

FUNCTION, HISTORY, AND ECOLOGY IN THE EXCEPTIONAL  
DIVERSIFICATION OF MURINE RODENTS

A Dissertation

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*For my family: past, present, and future*

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## ABSTRACT

Life's diversity is not spread evenly across all lineages, and this unevenness is thought to be due, in part, to a few interwoven factors: biogeographic history, the evolution of successful functional traits, and the ecological opportunity these traits afford. My dissertation focuses on the evolution of a species-rich and morphologically diverse clade of mammals, the murine rodents (Murinae; Muridae; Rodentia) to address 1) morphological adaptations associated with niche transition to arboreality 2) the effect of repeated ecological transitions on murine diversification, and 3) the role of atypical ecological niches in the assembly of hyperdiverse communities. My dissertation has revealed that ecological specialization, such as arboreality, and morphological adaptation co-occur and foster the invasion of new niches. I have also found that specialization, particularly locomotor specialization such as arboreality and amphibiosy, increases with community richness, fostering diverse communities of closely related species that are able to partition rather than directly compete for similar resources. My dissertation highlights that lineages in this diverse clade of mammals repeatedly evolve towards predictable ecologies, providing a pathway for the increase of species richness in high-diversity tropical communities.

## CHAPTER 1: INTRODUCTION

The relationship between organismal form and life history is a cornerstone of biology.

For centuries scientists have sought to both describe and interpret the astounding phenotypic diversity in the tree of life. Functional demands and ecological interactions positively select for phenotypic changes in diverging or recently split populations. Over time these physical and ecological forces help generate the great morphological variety that enables organisms to thrive in virtually every global environment. Consequently, integrative research into the interactions between function, history, and ecology is required for a deep understanding of morphological diversification (Wainwright and Riley 1994).

My dissertation focuses on the evolution of a species-rich and morphologically disparate clade of mammals. I attempt to interlace function, history, and ecology from local communities to continent-scale processes. The rodent subfamily Murinae contains 700 currently recognized species, or 11% of extant mammal diversity. In ~15 million years, murines diversified into a vast range of sizes, shapes, diets, and locomotor modes, from 10g canopy-dwelling frugivores to 1kg amphibious molluscivores. The many successful murine colonizations across the Old World over the last several million years provide replicated examples of in-situ diversification that highlight examples of parallel evolution. The recent global invasion of human-commensal murines demonstrates their ecological flexibility. This diversity and breadth of life histories make Murinae an exciting system with which to explore the roles of function, history, and ecology on diversification (Rowe et al 2019, Roycroft et al 2020, Martinez et al 2020). My research is focused on the evolution of novel or convergent morphological features that allow a species to exploit its habitat, and the effects of these morphologies on diversification and community assembly.

Locomotion unites functional morphology with microhabitat use and hence ecological interactions, providing a window into evolutionary processes. In my first chapter, I identified functional traits associated with arboreality. Arboreal species represent a single functional guild that has evolved repeatedly across the murine radiation (Pages et al 2015). Climbing introduces a set of physical constraints on vertebrates that require unique phenotypic adaptations (Cartmill 1985, deAlencar et al 2017). Convergent functional traits in distantly related arboreal species can signify climbing adaptations, which then can be used to predict the locomotion of rarely observed or extinct species. In my first chapter I used Bayesian phylogenetic multilevel models (BPMMS) to analyze quantitative observations of climbing frequency and linear measurements of postcranial skeletons from 21 species of Philippine murines test the hypotheses that 1) Murine species that differ in their affinity for climbing also differ in skeletal morphology, and 2) proficient climbers have converged on one or more of the same morphological conditions. I found that several measurement ratios can accurately infer climbing, however hand shape and finger length can effectively predict locomotor behavior with exceptional precision, allowing for accurate locomotor inferences across this clade of poorly-studied mammals.

Integrated morphological changes often track with behavioral or ecological transitions. Correlated evolution of functional traits may alter the tempo of diversification by releasing a lineage from limiting ecological factors, or conversely, by constraining a species to an adaptive peak (Collar et al 2009, Gajdzik et al 2019). Assessing these alternate predictions necessitates a historical investigation into the effect of habitat transitions on trait integration, and the rates of integrated morphological evolution and lineage diversification. In my second chapter I used locomotion as a central node connecting morphology and ecology to test the effects of morphological evolution on species diversification. Specifically, I addressed the hypotheses that

1) Transitions between locomotor modes results in an increased rate of evolution in functionally integrated morphological traits, and 2) specialized locomotor modes, such as arboreal and amphibious, functionally limit morphologies and reduce diversification rates. I found that the most rapidly diversifying murine clades throughout time have a highly conserved, classic “rat-like” body plan which allowed for the successful expansion of murines across the Old World and, thanks to human commensalism, beyond. I generated the largest time-calibrated phylogenetic hypothesis of Murinae to date (435 species) and used BPMMs to test for morphological integration and constraint across four locomotor modes: Arboreal, General, Terrestrial, and Amphibious. I then used comparative methods to infer rates of morphological evolution and lineage diversification, as they are associated with locomotor modes. I found that niche transitions toward rare locomotor modes, such as climbing and swimming, lead to decreased diversification rates, suggesting that these specialized ecologies represent evolutionary “cul-de-sacs” that foster static persistence (Gajdzik et al 2019, Futuyma and Moreno 1988).

Species richness at the local scale varies widely, even in diverse tropical regions. On the oceanic island of Sulawesi, Indonesia, local Murinae species richness in apparently similar habitats ranges from 10 to 23 species. How can so many closely related species coexist in some of these communities, while others contain more modest numbers? Ecological theory (MarArthur 1965) predicts that community species richness can increase in one of two ways. First, niches might have greater overlap in richer assemblages, but the overall community functional volume, but the total volume of niche space occupied by all species in a community remains the same (“niche packing”) (Pigot et al 2016, Pellissier et al 2018). Alternatively, community functional volume can increase with species richness due to increased use of previously unoccupied ecological space (“niche expansion”; Kreft and Jetz 2007, Hurlbert and Jetz 2010). In Sulawesi,

species-rich communities appear to have greater morphological and dietary diversity than species-poor communities. This suggests “niche expansion,” but the hypothesis remains to be tested. For my third chapter, I collected stable isotope data, locomotor data, and cranial and postcranial morphology data to infer community functional hypervolumes for 6 Sulawesi communities to test the hypotheses that 1) murine species in the most diverse communities occupy ecological niche spaces that are empty in the less-diverse communities, and 2) total community functional volumes will be positively correlated with local species richness (“niche expansion”).

# C<sup>1</sup>HAPTER 2: A SIMPLE SKELETAL MEASUREMENT EFFECTIVELY PREDICTS CLIMBING BEHAVIOR IN A DIVERSE CLADE OF SMALL MAMMALS\*

## Introduction

Climbing is a key behavior that facilitates access to above-ground resources and hence, ecological opportunity. As such, the tendency to climb may have altered patterns of competition and processes of diversification in the evolutionary history of many vertebrate clades, including mammals (Jenkins 1974a; Scheffers et al. 2013; Bars-Closel et al. 2017; de Alencar et al. 2017). Scansoriality — the propensity to climb — may be the ancestral locomotor mode of placental mammals (O’Leary et al. 2013), and recent paleontological work suggests climbing facilitated placental diversification (Ji et al. 2002; Luo et al. 2011). However, because locomotory behavior does not fossilize, our understanding of the role of climbing in the history of placental radiation is derived from indirect inferences from skeletal morphology (Ji et al. 2002, Luo et al. 2003, Kirk et al. 2008, Samuels & Van Valkenburgh 2008, Chen & Wilson 2015, Meng et al. 2017).

Similar to the situation for extinct mammals, the locomotor behavior of many living species is unknown. Most small mammals (< 5 kg) are nocturnal and secretive, making observations difficult, and it is not uncommon for researchers to discover climbing behavior in common, widespread species long thought of as exclusively terrestrial (Ingles 1960; Nations & Olson 2015; Costa et al. 2017).

Exploiting the arboreal niche requires the ability to navigate the trunks and branches of trees while simultaneously performing basic activities such as feeding. Arboreal substrates range

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from horizontal to vertical and vary dramatically in diameter and texture. In vertebrates there are a variety of solutions to the physical challenges of arboreality, such as the adhesive toepads found in some squamates. In general, climbing mammals rely on increased grip and claw purchase, improved depth perception, and the use of the tail for balance, stability, or grasping (Cartmill 1985, Tulli et al. 2015). As the differences between terrestrial locomotion and climbing are substantial, it is thought that both behavioral and morphological adaptations occur in concert with transitions between these ecological states. Signal of morphological adaptations to arboreal locomotion may be found in the postcranial skeletons of climbing mammals (Cartmill 1985; Jenkins 1974a).

Identifying which, if any, skeletal characters accurately predict climbing behavior would facilitate locomotor inferences for both extinct species and living species that lack observational data. Connecting morphology with locomotor behaviors requires a study system with species spanning a range of body sizes, quantitative observations of the propensity to climb, and a strong understanding of phylogenetic relationships to account for the non-independence of traits (Harvey & Pagel 1991). Although primates represent just one of numerous independent origins of scansoriality in mammals, they have been the subject of most climbing studies to date (Jenkins 1974a, 1974b; Gebo 1996, 2004; Bloch & Boyer 2002; Kirk et al. 2008). Most primate species have such extreme adaptations to climbing that they may be poor models for how climbing generally evolves (Jenkins 1974b). and, therefore, the transition from the ground to the trees has been investigated in various small, non-primate species, which vary in size from ~15g to 6kg (Argot 2002; Urbani & Youlatis 2013).

Skeletal traits traditionally associated with climbing in non-primate models include equal limb proportions, long digits, long tail, and mobile ankle joints (Argot 2002; Ji et al. 2002; Sargis

2002a, 2002b; Kirk et al. 2008; Samuels & Van Valkenburgh 2008; Woodman and Stabile 2015). However, when analyzed in multivariate morphospace, as is common practice in other vertebrate systems (e.g., Mahler et al. 2013; Ingram & Kai 2014), small climbing and terrestrial forms often overlap (Kirk et al. 2008; Samuels & Van Valkenburgh 2008; Verde Arregoitia et al. 2017). This pattern is potentially explained by the less extreme adaptations required to support small body mass and by the less severe consequences of falls in smaller animals (Jenkins 1974a). Multivariate ordination methods, such as principal components analysis, may also blur the significance of morphological traits (Uyeda et al. 2015). For example, if traits A, B, and C have high loadings on the first axis, and arboreal species tend to have high scores for this axis, it is challenging to disentangle which, if any, of these three traits can be used to infer climbing affinity.

Unlike other ecomorphological model systems, such as *Anolis* lizards (Losos 2009), small mammal body mass may span three orders of magnitude (see below). This may be important as smaller-bodied arboreal and terrestrial species have been shown to be more similar morphologically than larger-bodied species, likely due to the mechanics of locomotion (Kirk et al. 2008). Additionally, non-primate models span the mammalian phylogeny—from marsupials to murids, or roughly 175 Myr of evolutionary time (Meredith et al. 2011)—and it remains unclear whether shared traits are due to morphological convergence or are simply historical artifact. Recent work has successfully used 3-dimensional morphometrics and muscular structure to identify differences indicative of climbing in non-primate mammals (Fabre et al. 2013; Taverne et al. 2018), but these methods lack the simplicity needed to infer locomotion for the numerous extant and extinct species with no behavioral data. Ideally, inferences of climbing

behavior should be based on simple characters that commonly fossilize and are either indicative of climbing regardless of size or are known to be relevant for organisms of a given size.

The rodent subfamily Murinae (Rodentia, Muridae) contains 704 recognized species, 11% of extant mammals, that encompass a wide range of locomotor ecomorphologies, from semi-aquatic and semi-fossorial to arboreal (Musser & Carleton 2005; Pagés et al. 2015; Rowe et al. 2016; Burgin et al. 2018). Climbing murines vary in mass and behavior, from the large canopy-dwelling cloud rats (*Phloeomys*, up to 2.7kg), to the tiny bamboo-nesting Ranee mice (*Haeromys*, <10g). Terrestrial murines span a similar breadth of body sizes. This size range provides an opportunity to quantify traits unique to, and shared between, functional groups, as well as whether and how those traits vary with respect to body size.

The Philippines is home to roughly 80 currently recognized, mostly endemic murine species (Heaney et al. 2016) resulting from five radiations within four murine “divisions” (Jansa et al. 2006; Rowe et al. 2016). Three of these clades—cloud rats, earthworm mice, and "true" rats—contain both terrestrial and scansorial forms, allowing for direct comparison between closely related but behaviorally divergent species. Uniquely, these species are well represented by voucher specimens with complete postcranial skeletons and detailed records of above-ground and on-ground trapping efforts that effectively document which species climb and with what frequency (Ruedas 1995; Balete et al. 2009, 2011, 2013a, 2013b; Alviola et al. 2011; Duya et al. 2011; Rickart et al. 2011, 2013, 2016; Heaney et al. 2013a, 2013b). This provides a rare opportunity in small mammals to quantify observations of the frequency of climbing behavior, with numeric integration of behavior into linear models, thereby avoiding the simple, but potentially misleading binary scheme of “arboreal” versus “terrestrial.”

In this study, we leverage quantitative observations of climbing behavior, DNA sequence data, and available postcranial skeletons to evaluate whether climbing behavior can be predicted from skeletal measurements alone across a range of body sizes. We construct a phylogenetic generalized linear model of climbing in Philippine murines and then use it to predict locomotor mode in additional murine species for which only qualitative descriptions of locomotor behavior are available.

## **Material and Methods**

*Morphological Sampling* - One of us (JAN) collected 21 linear measurements (Fig. 1.1, Supplemental Appendices 1.1 – 1.2) from appendicular skeletons of 186 murine specimens representing 20 species of Philippine species and 27 additional murines (1–14 individuals per species). We measured the right side (when available) of adult specimens with fused epiphyses on long bones and complete molar eruption. Limited specimen availability did not allow us to control for sex. All measurements were taken using Mitutoyo digital calipers (precision = 0.01mm) and repeated until a stable measurement was obtained three consecutive times. We used this single measurement in additional analyses. These 21 measurements were transformed into 16 indices (Table 1.1, Supplemental Appendices 1.1 – 1.2), as is common practice (Elissamburu & Vizcano 2004; Samuels & Van Valkenburgh 2008; Hopkins & Davis 2009; Coutinho et al. 2013; Woodman & Stabile 2015, Slater and Friscia 2018). Indices also allow us to avoid using body-size corrected regression residuals of single linear measurements as data, a practice that has raised concerns (Garcia-Berthou 2001; Freckleton 2009). Some published indices use measurements of small elements, such as claws (e.g., Samuels & Van Valkenburgh 2008). However, we found that these elements are frequently damaged or missing, and their small size precluded measurement accuracy with hand-held calipers, and thus we excluded them.

As tail length is thought to be associated with climbing (Cartmill 1985), we included a tail-length index using data drawn from specimen tags and field notes. All specimens used in this study are housed in the Field Museum of Natural History, Chicago, the Louisiana State University Museum of Natural Science, Baton Rouge, the Museum Zoologicum Bogoriense, Cibinong, and the American Museum of Natural History, New York.

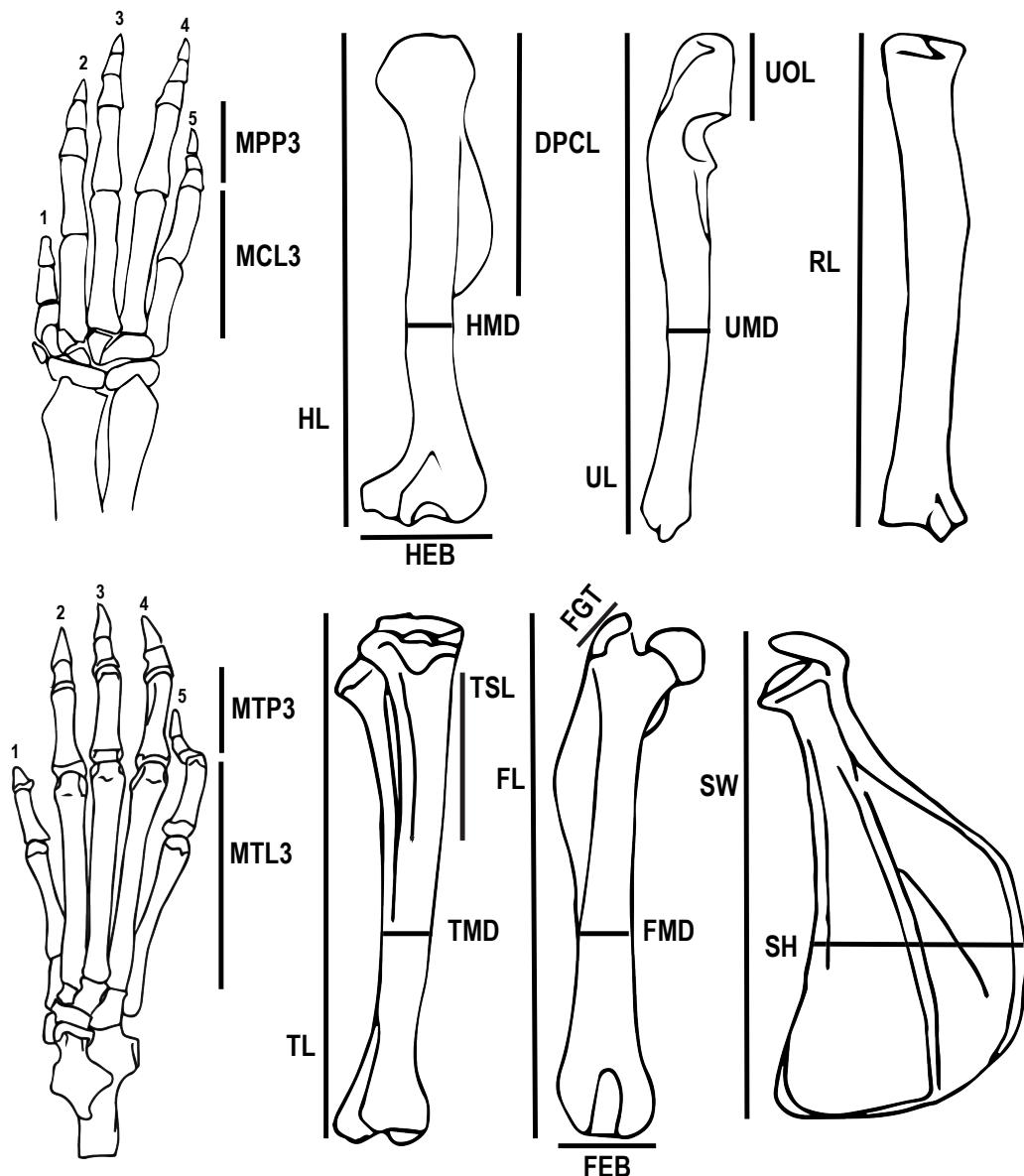


Figure 1.1. Linear measurements of postcranial elements used for this study. Measurements were converted to indices (Table 1.1). From upper left to lower right, elements are manus, humerus, ulna, radius, pes, tibia, femur, and scapula.

*Climbing Behavior* - Surveys of Philippine small mammals conducted from 1995 to 2011 include published trapping records for every species collected (Balete et al. 2009, 2011, 2013a, 2013b; Alviola et al. 2011; Duya et al. 2011; Rickart et al. 2011, 2013, 2016; Heaney et al. 2013a, 2013b). These records include total trapping effort, both on the ground (terrestrial) and above the ground (arboreal), and

the total number of captures for each trap position for each species (Supplemental Appendix 1.3). Additional details of localities and trapping methods can be found in the citations above. We calculated a climbing probability for each species as:

$$\text{Climb Index} = (\text{AC} / \text{AT}) / ((\text{AC} / \text{AT}) + (\text{GC} / \text{GT}))$$

where AC = arboreal captures, AT = arboreal trapnights, GC = ground captures, GT = ground trapnights, and trapnights = number of traps × number of nights. This formula gives a unitless climbing probability value ranging from 0 (terrestrial only) to 1 (arboreal only) for each species. One species, *Phloeomys pallidus*, the Northern Luzon giant cloud rat, was excluded from these calculations because it is too large to capture in the traps used. However, it is well known to be primarily arboreal (Heaney et al. 2016) and was given a score of 1. Though not recorded in the citations above, *Apomys gracilirostris* is currently known only from terrestrial captures (Ruedas 1995, LHR Field Notes) and was given a score of 0. For non-Philippine species, which generally lack detailed trapping data, we scoured the literature for information on climbing behavior and qualitatively scored each species into one of three groups: “Terrestrial”, “General”, and “Arboreal.” (Supplemental Appendix 1.2). Here “Arboreal” means that climbing is an integral life history trait for the species, “General” refers to species that are known to opportunistically

climb but are not thought to require climbing for survival, and “Terrestrial” indicates species that are not thought to climb due to habitat, behavioral, or dietary niche.

Table 1.1. Definitions of morphological indices. Measurements are illustrated in Fig. 1.1. All indices except for PES, SI, and TAIL were defined by Samuels & Van Valkenburgh (2008).

Index	Description	Formula	Abbreviation
SMI	Shoulder moment index: Indicates quantity of muscle attachment in the shoulder	Deltopectoral crest length / Humerus length	DPCL / HL
BI	Brachial index: Difference of proximal and distal portions of the forelimb	Radius length / Humerus length	RL / HL
HRI	Humeral robustness index: Robusticity of the humerus.	Humeral midshaft diameter / Humerus length	HMD / HL
HEB	Humeral epicondylar breadth: Indicates relative area of muscle attachment available on the forelimb.	Humeral epicondyle breadth / Humerus length	HEB / HL
OLI	Olecranon length index: Indicates relative area for muscle attachment in the elbow.	Length of olecranon / functional ulnar length	UOL / (UL - UOL)

table cont'd

Index	Description	Formula	Abbreviation
URI	Ulnar robustness index: Robusticity and available muscle attachment area of the ulna.	Ulnar midshaft diameter / Ulna length	UMD / (Ul - UOL)
MANUS	Manus proportion index: Relative digit length of the hand.	Proximal manual phalanx length (3rd ray) / metacarpal length (3rd ray)	MPP3 / MCL3
CI	Crural index: Relative proportions of the proximal and distal portion of the hindlimb.	Tibia length / Femur length	TL / FL
FRI	Femoral robustness index: Robusticity and muscle attachment area of the femur.	Femur midshaft diameter / Femur length	FMD / FL
GI	Gluteal index: Indicated quantity of muscle attachment from the gluteus to the hind leg.	Length of distal extension of femoral trochanter / Femur length	FGT / FL

table cont'd

Index	Description	Formula	Abbreviation
FEB	Femoral epicondylar breadth: Indicates relative area of muscle attachment available on the hindlimb.	Femoral epicondylar breadth / Femur length	FEB / FL
TRI	Tibial robustness index: Robusticity and muscle attachment are of the tibia.	Tibia midshaft diameter / Tibia length	TMD / TL
TSI	Tibial spine index: Indicates relative muscle attachment area of the knee and hip.	Length of distal extension of tibial spine / Tibia length	TSL / TL
PES	Pes proportion index: Relative digit length of the foot.	Proximal pedal phalanx length (3rd ray) / metatarsal length (3rd ray)	MTP3 / MTL3
IM	Intermembral index: Relative length of the forelimb to hindlimb.	(Humerus length + Radius length) / (Femur length + Tibia length)	(HL + RL) / (FL + TL)

table cont'd

Index	Description	Formula	Abbreviation
TAIL	Tail length index: Relative tail length.	Tail length / Total length of organism	Tail / Total
SI	Scapular shape index: Indicates the roundness of the scapula.	Scapula height / Scapula width	SH / SW

*Phylogenetic Reconstruction* - We downloaded DNA sequence data from one mitochondrial (CytB) and four nuclear genes (Rag1, GHR, BRCA1, and IRBP) from GenBank for all species in the morphological sampling, with two additional species, *Hapalomys delacouri* and *Gerbillus gerbillus*, included as outgroups (Fabre et al. 2013; Pagés et al. 2015). Sequences were aligned with MAFFT and visually inspected using Geneious v.7.1. We found no ambiguous regions of the alignment. We selected the best-fit models of sequence evolution for each gene using the models = BEAST command in PartitionFinder 2 (Lanfear et al. 2017). A dated phylogeny was estimated using BEAST 2.0 (Bouckaert et al. 2014) with a concatenated alignment, relaxed lognormal clock, and birth-death speciation model. The temporal framework was estimated using three fossil calibration points (*Antemus chijiensis*, Offset = 13.24, Log = 1.0, Mean = 3.2; cf. *Karnimata* sp., Offset = 10.47, Log = 1.0, Mean = 4.0; *Mus* sp., Offset = 7.29, Log = 1.0, Mean = 4.9) from a previous phylogeny of Muridae (Aghova et al. 2017). Four independent runs of BEAST 2 were run for 200 million generations. Convergence was evaluated using Tracer v1.6.0 (Rambaut et al. 2018) to confirm that effective sample sizes exceeded 1000, that the trace of the log-likelihood had plateaued, and that each chain reached the same plateau. We used TreeAnnotator v2.4.3 to discard the first 20% of trees as burnin, and to generate a time-calibrated maximum clade credibility tree (Fig. 1.2).

*Bayesian Generalized Linear Multilevel Modelling* - We modeled the relationship between morphology and climbing using phylogenetic Bayesian multilevel models, with Climb Index as our response and the morphological indices as our predictors. Multilevel models have several advantages over other methods, as they can incorporate both intraspecific morphological variation and phylogenetic relationship as group-level effects. Intrapecific variation is accounted for by using measurement data from all specimens, grouped by species, rather than using only

the species' means. This provides a pooled estimate for each species, which is then pooled into the overall effect of the predictor on the response (Gelman & Hill 2006, McElreath 2016). A similar property allows the phylogenetic covariance matrix to be used as a group-level effect (de Villemereuil et al. 2012). Bayesian multilevel models are effective with Gaussian and non-Gaussian predictor variables (Hadfield & Nakagawa 2010) and center-scaling multiple parameters to zero in Bayesian statistics produces conservative estimates while eliminating multiple comparison issues (Gelman & Tuerlinckx 2000).

We placed a logit link on the response variable, which bound the climbing probability estimates between 0 and 1. To avoid increased variance due to possible multicollinearity of some variables (McElreath 2016), we ran one regression model per morphological index rather than a multiple regression model containing all predictor variables. We used the R package MCMCglmm (Hadfield 2010) to generate our models. Error may be introduced into phylogenetic comparative analyses through uncertainty in the phylogenetic tree topology (de Villemereuil et al. 2012). Therefore, we used the R package mulTree (Guillerme & Healy 2014) to run our MCMCglmm models with 100 randomly sampled time-calibrated phylogenetic trees from the posterior distribution of the BEAST2 analysis. This results in 100 models for each of the 17 indices. Our model is:

$$\text{logit}(\Pr(Y=1)) = \alpha + \beta_n x_n + R_p + R_s + \epsilon$$

where  $Y$  is a vector of climbing probabilities,  $\alpha$  is the intercept,  $\beta_n$  represents the regression coefficient of each measurement ratio  $x_n$  for each sample, scaled to zero and fitted with a scaled Cauchy prior (Gelman et al. 2008; Ross et al. 2013; Carter & Worthington 2016),  $R_p$  is a group-level effect of interspecific relationships using an inverse phylogenetic variance-covariance matrix from each of the 100 trees (Hadfield 2010; Carter & Worthington 2016), and  $R_s$  is a

group-level effect of intraspecific variation. Both group-level effects are fitted with a parameter-expanded chi-squared prior (de Villemereuil et al. 2013; Carter & Worthington 2016).  $\epsilon$  represents residual variance and is fixed to 1 for binary data (Hadfield et al. 2013). A significant relationship between climbing index and a morphological index is shown by a posterior probability ( $\beta_n$ ) that does not overlap zero. We ran two independent chains for each set of 100 models. `mulTree` checked for convergence using the Gelman-Rubin potential scale reduction factor (Gelman & Rubin 1992) from the R package `CODA` v. 0.19 (Plummer et al. 2006). Our results were summarized using `mulTree`. We provide R scripts of the model on GitHub.

*Climbing Prediction for Non-Philippine Species* - We tested whether morphological indices correlated with the Climb Index of Philippine murines can accurately predict what is known of the climbing behavior for other species of murines that lack detailed observational data (see above). We used morphological indices that are associated with climbing (i.e. 95% credible interval not overlapping zero) in Philippine murines to construct a model using the categorical climbing scores described above (Supplemental Appendix 1.3, Supplemental Figure 1.1).

We fit a phylogenetic Bayesian ordinal mixed model using the categorical distribution family with a probit link function in the R package `brms` (Bürkner 2017; Bürkner & Vuorre 2018). Ordinal regression models are commonly used when categorical responses have a natural order. They are more robust than linear regression models that treat discrete categories as metric (Bürkner & Vuorre 2018). The categorical family assumes a directional trend in the individual categories; in this case, an increase in climbing from Terrestrial to General to Arboreal. Our model is:

$$\text{probit}(\Pr(Y_i \leq j)) = \theta + \beta_1 x_1 \dots \beta_j x_j + R_p + R_s$$

where  $\beta_1(x)$  attains the continuous values from the morphological indices. This ordinal model provides the cumulative probability of the  $i$ th rating falling in the  $j$ th category or below, where  $i$  indexes all measured specimens ( $n = 187$ ),  $j = 1, \dots, J$  represents the locomotor categories ( $J = 3$ ) and  $\theta_j$  is the intercept or threshold for the  $j$ th cumulative logit:  $\text{logit}(P(Y_i \leq j))$ . As in the model above,  $R_p$  and  $R_s$  are group-level effects of phylogeny and intraspecific variation, respectively. As with logistic regression, the residual error is fixed and not estimated in ordinal models. We again ran each predictor variable individually in its own model to prevent the increased variance that multicollinearity may create. To incorporate phylogenetic uncertainty, we used the same random sample of 100 time-calibrated phylogenetic trees that was used in the logistic model. Custom scripts executed each model 100 times. We ran four independent chains of each model and checked for convergence using the potential-scale-reduction factor (Brooks & Gelman 1998). We used the posterior estimates of the group-level effect to estimate the phylogenetic signal (Pagel's  $\lambda$ ; Pagel 1994; Bürkner 2017) for each of the predictor variables using the mixed-model approach (Housworth et al. 2004; Hadfield & Nakagawa 2010; Bürkner 2017). This measurement estimates the effect of relatedness on morphology and determines if the trait is strongly associated with phylogenetic relatedness. We used the `pp_check` function from `brms` to validate our model by comparing observed data to simulated data from the posterior predictive distribution. We compared the predictive ability of each model using k-folds cross validation using  $k=10$ . This method divides the data into 10 subsets (default in `brms`), then validates the results of the nine subsets for each missing subset.

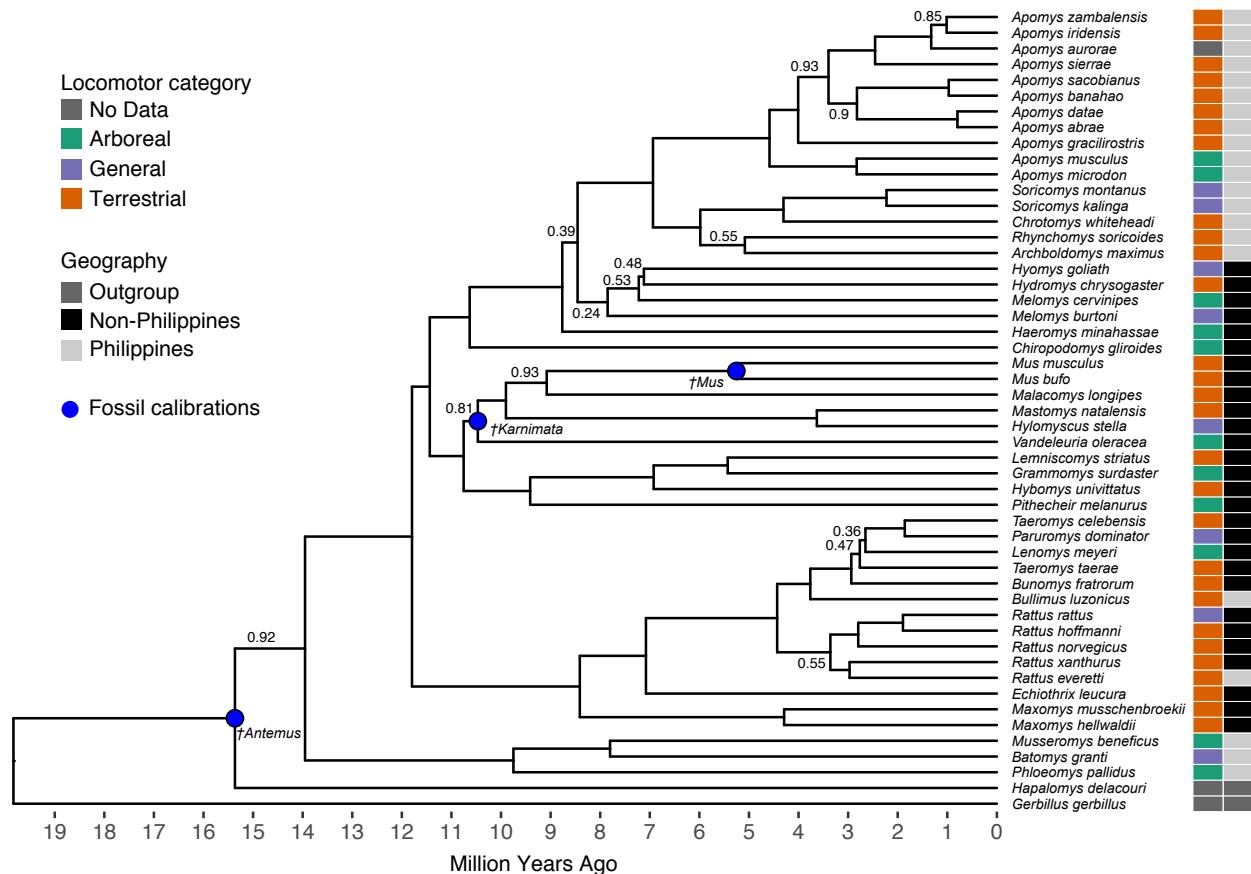


Figure 1.2. Maximum clade credibility tree, showing posterior probabilities  $<0.95$ , the position of fossil calibrations, and the tip states for locomotor category and biogeographic origins.

## Results

The General time reversible with a proportion of invariant sites and gamma distributed rate variation, GTR + I +  $\Gamma$ , model of sequence evolution was found to be the best fit for all five gene partitions of the alignment. All four BEAST2 runs converged and every run led to ESS values  $> 1000$  for each parameter. Our time-calibrated maximum clade credibility tree agrees with the timing and topology of published murine phylogenetic estimates (Fabre et al. 2013; Rowe et al. 2016; Aghova et al. 2017; Rowsey et al. 2018). Posterior probability of clade support was largely above 95%, though a few nodes were poorly supported (Fig. 1.2).

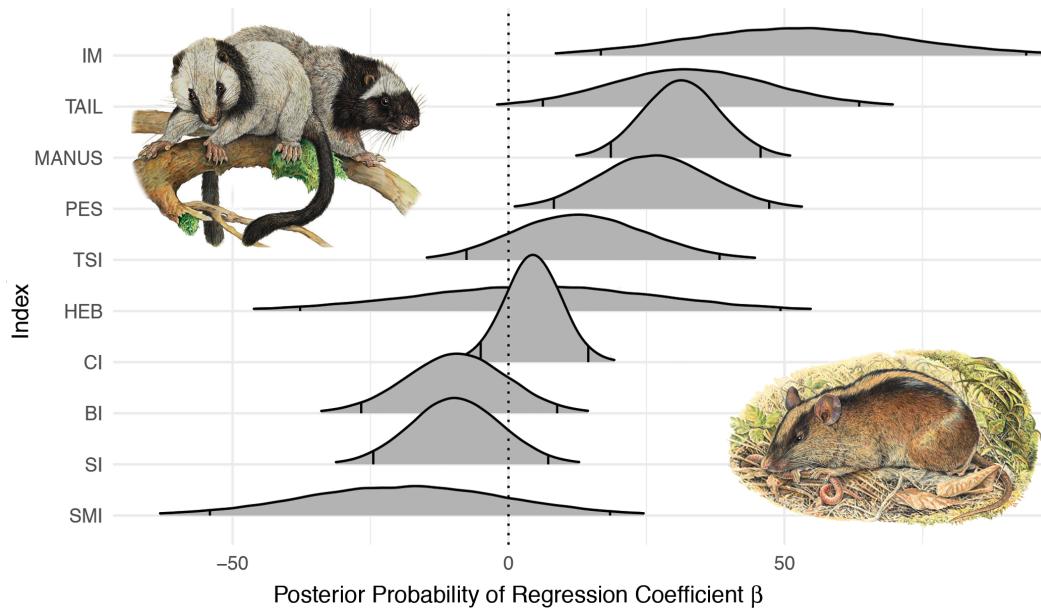


Figure 1.3. Results of logistic regression models in MCMCglmm. Density plots display the posterior probability of the  $\beta$  regression coefficient for each morphometric index, with 95% credible intervals delimited by vertical bars. Eight variables with large variance are not shown (see Table 1.2). Two Philippine murines are illustrated to show the degree of morphological disparity: upper left is the arboreal *Phloeomys pallidus*, and bottom right is the terrestrial *Chrotomys whiteheadi*. Illustrations by V. Simeonovski.

The Bayesian generalized mixed model fitted in MCMCglmm regressing the Climb Index of Philippine species with morphological indices all showed evidence of convergence (Gelman-Rubin statistic = 1) and had a high effective sample size for each parameter ( $>1000$ ). The models resulted in four measurements with a strong effect (i.e. 95% Credible interval of intercept and regression coefficient not overlapping zero) (Fig. 1.3). These four indices are MANUS (length of 3rd proximal phalanx of hand / length of 3rd metacarpal; a measure of relative finger length), PES (length of 3rd proximal phalanx of foot / length of 3rd metatarsal; a measure of relative toe length), IM (length of forelimb / length of hindlimb; a measure of limb uniformity), and TAIL (length of tail / total length; relative tail length). There was a high variance for many of the indices we calculated, reflecting interspecific variation, similarity between closely related species, and the negligible relationship between most indices and Climb

Index (Fig. 1.3, Table 1.2). The GI index coefficient has a negative credible interval that does not overlap zero (Table 1.2). However, because the intercept value does overlap zero and the credible interval of the regression coefficient is large, we excluded this measurement from future models.

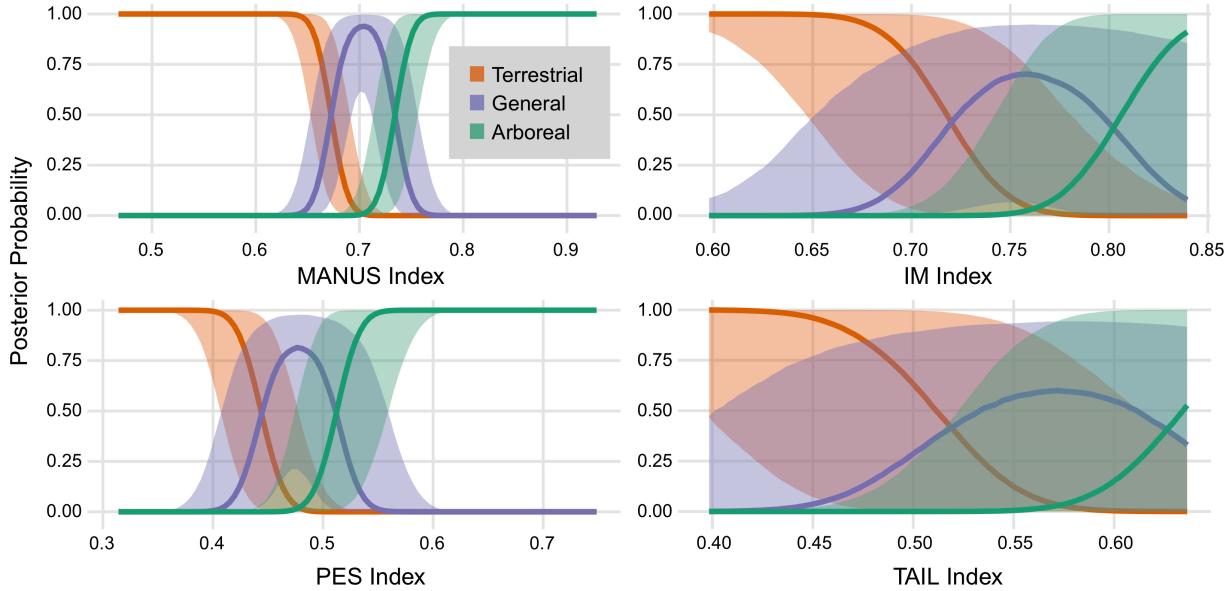


Figure 1.4. Marginal effect plots of ordinal models for the four strongest predictors of locomotion. 95% credible intervals are displayed around the mean trend lines. X-axis scales are bound by the observed values for each of the four indices.

Additional ordinal models were fit using the four variables MANUS, PES, IM, and TAIL. Ordinal mixed models were used to estimate how well the four variables fit with predicted categorical locomotor modes in species that lack quantitative climbing assessments. All models converged properly, each parameter had a high effective sample size ( $>1000$ ), and posterior-predictive checks showed good model fit (Supplemental Figure 1.2). We fit regularizing normal priors on the group-level effects ( $N(0, 1.5)$ ) to prevent MCMC chains from searching unreasonable areas of parameter space (Gelman 2006; McElreath 2016). Each of the four variables has a positive effect on locomotor mode in murines (Table 1.3), however, marginal

Table 1.2. Results of MCMCglmm logistic regression of morphological index vs. arboreality.  $\alpha$  is the intercept, and  $\beta$  is the regression coefficient of the index. HPD represents the highest density of the posterior distribution. Coefficients that do no overlap 0 are in bold.

