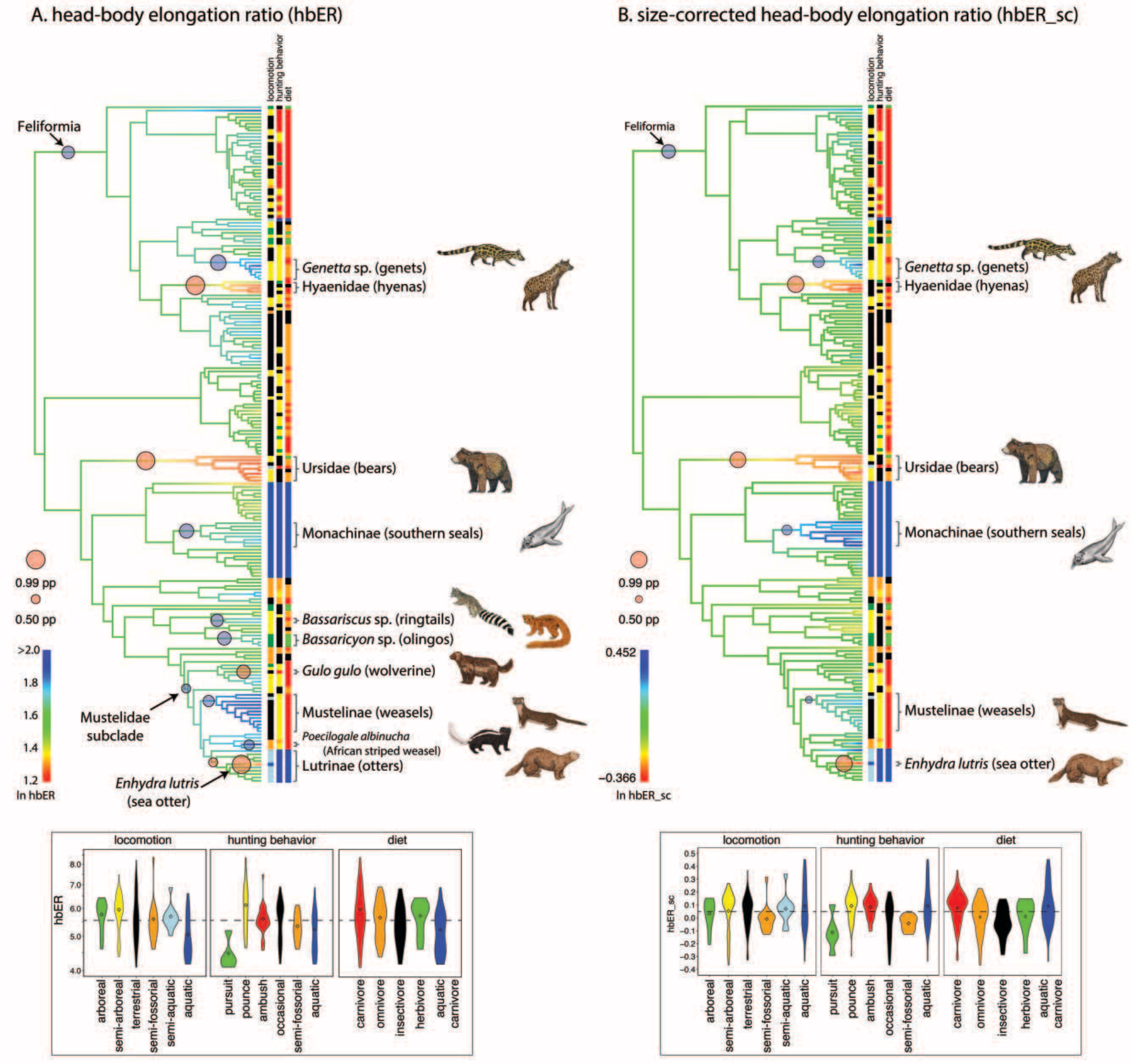

Figure 2: Evolutionary shifts in head-body elongation ratio (hbER; *A*) and size-corrected hbER (hbER_sc; *B*) across the carnivoran phylogeny, as identified by bayou. Pink and blue circles indicate shifts toward more robust (lower hbER/hbER_sc) or more elongate (higher hbER/hbER_sc) body shape optima, respectively. Circle sizes represent posterior probability (all pp > 0.5). Branch colors represent the ancestral state reconstruction of hbER/hbER_sc. Colored rectangles represent locomotor, hunting, and dietary ecologies. Locomotion: blue = aquatic; light blue = semiaquatic; green = arboreal; yellow = semiarboreal; orange = semifossorial; black = terrestrial. Hunting behavior: green = pursuit; yellow = pouncing; red = ambush; black = occasional; orange = semifossorial; blue = aquatic. Diet: blue = aquatic carnivory; red = carnivory; orange = omnivory; black = insectivory; green = herbivory. Insert figures show violin plots of hbER and hbER_sc by locomotor, hunting, and dietary ecologies.

