

A simple skeletal measurement effectively predicts climbing behaviour in a diverse clade of small mammals

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Arboreal locomotion allows access to above-ground resources and might have fostered the diversification of mammals. Nevertheless, simple morphological measurements that consistently correlate with arboreality remain indefinable. As such, the climbing habits of many species of mammals, living and extinct, remain speculative. We collected quantitative data on the climbing tendencies of 20 species of murine rodents, an ecologically and morphologically diverse clade. We leveraged Bayesian phylogenetic mixed models (BPMMs), incorporating intraspecific variation and phylogenetic uncertainty, to determine which, if any, traits (17 skeletal indices) predict climbing frequency. We used ordinal BPMMs to test the ability of the indices to place 48 murine species that lack quantitative climbing data into three qualitative locomotor categories (terrestrial, general and arboreal). Only two indices (both measures of relative digit length) accurately predict locomotor styles, with manus digit length showing the best fit. Manus digit length has low phylogenetic signal, is largely explained by locomotor ecology and might effectively predict locomotion across a multitude of small mammals, including extinct species. Surprisingly, relative tail length, a common proxy for locomotion, was a poor predictor of climbing. In general, detailed, quantitative natural history data, such as those presented here, are needed to enhance our understanding of the evolutionary and ecological success of clades.

ADDITIONAL KEYWORDS: arboreal – comparative method – ecomorphology – manus index – Murinae – Philippines – phylogenetic mixed models.

INTRODUCTION

Climbing is a key behaviour that facilitates access to above-ground resources and hence, ecological opportunity. As such, the tendency to climb might 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, i.e. the propensity to climb, might be the ancestral locomotor mode of placental mammals (O’Leary *et al.*, 2013), and recent paleontological work suggests that climbing facilitated placental mammal diversification (Ji *et al.*, 2002; Luo *et al.*, 2011). However, because locomotory

behaviour does not fossilize, our understanding of the role of climbing in the history of placental mammal 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 behaviour 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 behaviour 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

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feeding. Arboreal substrates range 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). Given that the differences between terrestrial locomotion and climbing are substantial, it is thought that both behavioural and morphological adaptations occur in concert with transitions between these ecological states. A signal of morphological adaptations to arboreal locomotion might be found in the postcranial skeletons of climbing mammals (Jenkins, 1974a; Cartmill, 1985).

Identifying which, if any, skeletal characters accurately predict climbing behaviour would facilitate locomotor inferences for both extinct species and living species that lack observational data. Connecting morphology with locomotor behaviours 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 only one of numerous independent origins of scansoriality in mammals, they have been the subject of most climbing studies to date (Jenkins, 1974a, b; Gebo, 1996, 2004; Bloch & Boyer, 2002; Kirk *et al.*, 2008). Most primate species have such extreme adaptations to climbing that they might be poor models for how climbing generally evolves (Jenkins, 1974b); therefore, the transition from the ground to the trees has been investigated in various small, non-primate species, which vary in size from ~15 g to 6 kg (Argot, 2002; Urbani & Youlatos, 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, b; Kirk *et al.*, 2008; Samuels & Van Valkenburgh, 2008; Woodman & Stabile, 2015). However, when analysed 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 low 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. This might be important, because smaller-bodied arboreal and terrestrial species have been shown to be more similar morphologically than larger-bodied species, probably owing to the mechanics of locomotion (Kirk *et al.*, 2008). Additionally, non-primate models span the mammalian phylogeny, from marsupials to murids, or ~175 Myr of evolutionary time (Meredith *et al.*, 2011), and it remains unclear whether shared traits are attributable to morphological convergence or are simply historical artefact. Recent work has successfully used three-dimensional morphometrics and muscular structure to identify differences indicative of climbing in non-primate mammals (Fabre *et al.*, 2013a; Taverne *et al.*, 2018), but these methods lack the simplicity needed to infer locomotion for the numerous extant and extinct species with no behavioural data. Ideally, inferences of climbing behaviour 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 behaviour, from the large canopy-dwelling cloud rats (*Phloeomys*; ≤ 2.7 kg), to the tiny bamboo-nesting Rane mice (*Haeromys*; < 10 g). 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 and to determine whether and how those traits vary with respect to body size.

The Philippines is home to ~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 behaviourally 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 document effectively which species climb and with what frequency (Ruedas, 1995; Balete *et al.*, 2009, 2011, 2013a, b; Alviola *et al.*, 2011; Duya *et al.*, 2011; Rickart *et al.*, 2011, 2013, 2016; Heaney *et al.*, 2013a, b). This provides a rare opportunity in small mammals to quantify observations of the frequency

of climbing behaviour, with numerical integration of behaviour into linear models, thereby avoiding the simple, but potentially misleading, binary scheme of 'arboreal' vs. 'terrestrial'.

In this study, we leverage quantitative observations of climbing behaviour, DNA sequence data and available postcranial skeletons to evaluate whether climbing behaviour 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 behaviour are available.