Index	$\alpha$ HPD	$\alpha$ 95% CI	$\beta$ HPD	$\beta$ 95% CI
SMI	6.83	(-9.19, 24.09)	-17.9265	(-56.75, 18.71)
BI	9.02	(-10.62, 29.37)	-9.2968	(-28.01, 8.97)
HRI	0.40	(-11.19, 12.19)	-12.8783	(-158.14, 125.72)
HEB	-2.26	(-14.28, 10.43)	5.1928	(-40.87, 49.66)
OLI	5.25	(-6.79, 17.60)	-39.7650	(-115.03, 35.70)
URI	3.11	(-4.20, 10.61)	-92.3513	(-254.33, 63.85)
<b>MANUS</b>	<b>-22.50</b>	<b>(-32.89, -12.43)</b>	<b>31.3188</b>	<b>(17.36, 45.57)</b>
CI	-6.32	(-19.11, 6.87)	4.3958	(-5.79, 14.53)
FRI	-2.98	(-15.51, 9.98)	25.4993	(-141.26, 199.25)
GI	6.79	(-1.26, 15.84)	-100.6809	(-207.47, -3.17)
FEB	-9.26	(-24.00, 5.21)	46.4478	(-30.54, 123.41)
TRI	-0.77	(-10.05, 8.40)	-0.1562	(-177.16, 179.13)
TSI	-5.05	(-14.09, 3.30)	12.4924	(-10.02, 37.30)
<b>PES</b>	<b>-12.35</b>	<b>(-21.35, -3.10)</b>	<b>26.4282</b>	<b>(6.46, 47.04)</b>
<b>IM</b>	<b>-38.40</b>	<b>(-67.13, -10.09)</b>	<b>52.4149</b>	<b>(13.17, 92.99)</b>
<b>TAIL</b>	<b>-16.51</b>	<b>(-32.06, -2.29)</b>	<b>32.1920</b>	<b>(3.63, 63.20)</b>
SI	6.23	(-6.40, 18.71)	-9.7533	(-25.89, 7.06)

effects plots demonstrate that both TAIL and IM have large credible intervals, which diminish their value for inferring locomotor state (Fig. 1.4). These results are confirmed with k-folds cross validation, which shows that MANUS is the best-fitting model for climbing in murine rodents (though the standard errors of MANUS and PES overlap, Table 1.4), and that TAIL is the poorest-fitting of the four ordinal models.

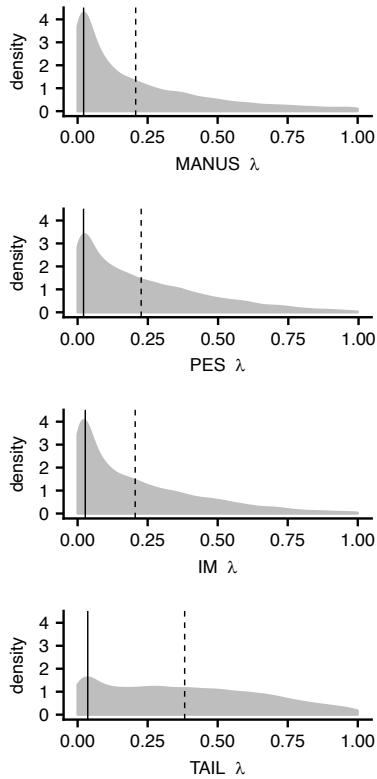


Figure 1.5. Posterior distribution of Pagel's  $\lambda$  for each of the four morphometric indices that predict locomotor category. Vertical lines indicate mean (dashed) and highest posterior density (solid).

There was high variance in the posterior distribution of Pagel's  $\lambda$  values for all indices due to the long tails of the posterior distribution of the group-effect parameters. However, we recovered a highest posterior density (HPD) of  $\lambda = 0.021$ , and a mean of  $\lambda = 0.21$  for the estimate of phylogenetic signal of MANUS (Fig. 1.5, Table 1.5). Similar values were estimated for PES and IM, but TAIL produced a higher Pagel's  $\lambda$  (Fig. 1.5).

Table 1.3. Results from brms ordinal regression for four indices

Index	$\alpha$ [1] Mean	$\alpha$ [1] 95% CI	$\alpha$ [2] Mean	$\alpha$ [2] 95% CI	$\beta$ mean	$\beta$ 95% CI
MANUS	53.74	(33.13, 80.61)	58.72	(13.23, 36.37)	79.96	(49.50, 119.63)
PES	26.45	(14.09, 41.19)	30.63	(17.45, 46.94)	59.84	(32.76, 93.75)
TAIL	14.98	(3.37, 27.79)	18.74	(6.61, 32.60)	29.78	(7.53, 54.13)
IM	28.75	(5.81, 53.12)	32.46	(9.28, 57.65)	40.29	(8.24, 74.39)

## Discussion

Arboreal locomotion has evolved repeatedly in mammals and is thought to have fostered their diversification by facilitating access to untapped resources (Luo et al. 2011; Meredith et al. 2011). However, many mammal species have not been—or cannot be—observed (e.g. fossil species) and thus we need indirect approaches to predict these species' ecological traits. We tested the predictive power of 17 morphological indices on a quantitative measure of climbing probability from murine rodents from the Philippines. We then used the variables strongly associated with climbing to test our ability to accurately assign other murine species to a categorical locomotor mode. Of the 17 indices, only MANUS, PES, TAIL, and IM were strongly associated with climbing probability in Philippine murines. This result is based on posterior probabilities of regression coefficient  $\beta$  values and intercept values that do not overlap zero. MANUS and PES also effectively predicted categorical locomotor mode across the murine radiation, regardless of body size and phylogenetic position. We show that a MANUS ratio  $> 0.7$  nearly always indicates some level of climbing behavior in murines. Given the high predictive ability (Fig. 1.4), and low phylogenetic signal, we conclude that the MANUS index is a simple and effective way to infer climbing behavior in murines. Our results suggest that increased digit

length, as indexed by MANUS and PES, is an adaptive shift associated with the transition to arboreality.

Table 1.4. K-Fold Information Criteria (IC) scores, standard error, and model differences

Model	K-Fold IC	SE
MANUS	41.19	8.64
PES	48.26	8.08
IM	50.14	10.23
TAIL	60.91	10.26
Model Differences		
MANUS - PES	-7.07	7.78
MANUS - IM	-8.95	9.43
MANUS - TAIL	-19.71	10.61
PES - IM	-1.88	5.83
PES - TAIL	-12.64	5.26
IM - TAIL	-10.77	5.54

The observed relationship between finger length and climbing is not new, as having long fingers relative to hand size is thought to increase grasping ability, a critical aspect of climbing (Cartmill 1985). In fact, some variation of this measurement ratio has been used to estimate locomotor mode in a wide range of extant and extinct taxa (e.g., Bloch & Boyer 2002; Ji et al. 2002; Luo et al. 2003, 2011; Gebo 2004; Weisbecker & Warton 2006; Luo 2007; Sargis et al. 2007; Kirk et al. 2008; O’Leary et al. 2013; Meng et al. 2017). To our knowledge, however, this is the first study to quantitatively test the assumption that hand proportions and climbing

behavior are correlated across a morphologically disparate group of mammals. Perhaps most striking is that “General” species consistently have intermediate finger length values, which suggests that this locomotor mode may represent an intermediate step between terrestrial and arboreal mammals. Our quantitative, continuous climbing data clearly demonstrate a strong log-linear relationship with finger length, revealing how detailed natural history data can elucidate ecomorphological signal that may be obscured by forcing naturally continuous life-history traits into categories.

Table 1.5. Estimated Pagel’s  $\lambda$  values for four indices

Index	HPD	Mean	95 % CI
MANUS	0.021	0.21	(0, 0.84)
PES	0.026	0.23	(0, 0.76)
IM	0.023	0.21	(0, 0.74)
TAIL	0.036	0.38	(0, 0.94)

Skeletal features previously associated with climbing in rodents and other small mammals include equally proportioned limbs (IM ~ 1), a short olecranon process (OL), long humerus (BI), and grasping hands and feet (MANUS and PES; Sargis 2001, 2002b; Samuels & Van Valkenburgh 2008; Tulli et al. 2015). Though we find some (but not all) of these to be positively associated with climbing in Philippine murines, we hypothesize that the lack of strong association between most measurements, and the low predictive ability of TAIL and IM, are due to the large phenotypic variation across murine rodents. The Philippine species in this study display the full range of body size found in extant murines and exhibit a wide spectrum of locomotor and feeding adaptations (Heaney et al. 2016). Surprisingly, we found that commonly referenced features of arboreality such as gracile long bones and a shortened olecranon process do not effectively predict climbing behavior. Perhaps other measurements are important in more

phenotypically conserved groups, though our results demonstrate that MANUS effectively predicts climbing behavior regardless of body size or ecomorphology in murines.

The common assumption that tail length is associated with climbing in small mammals (e.g., Kingsley et al. 2017) has received little empirical support (but see Horner (1954) for one experimental example). Our results support a positive relationship of tail length with climbing in Philippine murines, however, we find large variance (Supplemental Figure 1.1) and low predictive ability (Fig. 1.4) for this trait across all locomotor categories. Additionally, variation in TAIL is more strongly associated with phylogenetic relatedness than any of the other three indices ( $\lambda_{\text{mean}} = 0.38$ , Table 1.5, Fig. 1.5) and, without additional research, we caution against using this single metric to infer climbing in mammals.

Though not without variance, phylogenetic signal in the MANUS index is low. Low signal may be interpreted in a variety of ways (Kamilar and Cooper 2013), but we suggest that a Pagel's  $\lambda$  HPD of 0.021 (Table 1.5, Fig. 1.5) indicates that finger length is a phylogenetically labile trait. Finger length is probably more tightly related to ecology, and climbing species—regardless of phylogenetic distance—are expected to have relatively longer fingers than their terrestrial counterparts. Metrics of relative finger length are often compared between fossil and extant taxa across vast phylogenetic distances (Ji et al. 2002; Luo et al. 2011). Though our understanding of locomotory styles of extinct species will always require inference, our findings here suggest that relative finger length is a simple and effective way to infer climbing behavior in murines, and perhaps in mammals more generally.

# CHAPTER 3: LOCOMOTORY MODE TRANSITIONS ALTER PHENOTYPIC EVOLUTION AND LINEAGE DIVERSIFICATION IN AN ECOLOGICALLY RICH CLADE OF MAMMALS

## Introduction

An organism is a complex assemblage of interconnected traits that frequently covary in predictable patterns across the tree of life. Morphological change and habitat transition often occur in unison over evolutionary time scales (Losos 2009, Collar et al. 2011) and these transitions may alter the tempo of diversification (Stroud and Losos 2016, Alencar et al. 2017). Historically, much of the research exploring links among phenotype, ecology, and diversification focused on a single trait or key innovation (Heard and Hauser 1995). However, investigating integrated functional systems with more direct connections to organismal ecology may better elucidate the relationship between morphological form and diversification (Heard and Hauser 1995, Piglucci 2003, Goswami et al. 2014).

Although some niche transitions promote diversification (Schluter 2000, Near et al. 2012), others have little effect on a clade's evolutionary success, or may even hinder its diversification (Collar et al. 2009, Alhajeri and Steppan 2018). The “dead-end” or “cul-de-sac” hypothesis suggests that adaptive phenotypic change may push an organism toward an isolated adaptive peak, thereby decreasing the likelihood of further phenotypic differentiation (Simpson 1944, Buckling et al. 2003, Colles et al. 2009, Gajdzik et al. 2019). A large clade containing numerous, independent transitions toward, but not away from, specialization, along with low or negative net diversification rates, would lend credence to this hypothesis (Futuyma and Moreno 1988). Confirming the presence of shared trait dimensions between species that occupy similar behavioral or ecological niches is the first step in understanding integrated morphological adaptations and their impacts on diversification.

In mobile animals, trait combinations can inform how a species moves through its surroundings to access resources (Hildebrand et al. 1985). If organismal body plans reflect locomotory habits, then morphological shifts should occur in tandem with locomotor mode transitions. Evidence of rapid changes in morphological dimensions temporally associated with an ecological or locomotory shift supports the hypothesis of an adaptive process (Ricklefs and Miles 1994), while shared directional shifts in two or more traits suggests trait integration and a form-function association (Pigot et al. 2020).

One oft-studied case of locomotor adaptation is climbing in vertebrates. Arboreality introduces unique ecological challenges, such as navigating narrow, hazardous substrates, and is thought to promote behavioral and morphological adaptations (Cartmill 1974, 1985, Lillywhite and Henderson 1993, Nations et al. 2019). Numerous tetrapod clades have transitioned to an arboreal lifestyle (Cartmill 1985) and arboreality is often associated with convergent phenotypic evolution, including changes in digit, foot, and tail lengths in squamates and mammals (Hayssen 2008, Losos 2009, Harrison et al. 2015, Alencar et al. 2017, Nations et al. 2019, Mincer and Russo 2020). However, exceptions exist. For example, a large clade of salamanders shows no apparent morphological differences between arboreal and terrestrial taxa (Baken and Adams 2019), and the correlation between tail length and climbing in marsupials is weaker than in other vertebrates (Weisbecker et al. 2019). Therefore, one-to-one links between morphological measurements like foot and tail length and locomotion are not universal across tetrapods, and detailed investigations of potentially integrated traits may capture patterns not seen in other taxa or in single elements (Fabre et al. 2017).

Here we use the Old-World rats and mice (Rodentia: Muridae: Murinae), a relatively young (~15 million years; Aghova et al. 2018) and species-rich clade (nearly 700 species; Burgin

et al. 2018) to explore trait evolution and integration in the context of locomotion, and to determine how locomotion affects both phenotypic and lineage diversification. Although Murinae is best known for two human laboratory animals and commensal species (*Mus musculus* and *Rattus norvegicus*), its members represent a rich array of diets, morphologies, locomotory modes, and preferred habitats (Rowe et al. 2016, Martinez et al. 2018).

We leverage recent advances in taxonomic sampling along with four common, standard morphological measurements to test whether external morphological traits of murines covary, whether single or multiple traits are correlated with locomotion, and whether locomotor mode shifts affect the evolutionary success of lineages. More specialized locomotor modes, such as Arboreal and Amphibious, are thought to require distinct combinations of morphological traits. Longer tails may aid in climbing by enhancing counterbalance and tactility, while shortened, often wider hind feet aid in gripping narrow branches (Hickman 1979, Cartmill 1985). Long, thin bodies may improve the ability to bridge gaps in the canopy (Cartmill 1985, Gebo 2004, Youlatos et al. 2015). Long, often laterally compressed tails and long hind feet are used for propulsion in amphibious small mammals (Hickman 1979, Samuels and van Valkenburgh 2008), and a larger body improves thermal inertia in aquatic environments (Dunstone 1998). As such, we predicted that species in these specialized categories (Arboreal and Amphibious) will display narrow optimal trait values and lower rates of morphological evolution, reflecting stabilizing selection associated with performance in each habitat (Alencar et al. 2017, Ord et al. 2020).

## Methods

*Phylogenetic hypothesis of Murinae* - To construct a phylogenetic hypothesis of Murinae, we downloaded sequence data of four nuclear loci (*BRCA*, *IRBP*, *GHR*, and *RAG1*) and one mitochondrial gene (*CytB*) from GenBank for all available Murinae. To represent each species,

we obtained sequences from the same individual when available. We included *Gerbillus gerbillus* as an outgroup. Sequences were concatenated by species and aligned using Muscle software in Geneious v.7.1. All sequences were visually inspected for alignment errors in Geneious. Our concatenated alignment included 434 murine species and one outgroup, with mitochondrial *CytB* for 93% of species (405 of 435), and at least 1 nuclear gene for 86% of species (376 of 435). We used ModelFinder (Kalyaanamoorthy et al. 2017) to search for best-fit gene and codon partitions and DNA substitution models, and IQtree v.1.6.9 (Nguyen et al. 2015) to estimate a maximum likelihood phylogeny. Preliminary ModelFinder results suggested we partition by both gene and codon position, but this led to poor parameter estimates in downstream phylogenetic estimates (see below), likely due to overparameterization of a sparse alignment. Therefore, we repeated the above process with a maximum of five partitions, or one for each gene. To estimate a time calibrated phylogeny of Murinae, we used BEAST2 v.2.5.1 (Bouckaert et al. 2014), with the relaxed log-normal clock. We unlinked sequence evolution models, linked clock and tree models, and set models based on ModelFinder results. We time-calibrated our phylogeny with seven vetted fossil calibrations and their recommended log-normal priors (Aghova et al. 2018). To decrease sampling time, we first smoothed the tree from our IQtree analysis with the *chronos()* function in the R package ape v.5.3 (Paradis et al. 2004), setting the root to 15 Ma (Aghova et al. 2018). We used this ultrametric phylogeny as a starting tree, allowing the MCMC sampling to search for topological and branch-length improvements. Four independent runs of 200 million generations each, with samples drawn every 1000 generations, were completed with the CIPRES portal (Miller et al. 2010). We discarded the first 20% of trees and parameter values as burnin and thinned by a factor of 10 using TreeAnnotator. Convergence was evaluated using Tracer (Rambaut et al. 2014) to confirm that effective sample

sizes (ESS) exceeded 1000, that the trace of the log-likelihood (and other parameters) had plateaued, and that each chain reached the same plateau. We summarized the results as a maximum clade credibility tree using TreeAnnotator.

*Locomotor modes and morphological measurements of murine species* - To determine the locomotor mode of murines we scoured peer-reviewed literature and books for information on locomotor behavior and classified 423 species into one of four groups: “Arboreal,” “General,” “Terrestrial,” and “Amphibious.” (Supplemental Appendix Table 2.2). Here “Arboreal” means that climbing is an integral life-history trait for the species. “General” species are known to navigate a variety of substrates and opportunistically climb or swim (Russell et al. 2005), but do not require climbing or swimming (i.e. for nesting or feeding). “Terrestrial” indicates species that are not known to climb due to habitat use or behavioral or dietary niche, and “Amphibious” indicates a dependency on aquatic habitats for feeding. For example, if we read a report saying, “species A feeds on seeds on the ground but was once observed climbing to feed on fruit” then they would be labeled “General.” Our categories depart from a common “Arboreal- Scansorial-Terrestrial” classification. Arboreal means “inhabiting trees”, and Scansorial means “climbing,” so therefore all Arboreal species are Scansorial, but not all Scansorial species are Arboreal, which can lead to confusion. Our more discrete categories avoid this confusion and better describe both locomotion and microhabitat use.

We assembled four morphological measurements: head body length (HBL), tail length (TL), hind foot length (HFL), and mass for 373 of the 423 species with locomotor classification. These measurements are traditionally taken in the field from vouchered specimens and have served as key traits for species identification and ecological inference, providing an opportunity to collect a large sample size. Data were obtained from both specimen labels and the primary

literature (Supplemental Appendix Table 2.2). Sexual size dimorphism is not common in Murinae (Carlton and Martinez 1991, Musser et al. 2008, Carlton et al. 2015) though it has been observed in some species (Balete et al. 2006). However, we used measurements from adult male specimens whenever available or identified as such. There was an average of 2.4 primary literature sources per species (range = 1 – 6), though each primary source reported averages taken from numerous specimens (Supplemental Appendix Table 2.2). We combined measurements from each source, then took the average. As tail and hind foot lengths scale with body length, we calculated ratios of these measurements (*sensu* Mosimann 1970) to mitigate the influence of size in some of our analyses. Relative tail length (RTL) is tail length divided by total length (HBL + TL), and relative hind foot length (RHF) is HFL divided by HBL. As murine body mass ranges from 10 to 2500g, we log transformed masses. We scaled all measurements and ratios to unit variance with the *scale* function in R v3.5 and v4.0 (R Core Team 2020).

*Ancestral State Estimation of Locomotor Mode and Transitions* - We estimated the ancestral states of locomotor mode across the phylogeny of Murinae using stochastic character mapping (Bollback 2006) in the R library phytools v0.6-99 (Revell 2012). We used a trimmed phylogeny of the 423 species with locomotor data in our stochastic character mapping. To incorporate phylogenetic uncertainty, we took a random sample of 100 trees, with the outgroup removed, from the posterior distribution of our BEAST2 analysis. To determine the best transition rate model, we used fitMK() in phytools to fit three Markov models with different patterns of discrete trait evolution — “equal rates”, “symmetrical”, and “all rates differ” — and compared their predictive performance using Akaike Information Criterion (AIC) weights. We used the model of discrete trait evolution with the highest predictive performance to estimate a transition matrix in simmap. We estimated the transition rate for each tree using the  $Q = “empirical”$  setting. As

all Amphibious taxa are phylogenetically nested and a clearly derived state within Murinae (Rowe et al. 2014, Martinez et al. 2020) we treated an Amphibious ancestor as unlikely and set the root state prior to  $pi = 0.333, 0.333, 0.333, 0.0001$  for Arboreal, General, Terrestrial, and Amphibious, respectively. One hundred iterations on each of 100 trees resulted in 10,000 stochastic character maps. We summarized the character maps for each tree (100 summaries) to generate a posterior estimate of the locomotor mode at each node and the mean transition rate between each state.

*Morphological correlates of locomotion* - To test the hypothesis that discrete locomotor modes have unique morphologies, we fit a series of phylogenetic Bayesian multilevel models with Stan (Carpenter et al. 2017) in the R library brms (Bürkner 2017). Using locomotor mode as the predictor, we fit four models, each with a different trait (HBL, RTL, RHF, and log mass) as the response variable. We used the phylogenetic correlation matrix from a trimmed murine phylogeny of 373 species (those with morphological measurements and locomotor data) as a group-level effect to account for the non-independence of species (de Villemereuil et al. 2012, Bürkner 2017). We ran one model for each of 100 trees from the posterior distribution (as above) to incorporate phylogenetic uncertainty (Nakagawa and De Villemereuil 2018). We fit regularizing normal priors on the population-level effects  $N(0, 1.5)$  (Gelman 2006, McElreath 2016) and used the student-t distribution family to describe the response variable, a method often termed ‘robust regression’ (Kruschke 2013, Bürkner 2018). For each trait, each of the 100 models included four chains run for 5000 iterations, with 2500 warm-up and 2500 sampling iterations, which were thinned by a factor of 10, yielding 100,000 posterior samples. For regression with categorical predictors, brms assigns a random category (locomotor mode in this case) as the intercept (“dummy variable”), so we removed the intercept parameter from the

model to generate a posterior distribution of phylogenetically corrected mean trait values for each locomotor group. We assessed convergence with ESS and a Gelman-Rubin diagnostic of  $\hat{R}$  1.01. We used the posterior distributions of the mean trait values to determine if different locomotor modes have different morphologies by calculating the differences between each of the posterior distributions, i.e. contrasts (Kruschke 2013, McElreath 2016, Roycroft et al. 2019) using the *compare\_levels* function in the R library *tidybayes* (Kay 2020). If the 95% credible interval of the difference distributions does not overlap zero, then we can say that the traits differ between locomotor modes. This method is analogous to the Bayesian ANOVA or Bayesian robust t-test (Kruschke 2013).

*Trait covariation and functional evolution* - Traits that are more functionally related have a higher size or shape correlation than traits that are less functionally related (Van Valen 1965). To quantify trait covariation, we estimated the size correlation between four morphological traits of 373 murine species using phylogenetic multiresponse models (i.e. models with multiple response variables, Nakagawa and Santos 2012, de Villemereuil and Nakagawa 2014, Bürkner 2017, Brommer et al. 2019). We estimated the correlation between the absolute size of phenotypic measurements (TL, HFL, HBL, and log mass) both within and across locomotor modes. A high correlation between the size of two measurements within a locomotor mode indicates an optimal ratio of traits, and therefore a functional relationship (Van Valen 1965, Randau and Goswami 2018). All measurements, (tail length, HFL, HBL, and log mass) were scaled to unity using the *scale* function in R. We removed the intercept from the model, included no population-level effects (i.e. response variables), and used the phylogenetic correlation matrix as a group-level effect. We used brms to build the model, using four morphological traits as response variables. With multiresponse models, brms produces a posterior distribution of estimated correlations

comparable to Pearson's correlation coefficient (Bürkner 2017, Brommer et al. 2019). In addition to our model with all available murine taxa, we ran four identical multiresponse models for each locomotor mode using only the trait data and species in each locomotor regime.

*Locomotion and the mode of trait evolution* - To test for morphological diversification and constraint within locomotor modes we fit a series of models of trait evolution using the R library OUwie v.1.57 (Beaulieu et al. 2012, Beaulieu and O'Meara 2019) with each locomotor mode representing a unique regime. For Brownian Motion (BM) models, traits evolve according to the rate parameter  $\sigma^2$ . Ornstein-Uhlenbeck (OU) models contain a nondirectional rate parameter  $\sigma^2$ , the optimal value of the trait  $\theta$ , and the strength of selection  $\alpha$ . We fit five models in OUwie: BM1) a single  $\sigma^2$  estimate for all locomotor regimes; BMS) independent  $\sigma^2$  rates for each regime; OU1) OU model with a single  $\theta$ ,  $\alpha$ , and  $\sigma^2$  shared by all locomotor regimes; OUM) OU model with independent  $\theta$  values for each locomotor regime, but a single  $\sigma^2$  and  $\alpha$  shared by all states; and OUMV) OU model with different  $\theta$  and  $\sigma^2$  for each locomotor regime, but a single  $\alpha$ . In preliminary analyses two OUwie models that assumed a varying  $\alpha$ , OUMA and OUMVA, returned sub-optimal log-likelihood values and negative values in the eigenvalue decomposition of the Hessian matrix and therefore were not considered further per author recommendations (Beaulieu and O'Meara 2019). Using a trimmed phylogeny of 373 murines with morphological and locomotor data, we generated 100 stochastic character maps from a random set of 100 trees from our posterior distribution using phytools with the same Q matrix and root priors as in Ancestral State Estimation of Locomotor Mode and Transitions above. We used our four phenotypic traits (mean-centered and scaled HB, RTL, RHF, and log mass) as our input traits and locomotor mode as our input regimes. We set up one OUwie model per trait, used custom scripts to loop each OUwie model over our set of 100 stochastic character maps, compared the

five OUwie trait evolution models using AICc, and calculated the mean and 95% probability ranges of each parameter. We report the results of the best-fit model. To verify the stability of our OUwie model results, we calculated 10 parametric bootstraps across 5 randomly selected stochastic character maps, for a total of 50 bootstraps for each trait, using the *OUwie.bootstrap* function, then estimated the 95% probability intervals of these bootstraps. To confirm that our parameter estimates ( $\theta$ ,  $\alpha$ , and  $\sigma^2$ ) differed between locomotor regimes, we compared the differences between the posterior distributions of the mean estimates of each parameter across locomotor modes using the “Bayesian ANOVA” linear modeling approach for categorical predictor variables described above. Briefly, we ran Bayesian linear models in brms (Bürkner 2017) using the parameter estimate as the responses and the categorical locomotor mode as the predictors, and compared the posterior distributions of the mean estimates using *compare\_levels* in *tidybayes* (Kay 2020).

Interpretation of the OU model parameters is aided by calculating two additional variables: phylogenetic half-life ( $\ln(2) / \alpha$ ), or the time it takes a trait to evolve half way to the optimal  $\theta$ , and stationary variance ( $\sigma^2 / 2\alpha$ ), or the expected variance of the trait when the evolutionary process is at equilibrium (Hansen 1997, Gearty et al. 2018). We calculated these two variables for each OU model selected by AICc.

*Locomotion’s influence on diversification* - We used character-state dependent diversification models to test whether transitions to specialist states (i.e. Arboreal and Amphibious) limit evolvability. Character-state dependent diversification models, also known as SSE models, describe the joint evolution of a character and the phylogeny (Maddison et al. 2007, FitzJohn et al. 2009, Freyman and Höhna 2018, Freyman and Höhna 2019). However, they may be subject to false-positive results (Maddison and FitzJohn 2015, Rabosky and Goldberg 2015). One

possibility is that the diversification parameters are caused by an unmodeled character, which we addressed by using hidden state models (Beaulieu and O'Meara 2016, Caetano et al. 2018). We used a hidden Markov model with two hidden states (Beaulieu and O'Meara 2016; Caetano et al. 2018), resulting in eight states: Arboreal, General, Terrestrial, and Amphibious associated with hidden state A, and the same four locomotor modes with hidden state B. We used the dnCDBDP() command in RevBayes v.1.0.9 (Höhna et al. 2014, Höhna et al. 2016), which uses a full Bayesian approach to model speciation and extinction rates of each character, transition rates between locomotor modes, and transition rates between the two hidden states. We incorporated a random sample of 100 trimmed trees from our BEAST2 posterior distribution of trees to incorporate phylogenetic uncertainty. As we lack locomotor data for 11 taxa, we used only 423 of the 434 murine species in our phylogenetic reconstruction. Each model on each tree was run for 4500 generations, with the first 500 discarded as burnin. We combined the results of all trees, providing posterior distributions of 400,000 estimates per parameter, then thinned these by a factor of 100 for ease in subsequent analyses and plotting.

## Results

*Phylogenetic relationships and character states* - The phylogenetic estimate from IQtree incorporated an independent substitution model for each of our five potential partitions. All parameters in the BEAST2 runs properly converged (ESS > 1000 in combined log). Our maximum clade credibility (MCC) estimate was generally well supported (Figure 2.1, higher resolution in Supplemental Figure 2.1), and, despite increasing the taxon sampling over previous studies (e.g. from 268 species in the largest previous murine phylogeny, Rowe et al. (2019), to 423 in this study), topological and temporal estimates are congruent with recent phylogenetic hypotheses (Aghova et al. 2018, Rowe et al. 2019). We used the tribe and division names

proposed in Rowe et al. (2019) with some exceptions. We did not recover a monophyletic Oenomys division (*Oenomys*, *Thamnomys*, *Grammomys*, *Thallomys*) (*sensu* Musser and Carleton 2005) and henceforth we refer to the Grammomys division as containing the genera *Grammomys*, *Thamnomys*, and *Thallomys*, and the Golunda division as containing *Golunda* and *Oenomys* (Figure 1.1). The Colomys division (*Colomys*, *Zelotomys*) is nested within the Stenocephalemys division, a pattern also recovered in both in Aghova et al. (2018) and Rowe et al. (2019).

We recorded a locomotor mode for 647 of the 700 murine species (15% Arboreal, 20% General, 63% Terrestrial, 2% Amphibious). Of these, 423 species were used in the Ancestral State estimates (15% Arb., 22% Gen., 61% Ter., 2% Amph.) and 373 in morphological analyses (15% Arb., 23% Gen., 60% Ter., 3% Amph.) (Appendix II). The proportion of species amongst locomotor modes remained fairly constant within each reduced dataset. Thus, our taxon sampling is representative of locomotor mode distribution across Murinae.

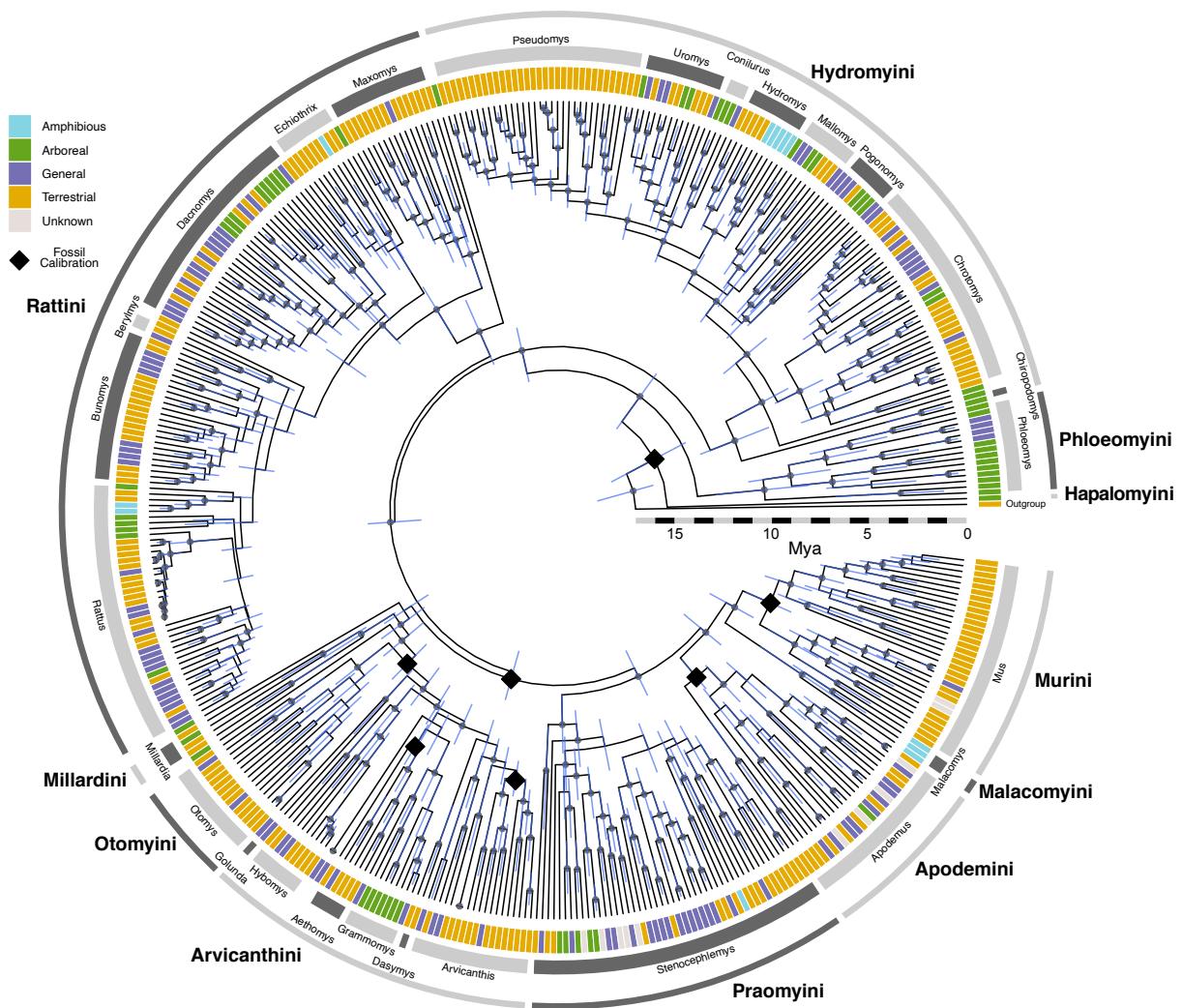


Figure 2.1: Time-calibrated maximum clade credibility tree of Murinae. Colored bars at the tips represent locomotor mode (see legend), while tribes (outer ring) and divisions (inner ring) are marked around the tree in alternating dark and light grey. Black diamonds signify fossil calibrations, grey dots indicate nodes with 95% credible support, and blue bars are 95% credible intervals of node ages. Not all taxa in the tree belong to divisions or tribes used in this manuscript. A higher resolution image with tip labels is available as Supplemental Figure 2.1.

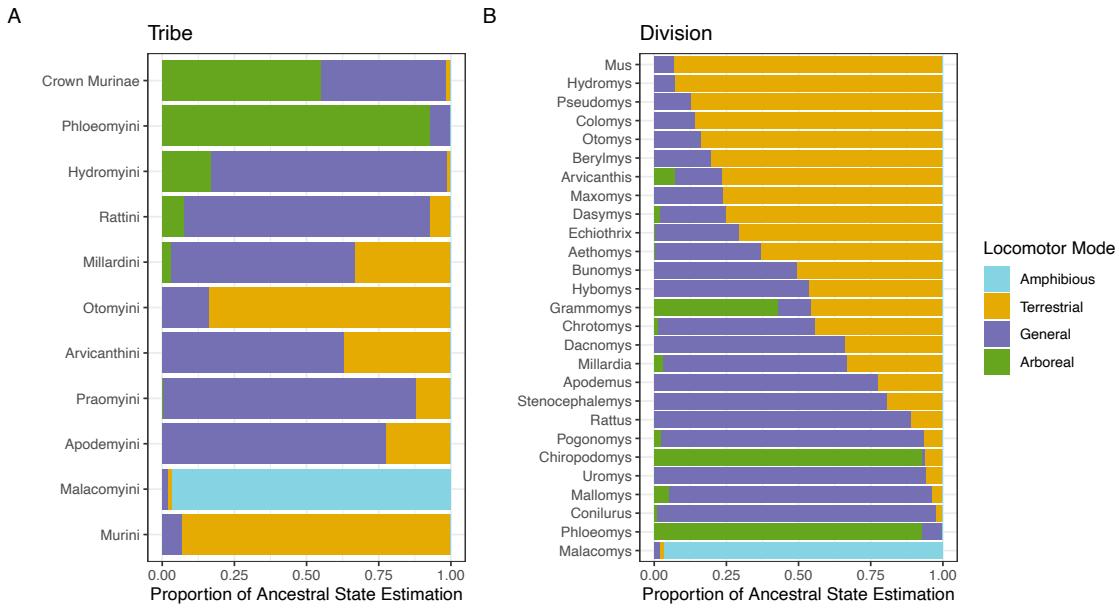


Figure 2.2: A) Estimated ancestral states of murine tribes. Crown Murinae is followed by tribes in descending order by crown age, and B) estimated ancestral states of murine divisions, sorted for easy visualization.

#### *Ancestral Character States and State Transitions - The “all rates differ” transition model*

received >99% of the AIC weight, therefore we ran stochastic character maps using the “ARD” model. We extracted the ancestral states of the murine tribes and divisions from Rowe et al. (2019) with the changes mentioned above. Several divisions from Rowe et al. 2019 (*Hapalomys*, *Haeromys*, *Micromys*, and *Srilankamys*) were represented by a single taxon in our phylogenetic estimate and therefore had no ancestral state estimate. We found that the root state of Murinae is either Arboreal (proportion of ancestral state estimates = 0.54) or General (0.44)(Figure 2.2), though this ambiguity may be due to our minimal outgroup sampling. Perhaps not surprisingly, the old and relatively depauperate tribe Phloeomyini has a high probability (0.93) of an Arboreal most recent common ancestor (MRCA; Figure 2.2). Hydromyini and Rattini both have high probabilities of a General MRCA (0.82 and 0.85 respectively), while Otomyini and Murini likely

had a Terrestrial MRCA (0.84 and 0.93 respectively) (Figure 2.2). The small clade of Malacomyini, comprised of only three Amphibious species, is estimated to have had an Amphibious MRCA (0.96). Divisions were split between Terrestrial, General, and ambiguous ancestral states, with two divisions having an estimated Arboreal ancestor and one division with an Amphibious ancestor.

Summarizing the 10,000 stochastic character maps produced a mean of 175, median of 174, locomotor mode transitions per tree. Locomotor mode shifts only occurred in a “linear” pattern between Arboreal and General, General and Terrestrial, and Terrestrial and Amphibious, despite no constraints in the model requiring transitions to occur this way. The General-to-Arboreal transition rate is over four times that of the reverse. Transitions from General to Terrestrial were nearly twice that of the reverse (Table 2.1). Transition rates between General and Arboreal were lower than between General and Terrestrial. Transitions to the Amphibious state were rare, and Amphibious species have never left this specialized mode, according to our inferences.

Table 2.1: Mean transition rates between locomotor modes from stochastic character maps. Matrix is read from row to column, so that first value in row Arboreal is the rate from Arboreal (row) to General (column).

Mode	Arboreal	General	Terrestrial	Amphibious
Arboreal	-	0.003	0.000	0.000
General	0.013	-	0.030	0.000
Terrestrial	0.000	0.017	-	0.002
Amphibious	0.000	0.000	0.000	-

*Morphological patterns of locomotion* - Bayesian linear models of mean trait values for each locomotor mode converged for all four models (ESS > 10,000 for merged models,  $\hat{R} = 1$ ). Amphibious murines have the highest mean HBL and General species are longer than Terrestrial or Arboreal species, whereas the latter two have very similar mean HBLs (Table 2.2, Figure 2.3). However, at the 95% credible level, the difference in HBL between any of the locomotor modes overlaps zero (Figure 2.4A). Body mass was similar for all locomotor modes (Table 2.2). Amphibious species have a higher than average mass, and Arboreal species a slightly lower than average mass, however, none of the pairwise comparisons differ from zero at the 95% credible level (Figure 2.4B). For RTL we observed greater differences among locomotor modes (Table 2.2). Arboreal species have the longest tails, Terrestrial species have the shortest tails, and General and Amphibious species fall in between (Table 2.2, Figure 2.3). In contrasts, the RTL of Arboreal species is longer than both Terrestrial and General species at the 95% credible level, and longer than the RTL of Amphibious species at a 90% credible level (Figure 2.3, Figure 2.4C). The Amphibious RTL estimate has a large credible interval and differences between them and General or Terrestrial species are less decisive (Figure 2.4C). Amphibious species have the longest RHF, Arboreal and General species have the shortest RHF, and Terrestrial species are centered around zero, or the mean of all murines (Table 2.2, Figure 2.3). Contrast plots highlight these differences, revealing that General and Arboreal RHFs are smaller at the 95% credible level than Terrestrial or Amphibious RHFs, and Terrestrial are smaller than Amphibious at the 90% credible level (Figure 2.4D).

Table 2.2: Mean estimates and 95% credible intervals for each locomotor mode and measurement from phylogenetic multilevel models. The column provides the estimated error and 95% credible interval for each model.