The data-driven approach of bayou revealed that carnivorans exhibited evolutionary shifts in head ER, sacral AEI, and body depth but did not find strong evidence for additional evolutionary shifts in cervical AEI, thoracic AEI, or lumbar AEI (fig. 3). Musteline weasels exhibited an evolutionary shift toward more elongate crania ($\Theta_{\text{ancestral}} = 2.9$ [2.8 to 3.1]; $\Theta = 4.3$ [3.2 to 6.9], pp = 0.67); bears exhibited a shift toward a more elongate sacral region ($\Theta_{\text{ancestral}} = 1.8$; $\Theta = 2.9$ [2.4 to 3.3], pp = 0.76), whereas skunks (Mephitidae subclade) exhibited a shift toward a more robust sacral region ($\Theta = 0.9$ [0.7 to 1.0], pp = 0.64). Feliforms ($\Theta_{\text{ancestral}} = 1.1$ cm [1.0 to 1.1]; $\Theta = 0.9$ cm

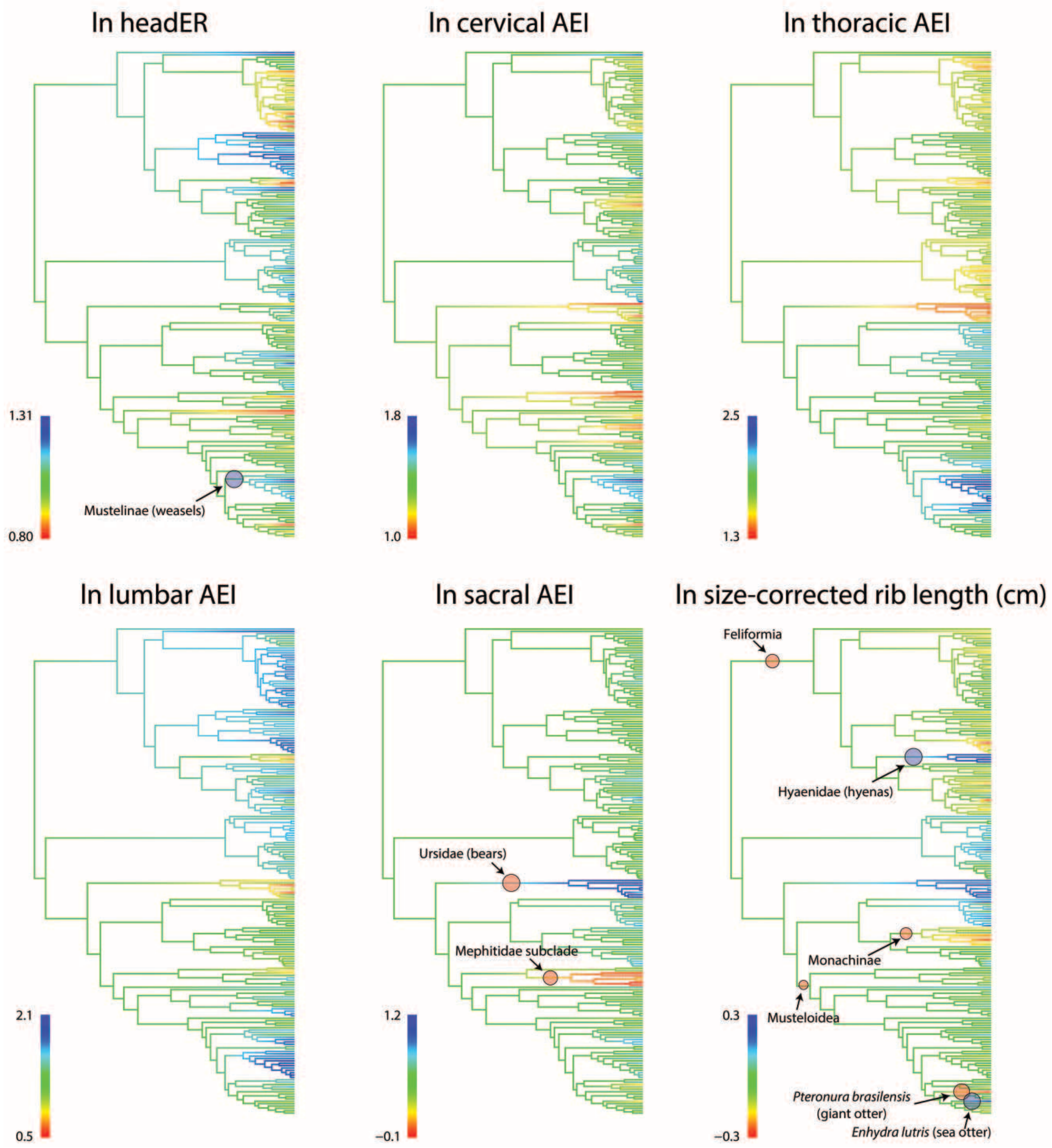

Figure 3: Evolutionary shifts in the morphological components underlying body shape optima across the carnivoran phylogeny as identified by bayou. Pink and blue circles indicate shifts toward higher and lower trait optima, respectively. Circle sizes represent posterior probability (all pp > 0.5). Branch colors represent the ancestral state reconstruction of each trait. AEI = axial elongation index (Ward and Brainerd 2007); head ER = head elongation ratio.

[0.9 to 0.9], pp = 0.79), southern seals ($\Theta = 1.0$ cm [1.0 to 1.1], pp = 0.73), musteloids ($\Theta = 1.0$ cm [0.9 to 1.0], pp = 0.69), and the giant otter (*Pteronura brasiliensis*, $\Theta = 0.8$ cm [not applicable; single species], pp = 0.92) exhibited evolutionary shifts toward reduction in relative body depth, whereas hyenas ($\Theta = 1.4$ cm [1.2 to 1.5], pp = 0.99) and the sea otter ($\Theta = 1.2$ cm [not applicable; single species], pp = 0.98) exhibited evolutionary shifts toward increased relative body depth. The bayou models for sacral AEI and body depth were overwhelmingly favored compared with their ecology-based OUM counterparts (mAICcW > 0.96; table S4). In contrast, head ER received nearly equal support for the $\mathrm{OUM_{hunting}}$ model (mAICcW = 0.38), the bayou model (mAICcW = 0.33), and the OU1 model (AICcW = 0.21).

Discussion

Biologists have long hypothesized that distinct trophic ecologies can drive adaptive evolution of different body shapes. Surprisingly and contrary to what was predicted, I found that adaptive models of locomotory, hunting, and dietary ecologies were relatively poor predictors of evolutionary shifts in body shape optima across the clade. In contrast, body size appeared to have some influence on body shape evolution across carnivorans, as analyses with both hbER and size-corrected hbER data sets led to slight differences in evolutionary shifts of body shape. Furthermore, aquatic and terrestrial carnivorans exhibit opposing allometric patterns in body shape, and these differences may be driven by differences in gravitational constraints found in the terrestrial versus aquatic environments (see below).

Although the model selection approach (excluding the bayou model) favored a multipeak OU model with distinct adaptive peaks for hunting behaviors, only 52.3% of the 500 replications had the $\mathrm{OUM_{hunting}}$ model as the best model; in fact, nearly 40% of the replications had the BM1 or OU1 model as the best model. Consistent with this discrepancy are the calculations of bootstrapped 95% confidence intervals that revealed overlapping optimal body shape values between hunting behaviors. There are a few reasons why the multipeak $\mathrm{OUM_{hunting}}$ model may have been selected as the preferred model. First, pursuit hunting regime may actually be driving the preference for the $\mathrm{OUM_{hunting}}$ model because these carnivorans exhibit more robust bodies than other carnivorans (fig. 2*A*). Unfortunately, this signal may be masked because of poor estimations of the optimum. There are only five species within this hunting regime, leading to poor, unrealistic estimations of the optimal hbER for the pursuit hunting regime. In addition, uncertainty in optimal estimations can also arise when species in the regime are spread across the phylogeny. That the five pursuit carnivorans are spread across the entire carnivoran phylogeny and share a common ancestor over 48 million years ago may contribute to high uncertainty in optimal estimates resulting in overlapping optima. Overlapping optima of the preferred OU model may also suggest that the processes underlying body shape evolution is more complex than hypothesized by specific OUM models. This is corroborated by findings that an OU model with regimes identified by bayou is a better fit than the $\mathrm{OUM_{hunting}}$ model (mAICcW = 0.75), although many of the evolutionary shifts identified by bayou also exhibited wide 95% confidence intervals and unrealistic optima because of large number of shifts relative to the number of species and other problems described above. Nevertheless, these models indicated that the complexity and variation of the body shape landscape cannot be effectively captured by a priori hunting behavioral regimes.