Measurement	Arboreal	General	Terrestrial	Amphibious	Sigma
log(Mass)	-0.17 (-0.91, 0.57)	0.05 (-0.69, 0.79)	0.02 (-0.72, 0.75)	0.38 (-0.48, 1.25)	0.15 (0.08, 0.22)
Head Body	-0.25 (-0.82, 0.32)	-0.14 (-0.71, 0.42)	-0.26 (-0.82, 0.30)	0.10 (-0.59, 0.80)	0.11 (0.06, 0.16)
Hind Foot	-0.34 (-1.06, 0.39)	-0.29 (-1.01, 0.44)	-0.05 (-0.77, 0.67)	0.66 (-0.34, 1.65)	0.32 (0.21, 0.43)
Tail	0.49 (-0.24, 1.22)	0.00 (-0.73, 0.73)	-0.32 (-1.04, 0.41)	-0.04 (-0.91, 0.83)	0.32 (0.23, 0.40)

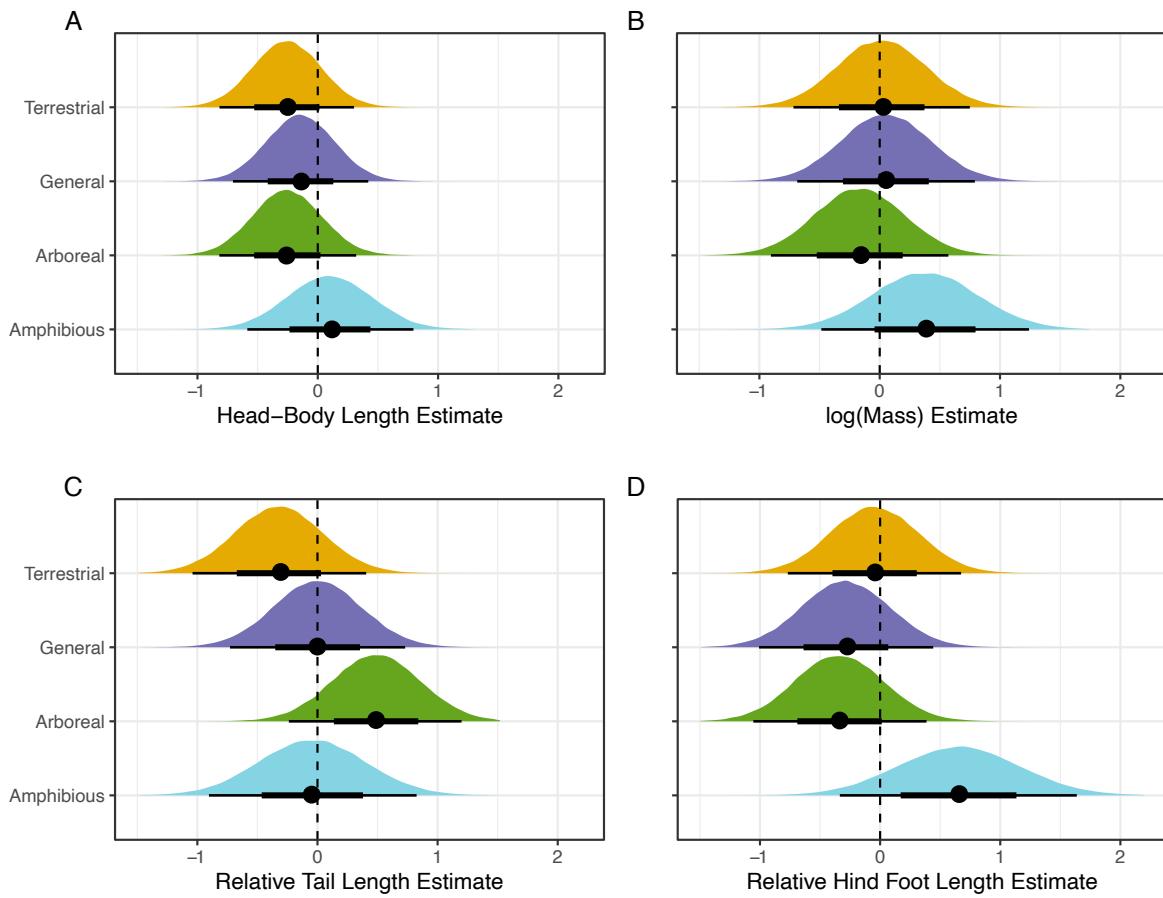


Figure 2.3: Density plots of phylogenetic mean trait values for the four locomotor modes. Black circles represent the median values and horizontal black bars are the 65% (thick) and 95% credible intervals (thin). All measurements are mean centered and scaled to 1 standard deviation.

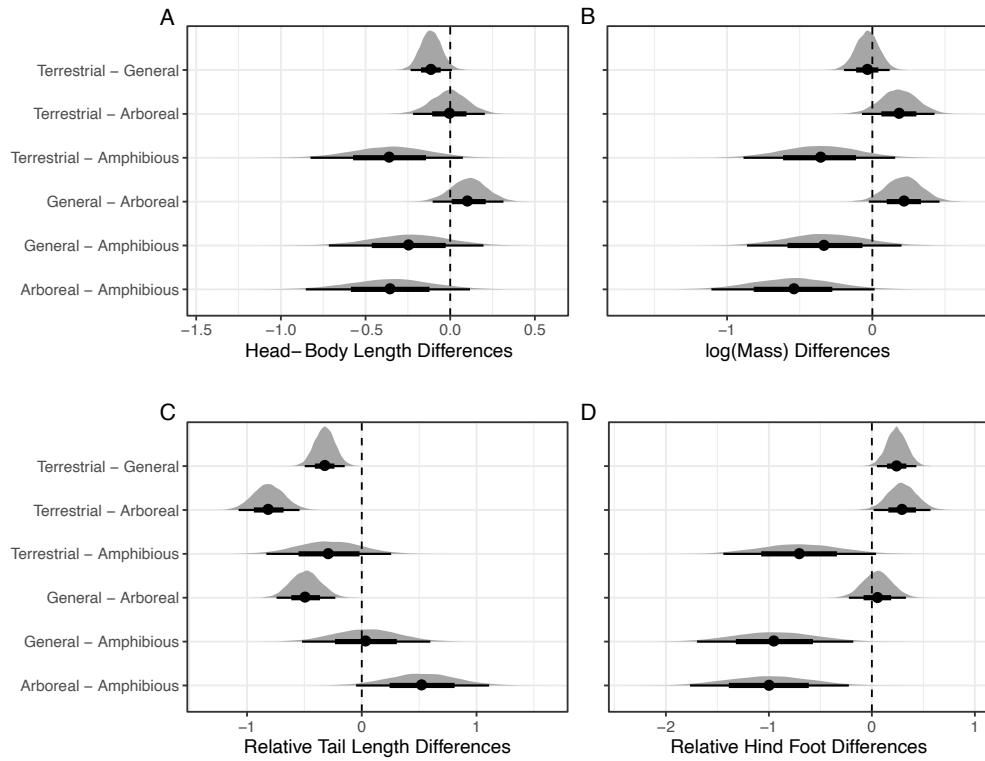


Figure 2.4: Density plots of differences (contrasts) between phylogenetic mean trait values for the four locomotor modes (see Figure 2.3). Points are medians, wide bars the 65% credible intervals, and narrow bars are 95% credible intervals. If the distributions of the differences do not overlap zero at the 95% credible level, then we can say there is a reliable difference between the two values. A) HBL differences, B) log(Mass) differences, C) RTL differences, and D) RHF differences.

*Trait covariance and functional evolution* - All models of trait covariation converged ( $\text{ESS} > 800$ ,  $\hat{R} = 1$  for all parameters). We found high correlation among traits for all of Murinae (Table 2.3) with a mean correlation of 0.87. However, the strength of covariance among traits varied with locomotor modes. Overall, traits were least correlated in Terrestrial taxa and most correlated in Arboreal and General taxa (Table 2.3). As expected, HBL and mass were highly correlated in all locomotor modes. Arboreal and General taxa had a greater correlation between tail length and body length than did Terrestrial taxa (Table 2.3). The correlation between TL and HFL also was greater in Arboreal and General species than in Terrestrial species. The correlation

between HBL and HFL shows a similar pattern of high covariance in Arboreal and General taxa, but lower correlation in Terrestrial taxa. Due to small sample size, Amphibious taxa correlation estimates had wide credible intervals that prevented interpretation of possible trait correlation.

Table 2.3: Phylogenetic covariance correlation coefficients (mean and 95% credible intervals) for traits by locomotor mode (columns 1-4) and for all murines (column 5).

Correlations	Arboreal	General	Terrestrial	Amphibious	All
Head Body & Tail	0.93 (0.86, 0.97)	0.93 (0.85, 0.98)	0.74 (0.63, 0.84)	0.62 (-0.09, 0.95)	0.92 (0.88, 0.95)
	0.95 (0.92, 0.98)	0.96 (0.93, 0.98)	0.89 (0.85, 0.93)	0.62 (-0.13, 0.96)	0.96 (0.95, 0.98)
Head Body & Hind Foot	0.93 (0.85, 0.97)	0.92 (0.83, 0.97)	0.88 (0.80, 0.95)	0.69 (-0.21, 0.97)	0.96 (0.93, 0.98)
	0.94 (0.90, 0.97)	0.97 (0.94, 0.99)	0.93 (0.91, 0.95)	0.55 (-0.26, 0.92)	0.95 (0.93, 0.97)
Tail & Hind Foot	0.90 (0.79, 0.95)	0.90 (0.79, 0.96)	0.71 (0.60, 0.81)	0.34 (-0.46, 0.84)	0.87 (0.82, 0.92)
	0.86 (0.77, 0.93)	0.95 (0.90, 0.98)	0.88 (0.83, 0.92)	0.39 (-0.40, 0.87)	0.94 (0.91, 0.96)
Hind Foot & Mass					

*Rates of trait evolution associated with locomotor modes* - The OUMV model, with locomotor-mode specific evolutionary rates  $\sigma^2$  and optima  $\theta$ , but a universal strength of pull parameter  $\alpha$ , had by far the best AICc scores across all four traits (scaled RTL, scaled RHF, scaled HBL, and log(Mass), Table 2.4). Therefore, we only present the results of this model (Figure 2.5). Our model estimates and probability intervals were similar to our parametric bootstrap estimates and

probability intervals across all traits. Our OUwie model and parametric bootstrap values are highly congruent (mean difference  $\pm$  0.01) and are all reliably above zero.

Our HBL OUMV model estimated a universal mean  $\alpha$ = 0.09 (95% probability = 0.05, 0.19) and universal phylogenetic half-life mean of 7.44 my (3.64 my, 14.25 variance mean of 0.86 (0.53, 1.23). Terrestrial species have the lowest rate of HBL stochastic evolution at 0.14 (0.10, 0.37), an HBL  $\theta$  mean of -0.47 (-0.71, -0.20), and the lowest stationary variance at 0.81 (0.59, 1.21). Amphibious species have an optimal HBL mean of 1.62 (0.86, 3.06), a stochastic evolution rate mean of 0.35 (0.24, 0.50), and a stationary variance mean of 1.92 (1.02, 3.59). All of the pairwise differences in HBL  $\theta$  and  $\sigma^2$  values were robust except for a non-credible difference between Amphibious and Arboreal HBL  $\sigma^2$  (Supplemental Figure 2.2).

Table 2.4: Corrected Akaike Information Criteria (AICc) scores for each of the five models of trait evolution from OUwie analyses. The OUMV model has the lowest AICc value for all four traits (in bold).

Trait	BM1 AICc	BMS AICc	OU1 AICc	OUM AICc	OUMV AICc
Head Body Length	31.80	16.40	25.44	15.57	<b>0.01</b>
Log(Mass)	25.99	9.51	-2.23	-2.65	<b>-8.69</b>
Relative Tail Length	78.93	11.10	34.20	-8.38	<b>-31.45</b>
Relative Hind Foot Length	54.95	24.46	-41.44	-44.25	<b>-52.65</b>

Mass has the lowest  $\alpha$  at 0.08 (0.05, 0.16), and the highest phylogenetic half-life at 9.17 my (4.45 my, 15.38 my) of any trait, suggesting a weak pull towards the optimal mass of each locomotor mode. Arboreal species have a mass  $\theta$  mean of 3.95 (3.29, 4.37), the highest stochastic evolution rate at 0.29 (0.20, 0.47), and the highest stationary variance at 1.86 (1.37, 2.6). General species have a mass  $\theta$  mean of 4.39 (4.16, 4.75), the lowest  $\sigma^2$  at 0.12 (0.09, 0.21), and the lowest stationary variance at 0.82 (0.49, 1.17). Terrestrial species have a  $\theta$  mean of 3.91

(3.45, 4.23), a  $\sigma^2$  mean of 0.18 (0.12, 0.28), and a stationary variance mean of 1.24 (1.00, 1.58). Amphibious species have the highest optimal mass at 6.08 (5.19, 7.49), a  $\sigma^2$  mean of 0.21 (0.15, 0.28), and a stationary variance mean of 1.26 (0.07, 2.46). All pairwise differences in log (Mass)  $\theta$  values were robust. All  $\sigma^2$  differences were robust except for non-credible  $\sigma^2$  difference between Terrestrial and Amphibious species (Supplemental Figure 2.2).

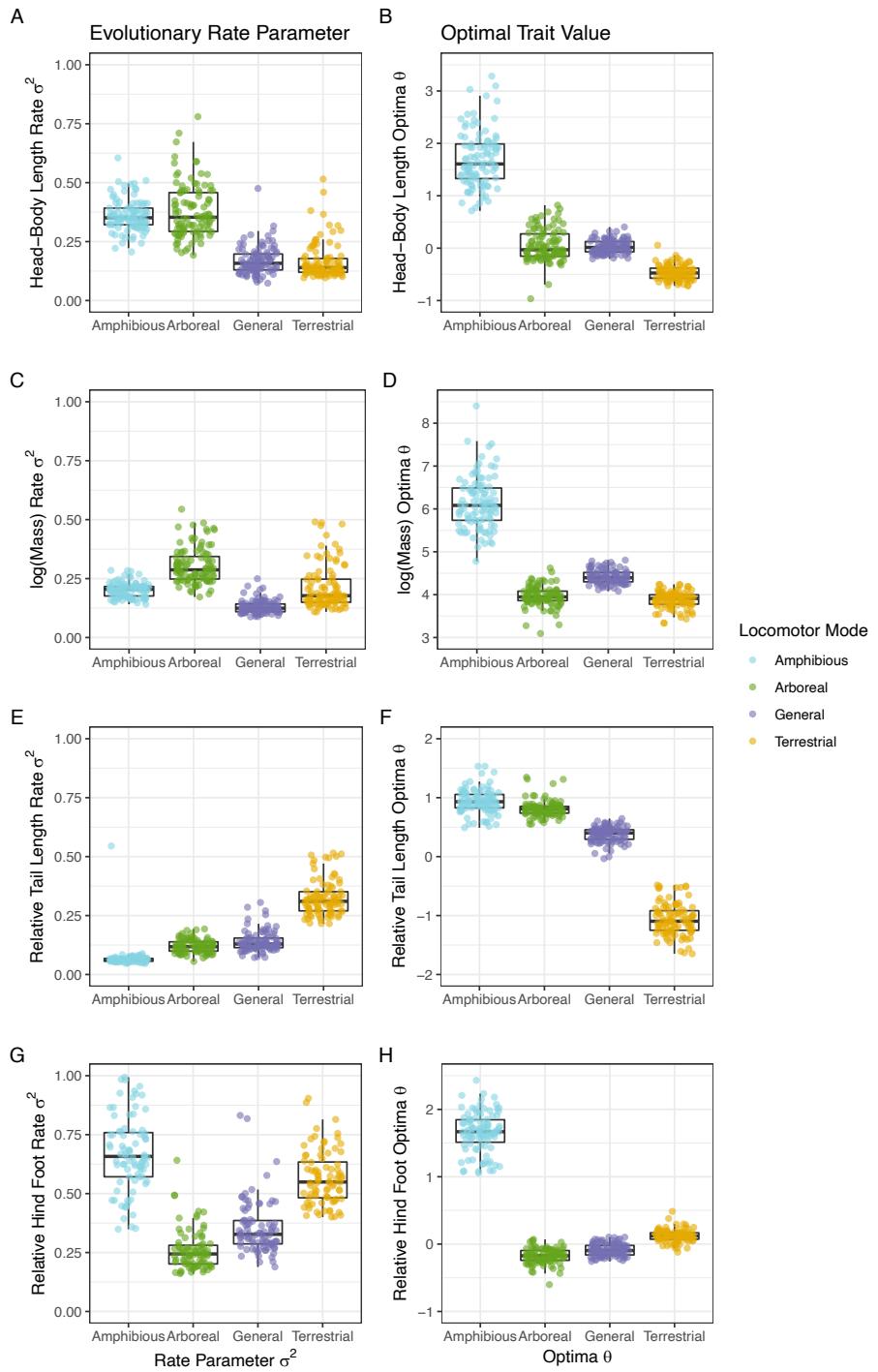


Figure 2.5: Results from 100 independent OUwie OUMV analyses. Colored dots represent the outcomes of each analysis, and box plots provide the median (dark line in the box), 25<sup>th</sup> and 75<sup>th</sup> percentiles (top and bottom of boxes), and the largest or smallest values no further than 1.5 \* inter-quartile range from the center (whiskers). Head-Body Length, Relative Tail Length, and Relative Hind Foot Length are scaled to a mean of zero and a standard deviation of 1.

RTL has an  $\alpha$  mean of 0.13 (0.09, 0.20) and a phylogenetic half-life mean of 5.41 my (3.46, 8.13). Arboreal species have the second highest tail optimum at 0.81 (0.59, 1.29), a  $\sigma^2$  mean of 0.12 (0.08, 0.18), and a stationary variance mean of 0.45 (0.32, 0.59), less than  $\frac{1}{4}$  the of the HBL or log(Mass) variances. General species have a RTL  $\theta$  mean of 0.39 (0.07, 0.58), a  $\sigma^2$  mean of 0.13 (0.09, 0.21), and a stationary variance mean of 0.51 (0.37, 0.86). Terrestrial species have the lowest RTL optimum at -1.12 (-1.63, -0.72), the highest RTL  $\sigma^2$  at 0.31 (0.05, 0.51), and the highest RTL stationary variance at 1.23 (0.97, 1.51). Amphibious species have the highest RTL  $\theta$  at 0.94 (0.70, 1.43), the lowest RTL  $\sigma^2$  at 0.06 (0.05, 0.08), and the lowest RTL stationary variance at 0.23 (0.18, 0.36). All of the pairwise differences in RTL  $\theta$  and  $\sigma^2$  values were far from zero (Supplemental Figure 2.2).

RHF models have the highest  $\alpha$  at 0.22 (0.15, 0.34) and the shortest phylogenetic half-life at 3.22 my (2.04 my, 4.50 my) of any of the four traits, demonstrating a stronger pull towards the optimal foot size for each locomotor mode. Arboreal species have the lowest hind-foot length optimum of any locomotor mode at -0.16 (-0.42, 0.04), the lowest  $\sigma^2$  at 0.24 (0.17, 0.48), and the lowest stationary variance at 0.57 (0.45, 0.71). General species have a mean RHF  $\theta$  of -0.08 (-0.23, 0.10), a mean  $\sigma^2$  of 0.33 (0.21, 0.63), and a mean stationary variance of 0.76 (0.58, 1.01). Terrestrial species have an RHF optimum mean of 0.12 (-0.06, 0.30), an RHF  $\sigma^2$  mean of 0.55 (0.41, 0.88), and a stationary variance mean of 1.29 (1.14, 1.41). Amphibious species have the highest RHF  $\theta$  at 1.71 (1.40, 2.23), the highest RHF  $\sigma^2$  at 0.66 (0.36, 0.99), and a mean RHF stationary variance at 1.59 (0.94, 2.04). All of the pairwise differences in RHF  $\theta$  and  $\sigma^2$  values were robust (Supplemental Figure 2.2).

*Locomotion and Diversification* - All parameter estimates in our hidden character-state dependent diversification analysis appeared to converge. After thinning by a factor of 100,

character-dependent birth death models still demonstrate acceptable levels of convergence (ESS > 300 for 4000 samples), demonstrating consistent parameter estimates regardless of tree topology. Due to the long tails in the posterior distributions of diversification analysis parameter estimates (Figure 2.7), we present the more stable 90% credible intervals (Kruschke 2014). The mean transition rate of hidden state A to state B is 0.014 (90% C.I. = 0.0001 to 0.028) while the mean of the reverse is 0.531 (90% C.I. = 0.344 to 0.718) (Figure 2.6). We estimated the transition waiting time, or the inverse of the transition rate describing time between transitions. The highest posterior density (HPD) of transition waiting time from state A to state B is 52.15 million years (90% C.I. = 12.16 to 307.12) (Figure 2.6B). As Crown Murinae is estimated to be < 20 my, this long waiting time clearly demonstrated the low probability of a state A to state B transition. The HPD transition waiting time from state B to state A is 1.78 million years (90% C.I. = 1.24 to 2.59) (Figure 2.6C).

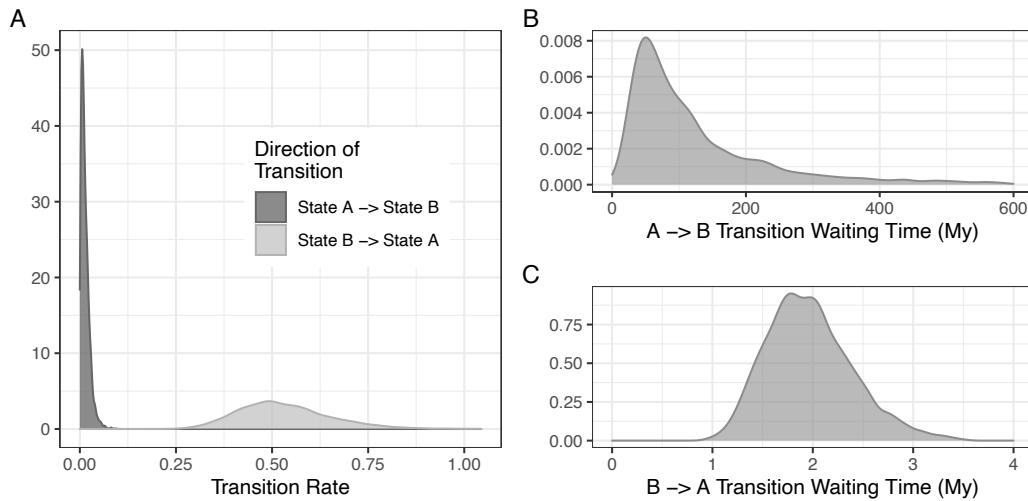


Figure 2.6: Transitions from state A to state B occur much more frequently than the reverse. A) Posterior distribution density plots of transition rates between hidden states A and B from character-state dependent diversification models; B) and C) density plots of transition waiting time (inverse of transition rate) from hidden state A to hidden state B, and the reverse,

respectively, in millions of years (My). Note large differences in the scales of B and C. Values > 600 My have been removed from plot B to simplify visual representation.

The estimated speciation rates of the eight character-state combinations (four locomotor categories by two hidden states) show the mean speciation rates in the rarely visited hidden state B are more than triple those of hidden state A (Figure 2.7). In state A, Terrestrial species have the highest speciation rate (mean of 0.233, (0.147 to 0.311)) followed by General (mean = 0.186, (0.050 to 0.308)) and Arboreal (mean = 0.156, (0.038 to 0.250)). The Amphibious state A speciation rate mean is similar to the Arboreal and General states, but it has a large credible interval (mean = 0.175, (0.000 to 0.435)) (Figure 2.7). In hidden state B, Terrestrial (mean = 0.989, (0.522 to 1.461)) and General (mean = 0.889, (0.615 to 1.128)) have the highest speciation rates, while Arboreal species have the lowest (mean = 0.516, (0.133 to 0.845)). Amphibious species in state B have an intermediate rate estimate with large variance (mean = 0.806, (0.176 to 1.398)).

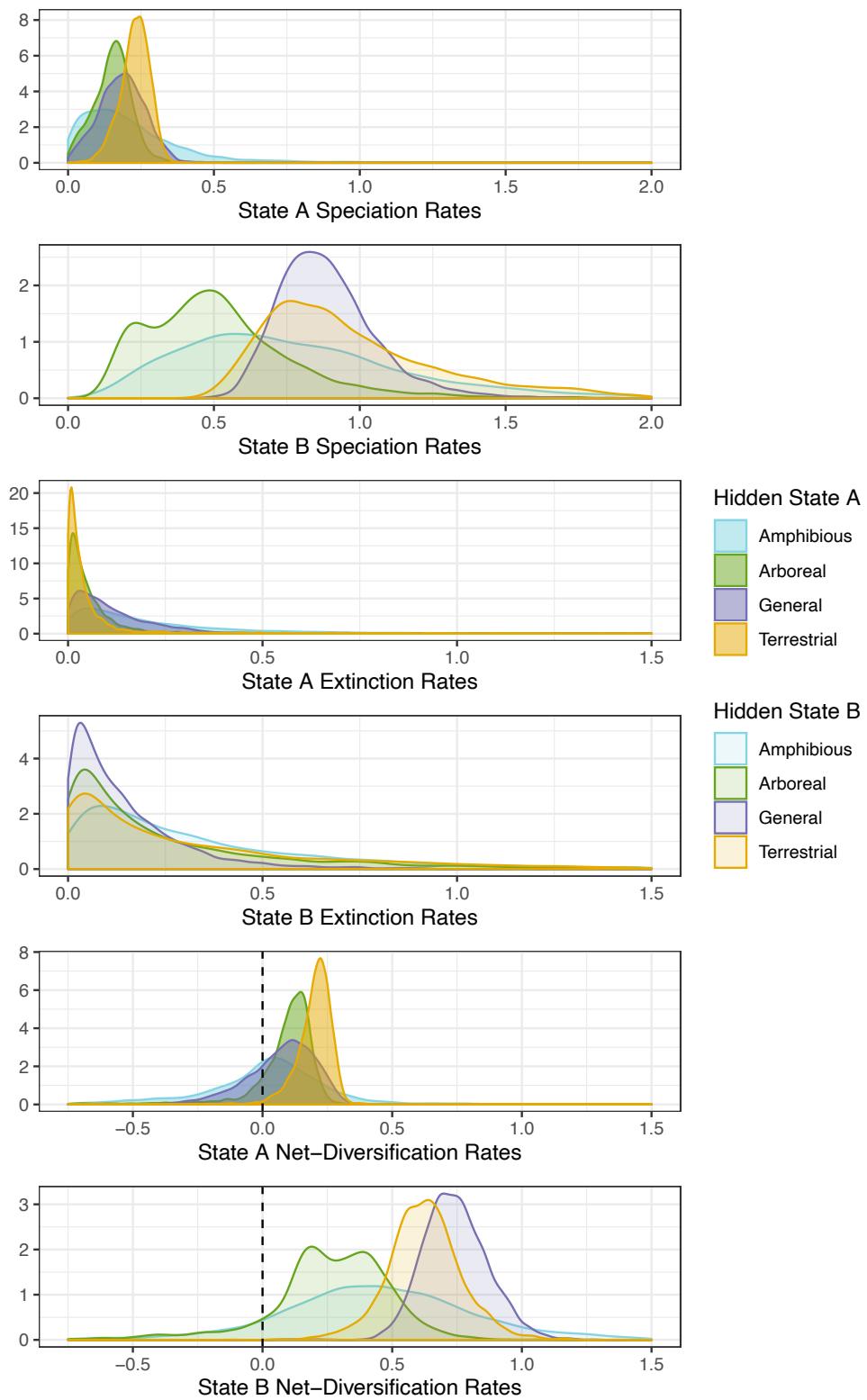


Figure 2.7: Posterior distribution density plots of rate estimates from character-state dependent diversification models.

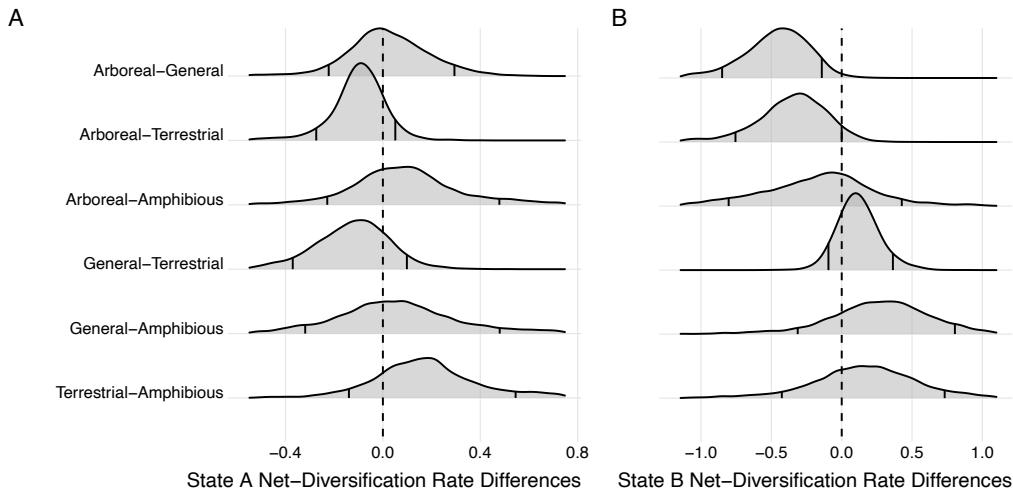


Figure 2.8: Density plots of the differences between net-diversification rate estimates for each locomotor mode. A) Though median values for Terrestrial are higher and median values for Arboreal are lower than other modes, the 90% Credible intervals all overlap zero, indicating undecided differences between all net-diversification rates. B) In State B, the Arboreal mode shows strong evidence of a slower diversification rate than General and Terrestrial.

The estimated extinction rates of all locomotor modes in both hidden states are centered near zero (Figure 2.7). The net diversification rates show slow diversification for hidden state A (Arboreal = 0.073, (-0.061 to 0.241), General = 0.074, (-0.128 to 0.280), Terrestrial = 0.200, (0.010 to 0.296), Amphibious = -0.008, (-0.486 to 0.390)). All state A diversification estimates have positive means, but only Terrestrial species show a credibly non-zero rate at the 90% level (Figure 2.7). All four locomotor modes show a generally positive diversification rate in state B with much higher mean values and credible intervals than in state A (Arboreal = 0.252, (-0.061 to 0.667), General = 0.744, (0.548 to 0.950), Terrestrial = 0.621, (0.408 to 0.870), Amphibious = 0.464, (-0.243 to 1.091)). Despite the high mean values, only Terrestrial and General species show a non-zero diversification rate at the 90% credible level (Figure 2.7).

## Discussion

*Do single or multiple traits covary with locomotion?* – Among murine rodents, an ecologically diverse and species rich group of mammals, we found that species in each locomotor category have different combinations of trait values. Some traits, such as tail and foot lengths, are highly correlated and have low evolutionary rates in some locomotor regimes. This suggests that these traits evolve in an integrated manner and that certain ecologies and habitats can lead to morphological specialization and reduced phenotypic evolution (Collar et al. 2009, Alencar et al. 2017). Arboreal species, for example, have long tails and short hind feet (Figures 2.4 and 2.5); these traits are tightly correlated (Table 2.3) with low rates of evolution (Figure 2.5) and low stationary variance (Table S2). Long tails and short, broad hindfeet fit morphological expectations for arboreal species (Hickman 1979, Cartmill 1985, Karantanis 2017). Although tail length alone may be an inadequate predictor of locomotion in murines (Nations et al. 2019), our results suggest that the evolution of long tails, in association with other traits, has been important for small climbing mammals. In addition, Arboreal taxa have more gracile body forms than General and Terrestrial species — optimal or mean HBL is similar for the three regimes, but Arboreal species have a lower optimal mass (Figure 2.5) — supporting the role of lighter, slimmer bodies in arboreal vertebrates. One of the key challenges of arboreality is bridging gaps in the forest canopy by reaching between branches (Cartmill 1985, Gebo 2004, Youlatos et al. 2015), and arboreal mammals and squamates often have a narrower body plan than terrestrial counterparts (Dublin 1903, Lillywhite and Henderson 1993, Alencar et al. 2017).

Arboreal species have the highest rate of HBL evolution, the broadest optimal HBL range, and the largest HBL stationary variance of any locomotor mode, suggesting no directional tendencies in the body size evolution of Arboreal species (HBL rate, Figure 2.5, Figure S2, Table

S1). The Arboreal regime contains the largest (*Phloeomys pallidus*, 2100g) and one of the smallest (*Haeromys minahassae*, 10g) taxa in our data set. Body size is a labile trait that can evolve rapidly (Slater and Friscia 2019), and in murines, body size (HBL and mass) evolves around twice as fast in Arboreal species compared to General species (Figure 2.4, Table S1). Transitions to Arboreal only occurred from General species (Table 2.1), and General species have a narrow optimum body size with low stationary variance (Figure 2.5, Table S1). Therefore, while some traits in Arboreal species such as RHF and RTL are highly correlated, selection may be relaxed on other traits such as body mass.

General species have intermediate tail lengths, short hind feet, and, as in Arboreal species, these two traits are tightly correlated (Table 2.3). Models of trait evolution show that General species have very narrow optimal trait values and low rates of phenotypic evolution for all four measurements (Figure 2.5), though the relatively low  $\alpha$  values for HBL and mass may influence these interpretations. These results, along with the high trait correlation values (Table 2.3), demonstrate that the General body plan is highly conserved. As all General species are known to climb at least occasionally, and these results provide additional support for the role of long tails and short, broad hind feet in navigating narrow or vertical surfaces. (Hickman 1979, Cartmill 1985). In other words, a modest tendency to climb may require similar adaptations as frequent climbing. The similarities between arboreal and “scansorial” species has been noted in other vertebrate clades, including carnivores (Samuels et al. 2013), frogs (Blackburn et al. 2013), and snakes (Lillywhite et al. 2012).

Terrestrial species have short tails, long hind feet, and larger, more rotund bodies (large mass relative to HBL). Tail length is comparatively decoupled from body size (both mass and HBL) in Terrestrial species, suggesting that terrestriality does not constrain tail length evolution

(Table 2.3, Figure 2.5). For instance, Terrestrial groups such as the Maxomys division have tail lengths that are similar to HBL, while many Otomys and Mus division species have tails less than half of HBL.

Though the paucity of Amphibious species resulted in wide parameter variance, these species have the largest values in every morphological measurement except tail length (Figure 2.4). In general, Amphibious rodents are larger than their Terrestrial relatives (Dunstone 1998, Pihlström 2008). Increased body size of amphibious species is seen across all rodents and in other vertebrate groups such as squamates and has been attributed to the need for improved heat conservation in water (Dunstone 1998, Meiri 2008, Pihlström 2008, Martinez et al. 2020). Most amphibious mammals, and amphibious vertebrates in general, swim using hind foot and tail propulsion (Hickman 1979, Samuels and van Valkenburgh 2008), which is thought to select for elongate hind feet and powerful, long tails that are often laterally compressed or augmented with stiff ventro-dorsally arranged vertically oriented hairs (Voss 1988, Rowe et al. 2014). Our observations of increased HBL, mass, RHF, and RTL support these existing hypotheses of convergent evolution in Amphibious species (Peterhans and Patterson 1995, Meiri 2008, Rowe et al. 2014, Martinez et al. 2020).

Although our chosen measurements provide only a rough sketch of body form, they still show strong evidence of trait covariance associated with locomotor mode. More detailed investigations into small mammal morphology, such as limb proportions, finite element analysis of muscle force, or biomechanical modeling of skeletal-element interactions, may reveal nuanced adaptations that are left unobserved with simple linear measurements. Nonetheless, our large sample size reveals clear differences in and covariances between body size, foot length, and tail length, in four distinct small mammal locomotor modes.

*Locomotion and evolutionary success-* Character-dependent diversification analyses show heterogeneity in diversification rates among locomotor modes and an association with unmodeled character states (Figures 2.7 and 2.8). Although interpreting hidden Markov models is challenging (Caetano et al. 2018), we see that the hidden states with high diversification rates (state B) are uncommon and short-lived, a pattern demonstrated by the rare transition to and frequent transition from state B (Figure 2.6). We interpret this to mean that some unmodeled character state, or trait, occasionally appears throughout murine history. Though there is no way to know the nature of the unmodeled trait, possibilities include increased access to novel areas via colonization, favorable environmental conditions, or dietary adaptations. Second, we do see that in state A, Terrestrial species have the highest and only credibly non-zero net-diversification rate (Figure 2.7), while in state B General and Terrestrial species have similarly high diversification rates (Figures 2.7 and 2.8). This parallels our stochastic character mapping results, where many diverse clades in the murine phylogeny have either General or Terrestrial ancestors, rather than Arboreal or Amphibious ancestors. Lastly, Arboreal diversification rates are much lower than Terrestrial in state A and reliably lower than General and Terrestrial species at the 90% level in state B (Figure 2.8).

Credible intervals on Amphibious diversification rate estimates are wide but, like Arboreal species, are lower than Terrestrial state A and lower than General and Terrestrial in state B (Figure 2.8). In fact, amphibiosity appears to be an evolutionary dead end in murines, as the diversification rates in both hidden states are low (Figure 2.7), and discrete character mapping reported no transitions away from this specialized state (Table 2.1). The finding of low diversification rates in the more specialized Arboreal and Amphibious modes differs from previous studies. For example, in the larger rodent clade Muroidea (in which Murinae is nested)

and the squamate clade Viperidae, locomotor specialization was not found to affect diversification (Alhajeri and Steppan 2018, Alencar et al. 2017). In other animals such as cichlids, butterflies, and neotropical furnariid birds (Claramunt et al. 2012, Ebel et al. 2015, Burress 2016) specialization appears to facilitate cladogenesis. Our findings add to the growing consensus that specialization leads to a variety of outcomes, including rapid speciation, increased extinction risk, and static persistence (Futuyuma and Moreno 1988, Smits 2015).

*The evolution of arboreality in Murinae-* Arboreality is a widespread locomotor strategy among vertebrates that has garnered broad general attention because of its relevance to human origins and to general concepts such as Dollo's law and ecological innovation (Haines 1958, Cartmill 1974, Zani 2000, DeSilva 2009, Moen et al. 2013, Urbani and Youlatis 2013, Venkataraman et al. 2013, Alencar et al. 2017, Scheffers and Williams 2018, Baken and Adams 2019). Within Murinae, Arboreal taxa are often on long phylogenetic branches with few species (Figure 2.1), a pattern that differs from other arboreal vertebrates (Samuels et al. 2013, Alencar et al. 2017, Moen and Wiens 2017, Ord et al. 2020). This is most apparent in the genus *Hapalomys*, which contains three species of Arboreal mice (one in our phylogeny) and is sister to nearly 700 species. Other examples of this pattern include the tribe Phloeomyini and genera *Chiropodomys*, *Haeromys*, *Micromys*, and *Vandeleuria* (Figure 2.1). The paraphyly and long branches of depauperate Arboreal clades has led to speculation that many Arboreal lineages are relicts of previously diverse clades (Musser and Newcomb 1983, Emmons 1993, Pagès et al. 2015). Our results provide some support to this hypothesis. Stochastic character maps highlight more transitions to (mean = 34/tree) than away from (mean = 9/tree) arboreality. Our character-dependent diversification analyses demonstrate a low diversification rate for Arboreal species, suggesting that this specialized locomotor mode has evolutionary cul-de-sac tendencies, but has

remained a viable specialization over long periods of time. Ancestral state estimation shows that none of the young or rapidly diversifying divisions, such as *Rattus*, *Mus*, *Bunomys*, *Chrotomys*, or *Pseudomys* have a  $> 0.01$  probability of an Arboreal ancestor (Figure 2.2). The few young Arboreal clades, such as *Chiromyscus* and *Margaretamys*, are deeply nested within larger groups containing few if any Arboreal taxa. This suggests that young, rapidly diversifying clades evolve from General or Terrestrial ancestors, with Arboreal species appearing after the clade's establishment. If this same pattern existed in the past, then Arboreal species on long branches probably do represent rare transitions in largely extinct clades. In Murinae, arboreality appears to be an adaptive peak that is difficult to descend (Figure 2.3, Table 2.1, Figure 2.5), but, as was documented in mammals at large (Smits 2015), is not a speciation sink (Figure 2.7). However, without a rich fossil record, the hypothesis that Arboreal lineages are relicts of historically more diverse clades may remain quantitatively untestable (Pages 2015).

*Generalized morphologies as reservoirs of diversification* – In Murinae we see that the most specialized locomotor modes, Arboreal and Amphibious, are less common than the General and Terrestrial modes. Murine locomotor mode transitions occur largely from generalist to specialist but are not irreversible (Table 2.1), a pattern that has been observed in a wide variety of organisms (Nosil and Mooers 2005, Day et al. 2016). Models of trait evolution demonstrate that the General body plan is highly conserved with strongly correlated traits (Figures 2.4-2.5, Table 2.3). As many murine tribes and divisions are estimated to have a General ancestor (Figure 2.2), the morphological stasis of General forms is relevant to the history of murines. For example, tribes Hydromyini and Rattini, two large clades (Figure 2.1, Rowe et al. 2019), both originated from what were likely average sized rats with TL proportional to HBL and average to short HFL — a body plan similar to many modern day *Rattus* species. Transitions away from the General

regime happen at over twice the rate of transitions to General (Table 2.1). Combined with the knowledge that murine clades have colonized novel habitats and land masses numerous times throughout their history (Rowe et al. 2019), this suggests that species often transitioned to Terrestrial or Arboreal following the successful colonization of a new region. Character-dependent diversification analyses showed that General species in the rare hidden state B have the highest diversification rates (Figures 2.7 and 2.8). The most rapidly diversifying murine clade is the *Rattus* genus of Southeast Asia and Australia (Upham et al. 2019), a clade that does contain a diversity of locomotor modes but is phenotypically conserved (Rowe et al. 2011). Our results suggest that the success of this highly conserved, yet functionally flexible body plan helped foster the breadth of taxonomic and phenotypic diversity seen in murines today.

## Conclusion

We used locomotion as a central node connecting morphology and ecology to understand trait correlation and test the effects of locomotion on species diversification. We found evidence of functional trait evolution with, for example, arboreal murines evolving short feet, long tails, and slender bodies. Similar morphological patterns have been shown in other clades of arboreal vertebrates (Collar et al. 2011, Lapiédra et al. 2013, Alencar et al. 2017, Verde Arregoitia et al. 2017), highlighting a case of parallel evolution in phylogenetically distant taxa with comparable microhabitat use. In specialist murines, correlated evolution of functional traits within locomotor modes may alter the tempo of diversification by functionally limiting morphologies and reducing diversification rates. However, in generalists, we found that correlated morphological evolution can lead to alternative combinations of characters that slow phenotypic evolution yet promote taxonomic diversification. Together, these contrasting processes have produced exceptional ecological and species diversity in the murine radiation. Our results suggest that the body plan of

General species, classically referred to as “rat-like”, facilitated the expansion of Murinae across the Eastern Hemisphere. The flexibility of this body plan is demonstrated through the recent and rapid global expansion, via human commensalism, of several General murine species, whereas commensalism in Arboreal, Amphibious, or Terrestrial murines is largely unknown. This pronounced history of evolutionary success afforded to the most ecologically labile species reveals a role for generalists as seeds of future morphological and ecological diversity.

# CHAPTER 4: THE ROLE OF NICHE PACKING AND EXPANSION IN THE ASSEMBLY OF COMMUNITIES IN AN ADAPTIVE RADIATION

## Introduction

An important question in ecology is understanding the relationship between species richness and niche breadth among species poor and rich communities. Ecological theory requires that species within a community differ in the mean and breadth of their resource use and habitat (MacArthur and Levins 1967); however, evidence for a consistent pattern of resource partitioning within species-rich communities remains elusive. Rich biological communities often comprise many closely related species, particularly in insular biogeographic settings where local geography has fostered localized adaptive radiations (Losos and Ricklefs 2009.) In isolated locations with limited immigration, the synergy of ecological opportunity and cladogenesis shape the resource use of individual species and fill local communities with many closely related species (Lack 1983, Schlüter 2000, Losos and Ricklefs 2009), providing an excellent opportunity to investigate the evolution of resource partitioning in community assembly.

The number of species in a given community is highly variable, even at the local scale, and the properties of communities' resource use may differ with species richness. Inter-community differences in resource use can be quantified as the difference in the overall breadth of community niche space. Here we view a species niche as an n-dimensional volume of resource use, functional traits, and climatic requirements (henceforth 'niche volume': Hutchinson 1957), and the overall community ecological volume as the sum of the volumes of the species therein. For high-diversity communities to exist, individual species may exploit habitats or resources that are either unavailable or unused in low-diversity communities, and estimates of community niche volume should be positively correlated with species richness ("Niche

Expansion”; MacArthur 1970). Alternatively, species in high-diversity communities may narrow their niche breadth and become more specialized or otherwise increase niche overlap in such a way that reduces competitive exclusion and leads to a higher density community niche volume (“Niche Packing”; MacArthur 1970). Importantly, niche packing and expansion are not necessarily mutually exclusive explanations of how resource use varies among communities; community niche volumes may increase in both size and density with increasing diversity (Figure 3.1, Pigot et al 2016).

Species richness often varies along environmental gradients, such as along mountain slopes (Rahbek 1995). Some plant and animal communities reach their peak richness in the lowlands (Rahbek 1995, Colwell et al 2004) while others reach peak diversity at mid elevations (Colwell and Lees 2000, Heaney 2001, Colwell et al 2004, McCain 2005, Burner et al 2018). Subtle environmental differences along elevational gradients, such as changes in temperature or precipitation, may limit the overall species richness of particular elevational bands and therefore the community as a whole. As richness changes with elevation, ecological community volumes may also change, providing evidence of niche packing or expansion.

Oceanic islands offer a unique opportunity to view the process of community assembly (Wilson 1959, 1961, Warren et al 2015). The scarcity of oceanic dispersal events limits the regional species pool to either direct colonists or their descendants generated via in-situ speciation (Losos and Ricklefs 2009, Rowe et al 2019). Indeed, the observation of niche variation between tropical island and mainland communities was foundational in the development of the theory of niche packing or expansion (Crowell 1962, Wilson 1961, MacArthur and Wilson 1963, MacArthur 1965, VanValen 1965). Islands often contain the descendants of multiple colonists and subsequent radiations of phylogenetically similar lineages,

resulting in a “radiations within a radiation” hierarchy that gives a window into the process of niche divergence between closely related species (Gillespie 2004, Losos 2009). Finally, many large islands are topographically and environmentally complex and therefore contain numerous ecological settings that can limit or expand the overall resource pool available for species or communities.

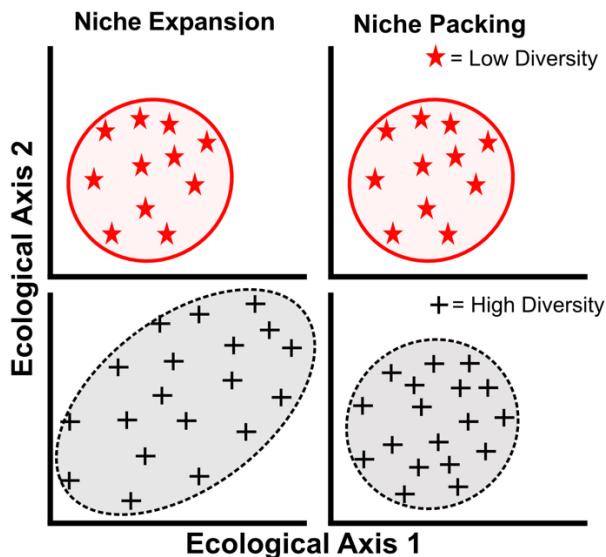


Figure 3.1: As community richness increases, community ecological volumes are thought to either “expand” to incorporate resources previously unused or unavailable, or “pack” as individual species narrow their niche breadths, leading to increased specialization within the volume. These two patterns are not mutually exclusive.

Functional traits, environmental conditions, and dietary preferences are commonly considered axes of niche volume in vertebrate communities (M'closky 1978, Ricklefs and Travis 1980, Pianka et al 2017). However, gathering specific functional trait data in some systems can be difficult. This is particularly true in communities of motile, nocturnal, or secretive species, where direct data on diet and behavior is nearly impossible to gather. However, functional morphology reflects resource use and therefore provides a window to a species' ecological niche (Ricklefs and Travis 1980, Pigot et al 2016). Differences in head shape (Kohli and Rowe 2019,

Van de Perre 2020), body size (Woodward and Hildrew 2002), and body shape (Ricklefs and Travis 1980, Nations et al 2020) indicate differences in functional and behavioral niches. Other indirect measures of resource use, such as trophic dimensions revealed through stable isotope ratios, provide estimates of dietary resources where direct observation or stomach-content analysis is intractable (Baltensperger et al 2015, Galetti et al. 2016). Additional quantified estimates of locomotion are informative as species may partition similar resources across forest strata or microhabitats (Losos 2009).

Here we investigate the patterns of community niche breadth among murine rodents (Murinae: Muridae: Rodentia) from the oceanic island of Sulawesi, a mountainous, topographically complex island (Figure 3.2). The rodent subfamily Murinae is a relatively young (~15 million years; Aghova et al. 2018) and species-rich clade (nearly 700 species; Burgin et al 2018) of rats and mice native to the Old-World. Best known for human commensal species (the house mouse *Mus musculus* and the brown rat *Rattus norvegicus*), murines in fact cover a diverse range of body size, dietary preference, and locomotor morphologies. The murine diversity of Sulawesi is exceptional, with 40 described species and, apart from human commensals, 100% endemism (Rowe et al 2019). In-situ diversification, following 8 oceanic dispersal events (Rowe et al 2019) in the past 6 million years or so (Nations et al 2020), is responsible for the preponderance of Sulawesi murine diversity. The murine fauna of Sulawesi includes some of the most remarkable and unusual rodent forms (Figure 3.2, Esselstyn et al. 2012, 2015) living in sympatry with more typical “rat-like” morphologies. Sulawesi murines have an array of cranial morphologies that reflect their dietary preferences (Esselstyn et al. 2012, 2015 + more). Their body sizes range from 10g to 500g, and apart from gliding they occupy all known small mammal locomotor modes (arboreal to

amphibious) and a wide range of diets (fruit to fungus, leaves to worms). The species richness of Sulawesi mountain communities, defined as the total number of murine species living on a mountain from 400 meters to the summit, ranges from 8 to 23, with the upper limit being perhaps the most diverse community of closely related terrestrial small mammals on Earth. Such a disparity in species richness between geographically and ecologically similar mountains on an isolated island provides a natural experiment for testing alternative processes of community assembly.

Many of the most distinct forms of Sulawesi murines are found in the most species-rich communities, including the long-snouted carnivorous “shrew-rats” of the *Echiothrix* division (Figure 3.2), while all communities contain many “conserved,” omnivorous murine forms, such as species in the *Maxomys* division and the genus *Rattus*. Therefore, we predicted that members of the richest communities are exploiting resources outside the range of exploited resources in low diversity communities, and we expect that overall community ecological volume will increase with greater diversity, supporting the community niche expansion hypothesis. Small mammal richness, and specifically murine richness, typically increases along an elevational gradient with its maximum at mid-elevations on other SE Asian islands (Heaney 2001, McCain 2005), though this pattern remains to be tested on Sulawesi. We expect that both species richness and community ecological volume will increase to a mid-elevation peak prior to decreasing at the highest elevations. We test these predictions using n-dimensional niche volumes assembled from ecological axes that reflect the complexity of biotic interactions and habitat use: skull shape (cranium shape + mandible shape), dietary niche ( $\delta^{15}\text{N} + \delta^{13}\text{C}$  isotopic ratios), body shape (external measurements), body size (mass + skull size), and locomotor mode (mode of

movement reflecting forest habitat or strata) (Stevens et al 2012, Galetti et al 2016, Kohli et al 2019, Stephens et al 2019).

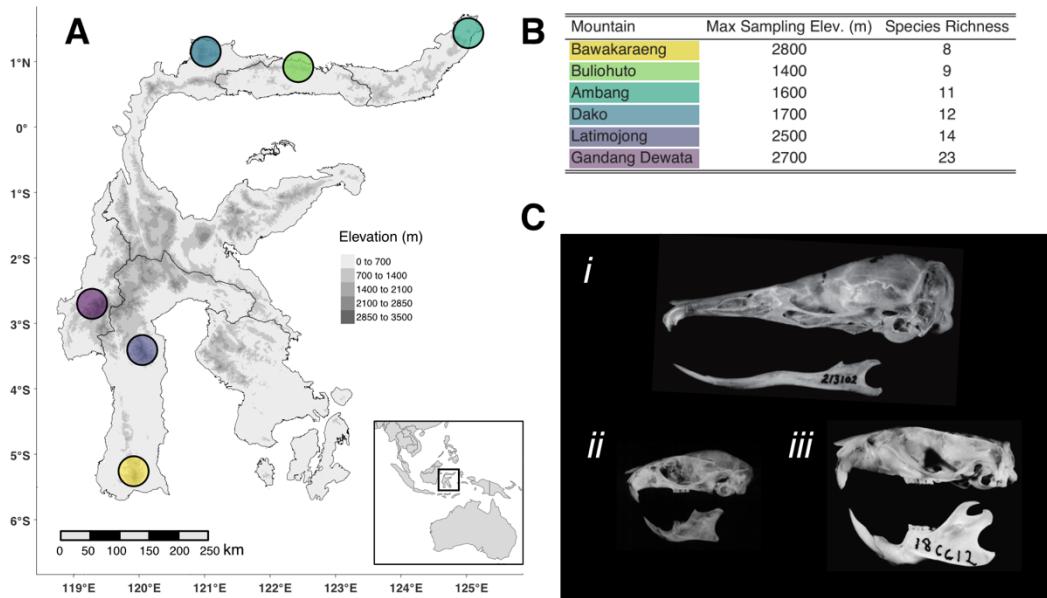


Figure 3.2: The oceanic island of Sulawesi contains a wide breadth of both endemic species and habitats. Six recent surveys of small mammals have revealed patterns of varying murine rodent species richness across the island. A) The locations of six recent small mammal surveys across Sulawesi. B) The mountain communities, maximum survey elevation, and number of murine rodent species. Each of the six mountains were surveyed up to 500m of the summit its rats. C) The diversity of Sulawesi murines is exceptional and includes unique forms that live alongside species with more “typical” morphologies. *i* - the toothless shrew rat *Paucidentomys vermidax* of the Echinothrix Division with an extremely elongate rostrum, *ii* – The tiny arboreal *Haeromys minahassae*, with a short rostrum and delicate size, and *iii* – *Rattus sp...* a more typical murine morphology.

## Methods:

*The distribution of species* - Small mammal surveys were conducted in 6 mountain regions in Sulawesi, Indonesia, from 2011 to 2016 (Ambang, Bawakaraeng, Buliohuto, Dako, Gandang Dewata, and Latimojong; Figure 3.2). Surveys began in lower primary forest, typically near the line of anthropogenic forest clearing, and extended up to montane forests. All surveys extended to within 500m elevation of the summit, and 3 of the 6 surveys extended to the summit. Surveys lasted an average of 17 days (11-25) and employed the same collection methods: a mix of snap

traps, live traps, and 30L pitfall buckets. Specimens were deposited in: Museum Zoologicum Bogoriense, Bogor, Indonesia; Museums Victoria, Melbourne, Australia; Museum of Vertebrate Zoology, Berkeley, USA; Field Museum of Natural History, Chicago, USA; and Louisiana State University Museum of Natural Science, Baton Rouge, USA. All of the murine rodent species known from these regions of Sulawesi (Musser 2014, Wilson et al 2019) were collected during these surveys, indicating a thorough sampling effort. An additional 4 new taxa from these expeditions have been described (Esselstyn et al 2012, Rowe et al 2014, Esselstyn et al 2015, Rowe et al 2016b). Specimen elevational ranges were compiled from a compendium of mammal distributional data (Wilson et al. 2019). The 6 recent surveys extended the elevational ranges of some species, and we updated our elevational data accordingly. We assembled a list of species from each locality and recorded their elevational ranges, beginning at 400m, for all mountains. Due to recent anthropogenic forest clearing some surveys started higher than 400m, however the lowest elevations of all 6 surveys were in lowland forest and therefore captured the expected diversity from 400m upward. Species' upper limits were rounded up to the next 100m.

*Morphological data collection* - We assembled external measurement data, including the mean, minimum, and maximum values of head-body length (mm), tail length (mm), hind foot length (mm), ear length (mm), and mass (g), from previously published sources (Wilson et al 2019, Nations et al 2020). Assuming a normal distribution  $\mu\sigma$ , we calculated a  $\sigma$  value for each trait with the minimum and maximum values representing 2 standard deviations from the mean trait values. Where trait values for only a few specimens exist, we used the  $\sigma$  values of other species with similar sized traits. We drew 500 samples from a normal distribution using the  $\mu$  and  $\sigma$  values for each trait for each species and used these distributions in subsequent analyses. In order to calculate ecologically relevant features of external measurements and mitigate the influence of

size in some of our analyses (Mosimann 1970), we calculated 3 ratios from the distributions: Relative tail length (tail length / (head-body length + tail length)), relative hind foot length (hind foot length / head-body length) and relative ear length (ear length / head-body length) (Nations et al 2020).

We used a 3-dimensional geometric morphometric approach to calculate the variation in skull shape for each species. We generated  $\mu$ CT scans of the cranium of 59 specimens from 35 species (1-3 scans per species) and the mandible of 57 specimens from 33 species (1-3 scans per species). Scans were generated from specimens collected in the 6 surveys, as well as from previously collected museum materials. Stacks of 2D Tiff files were imported into the program MorphoDig where 3D landmarks were placed on cropped volume renderings (Lebrun, 2018). We placed 67 cranial landmarks on the left side of the skull, unless damage required us to flip images on the z-axis. In separate renderings, we placed 20 landmarks on the left dentary of the mandible. Maps of all landmarks are provided in supporting information. Landmarks were exported from MorphoDig as .stv files and imported into R with the package geomorph (Adams et al 2020). Missing landmarks were estimated (only 5 of 3953 cranial landmarks and 3 of 1140 mandible landmarks were missing), a Generalized Procrustes Analysis (GPA) superimposition was performed, and shape coordinates were subjected to a principal components analysis. We retained the centroid size (an estimate of total size) and the scores from the first 5 principal components (>95% of shape variation) from the cranium and mandible.

*Stable isotope data collection* - Stable isotopic ratios from hair, which is inert after growth, provide a continuous record of dietary information over several weeks to months (Tiezen et al 1983). Approximately 1-2 grams of hairs were plucked from the rump of 291 dry museum specimens collected on the 6 focal surveys. All variety of hair types (underfur, guard hairs,

and/or spines) were collected when present. Isotopic signatures vary temporally and regionally (Fry 2006), therefore we collected multiple hair samples from each species from each locality (mean = 4.9 specimens/species/locality, range = 1-14). Nitrogen stable isotopes values identify trophic level, and generally increase by 3-5% per level (DeNiro and Epstein 1981). Carbon isotopes track a consumer's basal foraging resource and do not vary by trophic level (DeNiro and Epstein 1978). Combined, these two metrics provide a useful signal of dietary niche (Ben-David and Flaherty 2012). Contaminants and lipids were cleaned from the hair using a 2:1 chloroform methanol solution (Hückstädt et al 2012). Hair samples ( $0.6 \pm 0.025$  mg) were loaded into tin capsules and flash combusted on a Costech ECS 4010 elemental analyzer coupled to a Thermo-Fisher Delta Plus XP continuous-flow stable isotope ratio mass spectrometer. We normalized stable isotope values with the USGS-40 and USGS-41 glutamic acid reference material, using a sample precision of 0.1%. Stable isotope values, reported in delta notation ( $\delta$ ) in per mil units, were calculated with the following equation:

$$\delta X = \left[ \left( \frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 1000$$

with X representing  $^{13}\text{C}$  or  $^{15}\text{N}$ , and  $R_{sample}$  and  $R_{standard}$  representing the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratios of sample and standard. All samples were processed at the Stable Isotope Ecology Laboratory at Louisiana State University School of Oceanography & Coastal Sciences.

*Locomotor mode data collection* - Using previously published data, Sulawesi murines were classified into one of four discrete locomotor modes: Arboreal, which means climbing is integral to survival; General, or known to navigate a variety of substrates and habitat strata; Terrestrial, or not known to climb; and Amphibious, or a dependence on aquatic habitats for feeding (Nations et al 2019, 2020). Locomotor modes provide additional information on foraging mode

and defines, to the best of our knowledge for these nocturnal, secretive species, a categorical definition of microhabitat use (Nations et al 2020).

*Niche axes* - Comparison of species within a community should rely on traits that quantitatively define a species ecological niche (McGill et al 2006). In animals, functional traits such as morphological, physiological, or behavioral characters that affect a species' niche requirements can include measures of body size, diet, foraging mode, and locomotor mode (Belmaker & Jetz 2013, Kohli et al 2019). We combined our 19 trait variables into 4 continuous niche axes of trait variation: skull shape (cranium shape PC 1-5 and mandible shape PC 1-5), dietary niche ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic ratios), body shape (head-body length, relative tail length, relative hind-foot length, and relative ear length), and body size (log(mass), cranium centroid size, and mandible centroid size). The categorical locomotor data was considered as a 5<sup>th</sup> axis. Community ecology studies in similar vertebrate systems often use only one or two of these niche axes (e.g. Belmaker & Jetz 2013, Pigot et al. 2016, Galetti et al 2016, but see Pianka et al 2017). Combined, these 5 axes provide a robust estimation of inter and intraspecific ecological niche that goes beyond typical community ecology studies in similar vertebrate systems (Pianka et al 2017).

*Community ecological volumes* - Community ecological volume, synonymous with community ‘niche breadth’, ‘disparity’, or ‘trait space’, is an estimate of the overall size of an n-dimensional trait volume (Guillerme 2020). The trait variance is useful for comparing species niches within a community, or the breadth of the community as a whole (MacArthur & Levins 1967, Violette et al 2012), as it provides a measure of both relative density and volume that is independent of species richness (Pigot et al 2016). A recent simulation study found that the sum of the variance of each niche axis (*sensu* Foote 1992) effectively captures changes in both the volume and density of trait space and outperforms other commonly used metrics such as ellipse or convex hull volumes

(Guillerme et al 2020). We therefore estimated the variance of each niche axis by summing the individual trait variances.

The sample size of morphological and dietary data varied between species and mountain communities, and in some cases was limited to one individual, such as with the semi-aquatic *Waiomys mammasae* which is known only from the holotype (Rowe et al. 2014). To mitigate the uneven sampling, we estimated a posterior probability distribution of species trait values using partial-pooling in a multilevel Bayesian framework. The Bayesian partial-pooling modeling approach allowed us to 1) formally incorporate uncertainty into our trait predictions, 2) avoid averaging, which discards valuable information, and 3) use the trait-variance probability estimates from well-sampled species to inform the variance estimates of undersampled species (Gelman and Hill 2006, McElreath 2020). All analyses were conducted in the probabilistic programming language Stan (Carpenter et al. 2017) within the R library brms (Bürkner 2017).

Posterior probability distributions for 12 traits (cranium and mandible PC 1-5 scores, cranium and mandible centroid size, and  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic ratios) were estimated for each species using the same series of steps. First, all trait values were scaled to unit variance, which placed all measurements on the same scale and informed our prior predictions (McElreath 2020). We then separated stable isotope scores by community, as baseline isotopic signatures differ with geography (Fry 2006). We used robust regression with the student-t distribution to minimize the influence of rare outlying response values (Kruschke 2013, McElreath 2020). The posterior distribution of each trait for each species was estimated as:

$$\begin{aligned}
y_i &= Student(v, \mu_i, \sigma_i) \\
\mu_i &= \alpha_{species[i]} \\
\alpha_j &= Normal(\bar{\alpha}, \sigma) \\
\bar{\alpha} &= Normal(0, 1) \\
\sigma &= Normal(0, 1) \\
v &= 3
\end{aligned}$$

Where  $y_i$  is the outcome (scaled trait value of each sample),  $\alpha_{species[i]}$  is the unique value for each species,  $\alpha_j$  is the multilevel prior distribution for all species  $1\dots j$ ,  $\bar{\alpha}$  is the hyperparameter of the average trait value, and  $\sigma$  the hyperparameter of the average species error. The tail-shape parameter of the student-t distribution,  $v$ , was set to 3 to allow for rare, extreme observations. Each model included four chains run for 5000 iterations, with 2500 warm-up and 2500 sampling iterations. Proper chain convergence was demonstrated with an  $ESS > 1000$  and a Gelman-Rubin diagnostic  $\hat{R} \leq 1.01$ . After verifying proper convergence, posterior samples were thinned to 500 per species, resulting in a posterior distribution of 12 morphological traits (cranium PC 1-5, mandible PC 1-5, and centroid sizes) for each species, and a posterior distribution of two dietary traits ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) per species per community. Next, we divided species 12 morphological traits into communities, to match the isotope data, then refit output data through our model to predict estimates of species trait values (incorporating residual error) using the `add_predicted_draws` function in the R library `Tidybayes` (Kay 2020). Variance was calculated from the predicted values of each MCMC draw for each trait, resulting in 14 variance distributions for each community. The normal distributions of species' external measurement data were divided into communities, and the variance of each trait was calculated.

Each niche axis should contribute equally to overall community trait volume, regardless of the number of unique traits per axis. Therefore, variances for each trait ( $n=19$ ) within each niche axis ( $n=4$ ) were summed and divided by the number of traits (e.g.  $[\sigma^2_{\delta^{15}\text{NAmbang}} +$

$\sigma^2_{\delta^{13}\text{CAmbang}}$ ] / 2 = Ambang dietary niche area). Finally, we summed the values of the 4 continuous variable niche axes to form a total ecological volume for each community. We estimated the 89% density values for the variance of each niche axis and the total ecological volume. To quantify the degree to which each community varies from the next, we computed the differences, or contrasts, between the niche axes of each community. Locomotor mode variance was calculated directly for each community using the categorical locomotor mode values. As locomotor modes are categorical rather than distributions of posterior predictions, their variance is a single value rather than a distribution and cannot be combined into the total ecological volume estimates.

*Elevation and community ecological volumes* - Species turnover occurs along elevational gradients in the 6 Sulawesi murine communities. For each community, we used elevational range data to infer the species present at each 100 m elevational break and used the predicted trait distributions from above to estimate the variances of the 4 niche axes and the total ecological volumes for every 100 meters in each community. We estimated locomotor mode variance for each 100 meter break in each community. We also report the species richness at each 100m elevational break. The effect (i.e. slope) of elevation on the variance of each trait axis was estimated using a multilevel model with varying slopes, which uses partial pooling estimates a global slope and intercept for all communities, and an individual slope and intercept for each community. Our model is:

$$\begin{aligned}
y_i &= \text{Normal}(\mu_i, \sigma) \\
\mu_i &= \alpha_{community[i]} + \beta_{community[i]} Elevation_i \\
\begin{bmatrix} \alpha_{community} \\ \beta_{community} \end{bmatrix} &\sim MVNormal \left( \begin{bmatrix} \alpha \\ \beta \end{bmatrix}, \mathbf{S} \right) \\
\mathbf{S} &= \begin{pmatrix} \sigma_\alpha & 0 \\ 0 & \sigma_\beta \end{pmatrix} \mathbf{R} \begin{pmatrix} \sigma_\alpha & 0 \\ 0 & \sigma_\beta \end{pmatrix} \\
\alpha &= \text{Normal}(\mu_{Elevation_niche}, 1) \\
\beta &= \text{Normal}(0, 1) \\
\sigma &= \text{Normal}(0, 1) \\
\sigma_\alpha &= \text{Normal}(0, 1) \\
\sigma_\beta &= \text{Normal}(0, 1) \\
\mathbf{R} &= LKJcorr(1.5)
\end{aligned}$$

Where  $y_i$  is the variance for the community at elevation  $i$ ,  $\alpha_{community[i]}$  is the intercept,  $\beta_{community[i]}$  is the slope, and varying effects term is defined by the multivariate-normal distribution, conditioned on the correlation matrix  $\mathbf{S}$ . Elevation was scaled to unit variance prior to fitting models. We used the mean variance of each niche axis,  $\mu_{Elevation_niche}$ , as the mean prior for intercept  $\alpha$ . We used a Normal(0,1) prior on the remaining parameters, and a LKJ(1.5) prior on the correlation matrix  $\mathbf{R}$ . We fit a similar model for the effect of elevation on species richness using the poisson distribution to define the response variable (counts of species/elevation/community) rather than the continuous normal distribution. Models were fit in brms.

Table 3.1: Mean values of total ecological volume along with each of the 5 trait axes, with lower and upper 89% probability intervals in parentheses. Locomotor mode variance was directly estimated using the number of discrete locomotor modes (Arboreal, General, Terrestrial, and Amphibious) in each community.

Community	Total Ecological Volume	Dietary Niche Area	Skull Shape Volume	Body Shape Volume	Body Size Volume	Locomotor Mode Variance
Bawakaraeng	2.25 (1.80, 2.85)	0.63 (0.28, 1.14)	0.40 (0.25, 0.62)	0.36 (0.26, 0.49)	0.87 (0.71, 1.03)	0.24
Buliohuto	3.44 (3.07, 3.92)	0.24 (0.10, 0.45)	0.71 (0.56, 0.89)	1.09 (0.80, 1.45)	1.40 (1.24, 1.59)	0.53

table cont'd

Community	Total Ecological Volume	Dietary Niche Area	Skull Shape Volume	Body Shape Volume	Body Size Volume	Locomotor Mode Variance
Ambang	3.93 (3.41, 4.51)	0.98 (0.64, 1.41)	0.65 (0.52, 0.84)	1.05 (0.80, 1.35)	1.25 (1.11, 1.43)	0.47
Dako	3.79 (3.28, 4.49)	0.99 (0.56, 1.57)	0.72 (0.59, 0.86)	0.98 (0.76, 1.23)	1.11 (0.97, 1.25)	0.45
Latimojong	3.27 (2.82, 3.78)	1.15 (0.77, 1.57)	0.70 (0.57, 0.86)	0.73 (0.56, 0.94)	0.69 (0.61, 0.77)	0.68
Gandang Dewata	4.19 (3.83, 4.55)	1.18 (0.92, 1.18)	0.80 (0.68, 0.93)	1.19 (1.02, 1.41)	1.03 (0.94, 1.12)	0.89

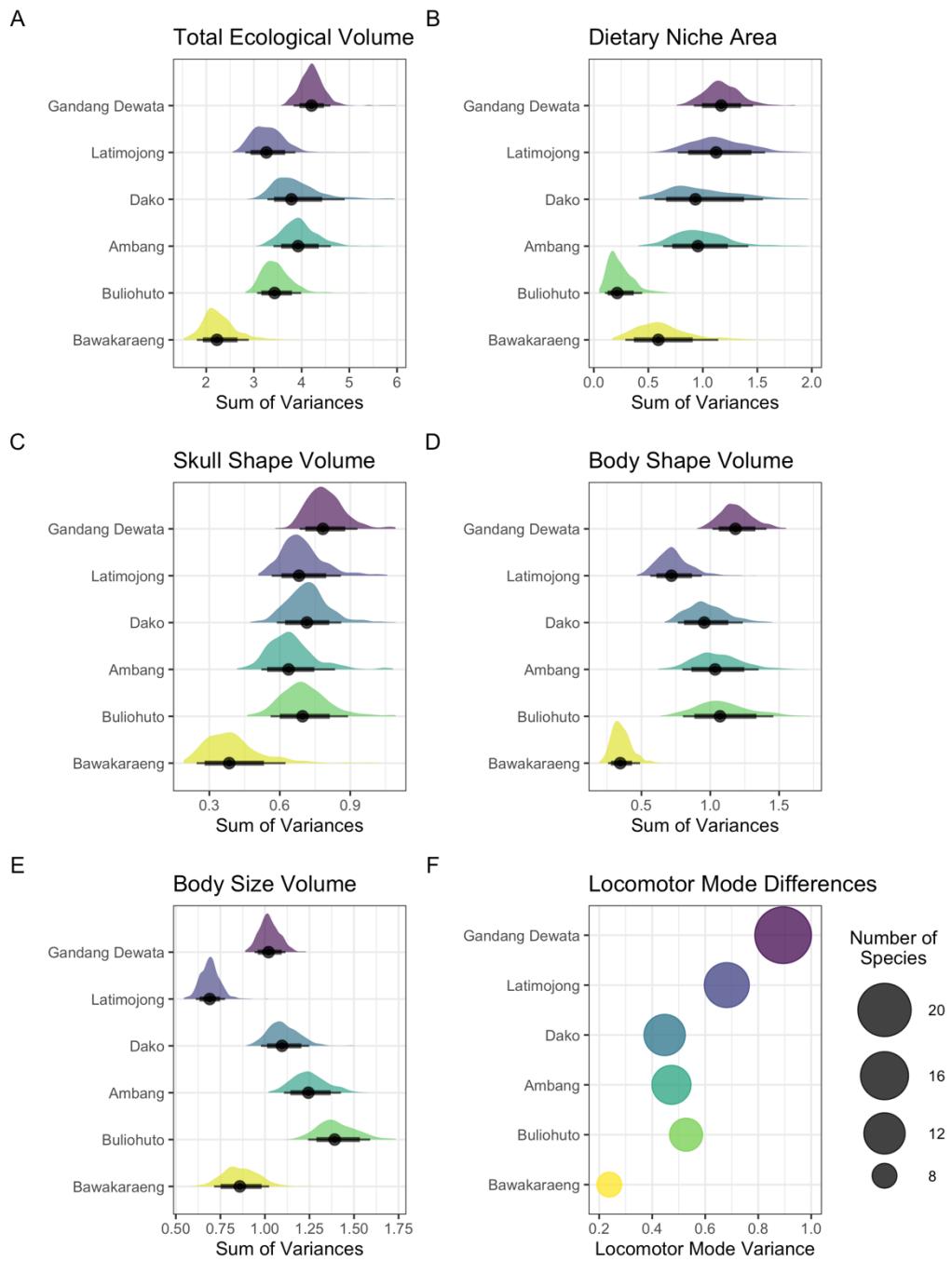


Figure 3.3: Total community ecological volume increases with species richness (A), though this is not true for all niche axes. Dietary niche area (B) and skull shape volume (C) increase with species richness, but this pattern does not hold in body shape (D) or body size (E). Locomotor mode variance (F) strongly increases with species richness, highlighting one mode of community niche volume expansion.

## Results

*Axes of trait variation* - The relationship between community richness and community ecological volumes varied across the individual 19 niche axes, with some axes showing strong positive relationships with community richness, and some axes showing similar variance between all communities (Figures 3.3 & 3.4, Table 3.1). The 5 focal trait axes — dietary niche, skull shape, body shape, body size, and locomotor mode — also demonstrated differing patterns; the most species rich community (Gandang Dewata) consistently has larger community niche variance than the least species rich community (Bawakaraeng), though the magnitude of the difference fluctuates (Figure 3.3A, Table 3.1). Overall, total ecological volume of the most species rich community, Gandang Dewata, has the greatest mean (Table 3.1), and, at the 89% probability level, is larger than three of the 5 communities (Figures 3.3A & 3.4C). However, the next four most species rich communities, Latimojong, Dako, Ambang, and Buliohuto, show no strong differences in total ecological volume (Figures 3.3A & 3.4C). The mean dietary area (sum of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  variance) slowly increases with species richness, however the differences between communities were low (Figures 3.3B & 3.4C), except for the small niche area of Buliohuto. The mean skull shape volume follows dietary niche area, slightly increasing with increasing richness, though differences between 5 of the 6 communities are not robust, with the low-diversity Bawakaraeng being substantially smaller than the others (Table 3.1, Figures 3.3C & 3.4C). The lowest richness and second highest richness communities had the lowest body shape volumes, and Gandang Dewata has the highest body shape volume mean but largely overlaps Dako and Ambang. Body size volume varied strongly between communities, but the sizes did not change with species richness (Figs 3.3E & 3.3C). Locomotor mode variation

followed a clear pattern niche expansion by increasing variance with increasing richness (Figure 3.3F).

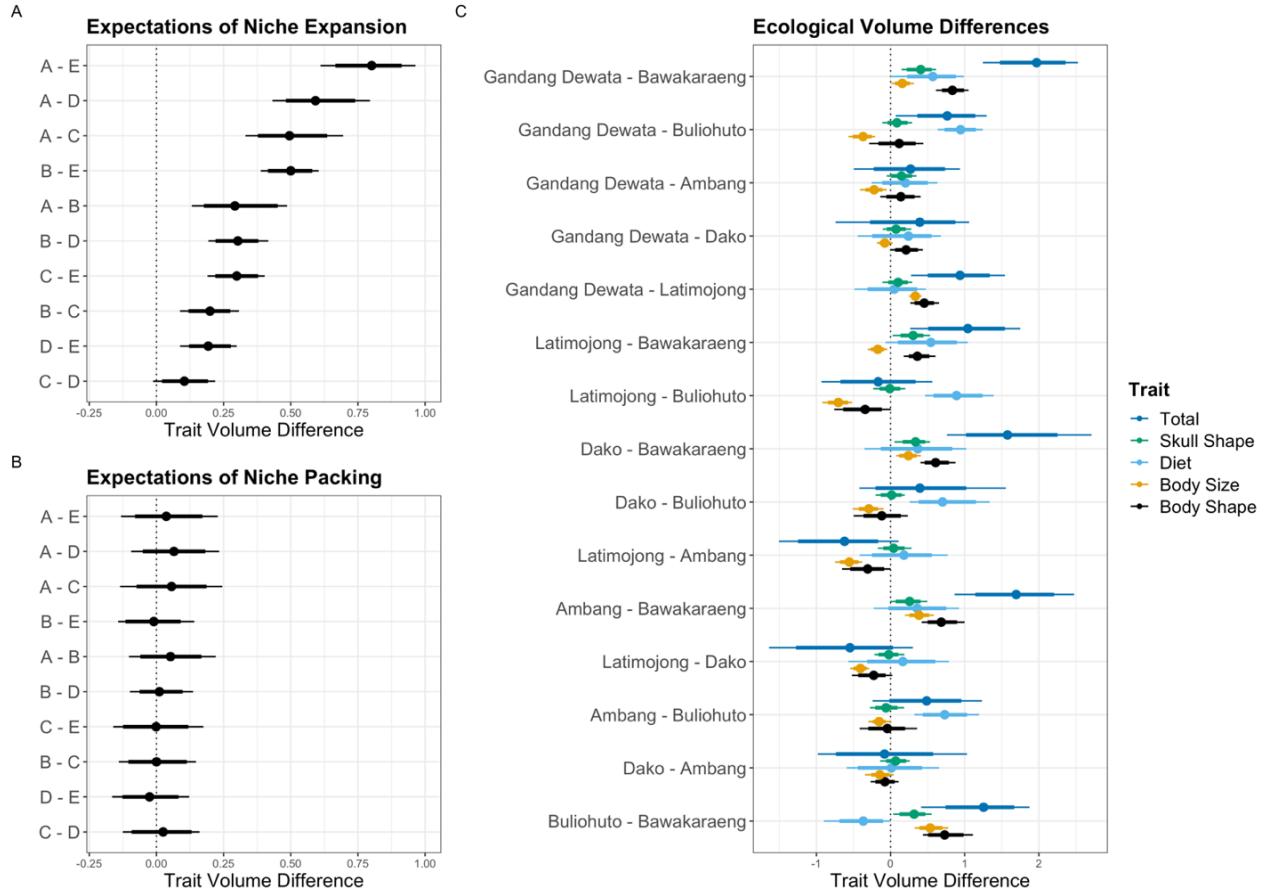
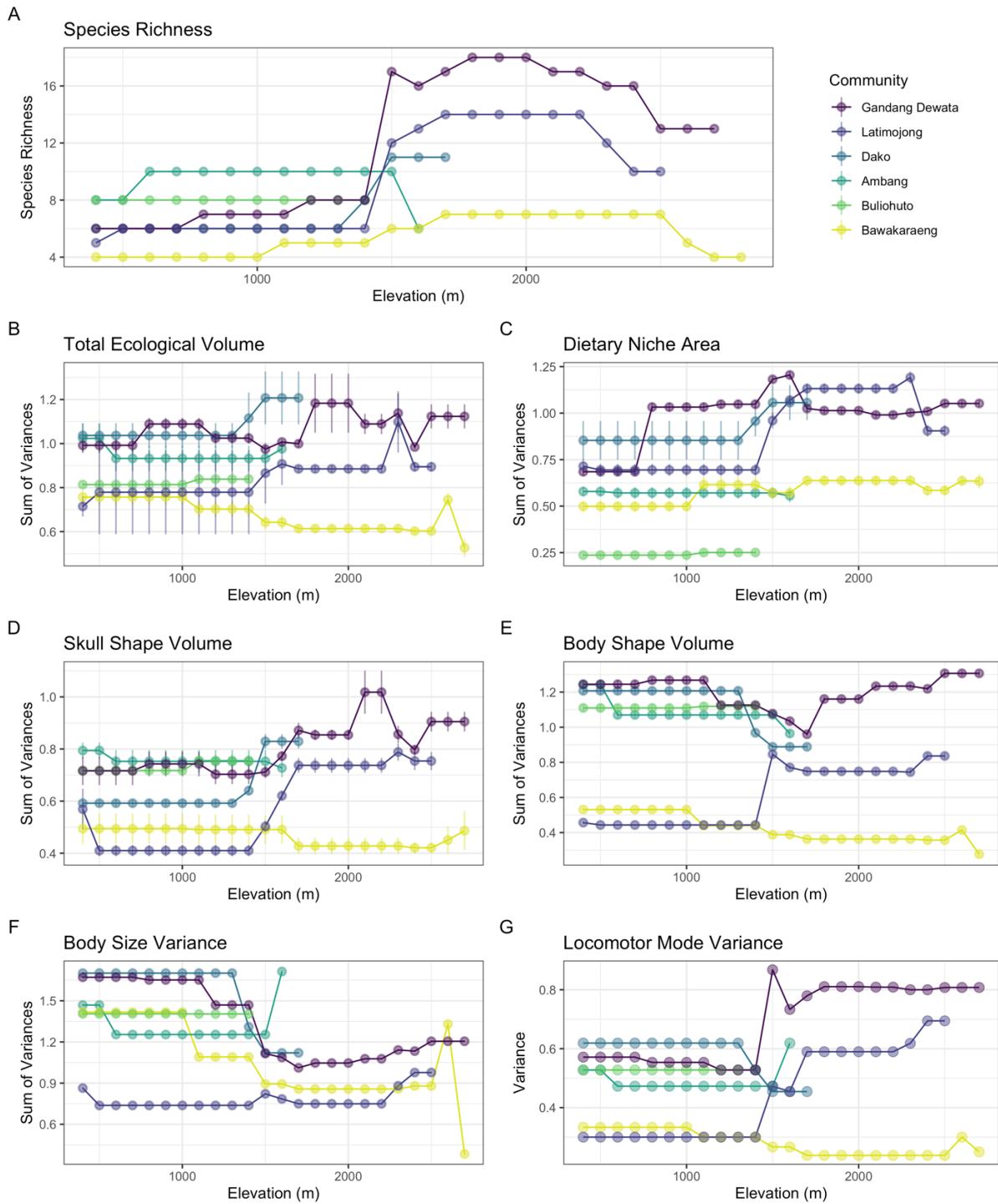


Figure 3.4: The pattern of niche packing or niche expansion between communities largely depends on the traits measured. Community differences on the y-axis are sorted by the magnitude of the difference in species richness, so the communities on the top are the most different in their number of species, and the communities on the bottom are most similar. A) Simulated data show a pattern of niche expansion, where the communities that are most different in richness are most different in trait volume. B) Simulated data demonstrate packing, or the opposite effect of A. C) Differences in the estimated variance, our metric of breadth, in 4 trait axes and their sum (Total) are shown for 6 Sulawesi murine communities. Colors represent different traits, points represent the mean difference, thick lines the 74% interval, and thin lines the 89% interval. We consider 89% intervals that are larger than zero a robust signal of expansion. No trait axis differences are all to the right of zero, nor do all trait differences overlap zero. Bawakaraeng, the least species rich community, has smaller trait axis values than other communities on most, but not all, trait axes, however the remainder of communities show no clear pattern.