Together, these results indicate that carnivorans with shared locomotor, hunting, or dietary ecologies do not evolve toward similar body shapes. Instead, evolutionary shifts in body shape primarily occur along clade branches, consistent with findings that the simulated data exhibited a much stronger $\mathrm{OUM_{hunting}}$ signal (mAICcW = 1.00) compared with the empirical data (mAICcW = 0.49 without bayou model comparison). While results from bayou suggest that phylogenetic history rather than the ecological traits analyzed in this study may have stronger influences on the evolution of carnivoran body shapes (fig. 2), it is important to note that many of the evolutionary shifts toward increased elongation exhibited low posterior probabilities. A possible reason for low posterior probability support may be that analyses with just extant taxa are unable to capture gradual, crownward transitions toward more elongate bodies. Therefore, future work incorporating ancestral estimation of body shape with the fossil record may uncover whether shifts toward more elongate bodies are gradual or instantaneous.

Body Shape as a Functionally Relevant Morphology?

That phylogeny rather than ecological traits appeared to better predict body shape shifts suggests that the reliability of body shape as a functionally relevant morphology should be considered on a clade-by-clade basis. Carnivoran clades serve as evolutionarily significant units (Humphreys and Barraclough 2014), and disparate evolutionary and ecological processes drive differences in morphological disparity between individual carnivoran families, particularly in the skull (Figueirido et al. 2009, 2011; Finarelli and Flynn 2009; Slater 2015; Law et al. 2018*a*; Slater and Friscia 2019). Therefore, distinct evolutionary and ecological processes may also drive the evolution of body shape optima within different carnivoran clades ranging from individual families to genera (see below). This hypothesis is consistent with the few empirical studies that previously tested relationships between body shape optima and ecologies in vertebrates. For example, Blankers et al. (2012) found that lungless salamanders within the subfamily Bolitoglossinae exhibited strong relationships between body shape and microhabitat, where arboreal species exhibit broader bodies and terrestrial species more slender bodies; however, these body shape–microhabitat relationships are not found in analyses across all salamanders (Blankers et al. 2012; Baken and Adams 2019). Similarly, although Friedman et al. (2016) found that pelagic zooplanktivorous surgeonfishes within the family Acanthuridae converged on an adaptive body shape optimum distinct from benthic surgeonfishes, Claverie and Wainwright (2014) found no evidence of associations between body shape optima and habitat or locomotor ecologies across 2,939 species of tropical reef fishes, although the latter was not statistically tested. These studies, together with the current study, provide little evidence that body shape evolution across large phylogenetic scales reflects adaptations to distinct locomotor, hunting, or dietary ecologies.

Like body size, body shape is a prominent feature of vertebrate morphology (Brown and Lasiewski 1972; Sharpe et al. 2015; Ward et al. 2015; Law et al. 2019; Morinaga and Bergmann 2020) that may conceal one-to-one mapping of morphology onto ecological characteristics across macroevolutionary scales. Several types of form-function relationships have been described to explain decoupling between morphology and ecology. Many-to-one mapping of form onto ecology (Alfaro et al. 2005; Wainwright et al. 2005) suggests that multiple body shape morphologies are functionally equivalent, enabling species with distinct body shapes to exploit similar resources and exhibit similar ecologies. For example, American badgers, black-footed ferrets, coyotes, and swift foxes are sympatric carnivorans with distinct body shapes, yet they feed on prairie dogs in the same grassland habitats (Kotliar et al. 1999). Equally possible is the one-to-many mapping of form onto ecology (Zelditch et al. 2017), where a single functionally versatile body shape can exploit diverse resources and not be restricted to a specialized resource. For example, the American mink exhibits an elongate body plan but is able to hunt in a variety of habitats, including chasing rodents in burrows, birds on the surface, and fishes in water (Larivière 1999). Last, many-to-many mapping (Bergmann and McElroy 2014; Zelditch et al. 2017) postulates that the multidimensionality of both morphology and ecology creates complex relationships between body shape and ecological diversity in which one-to-one, many-to-one, and one-to-many mappings can all occur simultaneously within a clade. Alternatively, allometric patterns driven by body size may be more important than a specific ecological regime, particularly in terrestrial species that must adapt to the mechanical demands of gravity. Larger species require robust body shapes to support their heavier bodies (Kardong 2014) and favor more dorsostability of the vertebral column (Halpert et al. 1987; Jones 2015*a*), whereas smaller species are free to evolve more elongate body shapes and exploit small, conscripted spaces (Horner and Biknevicius 2010; Horner et al. 2016). Therefore, the complexity of these form-function networks makes it difficult to decipher which ecological factors, if any, drive the evolution of overall body shapes, and it also suggests that whether body shape is a reliable trophic morphology for macroevolutionary analyses is dependent on phylogenetic level.