**Figure 3.5:** Species richness increases with elevation in most communities (A) but the 5 niche axes respond to changing elevation in different ways. Total ecological volume (A) is largely flat for all but Latimojong, while dietary niche (C), skull shape (D), and locomotor variance (G) increase with increasing elevation for species rich communities. Body shape volume (E) does not change with elevation increase for most communities, while body size variance (F) decreases with increasing elevation for 3 communities.

Table 3.2: Multilevel models show only moderate changes in ecological niche axes across elevational gradients. Dietary niche area increases with elevation, while the remaining traits demonstrate no robust change. Community results, partially-pooled group-level variables in the multilevel model, show alternative patterns of increasing or decreasing trait volumes with elevation. For example, Dako shows a decrease in Body Shape, Body Size, and Locomotor Mode with increased elevation, while Latimojong shows an increase in the same traits. Results from a multilevel poisson model show that species richness increases with elevation, most strongly in the high-richness community Gandang Dewata. Cells provide mean values from the posterior probability distributions, and parentheses show lower and upper 89% credible intervals. Effects where the 89% probability distribution fall above or below zero are shown in bold.

Global Parameters Intercept and Effect			Community Specific Effects					
Trait		Bawakaraeng	Buliohuto	Ambang	Dako	Latimojong	Gandang Dewata	
Total Ecological Volume	1.86 (1.05, 2.66)	0.17 (-0.51, 0.83)	-0.42 (-1.09, 0.25)	-0.10 (-0.82, 0.61)	-0.41 (-1.10, 0.31)	-0.10 (-0.79, 0.60)	<b>0.82</b> ( <b>0.16, 1.50</b> )	0.12 (-0.55, 0.81)
Dietary Niche	0.70 (0.47, 0.92)	<b>0.07</b> ( <b>0.0, 0.13</b> )	-0.06 (-0.13, 0.04)	-0.05 (-0.14, 0.04)	-0.04 (-0.13, 0.04)	<b>0.08</b> ( <b>0.0, 0.17</b> )	<b>0.07</b> ( <b>0.0, 0.14</b> )	0.01 (-0.06, 0.08)
Skull Shape	3.10 (2.69, 3.51)	0.20 (-0.08, 0.48)	-0.26 (-0.54, 0.02)	-0.21 (-0.55, 0.11)	<b>-0.37</b> ( <b>0.70, -0.07</b> )	0.27 (-0.04, 0.57)	<b>0.44</b> ( <b>0.16, 0.72</b> )	0.16 (-0.12, 0.45)
Body Shape	0.89 (0.62, 1.15)	-0.03 (-0.14, 0.08)	-0.04 (-0.15, 0.07)	0.03 (-0.09, 0.16)	-0.07 (-0.19, 0.05)	<b>-0.15</b> ( <b>-0.27, -0.03</b> )	<b>0.18</b> ( <b>0.07, 0.30</b> )	0.04 (-0.07, 0.15)
Body Size	1.24 (1.03, 1.44)	-0.12 (-0.24, 0.01)	-0.07 (-0.20, 0.06)	0.07 (-0.09, 0.23)	0.10 (-0.04, 0.26)	<b>-0.17</b> ( <b>-0.33, -0.03</b> )	<b>0.15</b> ( <b>0.02, 0.27</b> )	-0.07 (-0.21, 0.05)
Locomotor Mode	0.49 (0.37, 0.59)	0.02 (-0.06, 0.1)	-0.05 (-0.14, 0.03)	-0.02 (-0.11, 0.07)	-0.01 (-0.1 0.07)	<b>-0.10</b> ( <b>-0.19, -0.02</b> )	<b>0.12</b> ( <b>0.04, 0.2</b> )	0.07 (-0.01, 0.15)
Richness (poisson model)	8.28 (6.84, 9.85)	<b>1.21</b> ( <b>1.07, 1.34</b> )	<b>0.94</b> ( <b>0.82, 1.06</b> )	<b>1.06</b> ( <b>0.83, 1.34</b> )	<b>0.95</b> ( <b>0.78, 1.1</b> )	<b>0.98</b> ( <b>0.78, 1.22</b> )	<b>1.06</b> ( <b>0.86, 1.28</b> )	<b>1.25</b> ( <b>1.03, 1.52</b> )

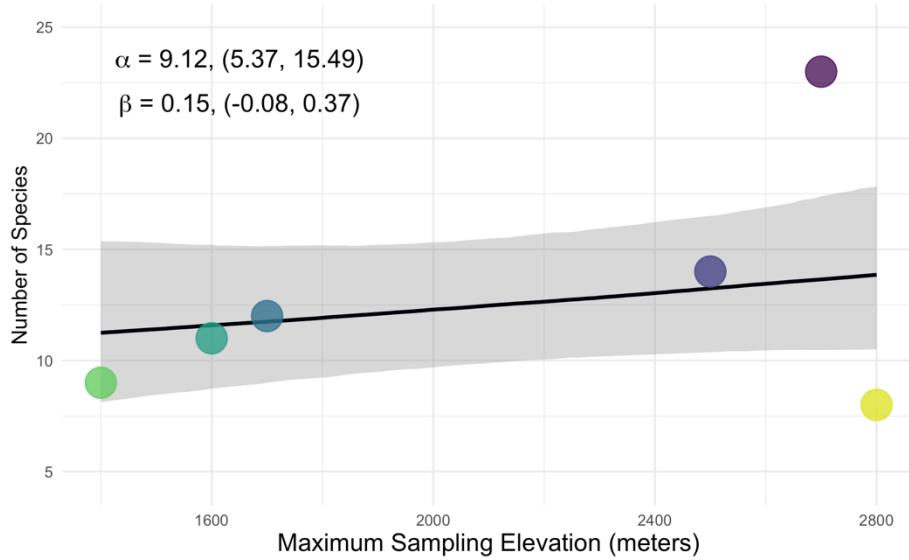


Figure 3.6: Poisson regression shows little effect of maximum sampling elevation on the total species richness of a community. As the peak sampling elevation increases, the number of species in the community slightly increases, though the 89% credible interval of the slope  $\beta$  is not distinguishable from zero. All mountain communities were samples to within 500 meters of the summit.

*Community volumes and elevational variation in species richness* - Species richness increases from low to middle elevations and then begins to drop at the highest elevations (Figure 3.5A), supporting the mid-domain effect hypothesis. However, mountain-wide species richness may not directly correlate with maximum elevation, as the mountain with the highest elevational sampling is the least species rich (Figure 3.5A). Changes in communities' ecological volumes along the elevational gradients vary. Total ecological volume is largely flat across the elevational gradient for 5 of the 6 communities, while Latimojong, the second most species-rich community, dramatically increases its community volume at the middle elevations, mirroring the positive relationship of species richness and elevation at that location (Figure 3.5B). Body shape follows a similar pattern to total trait variance, with only Latimojong showing a positive relationship with elevation (Figure 3.5E). Dietary niche area and skull shape volume increase along the elevational gradient in three communities with the greatest richness (Gandang Dewata,

Latimojong, Dako; Figure 3.5C). Body size variance drops precipitously with increasing elevation for 4 of the 6 communities (Figure 3.5F). Locomotor variance greatly increases along with richness in the three high richness communities but remains flat in the low richness communities (Figure 3.5G).

Multilevel modeling results show a weak effect of elevation on trait axes. The means of the global effect posterior distributions all overlap zero at the 89% credible level, with the singular exception being an increase in dietary niche area with increasing elevation (Table 3.2). Elevation shows a moderately negative effect on body size (Table 3.2). The partially pooled effects of each community show some non-zero positive and negative effects for different communities along the same niche axes (Table 3.2), though changing elevation did not result in robust variation in trait volumes in most communities. Poisson model of species richness counts show a positive overall increase of species richness with elevation. A separate poisson model of species richness shows no effect of maximum sampling elevation on richness (Figure 3.6).

## Discussion

Niche theory predicts that species within a community must differ in resource use if they are to coexist (MacArthur and Levins 1967). Therefore, increasing species richness in a community necessitates expansion of community niche volume to include resources previously unavailable or unused (niche expansion), the narrowing of species' niches to permit increased richness within the same volume (niche packing), or a combination of the two (Pigot et al 2016). Across 6 Sulawesi murine communities, ranging from 8 to 23 species, we find that niche expansion and niche packing act in concert on different ecological axes, though the pattern is inconsistent. Total trait volume, a volume of 5 axes assembled from 19 trait variables, slightly

increases with richness, but still shows substantial overlap between mountains (Figure 3.3A). Skull shape, body shape, and body size, all important metrics of ecomorphology, demonstrate some level of niche packing (Figure 3.3). In contrast, mean dietary niche area increases slowly with richness but the richest communities do not differ substantially in their variances (Figure 3.4C), suggesting that species in the richer communities both become more specialized and use food resources underexploited in less rich communities, supporting both expansion and packing.

Locomotor mode is the single trait axis that clearly demonstrates niche expansion (Figure 3.3F). Locomotor mode variance is nearly five-fold greater in Gandang Dewata (23 species) than Bawakaraeng (8 species), and two times greater in Gandang Dewata than Ambang (11 species; Figure 3.3F). Arboreality, Terrestriality, and Amphibiosity all provide access to similar resources in different microhabitats. For example, in Gandang Dewata, the amphibious *Waiomys mamasae*, the terrestrial *Paucidentomys vermidax*, and the arboreal *Sommeromys macrorhinos* all consume invertebrates and have similarly high  $\delta^{15}\text{N}$  values, yet it is unlikely they directly compete for resources. The arboreal herbivore *Margaretamys elegans* is more than twice the size of its sympatric congener *Margaretamys parvus*, demonstrating secondary niche separation within a specialized locomotor mode. Recent work demonstrates that, in Murinae, locomotor mode is tied to both morphological evolution and species diversification (Nations et al. 2020). Our results suggest that locomotor mode also promotes increased community richness by allowing species to overlap in other trait axes, such as diet, while remaining spatially segregated.

In 6 communities of murine rodents on Sulawesi, the means of niche volumes do increase with species richness (Figure 3.2), yet the niche expansion signal is not consistent or robust (Figure 3.4C), and different niche axes respond to increasing richness in a variety of ways: from a clear case of niche expansion (locomotor mode) to a moderately supported case of niche

packing (skull shape) to no discernable pattern (body size and shape). Our results support the view that niche packing and niche expansion act in concert (Pigot et al 2016) and should be viewed as two extremes on a continuum. As richness increases, murine rodent communities in Sulawesi increase their overall resource use while, at the same time, individual species narrow their niche breadths or increase niche overlap. Therefore, a dichotomous view of niche packing and expansion may not be appropriate, as noted in recent studies of tropical bird (Pigot et al 2016, Pellesier et al 2018) and mammal (Van de Perre 2020) communities.

In the tropics, the total number of species of small non-volant mammals (Stanley et al 1998, Heaney 2001, McCain 2005, Ramírez-Bautista & Williams 2018) and some other organisms (reviewed in Rahbek 1995) often increases with elevation, which may in turn affect the overall community ecological volume. In Sulawesi, the maximum elevation of the sampling location itself does not have a notable effect on murine species richness (Figure 3.6), however the two most species rich communities, Gandang Dewata and Latimojong, and the least species rich community, Bawakaraeng, do increase their richness along an elevational gradient. The three highest elevation communities all show a peak species richness around 2000m before decreasing in richness at higher elevation, a pattern observed in other similar SE Asian small mammal communities (Heaney 2001, McCain 2005). The response of trait axes to elevation is mixed and largely insignificant (Figure 3.5, Table 3.2). For all communities combined, the only positive effect of elevation is on dietary niche area (sum of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  variance). The slopes of the group-level effects from our multilevel model show that this effect is driven by Dako and Latimojong, both of which increase in species richness near mid elevations while simultaneously expanding their community dietary niche. Ultimately, the noisy effects of elevation on ecological

trait axes reinforces our findings that packing and expansion are not binary outcomes, but instead can act in concert on different trait axes in different communities.

The murine rodents of Sulawesi encompass some of the most unusual phenotypes in the entire murine radiation, and the presence of these species may exert a disproportional influence on the ecological volume of a community. For example, the carnivorous ‘shrew rats’ of the *Echiothrix* division, have exceedingly elongate rostrums and mandibles specialized for rooting out invertebrates (Figure 3.1; Esselstyn et al 2015), and their distinct skulls set them apart from other clades in the first 2 PC axis of both cranial and mandible shape (Supplemental Figure).

*Haeromys minahassae*, a diminutive, 10-15 g arboreal mouse, is also quite distinct from other species in the skull shape PC axes (Figure 3.2, Supporting Figure). Bawakaraeng, the least species-rich community, lacks both *H. minahassae* and a member of the *Echiothrix* division, resulting in a smaller skull shape volume. However, if a ‘shrew rat’ and an *H. minahassae* were added to the community, as in Buliohuto (9 species), the skull shape volume fills to nearly that of Gandang Dewata (23 species; Figures 3.3 & 3.4). Other niche axes were not as influenced by a single clade. For example, carnivorous shrew rats have high  $\delta^{15}\text{N}$ , as expected, but species from other clades in the same communities (*Bunomys*, *Rattus*) have similarly high  $\delta^{15}\text{N}$  (Supplemental Information).

Three murine communities in this study (Dako, Ambang, and Buliohuto) are located on Sulawesi’s northern peninsula, a long narrow stretch of land jutting out over 700 km to the north and east from the center core of the island (Figure 3.2). The land bridge between the northern peninsula and the central, eastern, and southeastern portions of the island emerged between 1-2 Ma. Prior to coalescence, the northern peninsula was likely a series of low lying, isolated islands (Nugraha et al 2018). G. G. Simpson (1964) described the ‘peninsula effect’ after observing a

decrease in mammalian fauna the further out a peninsula from the mainland, a pattern that has found favorable but not wholly consistent support (Jenkins & Rinne 2008). An important prediction of the peninsula effect is that peninsulas are “underinhabited in terms of available niches occupied by distant species” (Simpson 1964 pg. 73). We find that the three locations on the northern peninsula do not have the species richness (9, 11, and 12 species) found in the central core of Sulawesi (14 and 23 species), supporting the central theme of the peninsula effect. In contrast, we do not find under-inhabited niche space on the far reaches of the northern peninsula. The total ecological volumes of the three northern peninsula communities are similar to or larger than both Gandang Dewata and Latimojong (23 and 14 species; Figures 3.3 & 3.4). Despite geographic and, in some cases, genetic isolation of populations on the far reaches of the northern peninsula (Eldridge et al 2018, Giarla et al 2018), these murine communities have evolved to exploit a range of resources as wide as in any other community.

## **Conclusion:**

Our rich dataset of 19 ecological and morphological variables from 6 murine communities on Sulawesi revealed that the effect of richness on ecological trait volumes differs across ecological axes and communities. There were a few cases of niche expansion with moderate support, such as diet, though most traits had no discernable signal, supporting the hypothesis that niche packing and expansion are not binary outcomes of increasing richness, but instead represent finite ends on a niche-partitioning continuum. Locomotor mode variance, however, does increase with species richness, and provides a mechanism for diverse communities of closely related species to increase richness at a local scale. Put another way, niche packing on one axis (e.g. diet) may be the direct result of expansion on another axis (e.g.

locomotion), and therefore the breadths of independent trait axes in a niche hypervolume are not necessarily independent. When viewed in this light, discovering a signal of niche expansion or packing on all trait axes becomes increasingly unlikely. The rapid expansion of a single trait space, such as locomotor variance, may be sufficient to incorporate increased species richness into the community, even in some of the most diverse mammal communities of Earth.

## CHAPTER 5: CONCLUSIONS

Life's diversity is not spread evenly among clades. Some groups of organisms contain large numbers of species in all shapes and sizes, while others are represented by a few similar-looking species. This uneven distribution is thought to be due, in part, to a few interwoven factors: the biogeographic history of a lineage, the evolution of adaptive functional traits, and the ecological opportunity afforded to a population or community. My dissertation focuses on the evolution of a species-rich and morphologically disparate clade of mammals, the 700+ species of murine rodents, through investigations of function, history, and ecology.

My dissertation reveals the role of functional, historical, and ecological influences in generating the exceptional radiation of Murinae across the Old World while advancing methods for accurate behavioral inference for species which have not, or cannot, be directly observed. Morphological changes often track with behavioral or ecological transitions. The evolution of locomotion is important in understanding the diversification of mammals as the movement into novel niches helped propelled the remarkable mammal radiations of the Cenozoic. However, the locomotor behavior of many living species remains unknown, and quantitative relationships between important behaviors like climbing and morphology are lacking. In my first chapter I found that climbing behavior in murine rodents can be predicted, regardless of body size, by a ratio of two simple measurements of finger length (3rd proximal phalanx / 3rd metacarpal, Fig. 3.3). Low phylogenetic signal in this ratio indicates that finger length is a labile trait determined by ecology, indicating that it provides a simple and effective way to infer climbing behavior in murines, and perhaps other mammals more generally. I discovered a simple, highly convergent morphological trait that accurately predicts a specialized behavior in murines, highlighting the

role of adaptation in niche transition and establishing a quantitative functional trait beneficial for studies ranging from functional ecology to paleontology.

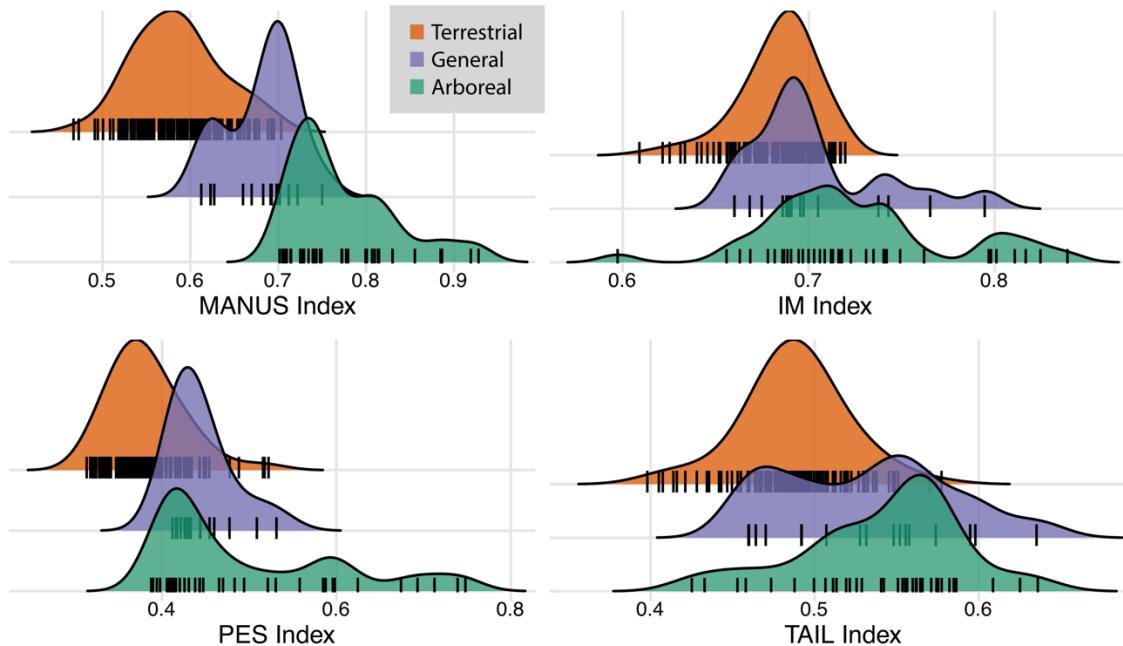
The transition to a novel environment is often associated with both morphological adaptation and increasing diversification rates. However, the opposite effect is not uncommon, where a transition to a new environment may actually decrease the ecological opportunity available to a clade. In my second chapter I estimated a time-calibrated phylogenetic hypothesis of Murinae to date (435 species) and used comparative methods to test for morphological integration across four locomotor modes and to infer rates of morphological evolution and lineage diversification, as they are associated with locomotor modes. I found unique combinations of trait values for each locomotor mode, and strong morphological covariation between the tail length and hind foot length in General and Arboreal species. Interestingly, General species, represented by the classic “rat-like” body plan, are the most constrained in all body size and shape metrics yet maintain high diversification rates, revealing that this versatile form may act as a source of future morphological diversity. Specialists (Arboreal and Amphibious), on the other hand, have decreased diversification rates.

Some murine rodent communities in Sulawesi exhibit exceptional diversity, while other communities have more modest numbers of species. Ecological theory requires that species within a community must differ in their resource or habitat use. I found that niche packing and niche expansion are not binary processes, but rather represent a continuum of correlated changes in resource use and community species richness. Some traits like morphological disparity tend to “pack” with species richness while others such as dietary niche “expand.”. Uncommon locomotor modes, such as arboreality and amphibiosity, occur mostly in species-rich communities, providing a way for species to exploit similar dietary niches without directly

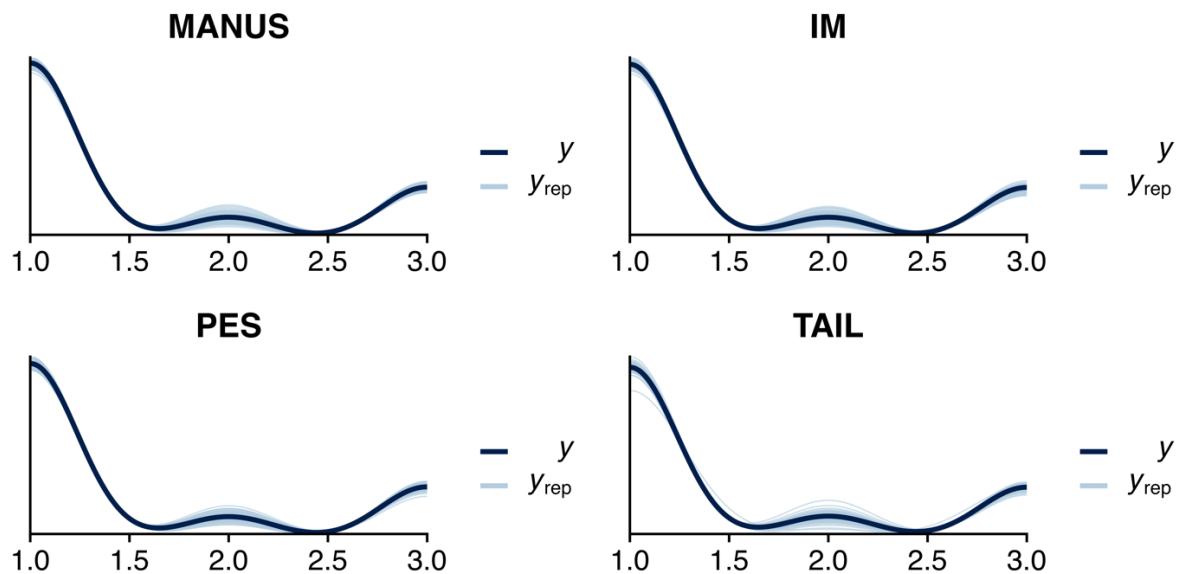
competing for resources and demonstrating the role of adaptive specialization in the assembly of crowded communities. Locomotion therefore provides a mechanism for diverse communities of closely related species to increase richness at a local scale, fostering the assembly of some of the most diverse mammal communities of Earth

My work highlights that, despite little room for diversification, murines have repeatedly evolve towards predictable ecologies with convergent morphological adaptations, providing a pathway for the increase of species richness in high-diversity tropical communities. In summary, my dissertation shows how phenotype and behavior interact with ecological specialization and lineage diversification in one of the most remarkable mammalian radiations.

## APPENDIX A SUPPORTING MATERIAL FOR CHAPTER 2



Supporting Figure 1.1: Raw index measurements of each specimens. Each locomotor mode is a unique histogram.



Supporting Figure 1.2: Posterior predictive checks for ordinal models in brms. All posterior samples (blue lines) show a good fit to the predicted  $y$  value (black line)

Supporting Table 1.1

Species	climb	SMI	BI	HRI	HEB	OLI	URI	MANUS
Apomys abrae	0	0.366	1.123	0.080	0.239	0.146	0.039	0.594
Apomys abrae	0	0.378	1.109	0.081	0.230	0.140	0.036	0.554
Apomys abrae	0	0.379	1.120	0.077	0.241	0.148	0.039	0.613
Apomys abrae	0	0.384	1.130	0.079	0.228	0.159	0.030	0.654
Apomys abrae	0	0.388	1.091	0.074	0.235	0.153	0.046	0.602
Apomys abrae	0	0.393	1.115	0.078	0.247	0.139	0.030	0.587
Apomys abrae	0	0.400	1.077	0.074	0.231	0.147	0.036	0.598
Apomys abrae	0	0.400	1.093	0.072	0.233	0.153	0.037	0.608
Apomys abrae	0	0.404	1.086	0.064	0.219	0.148	0.042	0.529
Apomys abrae	0	0.407	1.106	0.067	0.228	0.144	0.036	0.604
Apomys abrae	0	0.407	1.115	0.066	0.242	0.141	0.040	0.575
Apomys abrae	0	0.410	1.119	0.077	0.236	0.150	0.030	0.604
Apomys abrae	0	0.416	1.078	0.067	0.235	0.143	0.043	0.673
Apomys abrae	0	0.420	1.138	0.079	0.247	0.150	0.037	0.572
Apomys banahao	0	0.414	1.117	0.075	0.253	0.148	0.041	0.577
Apomys banahao	0	0.420	1.093	0.068	0.247	0.142	0.039	0.567
Apomys banahao	0	0.433	1.084	0.070	0.238	0.130	0.036	0.603
Apomys banahao	0	0.433	1.159	0.077	0.246	0.131	0.039	0.582
Apomys banahao	0	0.448	1.129	0.070	0.247	0.145	0.036	0.630
Apomys datae	0	0.387	1.135	0.079	0.230	0.141	0.039	0.547
Apomys datae	0	0.391	1.166	0.084	0.249	0.146	0.046	0.594
Apomys datae	0	0.395	1.122	0.075	0.267	0.165	0.030	0.580
Apomys datae	0	0.397	1.132	0.079	0.254	0.149	0.040	0.581
Apomys datae	0	0.401	1.168	0.066	0.249	0.141	0.041	0.550
Apomys datae	0	0.404	1.144	0.074	0.256	0.133	0.039	0.549

table cont'd

Species	climb	SMI	BI	HRI	HEB	OLI	URI	MANUS
Apomys datae	0	0.413	1.077	0.075	0.269	0.160	0.041	0.551
Apomys datae	0	0.414	1.132	0.069	0.248	0.152	0.043	0.621
Apomys datae	0	0.416	1.099	0.077	0.246	0.148	0.037	0.586
Apomys datae	0	0.416	1.150	0.076	0.257	0.146	0.045	0.648
Apomys datae	0	0.417	1.154	0.070	0.242	0.133	0.041	0.578
Apomys datae	0	0.421	1.116	0.065	0.263	0.158	0.040	0.543
Apomys datae	0	0.427	1.115	0.076	0.257	0.145	0.044	0.601
Apomys datae	0	0.439	1.106	0.075	0.268	0.150	0.051	0.559
Apomys datae	0	0.445	1.136	0.077	0.248	0.139	0.030	0.644
Apomys datae	0	0.446	1.142	0.084	0.258	0.143	0.051	0.606
Apomys datae	0	0.451	1.115	0.076	0.257	0.145	0.040	0.558
Apomys gracilirostris	0	0.421	1.081	0.076	0.271	0.163	0.043	0.618
Apomys gracilirostris	0	0.437	1.110	0.073	0.281	0.166	0.037	0.536
Apomys gracilirostris	0	0.442	1.080	0.079	0.273	0.158	0.043	0.542
Apomys gracilirostris	0	0.442	1.061	0.069	0.272	0.167	0.053	0.571
Apomys gracilirostris	0	0.453	1.108	0.074	0.276	0.154	0.045	0.593
Apomys iridensis	0	0.376	1.042	0.081	0.238	0.159	0.035	0.556
Apomys iridensis	0	0.400	1.054	0.076	0.237	0.156	0.045	0.646
Apomys iridensis	0	0.400	1.073	0.075	0.246	0.147	0.044	0.523
Apomys iridensis	0	0.405	1.085	0.077	0.247	0.137	0.033	0.637
Apomys iridensis	0	0.417	1.066	0.075	0.242	0.144	0.039	0.577
Apomys iridensis	0	0.420	1.090	0.070	0.231	0.142	0.042	0.604
Apomys microdon	1	0.401	1.064	0.074	0.260	0.131	0.037	0.702
Apomys microdon	1	0.404	1.071	0.079	0.260	0.151	0.035	0.814
Apomys microdon	1	0.414	1.045	0.073	0.249	0.134	0.031	0.740
Apomys microdon	1	0.416	1.075	0.084	0.248	0.146	0.035	0.780

table cont'd

Species	climb	SMI	BI	HRI	HEB	OLI	URI	MANUS
Apomys microdon	1	0.418	1.023	0.076	0.238	0.139	0.034	0.800
Apomys musculus	0.9	0.378	1.133	0.075	0.259	0.139	0.032	0.715
Apomys musculus	0.9	0.390	1.106	0.077	0.243	0.134	0.033	0.749
Apomys musculus	0.9	0.391	1.139	0.070	0.249	0.145	0.033	0.708
Apomys musculus	0.9	0.396	1.147	0.076	0.266	0.131	0.039	0.741
Apomys musculus	0.9	0.397	1.135	0.081	0.280	0.141	0.033	0.773
Apomys musculus	0.9	0.402	1.144	0.085	0.259	0.131	0.039	0.778
Apomys musculus	0.9	0.418	1.125	0.080	0.248	0.131	0.032	0.920
Apomys musculus	0.9	0.428	1.129	0.087	0.257	0.140	0.045	0.929
Apomys musculus	0.9	0.433	1.132	0.086	0.274	0.137	0.034	0.730
Apomys sacobianus	0	0.386	1.101	0.074	0.238	0.162	0.049	0.565
Apomys sacobianus	0	0.390	1.066	0.075	0.233	0.159	0.038	0.537
Apomys sacobianus	0	0.414	1.084	0.073	0.232	0.147	0.035	0.589
Apomys sacobianus	0	0.430	1.067	0.077	0.239	0.147	0.034	0.568
Apomys sacobianus	0	0.433	1.031	0.070	0.230	0.147	0.031	0.587
Apomys sierrae	0	0.385	1.053	0.071	0.239	0.161	0.042	0.569
Apomys sierrae	0	0.391	1.112	0.067	0.239	0.151	0.034	0.526
Apomys sierrae	0	0.402	1.044	0.070	0.245	0.149	0.040	0.577
Apomys sierrae	0	0.403	1.080	0.074	0.232	0.150	0.049	0.603
Apomys sierrae	0	0.419	1.108	0.073	0.230	0.145	0.039	0.557
Apomys sierrae	0	0.423	1.109	0.066	0.235	0.130	0.038	0.704
Apomys zambalensis	0	0.394	1.059	0.070	0.249	0.148	0.036	0.611
Apomys zambalensis	0	0.398	1.056	0.072	0.241	0.150	0.033	0.658
Apomys zambalensis	0	0.405	1.070	0.074	0.237	0.169	0.036	0.633
Apomys zambalensis	0	0.415	1.082	0.069	0.241	0.147	0.036	0.468
Apomys zambalensis	0	0.416	1.119	0.074	0.235	0.147	0.034	0.591

table cont'd

Species	climb	SMI	BI	HRI	HEB	OLI	URI	MANUS
<i>Apomys zambalensis</i>	0	0.443	1.094	0.070	0.236	0.143	0.041	0.592
<i>Archboldomys maximus</i>	0	0.441	1.062	0.086	0.327	0.182	0.040	0.676
<i>Archboldomys maximus</i>	0	0.448	1.051	0.089	0.327	0.181	0.043	0.658
<i>Archboldomys maximus</i>	0	0.450	1.134	0.099	0.356	0.186	0.055	0.696
<i>Batomys granti</i>	0.5	0.402	0.994	0.079	0.288	0.144	0.041	0.693
<i>Bullimus luzonicus</i>	0	0.437	1.082	0.074	0.244	0.165	0.044	0.520
<i>Bullimus luzonicus</i>	0	0.447	1.057	0.076	0.258	0.175	0.042	0.549
<i>Bullimus luzonicus</i>	0	0.453	1.086	0.075	0.226	0.158	0.039	0.522
<i>Bullimus luzonicus</i>	0	0.457	1.063	0.088	0.256	0.175	0.051	0.542
<i>Bullimus luzonicus</i>	0	0.466	0.988	0.072	0.220	0.160	0.044	0.535
<i>Bullimus luzonicus</i>	0	0.490	0.989	0.076	0.256	0.189	0.046	0.533
<i>Chrotomys whiteheadi</i>	0	0.481	1.025	0.098	0.293	0.187	0.047	0.616
<i>Musseromys beneficus</i>	1	0.451	1.153	0.089	0.267	0.133	0.038	0.811
<i>Phloecomys pallidus</i>	1	0.421	0.878	0.086	0.272	0.168	0.052	0.802
<i>Phloecomys pallidus</i>	1	0.452	0.823	0.079	0.297	0.160	0.055	0.816
<i>Phloecomys pallidus</i>	1	0.456	0.845	0.083	0.279	0.185	0.050	0.831
<i>Phloecomys pallidus</i>	1	0.479	0.866	0.083	0.281	0.159	0.054	0.887
<i>Rattus everetti</i>	0	0.444	1.028	0.084	0.241	0.163	0.044	0.568
<i>Rattus everetti</i>	0	0.454	0.995	0.082	0.239	0.166	0.041	0.602
<i>Rattus everetti</i>	0	0.459	0.962	0.085	0.232	0.163	0.049	0.693
<i>Rattus everetti</i>	0	0.464	1.060	0.086	0.245	0.156	0.040	0.666
<i>Rattus everetti</i>	0	0.474	0.963	0.085	0.246	0.171	0.053	0.601
<i>Rattus everetti</i>	0	0.476	0.969	0.090	0.249	0.174	0.048	0.603
<i>Rhynchomys soricoides</i>	0	0.465	1.079	0.090	0.307	0.176	0.061	0.625
<i>Rhynchomys soricoides</i>	0	0.477	1.178	0.084	0.333	0.167	0.055	0.519
<i>Rhynchomys soricoides</i>	0	0.488	1.153	0.088	0.316	0.171	0.048	0.513

table cont'd

Species	climb	SMI	BI	HRI	HEB	OLI	URI	MANUS
Rhynchomys soricoides	0	0.494	1.169	0.088	0.316	0.170	0.056	0.520
Rhynchomys soricoides	0	0.500	1.113	0.087	0.301	0.168	0.049	0.593
Rhynchomys soricoides	0	0.501	1.120	0.089	0.303	0.170	0.055	0.565
Rhynchomys soricoides	0	0.523	1.161	0.095	0.315	0.156	0.053	0.524
Soricomys kalinga	0.27	0.432	1.014	0.086	0.301	0.179	0.041	0.751
Soricomys kalinga	0.27	0.434	0.997	0.074	0.288	0.178	0.043	0.684
Soricomys kalinga	0.27	0.459	0.990	0.069	0.291	0.171	0.050	0.723
Soricomys montanus	0.15	0.457	1.018	0.083	0.287	0.184	0.036	0.703

Species	CI	FRI	GI	FEB	TRI	TSI	PES	IM	SI	Catalog
Apomys abrae	1.264	0.067	0.080	0.171	0.042	0.329	0.357	0.690	0.699	170907
Apomys abrae	1.279	0.074	0.070	0.160	0.047	0.278	0.396	0.681	0.733	188437
Apomys abrae	1.361	0.068	0.072	0.166	0.038	0.275	0.357	0.683	0.721	167342
Apomys abrae	1.317	0.067	0.078	0.165	0.042	0.322	0.355	0.676	0.685	170927
Apomys abrae	1.334	0.066	0.073	0.166	0.040	0.304	0.348	0.683	0.490	167355
Apomys abrae	1.355	0.066	0.082	0.185	0.040	0.270	0.350	0.684	0.789	170905
Apomys abrae	1.299	0.064	0.074	0.170	0.041	0.319	0.356	0.681	0.753	170929
Apomys abrae	1.321	0.071	0.071	0.171	0.039	0.294	0.355	0.689	0.675	170919
Apomys abrae	1.307	0.064	0.072	0.167	0.041	0.304	0.368	0.689	0.737	193876
Apomys abrae	1.348	0.068	0.074	0.167	0.038	0.311	0.375	0.686	0.719	193869
Apomys abrae	1.311	0.067	0.070	0.167	0.035	0.289	0.335	0.674	0.701	214361
Apomys abrae	1.302	0.063	0.071	0.165	0.044	0.283	0.372	0.672	0.680	170911
Apomys abrae	1.330	0.067	0.071	0.164	0.040	0.287	0.387	0.682	0.685	214362
Apomys abrae	1.360	0.075	0.080	0.173	0.041	0.298	0.320	0.682	0.646	167347
Apomys banahao	1.314	0.075	0.075	0.173	0.046	0.298	0.363	0.671	0.699	179478
Apomys banahao	1.327	0.064	0.065	0.184	0.042	0.274	0.359	0.688	0.705	218491

table cont'd

Species	CI	FRI	GI	FEB	TRI	TSI	PES	IM	SI	Catalog
Apomys banahao	1.267	0.070	0.071	0.180	0.044	0.327	0.377	0.695	0.742	179480
Apomys banahao	1.297	0.071	0.074	0.180	0.044	0.322	0.333	0.696	0.724	218490
Apomys banahao	1.324	0.066	0.075	0.174	0.046	0.298	0.360	0.682	0.692	218515
Apomys datae	1.306	0.067	0.076	0.158	0.041	0.326	0.322	0.683	0.638	175630
Apomys datae	1.341	0.084	0.069	0.179	0.044	0.288	0.331	0.708	0.706	175662
Apomys datae	1.333	0.065	0.075	0.187	0.044	0.328	0.355	0.697	0.680	188448
Apomys datae	1.334	0.075	0.067	0.178	0.050	0.273	0.379	0.712	0.756	188433
Apomys datae	1.330	0.065	0.074	0.168	0.038	0.335	0.361	0.689	0.675	170954
Apomys datae	1.352	0.079	0.067	0.170	0.042	0.310	0.342	0.691	0.683	170948
Apomys datae	1.314	0.068	0.081	0.164	0.045	0.324	0.318	0.697	0.669	188438
Apomys datae	1.306	0.069	0.076	0.166	0.040	0.313	0.371	0.690	0.682	170942
Apomys datae	1.311	0.059	0.071	0.174	0.048	0.248	0.369	0.695	0.665	188425
Apomys datae	1.355	0.074	0.076	0.169	0.042	0.303	0.339	0.682	0.724	193936
Apomys datae	1.319	0.064	0.075	0.158	0.040	0.231	0.350	0.696	0.661	170956
Apomys datae	1.290	0.068	0.080	0.178	0.044	0.300	0.339	0.687	0.708	188440
Apomys datae	1.263	0.071	0.074	0.169	0.045	0.299	0.340	0.698	0.672	175646
Apomys datae	1.318	0.072	0.096	0.178	0.046	0.332	0.338	0.700	0.707	193890
Apomys datae	1.357	0.073	0.071	0.169	0.045	0.288	0.353	0.694	0.750	193940
Apomys datae	1.371	0.080	0.078	0.179	0.046	0.333	0.339	0.689	0.738	193898
Apomys datae	1.342	0.081	0.078	0.173	0.047	0.302	0.338	0.694	0.665	214389
Apomys gracilirostris	1.387	0.067	0.081	0.162	0.036	0.298	0.318	0.661	0.696	222314
Apomys gracilirostris	1.376	0.072	0.064	0.181	0.039	0.334	0.337	0.649	0.736	222321
Apomys gracilirostris	1.345	0.071	0.070	0.182	0.043	0.327	0.352	0.660	0.732	222320
Apomys gracilirostris	1.368	0.070	0.065	0.184	0.041	0.325	0.371	0.663	0.728	222315
Apomys gracilirostris	1.393	0.073	0.075	0.174	0.042	0.317	0.375	0.658	0.716	222319
Apomys iridensis	1.200	0.071	0.078	0.176	0.047	0.338	0.353	0.683	0.685	206326

table cont'd

Species	CI	FRI	GI	FEB	TRI	TSI	PES	IM	SI	Catalog
Apomys iridensis	1.222	0.070	0.094	0.168	0.045	0.326	0.379	0.677	0.694	206324
Apomys iridensis	1.231	0.075	0.079	0.181	0.047	0.359	0.399	0.695	0.764	206335
Apomys iridensis	1.236	0.080	0.079	0.188	0.048	0.307	0.365	0.687	0.654	206336
Apomys iridensis	1.241	0.082	0.081	0.178	0.049	0.316	0.390	0.693	0.663	206330
Apomys iridensis	1.272	0.073	0.082	0.174	0.047	0.046	0.340	0.692	0.744	206325
Apomys microdon	1.308	0.067	0.076	0.171	0.043	0.325	0.448	0.703	0.771	214487
Apomys microdon	1.329	0.070	0.066	0.178	0.041	0.344	0.444	0.713	0.717	209585
Apomys microdon	1.274	0.066	0.069	0.172	0.042	0.310	0.415	0.695	0.697	189874
Apomys microdon	1.269	0.075	0.068	0.163	0.044	0.347	0.426	0.687	0.692	189875
Apomys microdon	1.263	0.068	0.078	0.169	0.045	0.350	0.395	0.712	0.692	209548
Apomys musculus	1.453	0.069	0.073	0.183	0.038	0.296	0.390	0.731	0.753	214411
Apomys musculus	1.373	0.070	0.071	0.180	0.042	0.309	0.408	0.709	0.700	175718
Apomys musculus	1.037	0.069	0.070	0.162	0.055	0.424	0.388	0.840	0.689	198853
Apomys musculus	1.457	0.070	0.061	0.177	0.040	0.311	0.413	0.689	0.695	214408
Apomys musculus	1.421	0.077	0.065	0.189	0.043	0.311	0.398	0.723	0.711	214410
Apomys musculus	1.407	0.067	0.067	0.181	0.043	0.349	0.414	0.718	0.717	214407
Apomys musculus	1.398	0.071	0.072	0.184	0.043	0.321	0.412	0.697	0.672	175719
Apomys musculus	1.390	0.078	0.070	0.177	0.041	0.326	0.439	0.700	0.756	218527
Apomys musculus	1.371	0.078	0.076	0.183	0.045	0.332	0.417	0.712	0.613	214409
Apomys sacobianus	1.219	0.074	0.084	0.169	0.045	0.290	0.340	0.669	0.760	216365
Apomys sacobianus	1.244	0.073	0.084	0.173	0.047	0.293	0.370	0.678	0.757	216363
Apomys sacobianus	1.219	0.066	0.087	0.163	0.043	0.317	0.360	0.666	0.745	216330
Apomys sacobianus	1.248	0.066	0.081	0.168	0.047	0.319	0.366	0.675	0.741	216345
Apomys sacobianus	1.240	0.069	0.078	0.177	0.051	0.298	0.342	0.673	0.714	212722
Apomys sierrae	1.253	0.069	0.086	0.183	0.042	0.258	0.373	0.693	0.737	209570
Apomys sierrae	1.247	0.063	0.070	0.164	0.044	0.282	0.385	0.677	0.680	186827