Similarly, my analyses suggested that adaptive models of locomotor, hunting, and dietary ecologies were poor fits to the morphological components underlying body shape variation. Although these multipeak OU models were the best fits for the majority of the vertebral components, optima from different regimes were statistically indistinguishable from each other. Furthermore, data-driven approaches revealed that there were also no evolutionary shifts in AEI values of the cervical, thoracic, and lumbar regions (table 1; fig. 2*A*). The lack of evolutionary shifts in these vertebral regions is surprising, especially in the thoracolumbar region, as elongation/shortening of this region contributed 55% to overall carnivoran body shape variation (Law 2021*a*). The thoracolumbar region is the primary structure used to support the body against gravity and transmit and receive propulsive forces to and from the limbs to generate locomotion (Kardong 2014). Therefore, changes in the thoracolumbar region should facilitate locomotor adaptations where elongation of these vertebral regions increased dorsoventral flexibility and maneuverability, whereas shortening facilitates dorsostability (Boszczyk et al. 2001; Jones 2015*a*, 2015*b*). That ecological traits related to locomotion poorly explained elongation and shortening of these vertebral regions is inconsistent with previous work in mammals demonstrating that locomotor ecologies influence the evolution of various aspects of the axial skeleton, such as vertebral shapes or vertebral counts (Boszczyk et al. 2001; Pierce et al. 2011; Galis et al. 2014; Randau et al. 2017; Jones et al. 2018; Vander Linden et al. 2019; Williams et al. 2019). A likely explanation is that vertebral AEI, which is calculated as the ratio between vertebral length and vertebral height, does not capture finer morphological features of the vertebral column, such as neural spines, transverse processes, and metapophyses to which locomotor muscles attach and, in turn, facilitate movement and performance during locomotion. For example, Jones et al. (2018) examined vertebral shapes in 52 species across broad mammalian clades (i.e., monotremes, metatherians, and representatives from all major eutherian clades) and found that terrestrial mammals exhibited relatively elongate neural spines and transverse processes, whereas fossorial and arboreal mammals exhibited well-developed metapophyses that enhance body stabilization during digging or climbing. Furthermore, ecological factors do appear to influence vertebral shapes within carnivoran clades, such as pinnipeds (seals, sea lions, and walrus; Pierce et al. 2011) and felids (Randau et al. 2016, 2017). Therefore, future investigations involving more detailed morphological quantification may discover that vertebral shape is a more reliable trophic morphology for macroevolutionary analyses across carnivorans. The use of simple cranial length to height ratios may similarly explain the poor fit of ecological multipeak models to head ER. Of all of the skeletal systems, the cranium is the most studied in carnivorans, and many researchers have revealed that specific cranial measurements and overall cranial shapes are strongly correlated to different ecological traits, such as diet (e.g., Friscia et al. 2007; Slater et al. 2009; Figueirido et al. 2013; Law et al. 2018*a*; Tseng 2018).