table cont'd

Species	CI	FRI	GI	FEB	TRI	TSI	PES	IM	SI	Catalog
Apomys sierrae	1.210	0.072	0.072	0.178	0.048	0.309	0.364	0.692	0.706	209579
Apomys sierrae	1.238	0.068	0.071	0.180	0.045	0.362	0.387	0.706	0.668	209586
Apomys sierrae	1.224	0.064	0.072	0.164	0.047	0.296	0.376	0.688	0.638	186825
Apomys sierrae	1.277	0.066	0.077	0.180	0.046	0.336	0.394	0.717	0.668	186821
Apomys zambalensis	1.297	0.075	0.092	0.189	0.044	0.298	0.384	0.657	0.671	183605
Apomys zambalensis	1.209	0.069	0.085	0.162	0.046	0.347	0.416	0.671	0.704	183601
Apomys zambalensis	1.250	0.072	0.079	0.176	0.048	0.314	0.375	0.652	0.688	183627
Apomys zambalensis	1.243	0.073	0.085	0.171	0.044	0.331	0.399	0.673	0.727	183635
Apomys zambalensis	1.247	0.068	0.075	0.168	0.048	0.314	0.390	0.684	0.646	179439
Apomys zambalensis	1.240	0.071	0.073	0.179	0.045	0.312	0.393	0.686	0.624	179441
Archboldomys maximus	1.298	0.077	0.074	0.176	0.048	0.277	0.410	0.669	0.697	193943
Archboldomys maximus	1.385	0.080	0.055	0.206	0.047	0.293	0.431	0.681	0.732	193944
Archboldomys maximus	1.357	0.082	0.073	0.198	0.046	0.284	0.390	0.667	0.719	193942
Batomys granti	1.130	0.078	0.064	0.222	0.054	0.369	0.478	0.766	0.760	214412
Bullimus luzonicus	1.110	0.069	0.093	0.181	0.055	0.404	0.374	0.712	0.802	209588
Bullimus luzonicus	1.137	0.070	0.093	0.198	0.052	0.329	0.370	0.694	0.846	214415
Bullimus luzonicus	1.159	0.069	0.087	0.190	0.052	0.351	0.394	0.708	0.827	209589
Bullimus luzonicus	1.116	0.077	0.095	0.176	0.060	0.367	0.401	0.695	0.862	188455
Bullimus luzonicus	1.129	0.078	0.089	0.186	0.052	0.381	0.410	0.720	0.891	185971
Bullimus luzonicus	1.086	0.080	0.099	0.193	0.059	0.350	0.386	0.673	0.834	188450
Chrotomys whiteheadi	1.127	0.077	0.090	0.176	0.052	0.371	0.422	0.714	0.778	62284
Musseromys beneficus	1.295	0.075	0.062	0.193	0.047	0.362	0.531	0.801	0.737	198857
Phloeomys pallidus	0.948	0.077	0.080	0.218	0.070	0.453	0.675	0.817	0.787	175730
Phloeomys pallidus	0.962	0.091	0.098	0.238	0.075	0.443	0.713	0.797	0.852	214420
Phloeomys pallidus	0.982	0.078	0.073	0.221	0.065	0.502	0.749	0.811	0.796	193967
Phloeomys pallidus	0.995	0.088	0.100	0.244	0.077	0.500	0.740	0.825	0.809	214419

table cont'd

Species	CI	FRI	GI	FEB	TRI	TSI	PES	IM	SI	Catalog
Rattus everetti	1.123	0.068	0.094	0.184	0.048	0.368	0.435	0.715	0.738	216581
Rattus everetti	1.134	0.071	0.106	0.176	0.051	0.422	0.422	0.696	0.719	183642
Rattus everetti	1.115	0.072	0.086	0.172	0.055	0.392	0.451	0.703	0.792	188468
Rattus everetti	1.146	0.079	0.092	0.194	0.051	0.370	0.455	0.711	0.853	191077
Rattus everetti	1.118	0.075	0.089	0.182	0.052	0.442	0.478	0.689	0.771	191078
Rattus everetti	1.082	0.072	0.104	0.180	0.056	0.383	0.449	0.712	0.817	189881
Rhynchomys soricoides	1.161	0.073	0.071	0.182	0.051	0.340	0.367	0.681	0.870	170980
Rhynchomys soricoides	1.214	0.079	0.087	0.207	0.056	0.309	0.381	0.707	0.843	193980
Rhynchomys soricoides	1.214	0.076	0.083	0.188	0.048	0.282	0.388	0.682	0.869	198886
Rhynchomys soricoides	1.153	0.074	0.084	0.176	0.048	0.312	0.353	0.677	0.835	214423
Rhynchomys soricoides	1.177	0.078	0.104	0.187	0.046	0.295	0.329	0.691	0.831	198887
Rhynchomys soricoides	1.214	0.065	0.097	0.190	0.044	0.302	0.369	0.673	0.803	198883
Rhynchomys soricoides	1.188	0.090	0.076	0.197	0.053	0.304	0.365	0.689	0.864	198884
Soricomys kalinga	1.341	0.081	0.053	0.199	0.045	0.360	0.510	0.705	0.666	175720
Soricomys kalinga	1.391	0.085	0.061	0.212	0.048	0.295	0.455	0.743	0.645	170965
Soricomys kalinga	1.383	0.072	0.068	0.192	0.044	0.331	0.461	0.738	0.662	170967
Soricomys montanus	1.345	0.072	0.051	0.188	0.045	0.333	0.444	0.698	0.639	188449

## Supporting Appendix 1.2

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
Apomys abrae	FMNH	170911	0.67188234	0.37224817	0.4889706	0.60358891	1	Terrestrial
Apomys abrae	FMNH	214361	0.6739587	0.33484505	0.5123967	0.57490637	1	Terrestrial
Apomys abrae	FMNH	170927	0.67613353	0.35465925	0.5131086	0.65434084	1	Terrestrial
Apomys abrae	FMNH	170929	0.68085798	0.35594406	0.4836364	0.59782609	1	Terrestrial
Apomys abrae	FMNH	188437	0.68087215	0.39606954	0.498155	0.5543672	1	Terrestrial
Apomys abrae	FMNH	214362	0.68176461	0.38739431	0.5076336	0.67343173	1	Terrestrial
Apomys abrae	FMNH	167347	0.68229256	0.32019704	0.483871	0.57166948	1	Terrestrial
Apomys abrae	FMNH	167355	0.68270233	0.34779566	0.5	0.6024735	1	Terrestrial
Apomys abrae	FMNH	167342	0.68299228	0.35714286	0.4923077	0.61256545	1	Terrestrial
Apomys abrae	FMNH	170905	0.68395696	0.34974425	0.5017668	0.58682635	1	Terrestrial
Apomys abrae	FMNH	193869	0.68596187	0.37545922	0.503876	0.60441426	1	Terrestrial
Apomys abrae	FMNH	193876	0.68865031	0.3679031	0.4828897	0.52922078	1	Terrestrial
Apomys abrae	FMNH	170919	0.68872631	0.35514019	0.5054545	0.60848287	1	Terrestrial
Apomys abrae	FMNH	170907	0.68952779	0.35724432	0.4738806	0.59375	1	Terrestrial
Apomys banahao	FMNH	179478	0.67134079	0.36279401	0.4681648	0.57704918	1	Terrestrial
Apomys banahao	FMNH	218515	0.68174988	0.35976505	0.4904215	0.63021869	1	Terrestrial
Apomys banahao	FMNH	218491	0.68760771	0.35897436	0.4641509	0.56655844	1	Terrestrial
Apomys banahao	FMNH	179480	0.69473851	0.37691238	0.4676806	0.60314685	1	Terrestrial
Apomys banahao	FMNH	218490	0.6957498	0.33263598	0.4943396	0.58225807	1	Terrestrial
Apomys datae	FMNH	193936	0.68215371	0.33883752	0.4807018	0.64779874	1	Terrestrial
Apomys datae	FMNH	175630	0.68256909	0.32154997	0.4760148	0.54662379	1	Terrestrial
Apomys datae	FMNH	188440	0.68650551	0.33914864	0.45	0.54276316	1	Terrestrial
Apomys datae	FMNH	170954	0.68877944	0.36096606	0.4981949	0.54954955	1	Terrestrial

table cont'd

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
Apomys datae	FMNH	193898	0.68926746	0.33883059	0.4676806	0.60616438	1	Terrestrial
Apomys datae	FMNH	170942	0.6896076	0.37050106	0.4781022	0.62068966	1	Terrestrial
Apomys datae	FMNH	170948	0.69111446	0.34165572	0.4793103	0.5488959	1	Terrestrial
Apomys datae	FMNH	214389	0.69352888	0.33836651	0.4599303	0.55787781	1	Terrestrial
Apomys datae	FMNH	193940	0.69419335	0.35289855	0.4595588	0.6442623	1	Terrestrial
Apomys datae	FMNH	188425	0.69499603	0.36881005	0.4779412	0.5856	1	Terrestrial
Apomys datae	FMNH	170956	0.6958578	0.35	0.48288973	0.57799672	1	Terrestrial
Apomys datae	FMNH	188448	0.69652856	0.35533708	0.4731183	0.5802099	1	Terrestrial
Apomys datae	FMNH	188438	0.69671752	0.31833223	0.4892086	0.55140187	1	Terrestrial
Apomys datae	FMNH	175646	0.6979405	0.34005376	0.4534884	0.6010274	1	Terrestrial
Apomys datae	FMNH	193890	0.70018916	0.33810498	0.4784173	0.55905512	1	Terrestrial
Apomys datae	FMNH	175662	0.70844924	0.33134773	0.4710425	0.59404097	1	Terrestrial
Apomys datae	FMNH	188433	0.71196188	0.37883008	0.4666667	0.58146965	1	Terrestrial
Apomys gracilirostris	FMNH	222321	0.64912281	0.33686301	0.5183946	0.53637902	1	Terrestrial
Apomys gracilirostris	FMNH	222319	0.65818236	0.37508197	0.5226481	0.59289176	1	Terrestrial
Apomys gracilirostris	FMNH	222320	0.66049855	0.35215947	0.5298246	0.54166667	1	Terrestrial
Apomys gracilirostris	FMNH	222314	0.66098371	0.31840796	0.5379538	0.61759729	1	Terrestrial
Apomys gracilirostris	FMNH	222315	0.66278366	0.37119114	0.4904215	0.57096774	1	Terrestrial
Apomys iridensis	FMNH	206324	0.67682647	0.37868971	0.5192982	0.64615385	1	Terrestrial
Apomys iridensis	FMNH	206326	0.68251969	0.35336713	0.5	0.55604076	1	Terrestrial
Apomys iridensis	FMNH	206336	0.68718481	0.36545925	0.52	0.63676471	1	Terrestrial
Apomys iridensis	FMNH	206325	0.6915078	0.34027326	0.5032051	0.60385757	1	Terrestrial
Apomys iridensis	FMNH	206330	0.69308912	0.39008142	0.4782609	0.57746479	1	Terrestrial
Apomys iridensis	FMNH	206335	0.69532593	0.39940828	0.4817518	0.52327448	1	Terrestrial
Apomys microdon	FMNH	189875	0.68709115	0.42647059	0.529148	0.78012685	3	Arboreal

table cont'd

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
Apomys microdon	FMNH	189874	0.69495361	0.4153264	0.5714286	0.74004193	3	Arboreal
Apomys microdon	FMNH	214487	0.70321229	0.44797688	0.5777778	0.70208333	3	Arboreal
Apomys microdon	FMNH	209548	0.71247312	0.39478585	0.6090909	0.8	3	Arboreal
Apomys microdon	FMNH	209585	0.71332209	0.44357213	0.5746606	0.81428571	3	Arboreal
Apomys musculus	FMNH	214408	0.68890089	0.41334769	0.5602094	0.74055416	3	Arboreal
Apomys musculus	FMNH	175719	0.69718855	0.41219769	0.5539216	0.91977077	3	Arboreal
Apomys musculus	FMNH	218527	0.70023178	0.43873085	0.5512195	0.92857143	3	Arboreal
Apomys musculus	FMNH	175718	0.70898235	0.40802676	0.5621891	0.74867725	3	Arboreal
Apomys musculus	FMNH	214409	0.71233237	0.41657922	0.5555556	0.73004695	3	Arboreal
Apomys musculus	FMNH	214407	0.71758665	0.41364606	0.5625	0.77806122	3	Arboreal
Apomys musculus	FMNH	214410	0.72300338	0.39841987	0.5567568	0.77284595	3	Arboreal
Apomys musculus	FMNH	214411	0.73117993	0.39031926	0.5195531	0.71498772	3	Arboreal
Apomys musculus	FMNH	198853	0.83952096	0.38830898	0.5660377	0.70801034	3	Arboreal
Apomys sacobianus	FMNH	216330	0.66566824	0.35968892	0.5310345	0.58908046	1	Terrestrial
Apomys sacobianus	FMNH	216365	0.66866913	0.34030683	0.4910394	0.56493507	1	Terrestrial
Apomys sacobianus	FMNH	212722	0.67271627	0.34168272	0.4909091	0.58730159	1	Terrestrial
Apomys sacobianus	FMNH	216345	0.67511312	0.36568695	0.5071429	0.56832298	1	Terrestrial
Apomys sacobianus	FMNH	216363	0.67813559	0.37044968	0.519685	0.53719008	1	Terrestrial
Apomys sierrae	FMNH	186827	0.67654357	0.38515406	0.4982332	0.52639296	1	Terrestrial
Apomys sierrae	FMNH	186825	0.6882858	0.37643678	0.4982206	0.5569044	1	Terrestrial
Apomys sierrae	FMNH	209579	0.69176581	0.36403509	0.4887218	0.57744361	1	Terrestrial
Apomys sierrae	FMNH	209570	0.69269178	0.37258953	0.5017668	0.56857143	1	Terrestrial
Apomys sierrae	FMNH	209586	0.7057964	0.38709677	0.4835165	0.60273973	1	Terrestrial
Apomys sierrae	FMNH	186821	0.71726333	0.39357143	0.4873646	0.70392749	1	Terrestrial

table cont'd

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
<i>Apomys zambalensis</i>	FMNH	183627	0.65202907	0.37516689	0.4892857	0.63338789	1	Terrestrial
<i>Apomys zambalensis</i>	FMNH	183605	0.65673514	0.38440111	0.4981818	0.61119516	1	Terrestrial
<i>Apomys zambalensis</i>	FMNH	183601	0.67110716	0.41593567	0.471831	0.65849673	1	Terrestrial
<i>Apomys zambalensis</i>	FMNH	183635	0.67339082	0.39869281	0.4641509	0.46769231	1	Terrestrial
<i>Apomys zambalensis</i>	FMNH	179439	0.68424215	0.38961039	0.49818182	0.59055118	1	Terrestrial
<i>Apomys zambalensis</i>	FMNH	179441	0.68613247	0.39285714	0.5035461	0.59243698	1	Terrestrial
<i>Archboldomys maximus</i>	FMNH	193942	0.66727273	0.3898451	0.4554455	0.69575472	1	Terrestrial
<i>Archboldomys maximus</i>	FMNH	193943	0.66862467	0.40978078	0.5070423	0.67555556	1	Terrestrial
<i>Archboldomys maximus</i>	FMNH	193944	0.68076199	0.4308653	0.4761905	0.65831435	1	Terrestrial
<i>Batomys granti</i>	FMNH	214412	0.76565822	0.47796024	0.4645161	0.69311377	2	General
<i>Bullimus luzonicus</i>	FMNH	188450	0.67322874	0.38595592	0.4470842	0.53256705	1	Terrestrial
<i>Bullimus luzonicus</i>	FMNH	214415	0.69415496	0.37039075	0.4665012	0.54867257	1	Terrestrial
<i>Bullimus luzonicus</i>	FMNH	188455	0.69526398	0.40062435	0.4420131	0.54162586	1	Terrestrial
<i>Bullimus luzonicus</i>	FMNH	209589	0.70750305	0.39406559	0.4642082	0.5218254	1	Terrestrial
<i>Bullimus luzonicus</i>	FMNH	209588	0.71171771	0.37397931	0.4877506	0.51995798	1	Terrestrial
<i>Bullimus luzonicus</i>	FMNH	185971	0.71998036	0.40981094	0.4821053	0.53537487	1	Terrestrial
<i>Bunomys fratrorum</i>	LSUMZ	38992	0.68743926	0.36083744	0.43466667	0.49172577	1	Terrestrial
<i>Bunomys fratrorum</i>	LSUMZ	38989	0.68973514	0.36062613	0.49577465	0.50125	1	Terrestrial
<i>Bunomys fratrorum</i>	LSUMZ	38991	0.69263688	0.36652917	0.48607595	0.50929368	1	Terrestrial
<i>Bunomys fratrorum</i>	LSUMZ	38988	0.69953465	0.34192038	0.49502488	0.49520384	1	Terrestrial
<i>Chiropodomys gliroides</i>	AMNH	240332	0.69084934	0.52199414	0.56521739	0.74425287	3	Arboreal
<i>Chiropodomys gliroides</i>	AMNH	240344	0.71645022	0.55851064	0.58673469	0.75	3	Arboreal
<i>Chrotomys whiteheadi</i>	FMNH	62284	0.71446925	0.42182663	0.4078014	0.61608498	1	Terrestrial
<i>Echinothrix leucura</i>	LSUMZ	39070	0.63377338	0.32301548	0.54567901	0.47368421	1	Terrestrial

table cont'd

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
<i>Grammomys surdaster</i>	LSUMZ	38504	0.65612565	0.40612245	0.56491228	0.74352941	3	Arboreal
<i>Grammomys surdaster</i>	LSUMZ	38503	0.66330391	0.40975104	0.54255319	0.72572816	3	Arboreal
<i>Grammomys surdaster</i>	LSUMZ	38506	0.66894052	0.42116402	0.56491228	0.71527778	3	Arboreal
<i>Grammomys surdaster</i>	LSUMZ	38508	0.67835294	0.41017316	0.58518519	0.71032746	3	Arboreal
<i>Grammomys surdaster</i>	LSUMZ	38511	0.68203828	0.42078189	0.5647482	0.71461187	3	Arboreal
<i>Grammomys surdaster</i>	LSUMZ	38509	0.68625718	0.43133047	0.58249158	0.72605791	3	Arboreal
<i>Haeromys minahassae</i>	LSUMZ	38298	0.7063655	0.444	0.62559242	0.88554217	3	Arboreal
<i>Haeromys minahassae</i>	LSUMZ	38299	0.74225703	0.46599132	0.63636364	0.83086053	3	Arboreal
<i>Hybomys univittatus</i>	LSUMZ	38541	0.6915363	0.44404332	0.45531915	0.66790353	1	Terrestrial
<i>Hydromys chrysogaster</i>	AMNH	35690	0.60929952	0.42198416	0.47920902	0.61395349	1	Terrestrial
<i>Hylomyscus stella</i>	LSUMZ	38559	0.66858488	0.41798942	0.5982906	0.69190601	2	General
<i>Hylomyscus stella</i>	LSUMZ	38858	0.6863648	0.41677255	0.55230126	0.69892473	2	General
<i>Hylomyscus stella</i>	LSUMZ	38557	0.68984221	0.42804428	0.63555556	0.69892473	2	General
<i>Hyomys goliath</i>	AMNH	208106	0.79497099	0.53198847	0.460371	0.7125951	2	General
<i>Lemniscomys striatus</i>	LSUMZ	38571	0.65276926	0.37732342	0.55128205	0.55936073	1	Terrestrial
<i>Lemniscomys striatus</i>	LSUMZ	38572	0.65952981	0.36403897	0.536	0.55723542	1	Terrestrial
<i>Lenomys meyeri</i>	LSUMZ	39074	0.73515982	0.62526024	0.52173913	0.74058127	3	Arboreal
<i>Lenomys meyeri</i>	LSUMZ	39076	0.74059095	0.58815427	0.50701754	0.7436182	3	Arboreal
<i>Lenomys meyeri</i>	LSUMZ	39075	0.74069134	0.59640636	0.5	0.73513514	3	Arboreal
<i>Lenomys meyeri</i>	MZB	40360	0.74149436	0.5987751	0.51368917	0.74058127	3	Arboreal
<i>Lenomys meyeri</i>	MZB	40363	0.74149436	0.5987751	0.51368917	0.74828375	3	Arboreal
<i>Lenomys meyeri</i>	LSUMZ	39077	0.74953532	0.58527955	0.526	0.72869955	3	Arboreal
<i>Malacomys longipes</i>	LSUMZ	38694	0.69741449	0.32847991	0.51149425	0.57458564	1	Terrestrial
<i>Malacomys longipes</i>	LSUMZ	38691	0.69802976	0.31416169	0.52054795	0.5445946	1	Terrestrial

table cont'd

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
<i>Malacomys longipes</i>	LSUMZ	38693	0.71319018	0.35141956	0.5	0.59064328	1	Terrestrial
<i>Malacomys longipes</i>	LSUMZ	38692	0.71752451	0.32506204	0.53776435	0.54062038	1	Terrestrial
<i>Mastomys natalensis</i>	LSUMZ	38714	0.69092543	0.37988281	0.49327354	0.63023256	1	Terrestrial
<i>Maxomys hellwaldii</i>	LSUMZ	38316	0.62173528	0.38565264	0.4836272	0.52518892	1	Terrestrial
<i>Maxomys hellwaldii</i>	LSUMZ	38317	0.62556618	0.38072418	0.48965517	0.54044118	1	Terrestrial
<i>Maxomys hellwaldii</i>	LSUMZ	39084	0.6313037	0.38287011	0.46686747	0.53403141	1	Terrestrial
<i>Maxomys hellwaldii</i>	LSUMZ	38319	0.64018465	0.38177753	0.49147727	0.55943153	1	Terrestrial
<i>Maxomys hellwaldii</i>	LSUMZ	38322	0.64587617	0.38820912	0.48533333	0.54260652	1	Terrestrial
<i>Maxomys musschenbroekii</i>	LSUMZ	38340	0.64266326	0.43278943	0.47777778	0.57503949	1	Terrestrial
<i>Maxomys musschenbroekii</i>	LSUMZ	38342	0.66615014	0.41125198	0.45955882	0.55592654	1	Terrestrial
<i>Maxomys musschenbroekii</i>	LSUMZ	38346	0.67252066	0.41125198	0.47037037	0.59663866	1	Terrestrial
<i>Maxomys musschenbroekii</i>	LSUMZ	38344	0.68934426	0.39314369	0.47985348	0.59703947	1	Terrestrial
<i>Melomys burtoni</i>	AMNH	155368	0.660425	0.41666667	0.50753769	0.71294118	2	General
<i>Melomys burtoni</i>	AMNH	155361	0.660425	0.41794088	0.57416268	0.7020316	2	General
<i>Melomys cervinipes</i>	AMNH	66021	0.59754457	0.47064485	0.48805461	0.70541082	3	Arboreal
<i>Mus bufo</i>	LSUMZ	38733	0.66893039	0.3699187	0.46478873	0.62295082	1	Terrestrial
<i>Mus bufo</i>	LSUMZ	38732	0.70468808	0.40955138	0.48148148	0.63666667	1	Terrestrial
<i>Mus musculus</i>	LSUMZ	25285	0.69655643	0.4057554	0.47019868	0.66202091	1	Terrestrial
<i>Mus musculus</i>	LSUMZ	34163	0.69963732	0.41940086	0.49655172	0.64285714	1	Terrestrial
<i>Mus musculus</i>	LSUMZ	34233	0.69984102	0.3799435	0.47368421	0.65517241	1	Terrestrial
<i>Mus musculus</i>	LSUMZ	25284	0.70018394	0.41838134	0.46060606	0.67868853	1	Terrestrial
<i>Mus musculus</i>	LSUMZ	34153	0.72003929	0.43300423	0.49673203	0.62721894	1	Terrestrial
<i>Musseromys beneficus</i>	FMNH	198857	0.80128924	0.53115727	0.5116279	0.81060606	3	Arboreal
<i>Paruromys dominator</i>	LSUMZ	38357	0.67506222	0.41269036	0.54857143	0.61318898	2	General

table cont'd

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
Paruromys dominator	LSUMZ	38356	0.68834282	0.4265873	0.55797101	0.62345091	2	General
Paruromys dominator	LSUMZ	38361	0.68925282	0.42215256	0.52798508	0.62781587	2	General
Paruromys dominator	LSUMZ	38360	0.6958296	0.43095005	0.53191489	0.62380952	2	General
Phloeomys pallidus	FMNH	214420	0.79712406	0.71315529	0.4332386	0.81552754	3	Arboreal
Phloeomys pallidus	AMNH	274635	0.79836621	0.69370933	0.45836154	0.85617701	3	Arboreal
Phloeomys pallidus	FMNH	193967	0.81120609	0.74854369	0.4255319	0.83075933	3	Arboreal
Phloeomys pallidus	FMNH	175730	0.81707797	0.67472119	0.4533153	0.80152672	3	Arboreal
Phloeomys pallidus	FMNH	214419	0.82499347	0.73979107	0.4738331	0.88700947	3	Arboreal
Pithecheir melanurus	MZB	4052	0.7181713	0.49482896	0.54081633	0.80747664	3	Arboreal
Rattus everetti	FMNH	191078	0.68866822	0.47817048	0.5192308	0.60148515	1	Terrestrial
Rattus everetti	FMNH	183642	0.69592832	0.42167957	0.5083682	0.60155383	1	Terrestrial
Rattus everetti	FMNH	188468	0.70335285	0.45090909	0.4710744	0.69326683	1	Terrestrial
Rattus everetti	FMNH	191077	0.71127104	0.45460238	0.5327696	0.66552511	1	Terrestrial
Rattus everetti	FMNH	189881	0.71223022	0.44853876	0.516269	0.60346821	1	Terrestrial
Rattus everetti	FMNH	216581	0.71456333	0.43462898	0.4925926	0.56810631	1	Terrestrial
Rattus hoffmanni	LSUMZ	39169	0.66288699	0.38430851	0.50268817	0.58941345	1	Terrestrial
Rattus hoffmanni	LSUMZ	39166	0.66563468	0.41786744	0.48	0.57597685	1	Terrestrial
Rattus hoffmanni	LSUMZ	39170	0.67462728	0.40472973	0.50284091	0.56925208	1	Terrestrial
Rattus norvegicus	LSUMZ	33986	0.69403918	0.45039683	0.47142857	0.61369193	1	Terrestrial
Rattus norvegicus	LSUMZ	34188	0.70737716	0.44347283	0.41432225	0.63378378	1	Terrestrial
Rattus rattus	LSUMZ	23697	0.69109266	0.44462409	0.5951087	0.66057839	2	General
Rattus rattus	LSUMZ	29378	0.70540541	0.43350864	0.55581948	0.6704918	2	General
Rattus xanthurus	LSUMZ	39199	0.7013656	0.51825293	0.57766143	0.66709347	1	Terrestrial
Rattus xanthurus	LSUMZ	39200	0.70417848	0.48881119	0.54811716	0.6887574	1	Terrestrial
Rattus xanthurus	LSUMZ	39205	0.70676692	0.5164557	0.57037037	0.69230769	1	Terrestrial

table cont'd

Species	Museum	Number	IM	PES	TAIL	MANUS	State	Locomotor Mode
Rattus xanthurus	LSUMZ	39196	0.71758122	0.5229151	0.52714932	0.63069544	1	Terrestrial
Rhynchomys soricoides	FMNH	198883	0.67290429	0.36872812	0.3983516	0.56521739	1	Terrestrial
Rhynchomys soricoides	FMNH	214423	0.67702612	0.35297691	0.4164134	0.51981707	1	Terrestrial
Rhynchomys soricoides	FMNH	170980	0.68100505	0.36686009	0.4434783	0.525	1	Terrestrial
Rhynchomys soricoides	FMNH	198886	0.68178213	0.38789809	0.4054054	0.51292517	1	Terrestrial
Rhynchomys soricoides	FMNH	198884	0.68876661	0.36474359	0.4285714	0.52401747	1	Terrestrial
Rhynchomys soricoides	FMNH	198887	0.6913775	0.32860666	0.4215116	0.59304085	1	Terrestrial
Rhynchomys soricoides	FMNH	193980	0.70674615	0.38098237	0.4359756	0.51877608	1	Terrestrial
Soricomys kalinga	FMNH	175720	0.70538319	0.50956938	0.46	0.75067751	2	General
Soricomys kalinga	FMNH	170967	0.73785872	0.46054181	0.4923077	0.72266667	2	General
Soricomys kalinga	FMNH	170965	0.74318956	0.45521472	0.4705882	0.68351064	2	General
Soricomys montanus	FMNH	188449	0.69753086	0.44431946	0.4924623	0.7025641	2	General
Taeromys celebensis	LSUMZ	39221	0.70199778	0.42802825	0.54932302	0.56521739	1	Terrestrial
Taeromys taerae	LSUMZ	39228	0.65622526	0.41569928	0.52272727	0.57861635	1	Terrestrial
Taeromys taerae	LSUMZ	39226	0.67336176	0.43171558	0.48444444	0.56477733	1	Terrestrial
Taeromys taerae	LSUMZ	39225	0.68967019	0.42577488	0.50211864	0.53410283	1	Terrestrial
Vandeleuria oleracea	AMNH	242256	0.76239182	0.48387097	0.57575758	0.77351916	3	Arboreal

Supporting Table 1.3

Species	Tree captures	Tree trapnights	Ground captures	Ground trapnights	climb_index	Climbing State	Reference
<i>Apomys_abrae</i>	3	1281	143	4512	0.06880881	T	(1, 2)
<i>Apomys_aurorae</i>	0	771	96	2891	0	T	(3)
<i>Apomys_bahahao</i>	3	1613	293	3390	0.02106554	T	(4)
<i>Apomys_datae</i>	19	5883	653	10728	0.05038573	T	(5, 6)
<i>Apomys_gracilirostris</i>	0	x	1	x	0	T	Field Notes LRH
<i>Apomys_iridensis</i>	1	839	85	3190	0.04281592	T	(7)
<i>Apomys_microdon</i>	55	4486	7	22570	0.97532748	A	(1-4, 6-11)
<i>Apomys_musculus</i>	59	7333	8	12567	0.92668072	A(3-5, 9, 11)(3-5, 9, 11)(3-5, 9, 11)	
<i>Apomys_sierrae</i>	1	1997	476	11851	0.01231371	T	(8-10)
<i>Apomys_zambalensis</i>	1	797	241	5755	0.02909034	T	(2, 11)
<i>Archboldomys_maximus</i>	0	4922	15	6904	0	T	(5)
<i>Batomys_granti</i>	5	5475	15	7882	0.32426873	G	(5, 6)
<i>Bullimus_luzonicus</i>	1	15446	130	34002	0.01665147	T	(1-9, 11)
<i>Chrotomys_whiteheadi</i>	0	9122	107	18073	0	T	(5, 6, 8, 10)
<i>MusseromysBeneficus</i>	3	456	0	1199	1	A	(8)
<i>Rattus_everetti</i>	6	14177	358	48086	0.05378866	T	(1-6, 8-11)
<i>Rynchomys_soricoides</i>	0	4792	30	4061	0	T	(5, 6)
<i>Soricomys_kalinga</i>	1	961	20	3824	0.16594341	G	(6)
<i>Soricomys_montanus</i>	1	1474	9	5067	0.27638684	G	(5)
<i>Apomys_gracilirostris</i>	0		1		0	T	(12)
<i>Phloeomys_pallidus</i>	1		0		1	A	(13)

Supporting Table 1.4

SciName	Climbing State	Reference
<i>Bunomys_fratrorum</i>	T	(14)
<i>Chiropodomys_gliroides</i>	A	(15, 16)
<i>Echiodhrix_leucura</i>	T	JAE Field Notes / (17)
<i>Grammomys_dryas</i>	A	(18)
<i>Haeromys_minahassae</i>	A	(19)
<i>Hybomys_univittatus</i>	T	(18)
<i>Hydromys_chrysogaster</i>	T	(20)
<i>Hylomyscus_stella</i>	G	(18)
<i>Hyomys_goliath</i>	G	(16, 20)
<i>Lemniscomys_striatus</i>	T	(18)
<i>Lenomys_meyeri</i>	A	(21, 22)
<i>Malacomys_longipes</i>	T	(18)
<i>Mastomys_natalensis</i>	T	(18)
<i>Maxomys_hellwaldii</i>	T	(16) / JAE field notes
<i>Maxomys_musschenbroekii</i>	T	(16, 23)
<i>Melomys_burtoni</i>	G	(24, 25)
<i>Melomys_cervinipes</i>	A	(16, 25)
<i>Mus_bufo</i>	T	(18, 26)
<i>Mus_musculus</i>	T	(13, 15, 16, 18, 25)
<i>Paruromys_dominator</i>	G	(16, 27)
<i>Pithecheir_melanurus</i>	A	(16)
<i>Rattus_hoffmanni</i>	T	(16, 28)
<i>Rattus_norvegicus</i>	T	(13, 15, 16, 18, 25)
<i>Rattus_rattus</i>	G	(15, 16, 18, 25)
<i>Rattus_xanthurus</i>	T	(16, 29)
<i>Taeromys_celebensis</i>	T	(29)
<i>Taeromys_taerae</i>	T	(14)
<i>Vandeleuria_oleracea</i>	A	(15)

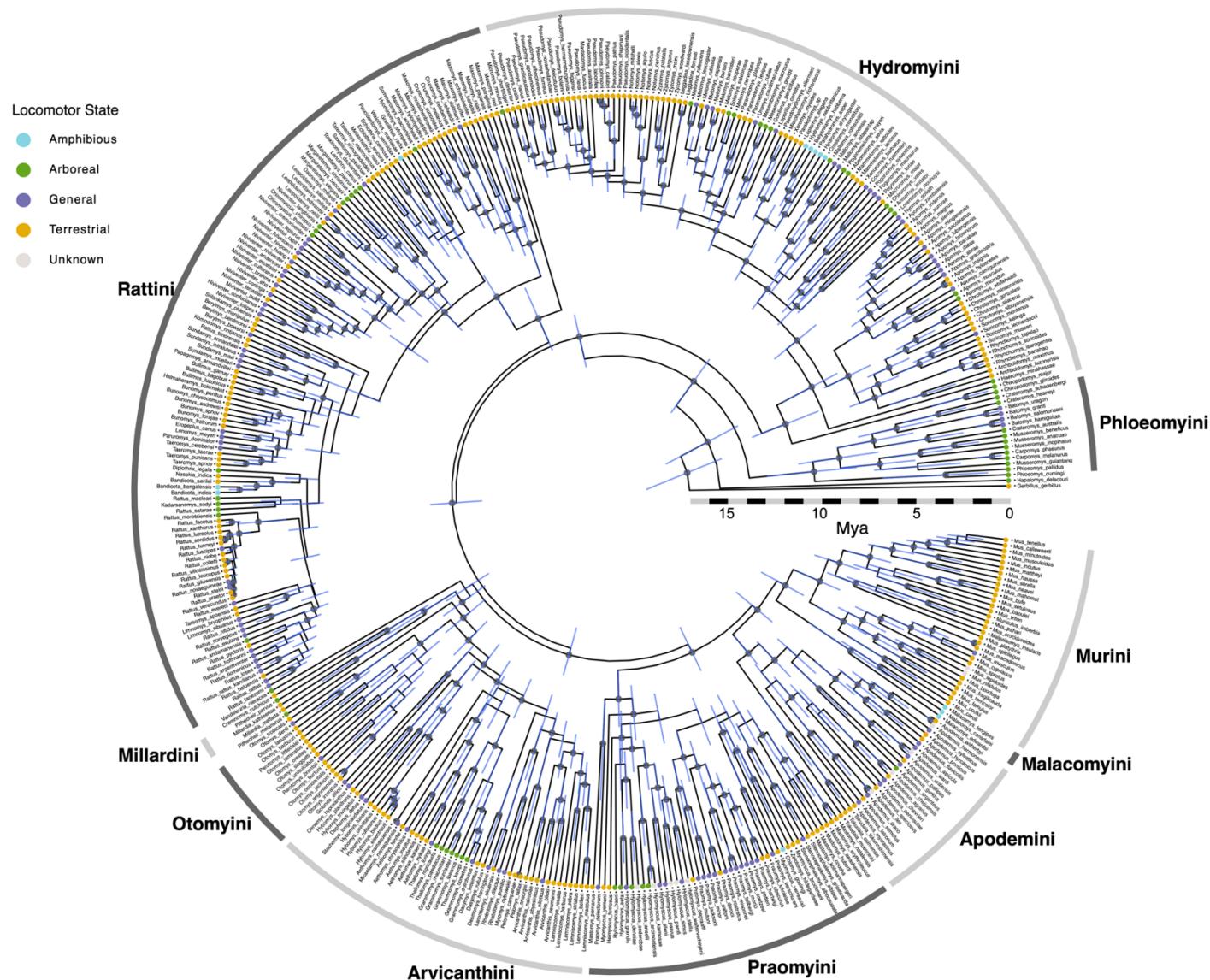
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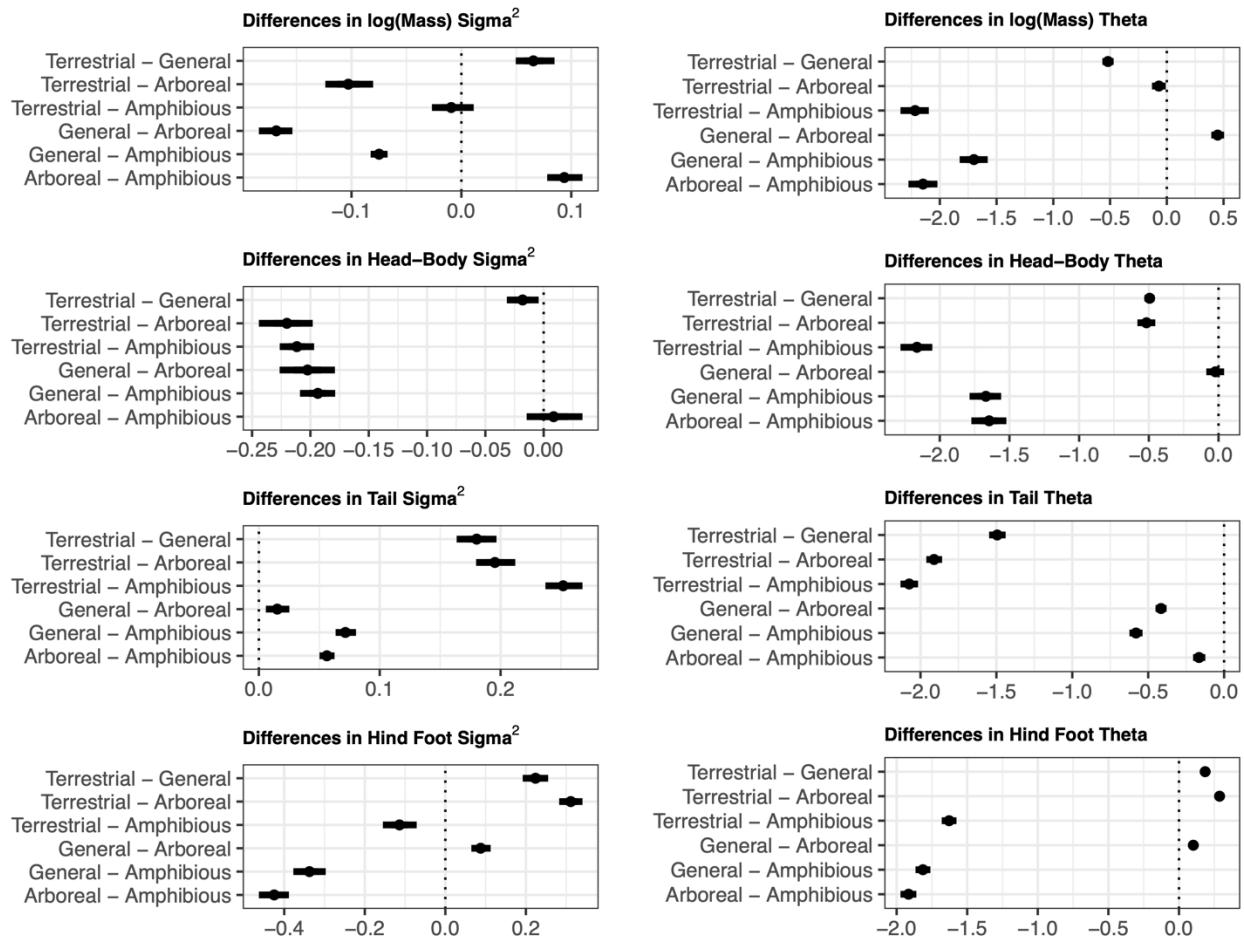
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**APPENDIX B**  
**SUPPORTING MATERIAL FOR CHAPTER 3**



Supporting Figure 2.1: Estimated phylogeny of Murinae with species labeled at the tips.