Evolution of Carnivoran Body Shapes and the Influence of Body Size

The data-driven approach of bayou indicated that evolutionary shifts in carnivoran body shapes primarily occur along clade branches (fig. 2*A*). Allometric relationships, in which larger species typically exhibit more robust body shapes (Law 2021*a*), may influence some of these evolutionary shifts. The two terrestrial families with the largest body sizes, bears (Ursidae) and hyaenas (Hyaenidae), exhibited evolutionary shifts toward 33% and 29% more robust body shapes, respectively. These robust body shapes along with dorsostability of the vertebral column are needed to support their heavier bodies against gravity (Halpert et al. 1987; Kardong 2014; Jones 2015*a*). In contrast, carnivorans with aquatic locomotor, hunting, and dietary ecologies exhibit no relationship to a weakly positive allometric relationship in which larger carnivorans exhibit more elongate bodies. A possibility for the decoupling between size and shape is a release from gravitational constraints in aquatic environments. The axial skeleton has a reduced role in body support in the buoyant environment and therefore enables adaptations toward more elongate bodies for increased maneuverability during swimming at even large body sizes (Jones and Pierce 2016). Consistent with these trends, southern seals (Monachinae) are the largest carnivorans yet exhibited shifts toward 15% more elongate bodies. Because larger bodies are able to retain relatively greater amounts of heat due to their relatively lower surface area to volume ratio (Ahlborn 2004), more elongate bodies would enable larger seals to reach optimal body shapes that would not compromise thermoregulatory needs or drag reduction during swimming (Fish 1993, 1996). Interestingly, there was no corresponding evolutionary shifts toward larger body sizes in either of these two clades. A variety of ecological and biomechanical factors may limit the evolution of larger body sizes that are currently represented in bears and hyenas; therefore, species may adapt through evolutionary changes in shape instead (Zelditch et al. 2017). That no evolutionary shifts toward larger body sizes occurred in bears, hyenas, or southern seals and evolutionary shifts remained significant when analyzed with size-corrected hbER provide evidence of how decoupling between body shape and size enables species to evolve optimal shapes for the biomechanical demands of environments if body size evolution is constrained. This hypothesis is supported by the relative short phylogenetic half-life (9.8 million years) of this OU bayou model relative to the carnivoran clade age (48.2 million years).

The superfamily Musteloidea exhibited multiple evolutionary shifts in body shape. Within Procyonidae, ringtails (*Bassariscus* species) and olingos (*Bassaricyon* species) exhibited independent shifts toward 19% and 15% more elongate bodies, respectively (fig. 2*A*). However, allometry may explain these shifts as they are no longer significant when using the size-corrected hbER (fig. 2*B*). Within Mustelidae, species exhibited evolutionary shifts toward 15% more elongate bodies followed by a secondary shift toward 38% and 54% more elongate bodies within musteline weasels (Mustelinae) and the African striped weasel (*Poecilogale albinucha*, Ictonychinae), respectively (fig. 2*A*). Elongate body shapes enable mustelids, particularly weasels, ferrets, and polecats, to actively chase down prey into burrows or crevices with greater locomotor efficiency (Horner and Biknevicius 2010; Horner et al. 2016). Evolutionary shifts to more elongate body plans have been hypothesized to serve as an innovation that facilitated the exploitation of novel grassland habitats and rodent prey during the mid-Miocene to Pleistocene, which ultimately led to the clade's increased species richness (Law et al. 2018*b*; Law 2019; Law et al. 2019). Nevertheless, performance testing is still needed to show the adaptive link between elongate body plans with subterranean locomotion. In contrast, some mustelids exhibited reversals toward more robust bodies, including the wolverine (*Gulo gulo*, Guloninae) and otters (Lutrinae), and the sea otter (*Enhydra lutris*) in particular. For otters, becoming too elongate may reduce swimming efficiency (Mises 1945; Webb 1975; Fish 1993); therefore, more robust bodies may be the optimal body shape that would not compromise thermoregulatory needs or drag reduction during swimming similar to phocid seals (Fish 1993, 1996). However, evolutionary shifts in mustelid body shape are strongly influenced by allometry, as analyses of size-corrected hbER revealed only two significant shifts in mustelids: toward more elongate bodies in weasels, and toward more robust bodies in the sea otter (fig. 2*B*).

Although allometry contributes to the evolution of carnivoran body shapes, the discrepancy between evolutionary shifts in hbER and size-corrected hbER cannot be completely explained by body size evolution. I found only two evolutionary shifts in carnivoran body size, and these evolutionary shifts did not correspond with the loss of significant evolutionary shifts in size-corrected hbER compared with analyses with hbER. Posterior probability support may influence these discrepancies, as posterior probabilities for shifts that were found in the hbER analyses but not the size-corrected hbER analyses ranged from 0.50 to 0.70.