Supporting Figure 2.2: Differences in sigma<sup>2</sup> and theta values for each locomotor mode. The posterior distributions of the mean were estimated for each parameter using Bayesian robust regression. The differences were calculated by subtracting the mean distributions. Each dot represents the mean difference, and each bar represents the 95% credible interval of the difference distribution.

Supporting Table 2.1: Taxa and locomotor modes.

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Abditomys latidens</i>	Arboreal	268.5	480.5	224.0	256.5	46.0	0.534	1.145	Heaney et al 2016 - Nowak 1991
<i>Abeomelomys sevia</i>	Arboreal	55.7	300.5	127.5	173.0	24.8	0.576	1.357	Flannery 1995a - Musser & Newcomb 1983
<i>Aethomys bocagei</i>	Terrestrial	79.9	354.0	165.0	189.0	36.0	0.534	1.145	Kingdon et al 2013 - Wilman et al 2014
<i>Aethomys chrysophilus</i>	General	77.9	294.0	138.0	156.0	31.0	0.531	1.130	Kingdon et al 2013
<i>Aethomys granti</i>	Terrestrial	NA	228.6	111.8	116.8	24.1	0.511	1.045	Kingdon et al 2013
<i>Aethomys hindei</i>	Terrestrial	149.1	314.0	158.0	156.0	32.0	0.497	0.987	Kingdon et al 2013
<i>Aethomys ineptus</i>	Terrestrial	107.6	309.0	147.0	162.0	30.0	0.524	1.102	Kingdon et al 2013 - IUCN 2017
<i>Aethomys kaiseri</i>	Terrestrial	92.7	266.2	146.5	119.7	25.2	0.450	0.817	Kingdon et al 2013
<i>Aethomys namaquensis</i>	General	51.7	259.3	107.5	151.8	25.3	0.585	1.412	Kingdon et al 2013
<i>Aethomys nyikae</i>	Terrestrial	90.2	309.2	143.4	165.8	28.6	0.536	1.156	Kingdon et al 2013
<i>Aethomys silindensis</i>	Terrestrial	82.8	351.3	173.6	177.7	33.6	0.506	1.024	Kingdon et al 2013 - IUCN 2017 - Wilman et al 2014
<i>Aethomys stannarius</i>	Terrestrial	92.0	300.0	148.0	152.0	31.0	0.507	1.027	Kingdon et al 2013 - IUCN 2017
<i>Aethomys thomasi</i>	Terrestrial	84.7	274.0	150.0	124.0	29.0	0.453	0.827	Kingdon et al 2013 - IUCN 2017 - Wilman et al 2014
<i>Anisomys imitator</i>	Arboreal	502.3	585.8	264.6	321.2	61.1	0.548	1.214	Flannery 1995a - Nowak 1991
<i>Apodemus agrarius</i>	Terrestrial	21.5	169.2	96.3	72.9	19.4	0.431	0.757	Kuncová & Frynta 2009
<i>Apodemus alpicola</i>	General	28.3	NA	NA	NA	NA			Reutter et al 2005
<i>Apodemus argenteus</i>	Arboreal	23.8	NA	NA	NA	NA			Sekijima 1995
<i>Apodemus chevrieri</i>	General	32.9	193.0	99.0	94.0	23.5	0.487	0.949	Nowak 1991 - Wilman et al 2014
<i>Apodemus draco</i>	General	23.8	202.5	92.5	110.0	22.5	0.543	1.189	Nowak 1991 - Francis & Barrett 2008
<i>Apodemus flavicollis</i>	General	30.0	NA	NA	NA	NA			Kuncová & Frynta 2009
<i>Apodemus gurkha</i>	General	28.3	NA	NA	NA	NA			Nowak 1991

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Apodemus hyrcanicus</i>	Terrestrial	25.8	NA	NA	NA	NA			IUNC 2017 - Gromov & Erbaeva. 1995 - Wilman et al 2014
<i>Apodemus latronum</i>	General	28.3	212.5	102.5	110.0	25.5	0.518	1.073	Nowak 1991 - Francis and Barrett 2008 - Xiao et al 2006
<i>Apodemus mystacinus</i>	Terrestrial	41.1	236.5	114.6	121.9	26.4	0.515	1.064	Kuncová & Frynta 2009
<i>Apodemus pallipes</i>	Terrestrial	23.8	181.0	91.0	90.0	20.5	0.497	0.989	Smith and Xie 2013 - Wilman et al 2014
<i>Apodemus peninsulae</i>	General	28.3	188.0	99.0	89.0	22.0	0.473	0.899	Nowak 1991
<i>Apodemus ponticus</i>	Terrestrial	28.3	191.2	89.9	101.3	22.7	0.530	1.128	Mohammadi et al 2014
<i>Apodemus semotus</i>	Terrestrial	25.3	238.7	116.8	121.9	26.4	0.511	1.044	Smith and Xie 2013
<i>Apodemus speciosus</i>	Terrestrial	38.8	211.7	111.2	100.5	24.0	0.475	0.904	Sekijima 1995
<i>Apodemus sylvaticus</i>	General	23.3	188.7	96.5	92.2	22.0	0.489	0.955	Kingdon et al 2013 - Kuncová & Frynta 2009
<i>Apodemus uralensis</i>	General	21.0	183.5	93.5	90.0	20.0	0.490	0.963	Smith and Xie 2013 - Heroldová & Tkadlec 2011
<i>Apodemus witherbyi</i>	Terrestrial	20.7	NA	NA	NA	NA			IUNC 2017 - Kuncova and Frenta 2009
<i>Apomys abrae</i>	Terrestrial	51.9	274.5	140.0	134.5	36.5	0.490	0.961	Heaney et al 2016 - Nowak 1991
<i>Apomys aurorae</i>	Terrestrial	75.0	278.5	137.5	141.0	35.0	0.506	1.025	Heaney et al 2016
<i>Apomys banahao</i>	Terrestrial	81.5	268.5	146.5	122.0	35.0	0.454	0.833	Heaney et al 2016
<i>Apomys brownorum</i>	Terrestrial	72.0	242.5	131.0	111.5	33.5	0.460	0.851	Heaney et al 2016
<i>Apomys camiguinensis</i>	Terrestrial	40.0	258.0	111.0	147.0	33.0	0.570	1.324	Heaney & Tabaranza 2006
<i>Apomys datae</i>	Terrestrial	70.4	276.0	150.7	135.8	35.8	0.492	0.901	Heaney et al 2016 - Nowak 1991
<i>Apomys gracilirostris</i>	General	43.1	310.0	150.0	160.0	38.0	0.516	1.067	Ruedas 1995 - Wilman et al 2014
<i>Apomys hylocetes</i>	Terrestrial	36.4	249.0	108.0	141.0	32.0	0.566	1.306	Heaney et al 2006
<i>Apomys insignis</i>	Terrestrial	36.9	252.0	105.0	147.0	33.0	0.583	1.400	Heaney et al 2006
<i>Apomys iridensis</i>	Terrestrial	96.0	292.0	147.5	144.5	37.5	0.495	0.980	Heaney et al 2016
<i>Apomys littoralis</i>	Terrestrial	25.5	220.0	100.0	120.0	25.0	0.545	1.200	Musser 1982a - Wilman et al 2014

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Apomys lubangensis</i>	Terrestrial	110.0	291.0	151.0	140.0	40.0	0.481	0.927	Heaney et al 2014
<i>Apomys magnus</i>	Terrestrial	110.0	288.5	145.0	143.5	39.0	0.497	0.990	Heaney et al 2016
<i>Apomys microdon</i>	Arboreal	35.5	241.5	107.0	134.5	27.0	0.557	1.257	Heaney et al 2016
<i>Apomys minganensis</i>	Terrestrial	79.0	262.5	135.5	127.0	33.0	0.484	0.937	Heaney et al 2016
<i>Apomys musculus</i>	Arboreal	20.6	197.5	88.5	109.0	22.5	0.552	1.232	Heaney et al 2016
<i>Apomys sacobianus</i>	General	63.4	296.0	153.5	142.5	37.5	0.481	0.928	Heaney et al 2016 - Nowak 1991
<i>Apomys sierrae</i>	General	92.0	277.0	141.0	136.0	36.5	0.491	0.965	Heaney et al 2016
<i>Apomys zambalensis</i>	General	99.5	302.5	162.0	140.5	37.5	0.464	0.867	Heaney et al 2016
<i>Archboldomys luzonensis</i>	Terrestrial	36.2	178.5	89.3	70.0	27.5	0.392	0.784	Heaney et al 2016 - Nowak 1991
<i>Archboldomys maximus</i>	Terrestrial	47.5	216.0	117.0	99.0	31.0	0.458	0.846	Heaney et al 2016
<i>Arvicanthis abyssinicus</i>	Terrestrial	92.9	250.9	140.5	110.4	26.4	0.440	0.786	Kingdon et al 2013
<i>Arvicanthis ansorgei</i>	Terrestrial	113.9	285.6	151.0	134.6	33.0	0.471	0.891	Kingdon et al 2013
<i>Arvicanthis blicki</i>	Terrestrial	128.0	261.0	161.0	100.0	30.8	0.383	0.621	Kingdon et al 2013
<i>Arvicanthis nairobae</i>	Terrestrial	91.0	239.0	138.0	101.0	26.0	0.423	0.732	Kingdon et al 2013
<i>Arvicanthis neumanni</i>	Terrestrial	85.0	246.5	146.0	100.5	27.5	0.408	0.688	Kingdon et al 2013
<i>Arvicanthis niloticus</i>	General	102.0	289.3	158.8	130.5	31.0	0.451	0.822	Kingdon et al 2013
<i>Arvicanthis rufinus</i>	Terrestrial	103.3	282.0	143.8	138.2	32.7	0.490	0.961	Kingdon et al 2013
<i>Baiyankamys habbema</i>	Amphibious	NA	317.0	147.0	170.0	36.0	0.536	1.156	Helgen 2005
<i>Bandicota bengalensis</i>	Amphibious	235.6	346.5	195.0	151.5	34.8	0.437	0.777	Nowak 1991 - Francis & Barrett 2008
<i>Bandicota indica</i>	Terrestrial	415.0	520.0	276.0	244.0	56.0	0.469	0.884	Lekagul & McNeely 1977 - Nowak 1991 - Francis & Barrett 2008
<i>Bandicota savilei</i>	Terrestrial	229.8	355.0	196.0	159.0	37.0	0.448	0.811	Lekagul & McNeely 1977 - Nowak 1991 - Francis & Barrett 2008
<i>Batomys dentatus</i>	General	196.0	380.0	195.0	185.0	36.0	0.487	0.949	Heaney et al 2016 - Wilman et al 2014
<i>Batomys granti</i>	General	174.4	348.5	199.5	149.0	36.3	0.428	0.747	Heaney et al 2016

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Batomys hamiguitan</i>	Terrestrial	173.0	302.0	183.0	119.0	35.0	0.394	0.650	Balete et al 2008
<i>Batomys russatus</i>	Terrestrial	115.0	256.0	146.0	110.0	30.0	0.430	0.753	Musser et al 1998
<i>Batomys salomonensi</i>	Terrestrial	185.8	315.0	175.0	140.0	37.0	0.444	0.800	Musser et al 1998
<i>Batomys uragon</i>	Terrestrial	335.0	335.5	186.0	149.5	37.0	0.446	0.804	Heaney et al 2016
<i>Berylmys berdmorei</i>	Terrestrial	235.0	373.0	205.0	168.0	38.0	0.450	0.820	Lekagul & McNeely 1977 - Nowak 1991 - Francis & Barrett 2008
<i>Berylmys bowersi</i>	General	382.7	544.6	266.3	278.3	58.8	0.511	1.045	Lekagul & McNeely 1977 - Nowak 1991 - Francis & Barrett 2008
<i>Berylmys mackenziei</i>	Terrestrial	265.0	454.0	210.0	244.0	49.0	0.537	1.162	Lekagul & McNeely 1977 - Nowak 1991 - Musser and Newcomb 1983
<i>Berylmys manipulus</i>	Terrestrial	116.0	323.5	160.0	163.5	55.5	0.505	1.022	Nowak 1991 - Francis & Barrett 2008 - Wilman et al 2014
<i>Bullimus bagobus</i>	Terrestrial	423.1	462.0	278.3	183.7	53.5	0.398	0.660	Nowak 1991
<i>Bullimus gamay</i>	Terrestrial	367.8	392.5	234.5	158.0	51.6	0.403	0.674	Wilman et al 2014
<i>Bullimus luzonicus</i>	Terrestrial	447.5	466.5	254.0	212.5	55.5	0.456	0.837	Heaney et al 2016
<i>Bunomys andrewsi</i>	Terrestrial	135.0	304.1	161.7	142.4	37.8	0.468	0.881	Musser - 2014
<i>Bunomys chrysocomus</i>	Terrestrial	106.0	301.0	160.0	141.0	34.8	0.468	0.881	Musser - 2014
<i>Bunomys coelestis</i>	Terrestrial	120.0	310.9	159.3	151.6	36.9	0.488	0.952	Musser - 2014 - Wilman et al 2014
<i>Bunomys fratrorum</i>	Terrestrial	152.7	341.4	170.4	171.0	40.0	0.501	1.004	Musser - 2014
<i>Bunomys karokophilus</i>	Terrestrial	133.2	338.2	173.8	164.4	39.3	0.486	0.946	Musser - 2014
<i>Bunomys penitus</i>	Terrestrial	144.9	342.4	173.5	168.9	40.2	0.493	0.973	Musser - 2014
<i>Bunomys prolatus</i>	Terrestrial	131.0	299.6	167.2	132.4	33.9	0.442	0.792	Musser - 2014 - Wilman et al 2014
<i>Bunomys torajae</i>	Terrestrial	116.8	343.1	177.8	165.3	37.6	0.482	0.930	Musser - 2014
<i>Carpomys melanurus</i>	Arboreal	165.0	363.5	182.0	181.5	33.0	0.499	0.997	Heaney et al 2016 – Nowak 1991
<i>Carpomys phaeurus</i>	Arboreal	123.0	329.0	177.8	164.3	31.5	0.499	0.924	Heaney et al 2016 -

									Nowak 1991
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table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Chiromyscus chiropus</i>	Arboreal	77.8	366.8	148.0	218.8	28.0	0.597	1.478	Lekagul & McNeely 1977 - Nowak 1991 - Smith and Xie 2013
<i>Chiromyscus thomasi</i>	Arboreal	90.0	377.5	162.5	215.0	28.0	0.570	1.323	Balakirev et al 2014
<i>Chiropodomys gliroides</i>	Arboreal	23.9	215.9	89.2	126.7	18.5	0.587	1.420	Lekagul & McNeely 1977 - Nowak 1991 - Musser 1979
<i>Chiropodomys major</i>	Arboreal	33.2	233.7	105.3	128.4	24.1	0.549	1.219	Nowak 1991 - Musser 1979
<i>Chiruromys vates</i>	Arboreal	45.7	272.5	110.0	162.5	24.3	0.596	1.477	Flannery 1995a - Nowak 1991
<i>Chrotomys gonzalesi</i>	Terrestrial	136.8	262.5	168.5	94.0	36.5	0.358	0.558	Heany et al 2016
<i>Chrotomys mindorensis</i>	Terrestrial	163.7	284.5	173.5	111.0	38.0	0.390	0.640	Heany et al 2016 - Nowak 1991
<i>Chrotomys sibuyanensis</i>	Terrestrial	104.0	242.0	160.0	82.0	34.0	0.339	0.513	Rickart et al. 2005
<i>Chrotomys silaceus</i>	Terrestrial	115.5	269.0	160.0	109.0	36.5	0.405	0.681	Heany et al 2016
<i>Chrotomys whiteheadi</i>	Terrestrial	149.7	282.0	167.0	115.0	38.0	0.408	0.689	Heany et al 2016
<i>Coccymys ruemmleri</i>	General	31.6	268.0	109.0	159.0	24.8	0.593	1.459	Flannery 1995a
<i>Colomys goslingi</i>	Amphibious	61.5	282.4	122.4	160.0	37.9	0.567	1.307	Kingdon et al 2013 - Nowak 1991
<i>Conilurus penicillatus</i>	Arboreal	190.5	371.5	188.5	183.0	48.0	0.493	0.971	Flannery 1995a - Strahan 1983
<i>Crateromys australis</i>	General	445.0	546.0	265.0	281.0	54.0	0.515	1.060	Musser et al 1998 - Wilman et al 2014
<i>Crateromys heaneyi</i>	Arboreal	124.0	599.5	279.5	320.0	63.5	0.534	1.145	Gonzales & Kennedy 1996
<i>Crateromys schadenbergi</i>	Arboreal	1450.0	681.5	360.8	405.7	77.5	0.595	1.124	Heany et al 2016 - Musser et al 1998
<i>Cremnomys cutchicus</i>	Terrestrial	59.8	258.0	117.0	141.0	0.5	1.205		Nowak 1991 - Wilman et al 2014
<i>Crossomys moncktoni</i>	Amphibious	166.7	404.0	188.0	216.0	51.2	0.535	1.149	Flannery 1995a
<i>Crunomys celebensis</i>	Terrestrial	48.3	193.6	112.6	81.0	25.0	0.418	0.719	Nowak 1991 -

									Achmadi et al 2014
<i>Crunomys fallax</i>	Terrestrial	37.5	184.0	105.0	79.0	0.4	0.752		Heany et al 2016 - Wilman et al 2014
<i>Crunomys melanius</i>	Terrestrial	54.5	190.8	110.0	80.8	26.0	0.423	0.735	Nowak 1991

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Crunomys suncoides</i>	Terrestrial	37.0	209.0	108.0	101.0	27.0	0.483	0.935	Rickart et al 1998
<i>Dacnomys millardi</i>	Terrestrial	168.3	452.9	198.6	254.3	44.8	0.561	1.280	Nowak 1991 - Smith and Xie 2013 - Musser 1981 - Wilman et al 2014
<i>Dasymys incomtus</i>	Terrestrial	131.5	299.1	154.3	144.8	33.8	0.484	0.938	Kingdon et al 2013
<i>Dasymys rufulus</i>	Terrestrial	78.0	289.4	144.3	145.1	33.2	0.501	1.006	Kingdon et al 2013
<i>Dephomys defua</i>	Arboreal	45.0	320.9	126.3	194.6	26.5	0.606	1.541	Kingdon et al 2013 - Nowak 1991
<i>Desmomys harringtoni</i>	General	77.4	264.6	136.3	128.3	27.6	0.485	0.941	Kingdon et al 2013
<i>Diplothrix legata</i>	Arboreal	76.5	560.0	275.0	285.0	0.5	1.036		Sugimura et al 2003 - Nowak 1991 - Wilman 2014
<i>Echiothrix centrosa</i>	Terrestrial	253.0	447.0	205.0	242.0	51.0	0.541	1.180	LSUMZ specimens - Musser & Durden 2014
<i>Echiothrix leucura</i>	Terrestrial	63.7	460.0	225.0	235.0	55.0	0.511	1.044	LSUMZ specimens - Musser & Durden 2014 - Wilman 2014
<i>Eropeplus canus</i>	General	275.0	543.0	266.0	277.0	48.0	0.510	1.041	LSUMZ specimens - Nowak 1991 - Wilman et al 2014
<i>Golunda ellioti</i>	General	62.1	212.1	128.4	83.7	25.9	0.395	0.652	Nowak 1991
<i>Gracilimus radix</i>	Terrestrial	41.0	277.0	118.0	159.0	29.0	0.574	1.347	Rowe et al. 2016
<i>Grammomys cometes</i>	Arboreal	48.5	286.0	118.0	168.0	24.0	0.587	1.424	Kingdon et al 2013
<i>Grammomys dolichurus</i>	General	39.5	284.5	115.3	169.2	23.5	0.595	1.467	Kingdon et al 2013 - Delany 1971
<i>Grammomys ibeanus</i>	Arboreal	42.4	303.0	120.4	182.6	22.5	0.603	1.517	Kingdon et al 2013
<i>Grammomys macmillani</i>	Arboreal	39.5	270.7	105.7	165.0	23.0	0.610	1.561	Kingdon et al 2013

<i>Grammomys surdaster</i>	Arboreal	36.0	283.0	110.0	173.0	23.0	0.611	1.573	Kingdon et al 2013
<i>Haeromys minahassae</i>	Arboreal	14.7	182.0	72.0	110.0	20.0	0.604	1.528	Musser 1990 - Wilman et al 2014
<i>Halmaheramys bokimekot</i>	Terrestrial	89.7	275.0	149.0	126.0	29.6	0.458	0.846	Fabre et al 2013
<i>Hapalomys delacouri</i>	Arboreal	64.3	279.5	129.5	150.0	23.0	0.537	1.158	Nowak 1991 - Smith and Xie 2013 - Wilman et al 2014

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Heimyscus fumosus</i>	Terrestrial	15.8	181.3	76.8	104.5	17.5	0.576	1.361	Kingdon et al 2013
<i>Hybomys badius</i>	Terrestrial	63.7	236.7	122.4	114.3	29.3	0.483	0.934	Kingdon et al 2013
<i>Hybomys lunaris</i>	Terrestrial	54.1	223.0	108.0	115.0	25.0	0.516	1.065	Kingdon et al 2013 - Huhndorf et al. 2007 - Wilman et al 2014
<i>Hybomys planifrons</i>	Terrestrial	50.3	221.0	124.0	97.0	30.6	0.439	0.782	Kingdon et al 2013
<i>Hybomys trivirgatus</i>	Terrestrial	58.0	224.0	124.0	100.0	31.8	0.446	0.806	Kingdon et al 2013
<i>Hybomys univittatus</i>	Terrestrial	52.4	224.7	121.4	103.3	27.9	0.460	0.851	Kingdon et al 2013
<i>Hydromys neobritannicus</i>	Amphibious	141.9	577.0	288.0	289.0	60.0	0.501	1.003	Wilman et al 2014
<i>Hylomyscus aeta</i>	Arboreal	24.4	232.6	95.7	136.9	21.4	0.589	1.431	Kingdon et al 2013
<i>Hylomyscus allenii</i>	General	19.6	214.9	83.6	131.3	19.8	0.611	1.571	Kingdon et al 2013
<i>Hylomyscus anselli</i>	Arboreal	28.5	247.0	101.0	146.0	21.0	0.591	1.446	Carelton & Stanley 2005
<i>Hylomyscus arcimontensis</i>	Arboreal	29.0	240.0	100.0	140.0	22.0	0.583	1.400	Carelton & Stanley 2005
<i>Hylomyscus baeri</i>	Arboreal	31.8	234.0	105.9	128.1	21.8	0.547	1.210	Kingdon et al 2013
<i>Hylomyscus denniae</i>	Arboreal	33.0	235.8	98.3	139.0	20.7	0.589	1.414	Kingdon et al 2013 - Huhndorf et al. 2007
<i>Hylomyscus grandis</i>	General	33.0	236.8	96.8	140.0	20.0	0.591	1.446	Kingdon et al 2013
<i>Hylomyscus parvus</i>	General	13.9	155.0	60.0	95.0	14.0	0.613	1.583	Kingdon et al 2013
<i>Hylomyscus stella</i>	General	19.4	222.0	91.5	130.5	18.0	0.588	1.426	Kingdon et al 2013
<i>Hyomys goliath</i>	General	844.6	636.5	324.5	312.0	59.4	0.490	0.961	Flannery 1995a - Nowak 1991
<i>Hyorhinomys stuempkei</i>	Terrestrial	235.0	403.5	193.5	210.0	53.0	0.520	1.085	Esselstyn et al 2015
<i>Kadarsanomys sodyi</i>	Arboreal	79.1	480.0	196.0	284.0	39.5	0.592	1.449	Nowak 1991 -

									Wilman et al 2014
<i>Komodomys rintjanus</i>	Terrestrial	73.9	327.4	175.9	151.5	36.5	0.463	0.861	Musser & Boaedi 1980 - Nowak 1991 - Wilman et al 2014
<i>Lamottemys okuensis</i>	Terrestrial	56.0	250.8	126.0	124.8	28.4	0.498	0.990	Kingdon et al 2013
<i>Leggadina forresti</i>	Terrestrial	21.9	176.0	104.0	72.0	19.0	0.409	0.692	Strahan 1983 - Nowak 1991 - Read 1984

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Leggadina lakedownensis</i>	Terrestrial	18.8	113.0	70.0	43.0	15.0	0.381	0.614	Strahan 1983 - Nowak 1991 - Van Dyck and Strahan 2008
<i>Lemniscomys barbarus</i>	Terrestrial	30.6	223.3	100.8	122.5	24.5	0.549	1.215	Kingdon et al 2013
<i>Lemniscomys bellieri</i>	Terrestrial	36.0	221.0	109.0	112.0	25.4	0.507	1.028	Kingdon et al 2013 - Ziegler et al 2002
<i>Lemniscomys macculus</i>	Terrestrial	28.4	208.2	99.2	109.0	22.6	0.524	1.099	Kingdon et al 2013
<i>Lemniscomys rosalia</i>	Terrestrial	51.2	268.9	136.8	132.1	26.9	0.491	0.966	Kingdon et al 2013
<i>Lemniscomys striatus</i>	Terrestrial	42.2	247.1	114.3	132.8	27.1	0.537	1.162	Kingdon et al 2013
<i>Lemniscomys zebra</i>	Terrestrial	36.1	226.0	102.0	124.0	24.5	0.549	1.216	Kingdon et al 2013
<i>Lenomys meyeri</i>	General	325.0	530.6	264.1	266.5	47.0	0.502	1.009	Flannery 1995b - Musser 2015 - LSUMZ Specimens
<i>Lenothrix canus</i>	Arboreal	163.5	420.0	192.5	227.5	42.0	0.542	1.182	Nowak 1991 - Wells et al 2004 - Musser & Newcomb 1983 - Francis and Barrett 2008
<i>Leopoldamys edwardsi</i>	General	325.9	546.0	246.0	300.0	48.0	0.549	1.220	Lekagul and McNeely 1977 - Nowak 1991 - Smith and Xie 2013
<i>Leopoldamys milleti</i>	Terrestrial	336.4	570.0	245.0	325.0	50.0	0.570	1.327	Francis and Barrett 2008 - Wilman et al 2014
<i>Leopoldamys neilli</i>	Terrestrial	219.0	487.0	217.0	270.0	42.0	0.554	1.244	Lekagul and McNeely 1977 - Francis and Barrett 2008 -
<i>Leopoldamys sabanus</i>	General	347.7	584.6	234.5	350.1	46.7	0.599	1.493	Lekagul and McNeely 1977 -

									Nowak 1991 - Pimsai et al 2014
<i>Leporillus conditor</i>	General	339.4	375.0	197.0	178.0	44.0	0.475	0.904	Strahan 1983 - Ryan et al 2003 - IUCN 2017
<i>Leptomys elegans</i>	Terrestrial	85.5	299.4	151.8	147.6	38.5	0.493	0.972	Flannery 1995a
<i>Limnomys bryophilus</i>	Terrestrial	64.1	300.0	130.0	170.0	32.6	0.567	1.308	Rickart et al 2003
<i>Limnomys sibuanus</i>	General	64.3	283.5	127.0	156.5	29.5	0.552	1.232	Nowak 1991 - Musser & Heaney 1992
<i>Lorentzimys nouhuysi</i>	Arboreal	15.0	186.6	74.2	112.4	18.6	0.602	1.515	Flannery 1995a - Nowak 1991

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Macruromys major</i>	Terrestrial	353.6	568.3	240.8	327.5	52.7	0.576	1.360	Flannery 1995a - Nowak 1991
<i>Malacomys cansdalei</i>	Amphibious	81.7	340.0	144.0	196.0	42.7	0.576	1.361	Kingdon et al 2013
<i>Malacomys edwardsi</i>	Amphibious	61.4	301.0	133.0	168.0	33.0	0.558	1.263	Kingdon et al 2013
<i>Malacomys longipes</i>	Amphibious	96.3	334.4	156.7	177.7	39.7	0.531	1.134	Kingdon et al 2013
<i>Mallomys aroaensis</i>	General	1732.0	804.0	410.0	394.0	72.0	0.490	0.961	Flannery 1995a - Nowak 1991
<i>Mallomys istapantap</i>	General	1970.2	747.0	411.0	336.0	70.5	0.450	0.818	Flannery 1995a - Nowak 1991
<i>Mallomys rothschildi</i>	Arboreal	1157.9	759.7	380.0	379.7	65.1	0.500	0.999	Flannery 1995a - Nowak 1991
<i>Malpaisomys insularis</i>	Terrestrial	71.3	NA	NA	NA	NA			Nowak 1991 - Wilman et al 2014
<i>Mammelomys lanosus</i>	Terrestrial	116.8	286.0	162.3	123.7	36.6	0.433	0.762	Flannery 1995a - Wilman et al 2014
<i>Mammelomys rattooides</i>	Terrestrial	212.2	326.0	200.0	126.0	38.0	0.387	0.630	Flannery 1995a - Flannery 1995b
<i>Margaretamys beccarii</i>	Arboreal	65.4	317.0	132.0	185.0	28.0	0.584	1.402	Nowak 1991 - Musser 1981
<i>Margaretamys christinae</i>	Arboreal	49.0	286.0	111.0	175.0	20.0	0.612	1.577	Mortelliti et al 2012
<i>Margaretamys elegans</i>	Arboreal	121.0	439.8	180.0	259.8	36.5	0.591	1.443	Nowak 1991 - Musser 1981
<i>Margaretamys parvus</i>	Arboreal	40.0	258.0	100.0	158.0	20.0	0.612	1.580	Nowak 1991 - Musser 1981
<i>Mastacomys fuscus</i>	Terrestrial	125.4	270.0	161.7	108.3	34.0	0.401	0.670	Strahan 1983 - Nowak 1991

<i>Mastomys awashensis</i>	Terrestrial	46.0	240.0	122.0	118.0	23.8	0.492	0.967	Kingdon et al 2013
<i>Mastomys coucha</i>	Terrestrial	42.4	185.0	100.0	85.0	20.0	0.459	0.850	Kingdon et al 2013
<i>Mastomys erythroleucus</i>	Terrestrial	56.9	225.7	118.0	107.7	23.0	0.477	0.913	Kingdon et al 2013 - Nowak 1991
<i>Mastomys huberti</i>	Terrestrial	59.1	253.0	139.0	114.0	25.1	0.451	0.820	Kingdon et al 2013
<i>Mastomys kollmannspergeri</i>	Terrestrial	105.9	260.0	142.0	118.0	27.2	0.454	0.831	Kingdon et al 2013
<i>Mastomys natalensis</i>	Terrestrial	90.4	216.0	108.0	108.0	22.3	0.500	1.000	Kingdon et al 2013

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Mastomys pernanus</i>	Terrestrial	19.0	144.0	78.0	66.0	16.1	0.458	0.846	Kingdon et al 2013 - Nowak 1991 - Wilman et al 2014
<i>Maxomys bartelsii</i>	Terrestrial	95.2	305.0	152.5	152.5	33.5	0.500	1.000	Musser 1979
<i>Maxomys dollmani</i>	General	120.0	362.2	158.9	203.3	26.8	0.561	1.279	Musser 1979
<i>Maxomys hellwaldii</i>	Terrestrial	203.0	385.4	206.1	179.3	37.4	0.465	0.870	Nowak 1991 - LSUMZ Specimens - Wilman et al 2014
<i>Maxomys hylomyoides</i>	Terrestrial	56.6	245.7	125.9	119.8	29.4	0.488	0.952	Nowak 1991 - LSUMZ Specimens - Wilman et al 2014
<i>Maxomys moi</i>	Terrestrial	147.0	344.7	167.9	176.8	37.8	0.513	1.053	Nowak 1991 - Francis & Barrett 2008 - Wilman et al 2014
<i>Maxomys musschenbroekii</i>	Terrestrial	84.8	274.0	145.5	128.5	34.5	0.469	0.883	Nowak 1991 - Corbett & Hill 1992 - Wilman et al 2014
<i>Maxomys ochraceiventer</i>	Terrestrial	159.0	306.3	152.8	153.5	32.5	0.501	1.005	Nowak 1991 - Nor 2001
<i>Maxomys pagensis</i>	Terrestrial	196.0	376.1	196.8	179.3	43.0	0.477	0.911	Nowak 1991 - Wilman et al 2014
<i>Maxomys panglima</i>	Terrestrial	159.0	399.8	197.9	201.9	41.5	0.505	1.020	Nowak 1991 - Esselstyn et al 2004
<i>Maxomys rajah</i>	Terrestrial	150.0	345.0	172.0	173.0	38.0	0.501	1.006	Lekagul and McNeely 1977 - Nowak 1991 -

									Francis & Barrett 2008
<i>Maxomys surifer</i>	Terrestrial	154.4	363.8	182.5	181.3	41.0	0.498	0.993	Lekagul and McNeely 1977 - Nowak 1991 - Francis & Barrett 2008 - Smith and Xie 2013
<i>Maxomys tajuddinii</i>	Terrestrial	66.0	220.6	106.8	113.8	28.6	0.516	1.066	Achmadi et al 2012 - IUCN 2017 - Wilman et al 2014
<i>Maxomys whiteheadi</i>	Terrestrial	49.2	218.0	115.0	103.0	26.0	0.472	0.896	Lekagul and McNeely 1977 – Nowak 1991 – Francis & Barrett 2008
<i>Melasmotherrix naso</i>	Terrestrial	47.5	206.8	118.0	88.8	27.5	0.429	0.753	Nowak 1991

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Melomys bannisteri</i>	Terrestrial	58.0	224.0	112.0	112.0	0.5	1.000		Wilman et al 2014
<i>Melomys bougainville</i>	Terrestrial	86.0	289.0	149.0	140.0	27.3	0.484	0.940	Flannery 1995b
<i>Melomys burtoni</i>	General	80.0	280.0	130.0	150.0	29.0	0.536	1.154	Strahan 1983 - Van Dyck and Strahan 2008
<i>Melomys capensis</i>	General	100.0	300.0	130.0	170.0	28.0	0.567	1.308	Strahan 1983 - Nowak 1991 - Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Melomys cervinipes</i>	Arboreal	120.0	286.7	140.0	146.7	28.7	0.512	1.048	Strahan 1983 - Nowak 1991
<i>Melomys leucogaster</i>	General	112.6	311.0	156.0	155.0	32.0	0.498	0.994	Flannery 1995a - 1995b
<i>Melomys rubicola</i>	Terrestrial	111.0	327.0	157.0	170.0	0.5	1.083		Nowak 1991 - Van Dyck and Strahan 2008
<i>Melomys rufescens</i>	Arboreal	64.0	273.3	136.3	137.0	27.2	0.501	1.005	Flannery 1995a - 1995b
<i>Mesembriomys gouldii</i>	Arboreal	800.0	675.0	300.0	375.0	67.0	0.556	1.250	Strahan 1983 - Nowak 1991
<i>Mesembriomys macrurus</i>	Arboreal	300.0	577.0	250.0	327.0	50.0	0.567	1.308	Strahan 1983 - Van Dyck and Strahan 2008 - IUCN 2017 - Watts & Aslin 1981
<i>Microhydromys richardsoni</i>	Terrestrial	9.6	169.3	83.0	86.3	19.7	0.510	1.040	Flannery 1995a
<i>Micromys minutus</i>	Arboreal	7.1	131.9	67.0	64.9	14.5	0.492	0.969	Nowak 1991 - Urbani et al 2013

<i>Millardia kathleenae</i>	Terrestrial	93.0	285.9	147.5	138.4	27.5	0.484	0.938	Nowak 1991 - Francis & Barrett 2008
<i>Millardia meltada</i>	Terrestrial	67.2	238.0	119.5	118.5	25.0	0.498	0.992	Nowak 1991 - Menon 2009 - Mishra & Dhanda 1975- Molur et al 2005
<i>Muriculus imberbis</i>	Terrestrial	18.5	125.0	74.0	51.0	16.5	0.408	0.689	Kingdon et al 2013
<i>Mus baoulei</i>	Terrestrial	9.2	102.8	65.9	36.9	13.3	0.359	0.560	Kingdon et al 2013 - Wilman et al 2014

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Mus booduga</i>	Terrestrial	13.7	130.8	75.5	55.3	15.6	0.423	0.732	Nowak 1991 - Francis & Barrett 2008 - Singh et al 2009
<i>Mus bufo</i>	Terrestrial	9.6	135.0	68.4	66.6	15.3	0.493	0.974	Kingdon et al 2013 - Lunde and Sarmiento 2002
<i>Mus callewaerti</i>	Terrestrial	9.1	133.6	88.8	44.8	15.3	0.335	0.505	Kingdon et al 2013 - Wilman et al 2014
<i>Mus caroli</i>	Terrestrial	14.3	154.0	76.0	78.0	18.0	0.506	1.026	Lekagul and McNeely 1977 - Francis & Barrett 2008 - Smith & Xie 2013
<i>Mus cookii</i>	Terrestrial	21.6	174.7	89.7	85.0	19.0	0.487	0.948	Lekagul and McNeely 1977 - Smith & Xie 2013
<i>Mus crociduroides</i>	Terrestrial	28.7	208.3	90.6	117.7	22.0	0.565	1.299	Nowak 1991 - Musser & Newcomb 1983 - Wilman et al 2014
<i>Mus cypriacus</i>	Terrestrial	15.0	156.0	84.0	72.0	18.0	0.462	0.857	Cucchi et al 2006
<i>Mus famulus</i>	Terrestrial	22.9	NA	NA	NA	NA			Nowak 1991 - Molur et al 2005 - Wilman et al 2014
<i>Mus fragilicauda</i>	Terrestrial	12.0	138.0	77.0	61.0	15.0	0.442	0.792	Francis & Barrett 2008
<i>Mus haussa</i>	Terrestrial	3.0	87.7	49.7	38.0	12.0	0.433	0.765	Kingdon et al 2013
<i>Mus indutus</i>	Terrestrial	6.5	95.2	53.2	42.0	14.0	0.441	0.789	Kingdon et al 2013
<i>Mus macedonicus</i>	Terrestrial	16.7	NA	NA	NA	NA			Frynta 1994
<i>Mus mahomet</i>	Terrestrial	10.2	120.5	67.0	53.5	15.0	0.444	0.799	Kingdon et al 2013 - Yalden & Largen 1992

<i>Mus mattheyi</i>	Terrestrial	9.5	90.4	52.0	38.4	12.1	0.425	0.738	Kingdon et al 2013 - Wilman et al 2014
<i>Mus minutoides</i>	Terrestrial	6.9	95.8	54.8	41.0	12.5	0.428	0.748	Kingdon et al 2013
<i>Mus musculoides</i>	Terrestrial	9.9	160.9	83.7	77.2	18.0	0.480	0.922	Kingdon et al 2013
<i>Mus musculus</i>	General	17.1	161.5	81.4	80.1	17.8	0.496	0.984	Kingdon et al 2013 - Strahan 1983 - Heaney et al 2016 - Lekagul and McNeely 1977 - Nowak 1991

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Mus neavei</i>	Terrestrial	8.0	127.2	88.8	38.4	13.0	0.302	0.432	Kingdon et al 2013
<i>Mus pahari</i>	Terrestrial	23.6	175.0	90.0	85.0	20.3	0.486	0.944	Lekagul and McNeely 1977 - Nowak 1991 - Smith and Xie 2013
<i>Mus platythrix</i>	Terrestrial	29.1	NA	NA	NA	NA			Nowak 1991 - Molur et al 2005
<i>Mus setulosus</i>	Terrestrial	11.2	137.3	81.8	55.5	14.1	0.404	0.678	Kingdon et al 2013
<i>Mus sorella</i>	Terrestrial	9.5	99.7	59.9	39.8	13.1	0.399	0.664	Kingdon et al 2013 - Wilman et al 2014
<i>Mus spicilegus</i>	Terrestrial	16.7	NA	NA	NA	NA			Nowak 1991 - Simeonovska-Nikolova 2000
<i>Mus spretus</i>	Terrestrial	15.6	201.8	139.7	62.1	16.0	0.308	0.445	Kingdon 2013
<i>Mus tenellus</i>	Terrestrial	9.5	92.2	53.8	38.4	12.6	0.416	0.714	Kingdon 2013
<i>Mus terricolor</i>	Terrestrial	8.3	132.0	68.0	64.0	15.0	0.485	0.941	Nowak 1991 - Singh et al 2009
<i>Mus triton</i>	Terrestrial	12.4	129.7	75.7	54.0	15.9	0.416	0.713	Kingdon et al 2013
<i>Musseromys anacuaao</i>	Arboreal	19.0	162.5	78.5	84.0	18.0	0.517	1.070	Heaney et al 2016
<i>Musseromys beneficus</i>	Arboreal	20.0	160.0	78.0	82.0	18.0	0.513	1.051	Heaney et al 2016
<i>Musseromys gulantang</i>	Arboreal	15.5	178.0	77.0	101.0	20.0	0.567	1.312	Heaney et al 2016 - Heaney et al 2009
<i>Musseromys inopinatus</i>	Arboreal	18.3	164.5	78.0	86.5	18.5	0.526	1.109	Heaney et al 2016
<i>Myomys dybowskii</i>	Terrestrial	110.5	338.2	198.4	139.8	34.6	0.413	0.705	Kingdon et al 2013

<i>Myomyscus angolensis</i>	Terrestrial	52.9	243.0	121.0	122.0	24.2	0.502	1.008	Kingdon et al 2013
<i>Myomyscus brockmani</i>	Terrestrial	29.5	213.5	90.0	123.5	22.0	0.578	1.372	Kingdon et al 2013
<i>Myomyscus verreauxii</i>	Terrestrial	42.5	249.0	106.0	143.0	24.0	0.574	1.349	Kingdon et al 2013
<i>Myomyscus yemeni</i>	Terrestrial	52.7	NA	NA	NA	NA			IUCN 2017 - Wilman et al 2014
<i>Nesokia indica</i>	Terrestrial	211.0	304.0	183.0	121.0	39.0	0.398	0.661	Kingdon et al 2013 - Nowak 1991 - Menon 2009 - Smith & Xie 2013

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Niviventer andersoni</i>	General	147.0	405.5	174.0	231.5	35.5	0.571	1.330	Nowak 1991 - Wilman et al 2014
<i>Niviventer brahma</i>	General	97.3	364.5	145.5	219.0	32.5	0.601	1.505	Smith and Xie 2013 - Musser 1981
<i>Niviventer confucianus</i>	General	32.5	334.8	147.5	187.3	30.0	0.559	1.270	Lekagul and McNeely 1979 - Nowak 1991
<i>Niviventer coninga</i>	General	80.7	390.5	172.5	218.0	33.5	0.558	1.264	Nowak 1991
<i>Niviventer cremoriventer</i>	General	72.3	328.1	147.5	180.6	24.8	0.550	1.224	Lekagul and McNeely 1979 - Francis & Barrett 2008 - Musser 1973 - Musser 1981 - Wells et al 2004
<i>Niviventer culturatus</i>	Terrestrial	81.2	325.0	140.0	185.0	32.0	0.569	1.321	Smith and Xie 2013 - Musser 1981
<i>Niviventer eha</i>	Terrestrial	53.6	301.0	121.0	180.0	29.5	0.598	1.488	Nowak 1991 - Smith and Xie 2013 - Wilman et al 2014
<i>Niviventer excelsior</i>	General	102.0	354.6	152.5	202.1	32.0	0.570	1.325	Nowak 1991 - Smith and Xie 2013 - Wilman et al 2014
<i>Niviventer fulvescens</i>	General	77.2	317.6	142.6	175.0	29.5	0.551	1.227	Lekagul and McNeely 1977 - Francis & Barrett 2008 - Smith and Xie 2013 - Musser et al 2006
<i>Niviventer hinpoon</i>	Terrestrial	61.0	282.0	140.0	142.0	26.5	0.504	1.014	Lekagul and McNeely 1979 - Musser 1981
<i>Niviventer langbianis</i>	Arboreal	69.8	348.0	145.0	203.0	0.6	1.400		Musser 1981 -

									Balakirev et al 2011 - Wilman et al 2014
<i>Niviventer lepturus</i>	General	84.8	NA	NA	NA	NA			Nowak 1991 - Wilman et al 2014
<i>Niviventer niviventer</i>	Terrestrial	100.0	358.5	146.5	212.0	0.6	1.447		Musser 1981 - Balakirev et al 2011
<i>Niviventer rapit</i>	General	79.7	354.0	143.0	211.0	32.0	0.596	1.476	Lekagul and McNeely 1979 - Nowak 1991
<i>Niviventer tenaster</i>	Terrestrial	103.0	360.0	155.0	205.0	33.5	0.569	1.323	Nowak 1991 - Francis & Barrett 2008 - Wilman et al 2014

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Notomys alexis</i>	Terrestrial	50.0	255.0	115.0	140.0	36.0	0.549	1.217	Strahan 1983 - Van Dyck and Strahan 2008
<i>Notomys aquilo</i>	Terrestrial	41.5	285.0	112.0	173.0	40.0	0.607	1.545	Strahan 1983 - Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Notomys cervinus</i>	Terrestrial	42.4	260.0	110.0	150.0	36.0	0.577	1.364	Strahan 1983 - Van Dyck and Strahan 2008
<i>Notomys fuscus</i>	Terrestrial	37.1	228.0	106.5	121.5	33.3	0.533	1.141	Strahan 1983 - Nowak 1991
<i>Notomys mitchellii</i>	Terrestrial	50.0	280.0	125.0	155.0	37.0	0.554	1.240	Strahan 1983 - Cockburn 1981 - Van Dyck and Strahan 2008
<i>Oenomys hypoxanthus</i>	General	88.4	330.1	158.8	171.3	32.0	0.519	1.079	Kingdon et al 2013
<i>Otomys anchietae</i>	Terrestrial	118.0	247.7	155.7	92.0	30.3	0.371	0.591	Kingdon et al 2013 - Wilman et al 2014
<i>Otomys angoniensis</i>	Terrestrial	104.1	299.0	220.0	79.0	25.5	0.264	0.359	Kingdon et al 2013
<i>Otomys barbouri</i>	Terrestrial	117.8	256.0	177.0	79.0	27.0	0.309	0.446	Kingdon et al 2013
<i>Otomys burtoni</i>	Terrestrial	90.0	234.0	156.0	78.0	30.0	0.333	0.500	Kingdon et al 2013
<i>Otomys denti</i>	General	140.0	267.0	162.5	104.5	28.8	0.391	0.643	Kingdon et al 2013
<i>Otomys irroratus</i>	Terrestrial	129.2	259.0	161.0	98.0	32.0	0.378	0.609	Kingdon et al 2013 - Bronner et al 1988
<i>Otomys jacksoni</i>	Terrestrial	127.2	NA	NA	NA	NA			Taylor et al 2011 - Wilman et al 2014
<i>Otomys lacustris</i>	Terrestrial	127.2	260.5	158.0	102.5	30.6	0.393	0.649	Kingdon et al 2013 - IUCN 2017 - Wilman et al 2014

<i>Otomys laminatus</i>	Terrestrial	188.5	308.0	199.0	109.0	30.0	0.354	0.548	Kingdon et al 2013
<i>Otomys occidentalis</i>	Terrestrial	77.0	221.0	143.0	78.0	28.0	0.353	0.545	Kingdon et al 2013
<i>Otomys orestes</i>	Terrestrial	127.2	236.5	156.7	79.8	27.1	0.337	0.509	Taylor et al 2011 - Carleton & Byrne 2006
<i>Otomys sloggetti</i>	Terrestrial	84.0	189.0	127.0	62.0	28.0	0.328	0.488	Kingdon et al 2013 - Nowak 1991
<i>Otomys tropicalis</i>	Terrestrial	111.3	259.5	178.0	81.5	28.7	0.314	0.458	Kingdon et al 2013
<i>Otomys unisulcatus</i>	Terrestrial	105.0	252.0	158.0	94.0	29.0	0.373	0.595	Kingdon et al 2013 - Nowak 1991

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Papagomys armandvillei</i>	Terrestrial	73.8	773.5	428.5	345.0	85.0	0.446	0.805	Nowak 1991 - Musser 1981b
<i>Parahydromys asper</i>	Amphibious	533.3	479.3	225.0	254.3	53.1	0.531	1.130	Flannery 1995a
<i>Paramelomys levipes</i>	Terrestrial	85.6	281.7	144.0	137.7	34.4	0.489	0.956	Flannery 1995a -
<i>Paramelomys platyops</i>	Terrestrial	107.8	282.7	170.2	112.5	30.0	0.398	0.661	Flannery 1995a - 1995b
<i>Paramelomys rubex</i>	Terrestrial	47.7	239.0	118.0	121.0	28.2	0.506	1.025	Flannery 1995a
<i>Parotomys brantsii</i>	General	129.4	255.2	157.5	97.7	30.7	0.383	0.620	Kingdon et al 2013
<i>Parotomys littledalei</i>	Terrestrial	116.0	261.0	153.0	108.0	27.0	0.414	0.706	Kingdon et al 2013
<i>Paruromys dominator</i>	General	304.6	486.5	223.5	263.0	51.9	0.541	1.177	Nowak 1991
<i>Paucidentomys vermidax</i>	Terrestrial	103.5	362.5	163.5	199.0	37.5	0.549	1.217	Esselstyn et al 2012
<i>Pelomys campanae</i>	Terrestrial	77.0	289.0	144.0	145.0	32.0	0.502	1.007	Kingdon et al 2013
<i>Pelomys fallax</i>	Terrestrial	112.7	280.0	147.0	133.0	32.0	0.475	0.905	Kingdon et al 2013 - Nowak 1991
<i>Phloeomys cumingi</i>	Arboreal	1896.2	711.5	417.5	294.0	79.5	0.413	0.704	Heany et al 2016 - Nowak 1991
<i>Phloeomys pallidus</i>	Arboreal	2097.1	738.5	404.0	334.5	85.0	0.453	0.828	Heany et al 2016 - Nowak 1991
<i>Pithecheir melanurus</i>	Arboreal	108.0	369.0	167.5	201.5	30.0	0.546	1.203	Nowak 1991 - Wilman et al 2014
<i>Pithecheir parvus</i>	Arboreal	106.0	357.0	164.0	193.0	28.0	0.541	1.177	Nowak 1991 - Francis & Barrett 2008 - Pimsai et al 2014 - Wilman et al 2014
<i>Pogonomelomys mayeri</i>	Arboreal	110.8	336.0	147.0	189.0	29.3	0.563	1.286	Flannery 1995a

<i>Pogonomys loriae</i>	General	94.7	370.3	151.0	219.3	26.6	0.592	1.452	Flannery 1995a - 1995b
<i>Pogonomys macrourus</i>	General	47.2	277.5	120.5	157.0	20.9	0.566	1.303	Flannery 1995a - 1995b
<i>Pogonomys sylvestris</i>	General	44.2	280.0	122.0	158.0	21.7	0.564	1.295	Flannery 1995a
<i>Praomys daltoni</i>	General	34.4	224.6	108.8	115.8	20.0	0.516	1.064	Kingdon et al 2013 - Happold 1987
<i>Praomys degraaffi</i>	Terrestrial	39.1	246.0	110.4	135.6	25.8	0.551	1.228	Kingdon et al 2013

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Praomys delectorum</i>	General	32.3	224.3	100.1	124.2	23.8	0.554	1.241	Kingdon et al 2013
<i>Praomys derooi</i>	Terrestrial	32.0	212.8	97.1	115.7	21.4	0.544	1.192	Kingdon et al 2013
<i>Praomys hartwigi</i>	General	48.0	287.1	125.0	162.1	26.5	0.565	1.297	Kingdon et al 2013
<i>Praomys jacksoni</i>	General	39.9	262.5	120.0	142.5	22.3	0.543	1.188	Kingdon et al 2013 - Lunde & Sarmiento 2002
<i>Praomys lukoleliae</i>	Terrestrial	41.7	265.0	123.8	141.2	30.2	0.533	1.141	Kingdon et al 2013
<i>Praomys minor</i>	General	41.8	231.0	102.0	129.0	21.7	0.558	1.265	Kingdon et al 2013 - Wilman et al 2014
<i>Praomys misonnei</i>	General	40.0	250.0	114.0	136.0	22.8	0.544	1.193	Kingdon et al 2013
<i>Praomys morio</i>	General	42.4	243.4	113.5	129.9	23.5	0.534	1.144	Kingdon et al 2013
<i>Praomys mutoni</i>	General	45.0	260.0	114.0	146.0	22.0	0.562	1.281	Kingdon et al 2013
<i>Praomys obscurus</i>	Terrestrial	47.2	282.0	121.0	161.0	27.1	0.571	1.331	Kingdon et al 2013
<i>Praomys petteri</i>	General	49.0	259.0	119.0	140.0	26.0	0.541	1.176	Kingdon et al 2013
<i>Praomys rostratus</i>	General	50.0	252.0	114.0	138.0	26.5	0.548	1.211	Kingdon et al 2013
<i>Praomys tullbergi</i>	General	35.4	241.0	109.0	132.0	25.0	0.548	1.211	Kingdon et al 2013
<i>Praomys verschureni</i>	General	50.8	264.3	121.3	143.0	30.1	0.541	1.179	Kingdon et al 2013
<i>Pseudohydromys ellermani</i>	Terrestrial	22.0	198.0	97.0	101.0	20.9	0.510	1.041	Flannery 1995a - Helgen & Helgen 2009
<i>Pseudomys albocinereus</i>	Terrestrial	32.8	215.0	105.0	110.0	25.0	0.512	1.048	Nowak 1991 - Van Dyck & Strahan 2008 Watts & Aslin 1981
<i>Pseudomys apodemoides</i>	Terrestrial	17.0	200.0	90.0	110.0	23.0	0.550	1.222	Strahan 1983 - Cockburn 1981 - Van Dyck & Strahan 2008

<i>Pseudomys australis</i>	Terrestrial	75.0	260.0	140.0	120.0	30.0	0.462	0.857	Strahan 1983 - Nowak 1991 - Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Pseudomys bolami</i>	Terrestrial	15.8	183.0	80.0	103.0	0.6	1.288		Nowak 1991 - Van Dyck and Strahan 2008
<i>Pseudomys calabyi</i>	Terrestrial	16.7	162.8	84.4	78.4	18.0	0.482	0.929	Ford and Johnson 2007 - Van Dyck and Strahan 2008

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Pseudomys chapmani</i>	Terrestrial	11.5	122.8	59.2	63.6	15.0	0.518	1.074	Strahan 1983 - Ford and Johnson 2007 - Van Dyck and Strahan 2008
<i>Pseudomys delicatulus</i>	Terrestrial	11.8	155.0	75.0	80.0	18.0	0.516	1.067	Flannery 1995a - Strahan 1983 - Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Pseudomys desertor</i>	Terrestrial	30.0	190.0	100.0	90.0	22.0	0.474	0.900	Strahan 1983 - Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Pseudomys fieldi</i>	Terrestrial	43.7	230.0	110.0	120.0	27.0	0.522	1.091	Strahan 1983 - Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Pseudomys fumeus</i>	Terrestrial	80.0	270.0	120.0	150.0	29.0	0.556	1.250	Strahan 1983 - Van Dyck and Strahan 2008
<i>Pseudomys gracilicaudatus</i>	Terrestrial	90.0	240.0	130.0	110.0	28.0	0.458	0.846	Strahan 1983 - Van Dyck and Strahan 2008 - Nowak 1991 - Watts & Aslin 1981
<i>Pseudomys hermannsburgensis</i>	Terrestrial	13.9	155.0	75.0	80.0	19.0	0.516	1.067	Strahan 1983 - Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Pseudomys higginsi</i>	Terrestrial	65.1	295.0	133.0	162.0	35.0	0.549	1.218	Strahan 1983 - Van Dyck and Strahan 2008 - Nowak 1991 - Watts & Aslin 1981
<i>Pseudomys johnsoni</i>	Terrestrial	16.0	171.0	76.0	95.0	17.4	0.556	1.250	Nowak 1991 - Ford and Johnson 2007 -

									Van Dyck and Strahan 2008
Pseudomys nanus	Terrestrial	52.2	207.0	107.0	100.0	25.0	0.483	0.935	Strahan 1983 - Van Dyck and Strahan 2008 - Nowak 1991
Pseudomys novachollandiae	Terrestrial	19.9	195.0	90.0	105.0	22.0	0.538	1.167	Strahan 1983 - Van Dyck and Strahan 2008 - Nowak 1991 - Watts & Aslin 1981
Pseudomys occidentalis	Terrestrial	45.0	218.0	89.0	129.0	27.0	0.592	1.449	Strahan 1983 - Van Dyck and Strahan 2008

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
Pseudomys oralis	Terrestrial	95.0	270.0	140.0	130.0	34.0	0.481	0.929	Strahan 1983 - Van Dyck and Strahan 2008 - Nowak 1991 - Watts & Aslin 1981
Pseudomys patrius	Terrestrial	14.0	135.0	63.0	72.0	0.5	1.143		Ford and Johnson 2007 - Van Dyck and Strahan 2008
Pseudomys shortridgei	Terrestrial	65.0	245.0	140.0	105.0	28.0	0.429	0.750	Strahan 1983 - Van Dyck and Strahan 2008 - Nowak 1991 - Watts & Aslin 1981
Rattus andamanensis	Arboreal	169.0	450.0	208.0	242.0	40.0	0.538	1.163	Lekagul and McNeely 1979 - Smith and Xie 2013 - Pimsai et al 2014
Otomys angoniensis	Terrestrial	104.1	299.0	220.0	79.0	25.5	0.264	0.359	Lekagul and McNeely 1979 - Nowak 1991 - Francis & Barrett 2008 - Pimsai et al 2014 - Aplin et al 2003 - I UCN 2017
Otomys barbouri	Terrestrial	117.8	256.0	177.0	79.0	27.0	0.309	0.446	Nowak 1991
Otomys burtoni	Terrestrial	90.0	234.0	156.0	78.0	30.0	0.333	0.500	Strahan 1983 - Rowe et al 2011 - IUCN 2017
Otomys denti	General	140.0	267.0	162.5	104.5	28.8	0.391	0.643	Heany et al 2016
Otomys irroratus	Terrestrial	129.2	259.0	161.0	98.0	32.0	0.378	0.609	Heany et al 2016 - Lekagul and McNeely 1979 - Taylor et al 1982 - IUCN 2017

Otomys jacksoni	Terrestrial	127.2	NA	NA	NA	NA			AMNH specimens - Wilman et al 2014
Otomys lacustris	Terrestrial	127.2	260.5	158.0	102.5	30.6	0.393	0.649	Strahan 1983 - Rader and Krockenberger 2006 - Rowe et al 2011 - IUCN 2017
Otomys laminatus	Terrestrial	188.5	308.0	199.0	109.0	30.0	0.354	0.548	Flannery 1995a

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
Otomys occidentalis	Terrestrial	77.0	221.0	143.0	78.0	28.0	0.353	0.545	Nowak 1991 - Musser 1982b Musser & Holden 1991 - Wilman et al 2014
Otomys orestes	Terrestrial	127.2	236.5	156.7	79.8	27.1	0.337	0.509	Flannery 1995a - 1995b - Strahan 1983 - Nowak 1991 - Rader and Krockenberger 2006
Otomys sloggetti	Terrestrial	84.0	189.0	127.0	62.0	28.0	0.328	0.488	Lekagul and McNeely 1979 - Nowak 1991 - Smith and Xie 2013
Otomys tropicalis	Terrestrial	111.3	259.5	178.0	81.5	28.7	0.314	0.458	Strahan 1983 - Nowak 1991 - Rowe et al 2011
Otomys unisulcatus	Terrestrial	105.0	252.0	158.0	94.0	29.0	0.373	0.595	Nowak 1979 - Musser & Newcomb 1983 - Andrews 1900 - IUCN 2017 - Wilman et al 2014
Papagomys armandvillei	Terrestrial	73.8	773.5	428.5	345.0	85.0	0.446	0.805	Flannery 1995b - Nowak 1991
Parahydromys asper	Amphibious	533.3	479.3	225.0	254.3	53.1	0.531	1.130	Flannery 1995a
Paramelomys levipes	Terrestrial	85.6	281.7	144.0	137.7	34.4	0.489	0.956	Heany et al 2016 - Lekagul and McNeely 1979 - Smith and Xie 2013 - Molur et al 2005 - IUCN 2017
Paramelomys platyops	Terrestrial	107.8	282.7	170.2	112.5	30.0	0.398	0.661	Kingdon et al 2013 - Strahan 1983 - Lekagul and McNeely 1979 -

									Nowak 1991 - Singleton et al 2003 - IUCN 2017
Paramelomys rubex	Terrestrial	47.7	239.0	118.0	121.0	28.2	0.506	1.025	Flannery 1995a - Nowak 1991
Parotomys brantsii	General	129.4	255.2	157.5	97.7	30.7	0.383	0.620	Flannery 1995a - 1995b

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
Parotomys littledalei	Terrestrial	116.0	261.0	153.0	108.0	27.0	0.414	0.706	Smith and Xie 2013 - Molur et al 2005 - Wilman et al 2014
Paruromys dominator	General	304.6	486.5	223.5	263.0	51.9	0.541	1.177	Kingdon et al 2013 - Strahan 1983 - Lekagul and McNeely 1979 – Nowak 1991 - IUCN 2017
Paucidentomys vermidax	Terrestrial	103.5	362.5	163.5	199.0	37.5	0.549	1.217	IUCN 2017
Pelomys campanae	Terrestrial	77.0	289.0	144.0	145.0	32.0	0.502	1.007	Flannery 1995a - 1995b - Strahan 1983
Pelomys fallax	Terrestrial	112.7	280.0	147.0	133.0	32.0	0.475	0.905	Flannery 1995a - Nowak 1991
Phloeomys cumingi	Arboreal	1896.2	711.5	417.5	294.0	79.5	0.413	0.704	Heany et al 2016 – Smith and Xie 2013
Phloeomys pallidus	Arboreal	2097.1	738.5	404.0	334.5	85.0	0.453	0.828	Kitchner et al 1991 - Wilman et al 2014
Pithecheir melanurus	Arboreal	108.0	369.0	167.5	201.5	30.0	0.546	1.203	Nowak 1991 - Francis & Barrett 2008 - IUCN 2017
Pithecheir parvus	Arboreal	106.0	357.0	164.0	193.0	28.0	0.541	1.177	Strahan 1983 - Rowe et al 2011 - Van Dyck and R. Strahan 2008
Pogonomelomys mayeri	Arboreal	110.8	336.0	147.0	189.0	29.3	0.563	1.286	Flannery 1995a
Pogonomys loriae	General	94.7	370.3	151.0	219.3	26.6	0.592	1.452	Strahan 1983 - IUCN 2017
Pogonomys macrourus	General	47.2	277.5	120.5	157.0	20.9	0.566	1.303	Nowak 1991 - Musser & Newcomb 1983 - Musser 1991

<i>Pogonomys sylvestris</i>	General	44.2	280.0	122.0	158.0	21.7	0.564	1.295	Kingdon et al 2013
<i>Praomys daltoni</i>	General	34.4	224.6	108.8	115.8	20.0	0.516	1.064	Heany et al 2016
<i>Praomys degraaffi</i>	Terrestrial	39.1	246.0	110.4	135.6	25.8	0.551	1.228	Heany et al 2016
<i>Praomys delectorum</i>	General	32.3	224.3	100.1	124.2	23.8	0.554	1.241	Heany et al 2016
<i>Praomys derooi</i>	Terrestrial	32.0	212.8	97.1	115.7	21.4	0.544	1.192	Heany et al 2016
<i>Praomys hartwigi</i>	General	48.0	287.1	125.0	162.1	26.5	0.565	1.297	Francis & Barrett 2008 - Musser et al 2005 - Nguyen et al 2015

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Praomys jacksoni</i>	General	39.9	262.5	120.0	142.5	22.3	0.543	1.188	Flannery 1995b
<i>Praomys lukoleliae</i>	Terrestrial	41.7	265.0	123.8	141.2	30.2	0.533	1.141	Musser & Durden 2002 - Rowe et al 2014
<i>Praomys minor</i>	General	41.8	231.0	102.0	129.0	21.7	0.558	1.265	Heany et al 2016
<i>Praomys misonnei</i>	General	40.0	250.0	114.0	136.0	22.8	0.544	1.193	Heany et al 2016
<i>Praomys morio</i>	General	42.4	243.4	113.5	129.9	23.5	0.534	1.144	Heany et al 2016
<i>Praomys mutoni</i>	General	45.0	260.0	114.0	146.0	22.0	0.562	1.281	Heany et al 2016
<i>Praomys obscurus</i>	Terrestrial	47.2	282.0	121.0	161.0	27.1	0.571	1.331	Nowak 1991 - Wilman et al 2014
<i>Praomys petteri</i>	General	49.0	259.0	119.0	140.0	26.0	0.541	1.176	Kingdon et al 2013
<i>Praomys rostratus</i>	General	50.0	252.0	114.0	138.0	26.5	0.548	1.211	Kingdon et al 2013 - Nowak 1991
<i>Praomys tullbergi</i>	General	35.4	241.0	109.0	132.0	25.0	0.548	1.211	Kingdon et al 2013
<i>Praomys verschureni</i>	General	50.8	264.3	121.3	143.0	30.1	0.541	1.179	Kingdon et al 2013 - Nowak 1991
<i>Pseudohydromys ellermani</i>	Terrestrial	22.0	198.0	97.0	101.0	20.9	0.510	1.041	Nowak 1991 - Francis & Barrett 2008 - Pimsai et al 2014
<i>Pseudomys albocinereus</i>	Terrestrial	32.8	215.0	105.0	110.0	25.0	0.512	1.048	Nowak 1991 - Musser & Newcomb 1983
<i>Pseudomys apodemoides</i>	Terrestrial	17.0	200.0	90.0	110.0	23.0	0.550	1.222	Nowak 1991 - Musser & Newcomb 1983 - Wilman et al 2014
<i>Pseudomys australis</i>	Terrestrial	75.0	260.0	140.0	120.0	30.0	0.462	0.857	IUCN 2017

<i>Pseudomys bolami</i>	Terrestrial	15.8	183.0	80.0	103.0	0.6	1.288		Musser & Newcomb 1983 - Musser - 2014
<i>Pseudomys calabyi</i>	Terrestrial	16.7	162.8	84.4	78.4	18.0	0.482	0.929	Wilman et al 2014
<i>Pseudomys chapmani</i>	Terrestrial	11.5	122.8	59.2	63.6	15.0	0.518	1.074	Wilman et al 2014
<i>Pseudomys delicatulus</i>	Terrestrial	11.8	155.0	75.0	80.0	18.0	0.516	1.067	Nowak 1991 - Musser and Heaney 1992 - Heaney et al 2006

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Pseudomys desertor</i>	Terrestrial	30.0	190.0	100.0	90.0	22.0	0.474	0.900	Nowak 1991 - Rowe et al 2014
<i>Pseudomys fieldi</i>	Terrestrial	43.7	230.0	110.0	120.0	27.0	0.522	1.091	Nowak 1991 - Musser 1969 - Rowe et al 2014
<i>Pseudomys fumeus</i>	Terrestrial	80.0	270.0	120.0	150.0	29.0	0.556	1.250	Kingdon et al 2013
<i>Pseudomys gracilicaudatus</i>	Terrestrial	90.0	240.0	130.0	110.0	28.0	0.458	0.846	Kingdon et al 2013
<i>Pseudomys hermannsburgensis</i>	Terrestrial	13.9	155.0	75.0	80.0	19.0	0.516	1.067	Kingdon et al 2013
<i>Pseudomys higginsi</i>	Terrestrial	65.1	295.0	133.0	162.0	35.0	0.549	1.218	Kingdon et al 2013
<i>Pseudomys johnsoni</i>	Terrestrial	16.0	171.0	76.0	95.0	17.4	0.556	1.250	Endo and Tsuchiya 2006 - Wilman et al 2014
<i>Pseudomys nanus</i>	Terrestrial	52.2	207.0	107.0	100.0	25.0	0.483	0.935	Nowak 1991
<i>Pseudomys novachollandiae</i>	Terrestrial	19.9	195.0	90.0	105.0	22.0	0.538	1.167	Endo and Tsuchiya 2006 - Wilman et al 2014
<i>Pseudomys occidentalis</i>	Terrestrial	45.0	218.0	89.0	129.0	27.0	0.592	1.449	Francis & Barrett 2008 - Musser & Lunde 2006
<i>Pseudomys oralis</i>	Terrestrial	95.0	270.0	140.0	130.0	34.0	0.481	0.929	Flannery 1995a - 1995b - Strahan 1983 - Rader and Krockenberger 2006 - IUCN 2017
<i>Pseudomys patrius</i>	Terrestrial	14.0	135.0	63.0	72.0	0.5	1.143		Lekagul and McNeely 1979 - Francis & Barrett 2008 - Molur et al 2005
<i>Pseudomys shortridgei</i>	Terrestrial	65.0	245.0	140.0	105.0	28.0	0.429	0.750	Rowe et al 2014
<i>Rattus andamanensis</i>	Arboreal	169.0	450.0	208.0	242.0	40.0	0.538	1.163	Flannery 1995a
<i>Rattus argentiventer</i>	General	156.1	375.0	194.5	180.5	37.5	0.48	0.928021	Heaney et al 2016 - Lekagul and McNeely 1979 -

									Nowak 1991 - Francis & Barrett 2008 - Pimsai et al 2014 - Aplin et al 2003 - IUCN 2017
Rattus baluensis	Terrestrial	107.5	358.5	170.2	188.3	32.4	0.53	1.106345	Nowak 1991
Rattus colletti	Terrestrial	146.5	286.5	161.4	125.1	30.1	0.44	0.775313	Strahan 1983 - Rowe et al 2011 - IUCN 2017

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
Rattus everetti	General	304.3	434.5	222.0	212.5	46.0	0.49	0.957207	Heany et al 2016
Rattus exulans	General	62.9	286.7	135.8	150.9	26.1	0.53	1.111193	Heany et al 2016 - Lekagul and McNeely 1979 - Taylor et al 1982 - IUCN 2017
Rattus facetus	Terrestrial	175.0	450.0	200.0	250.0	44.0	0.56	1.25	AMNH specimens - Wilman et al 2014
Rattus fuscipes	General	100.3	301.0	155.3	145.7	32.4	0.48	0.938003	Strahan 1983 - Rader and Krockenberger 2006 - Rowe et al 2011 - IUCN 2017
Rattus giluwensis	Terrestrial	75.0	305.0	170.8	134.2	30.0	0.44	0.785714	Flannery 1995a
Rattus hoffmanni	General	147.0	339.6	170.1	169.5	38.2	0.50	0.996473	Nowak 1991 - Musser 1982b / Musser & Holden 1991 - Wilman et al 2014
Rattus leucopus	Terrestrial	205.8	377.6	201.3	176.3	38.8	0.47	0.875807	Flannery 1995a - 1995b - Strahan 1983 - Nowak 1991 - Rader and Krockenberger 2006
Rattus losea	General	90.8	279.0	146.0	133.0	30.0	0.48	0.910959	Lekagul and McNeely 1979 - Nowak 1991 - Smith and Xie 2013
Rattus lutreolus	Terrestrial	107.5	272.0	158.5	113.5	30.0	0.42	0.716314	Strahan 1983 - Nowak 1991 - Rowe et al 2011
Rattus macleari	Arboreal	150.0	489.0	234.0	255.0	51.9	0.52	1.089744	Nowak 1979 - Musser & Newcomb 1983 - Andrews 1900 -

									IUCN 2017 - Wilman et al 2014
Rattus morotaiensis	Arboreal	151.1	406.5	194.5	212.0	37.6	0.52	1.089974	Flannery 1995b - Nowak 1991
Rattus niobe	Terrestrial	47.5	248.0	121.0	127.0	27.2	0.51	1.049587	Flannery 1995a
Rattus nitidus	General	114.5	348.0	171.0	177.0	37.5	0.51	1.035088	Heany et al 2016 - Lekagul and McNeely 1979 - Smith and Xie 2013 - Molur et al 2005 - IUCN 2017

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
Rattus norvegicus	General	335.7	390.5	213.5	177.0	39.0	0.45	0.82904	Kingdon et al 2013 - Strahan 1983 - Heany et al 2016 - Lekagul and McNeely 1979 - Nowak 1991 - Singleton et al 2003 - IUCN 2017
Rattus novaeguineae	General	133.9	334.8	172.8	162.0	30.8	0.48	0.9375	Flannery 1995a - Nowak 1991
Rattus praetor	Terrestrial	196.6	363.0	196.7	166.3	35.5	0.46	0.84545	Flannery 1995a - 1995b
Rattus pyctoris	Terrestrial	150.0	NA	NA	NA	NA			Smith and Xie 2013 - Molur et al 2005 - Wilman et al 2014
Rattus rattus	General	146.7	377.4	180.8	196.6	36.1	0.52	1.087389	Kingdon et al 2013 - Strahan 1983 - Lekagul and McNeely 1979 - Nowak 1991 - IUCN 2017
Rattus satarae	Arboreal	130.0	389.0	151.0	238.0	32.5	0.61	1.576159	IUCN 2017
Rattus sordidus	Terrestrial	164.9	297.0	169.0	128.0	30.6	0.43	0.757396	Flannery 1995a - 1995b - Strahan 1983
Rattus steini	General	153.1	318.0	174.0	144.0	35.4	0.45	0.827586	Flannery 1995a - Nowak 1991
Rattus tanezumi	General	152.3	397.5	202.5	195.0	38.0	0.49	0.962963	Heany et al 2016 - Smith and Xie 2013
Rattus timorensis	Terrestrial	160.3	NA	NA	NA	NA			Kitchner et al 1991 - Wilman et al 2014

<i>Rattus tiomanicus</i>	General	121.2	334.4	161.3	173.1	31.5	0.52	1.073156	Nowak 1991 - Francis & Barrett 2008 - IUCN 2017
<i>Rattus tunneyi</i>	Terrestrial	169.3	270.0	146.0	124.0	29.5	0.46	0.849315	Strahan 1983 - Rowe et al 2011 - Van Dyck and R. Strahan 2008
<i>Rattus verecundus</i>	Terrestrial	90.5	318.4	157.7	160.7	32.8	0.50	1.019023	Flannery 1995a

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Rattus villosissimus</i>	Terrestrial	207.0	303.5	158.0	145.5	32.0	0.48	0.920886	Strahan 1983 - IUCN 2017
<i>Rattus xanthurus</i>	Terrestrial	303.0	559.0	247.3	311.7	46.7	0.56	1.260412	Nowak 1991 - Musser & Newcomb 1983 - Musser 1991
<i>Rhabdomys pumilio</i>	General	40.0	231.0	115.8	115.2	24.0	0.50	0.994819	Kingdon et al 2013
<i>Rhynchomys banahao</i>	Terrestrial	145.0	312.5	184.5	128.0	39.5	0.41	0.693767	Heany et al 2016
<i>Rhynchomys isarogensis</i>	Terrestrial	122.4	287.5	187.0	105.0	37.0	0.37	0.561497	Heany et al 2016
<i>Rhynchomys soricoides</i>	Terrestrial	179.0	330.5	183.5	147.0	40.5	0.44	0.80109	Heany et al 2016
<i>Rhynchomys tapulao</i>	Terrestrial	142.5	299.0	175.0	124.0	39.0	0.41	0.708571	Heany et al 2016
<i>Saxatilomys paulinae</i>	Terrestrial	116.0	318.0	150.0	168.0	32.0	0.53	1.12	Francis & Barrett 2008 - Musser et al 2005 - Nguyen et al 2015
<i>Solomys salebrosus</i>	Arboreal	397.0	520.5	276.5	244.0	48.6	0.47	0.882459	Flannery 1995b
<i>Sommeromys macrorhinos</i>	Arboreal	26.8	282.5	100.0	182.5	30.0	0.65	1.825	Musser & Durden 2002 - Rowe et al 2014
<i>Soricomys kalinga</i>	General	25.0	195.0	102.0	93.0	24.0	0.48	0.911765	Heany et al 2016
<i>Soricomys leonardcoi</i>	Terrestrial	31.0	194.0	105.5	88.5	23.0	0.46	0.838863	Heany et al 2016
<i>Soricomys montanus</i>	Terrestrial	27.0	190.5	98.0	92.5	24.0	0.49	0.943878	Heany et al 2016
<i>Soricomys musseri</i>	Terrestrial	31.0	189.0	98.5	90.5	22.0	0.48	0.918782	Heany et al 2016
<i>Srilankamys ohiensis</i>	Terrestrial	79.3	NA	NA	NA	NA			Nowak 1991 - Wilman et al 2014
<i>Stenocephalemys albipes</i>	General	49.8	252.0	115.0	137.0	27.0	0.54	1.191304	Kingdon et al 2013
<i>Stenocephalemys albocaudata</i>	Terrestrial	137.0	305.0	164.0	141.0	32.0	0.46	0.859756	Kingdon et al 2013 - Nowak 1991

<i>Stenocephalemys griseicauda</i>	Terrestrial	92.375	296.0	154.0	142.0	30.0	0.5	0.92		Kingdon et al 2013
<i>Stochomys longicaudatus</i>	General	73.5	356.6	145.1	211.5	29.3	0.59	1.457615		Kingdon et al 2013 - Nowak 1991
<i>Sundamys annandalei</i>	General	197.5	397.5	182.5	215.0	37.5	0.54	1.178082		Nowak 1991 - Francis & Barrett 2008 - Pimsai et al 2014
<i>Sundamys infraluteus</i>	Terrestrial	418.5	574.0	260.0	314.0	58.0	0.55	1.207692		Nowak 1991 - Musser & Newcomb 1983

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Sundamys maxi</i>	General	361.0	528.2	241.5	286.7	53.1	0.54	1.187164	Nowak 1991 - Musser & Newcomb 1983 - Wilman et al 2014
<i>Sundamys muelleri</i>	General	300.4	547.5	243.8	303.7	47.0	0.55	1.245693	Nowak 1991 - Francis & Barrett 2008 - Musser and Newcomb 1983 - IUCN 2017
<i>Taeromys celebensis</i>	General	252.7	498.6	224.0	274.6	50.1	0.55	1.225893	Musser & Newcomb 1983 - Musser - 2014
<i>Taeromys punicens</i>	Terrestrial	138.0	NA	NA	NA	NA			Wilman et al 2014
<i>Taeromys taerae</i>	Terrestrial	247.0	NA	NA	NA	NA			Wilman et al 2014
<i>Tarsomys apoensis</i>	Terrestrial	76.7	286.8	145.5	141.3	31.5	0.49	0.971134	Nowak 1991 - Musser and Heaney 1992 - Heaney et al 2006
<i>Tateomys macrocercus</i>	Terrestrial	40.0	278.0	112.0	166.0	30.7	0.60	1.482143	Nowak 1991 - Rowe et al 2014
<i>Tateomys rhinogradooides</i>	Terrestrial	86.5	308.5	145.5	163.0	37.3	0.53	1.120275	Nowak 1991 - Musser 1969 - Rowe et al 2014
<i>Thallomys loringi</i>	General	80.0	303.0	144.0	159.0	27.0	0.52	1.104167	Kingdon et al 2013
<i>Thallomys nigricauda</i>	Arboreal	99.1	281.8	135.0	146.8	24.7	0.52	1.087407	Kingdon et al 2013
<i>Thallomys paedulcus</i>	Arboreal	75.0	306.5	140.3	166.2	25.3	0.54	1.184604	Kingdon et al 2013
<i>Thamnomys kempfi</i>	Arboreal	79.5	357.0	155.0	202.0	29.3	0.57	1.303226	Kingdon et al 2013
<i>Tokudaia muenninki</i>	Terrestrial	177.4	148.0	43.0	105.0	37.0	0.71	2.44186	Endo and Tsuchiya 2006 - Wilman et al 2014
<i>Tokudaia osimensis</i>	Terrestrial	101.2	265.3	151.0	114.3	30.7	0.43	0.756954	Nowak 1991
<i>Tokudaia tokunoshimensis</i>	Terrestrial	180.0	150.0	32.0	118.0	35.0	0.79	3.6875	Endo and Tsuchiya 2006 -

									Wilman et al 2014
<i>Tonkinomys daovantieni</i>	General	172.5	370.0	200.0	170.0	39.0	0.46	0.85	Francis & Barrett 2008 - Musser & Lunde 2006
<i>Uromys caudimaculatus</i>	General	633.4	571.7	267.7	304.0	54.8	0.53	1.1356	Flannery 1995a - 1995b - Strahan 1983 - Rader and Krockenberger 2006 - IUCN 2017
<i>Vandeleuria oleracea</i>	Arboreal	13.3	186.3	75.0	111.3	17.8	0.60	1.484	Lekagul and McNeely 1979 - Francis & Barrett 2008 - Molur et al 2005

table cont'd

Species	Locomotor State	Mass	Length	Head-Body	Tail	Hind Foot	Relative Tail	Relative Foot	Source
<i>Waiomys mamasae</i>	Amphibious	64.0	288.0	129.0	159.0	36.0	0.55	1.232558	Rowe et al 2014
<i>Xenuromys barbatus</i>	Terrestrial	987.7	578.0	316.0	262.0	62.9	0.45	0.829114	Flannery 1995a
<i>Xeromys myoides</i>	Terrestrial	45.5	217.3	117.3	100.0	25.0	0.460	0.853	Strahan 1983 - Nowak 1991 - IUCN 2017 - Watts & Aslin 1981
<i>Zelotomys hildegardae</i>	Terrestrial	57.6	210.4	110.0	100.4	22.3	0.477	0.913	Kingdon et al 2013
<i>Zyzomys argurus</i>	Terrestrial	60.0	245.0	120.0	125.0	25.0	0.510	1.042	Strahan 1983 - Nowak 1991 - IUCN 2017 - Watts & Aslin 1981
<i>Zyzomys maini</i>	Terrestrial	94.0	296.0	150.0	146.0	0.5	0.973		Van Dyck and Strahan 2008 - Watts & Aslin 1981
<i>Zyzomys palatalis</i>	Terrestrial	115.0	257.0	126.0	131.0	0.5	1.040		Van Dyck and Strahan 2008 - IUCN 2017
<i>Zyzomys woodwardi</i>	Terrestrial	135.0	265.0	150.0	117.0	30.0	0.442	0.780	Strahan 1983 - Van Dyck and Strahan 2008 - IUCN 2017

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## VITA

Jonathan Allen Nations was born in Fort Myers, Florida in 1981, though he only spent two weeks there before moving, perhaps influencing his love of travel and his general lack of a geographic center. Most of his childhood was spent in Huntsville, Alabama, and high school years in Duluth, Georgia. After high school he spent a year in Bolivia, working in a home for niños de la calle and learning Spanish. Over the next decade Jon was mostly in Seattle, Washington, with a yearlong sabbatical in Mexico and Central America where he worked as a tour guide. There were many additional trips around Latin America, the Pacific Northwest, and Southeast Asia. He began his studies at Seattle Central Community College in 2008. It was his time at Seattle Central that solidified his love of biology, and, through the mentorship of Dr. Joshua Whorley and Dr. Wendy Rockhill, was introduced to research, specifically museum research on small mammals. Jon went on to conduct the largest known survey of small mammals in Seattle City Parks, and spent time working in the collections of the Burke Museum of Natural History. During a brief foray into Musk Ox wrangling, Jon fell in love with Alaska, and he and his partner Perrin Teal-Sullivan moved to Fairbanks in 2011 to study at the University of Alaska Fairbanks. Jon worked at the University of Alaska Museum for 4 years with Curator of Mammals Dr. Link Olson. He spent many hours a week in the collections, led many collecting expeditions (both alone and with other undergraduates), and researched climbing behavior in Northern Red-Backed Voles, a small mammal that isn't 'supposed' to climb but definitely does. He graduated with honors in 2014 and earned the Biology Student of the Year award from UAF. With a growing interest in tropical biodiversity and a deep commitment to specimen-based research, Jon joined the lab of Dr. Esselstyn at LSU in the fall of 2015. Someday he hopes to settle down somewhere.