Conclusion

Body shape is one of the most prominent features of vertebrate morphology with important influences on the physiology, performance, and ecology of organisms (Brown and Lasiewski 1972; Sharpe et al. 2015; Ward et al. 2015; Law et al. 2019; Morinaga and Bergmann 2020). Although different body shapes are often hypothesized to be explained by adaptations to distinct ecological traits, I found that adaptive models of locomotor, hunting, or dietary ecologies were weak predictors of carnivoran body shape variation. A possible explanation is that the multidimensionality of both body shape morphology and ecology (Alfaro et al. 2005; Wainwright et al. 2005; Bergmann and McElroy 2014; Zelditch et al. 2017) makes it difficult to determine which ecological factors, if any, drive the evolution of body shapes. Therefore, these results suggest that body shape and the underlying morphological components that contribute to its variation as defined here are not reliable functionally relevant traits. Instead, analyses of other morphological traits, such as vertebral shape, may better capture the specific structures of the vertebral column that more directly facilitate ecological functions (Boszczyk et al. 2001; Pierce et al. 2011; Galis et al. 2014; Randau et al. 2017; Jones et al. 2018; Williams et al. 2019). Nevertheless, some ecological influences on body shape evolution cannot be ruled out because the water to land boundary appears to drive opposing body shape allometry in terrestrial and aquatic carnivorans. These opposing allometric relationships also highlight the contribution of body size in influencing body shape evolution.

Importantly, these results demonstrate the importance of accounting for phylogenetic history and unifying hypothesis testing and data-driven approaches in future investigations of macroevolutionary processes and patterns (Uyeda et al. 2018). Here, the data-driven approach suggested that the evolution of carnivoran body shapes is partially driven by phylogenetic history rather than toward distinct ecology-related optima. That evolutionary shifts in body shape occurred along taxonomically named clade branches is consistent with previous findings that carnivoran families serve as evolutionarily significant units (Humphreys and Barraclough 2014) and that disparate evolutionary and ecological processes often drive differences in morphological disparity between individual carnivoran families (Figueirido et al. 2009; Finarelli and Flynn 2009; Figueirido et al. 2011; Slater 2015; Law et al. 2018*a*; Slater and Friscia 2019). Overall, these results demonstrate the complex relationships between morphological evolution, ecological diversity, and phylogeny across large macroevolutionary scales. Future work incorporating paleontological data composed of both morphology and ecology can help further elucidate the independent evolutionary processes that drove the evolution of distinct body shapes within carnivoran clades.

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Data and Code Availability

Data are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.pg4f4qrpm; Law 2021*b*).

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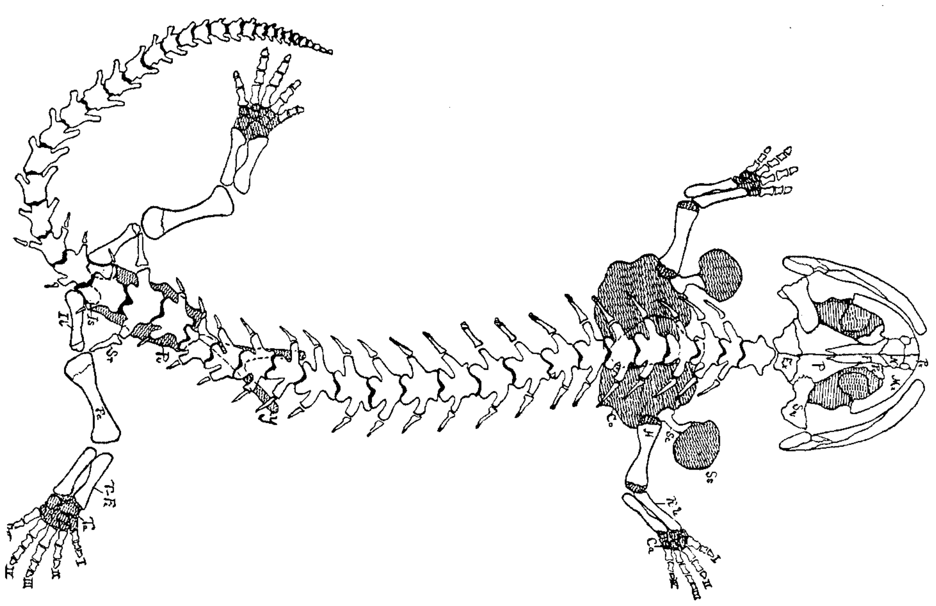

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