MATERIAL AND METHODS

MORPHOLOGICAL SAMPLING

One of us (J.A.N.) collected 21 linear measurements (Fig. 1; Supporting Information, Appendices S1–S3)

from appendicular skeletons of 186 murine specimens representing 20 species of Philippine murines 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 callipers (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; Supporting Information, Appendices S2 and S3), as is common practice (Elissamburu & Vizcano, 2004; Samuels & Van Valkenburgh, 2008; Hopkins & Davis, 2009; Coutinho *et al.*, 2013; Woodman & Stabile, 2015; Slater & Friscia, 2019). Indices also allowed us to avoid using body-size corrected regression residuals of single linear measurements as data, a practice that has

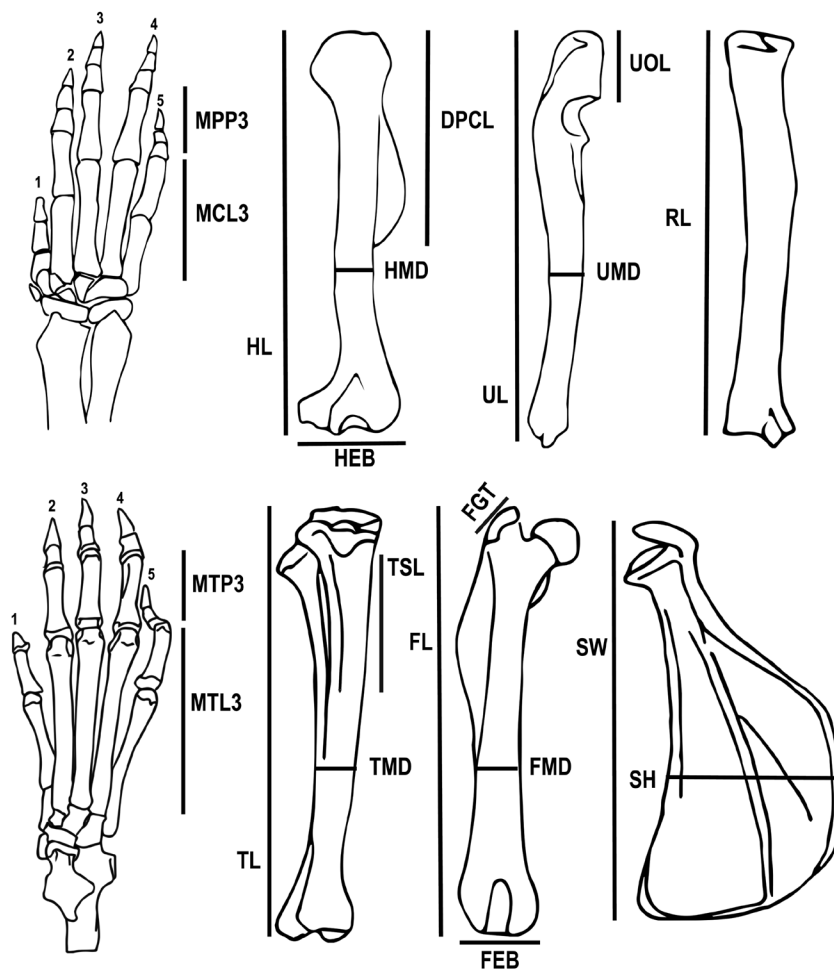


Figure 1. Linear measurements of postcranial elements used for this study. Measurements were converted to indices (Table 1). From upper left to lower right, elements are manus, humerus, ulna, radius, pes, tibia, femur and scapula.

Table 1. Definitions of morphological indices

Index	Description	Formula	Abbreviation
SMI	Shoulder moment index; indicates quantity of muscle attachment in the shoulder	Deltpectoral crest length/humerus length	DPCL/HL
BI	Brachial index; difference of proximal and distal portions of the forelimb	Radius length/humerus length	RI/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)
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 (third ray)/metacarpal length (third 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; indicates quantity of muscle attachment from the gluteus to the hindlimb	Length of distal extension of femoral trochanter/femur length	FGT/FL
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 area 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 (third ray)/metatarsal length (third 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)
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

Measurements are illustrated in [Figure 1](#). All indices except for PES, SI and TAIL were defined by [Samuels & Van Valkenburgh \(2008\)](#).

raised concerns (Garcia-Berthou, 2001; Freckelton, 2009). Some published indices use measurements of small elements, such as claws (e.g. Samuels & Van Valkenburgh, 2008). However, we found that these elements were frequently damaged or missing, and their small size precluded accuracy of measurement with hand-held callipers; thus, we excluded them. Given that 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 the present 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.

CLIMBING BEHAVIOUR

Surveys of Philippine small mammals conducted from 1995 to 2011 include published trapping records for every species collected (Balette *et al.*, 2009, 2011, 2013a, b; Alviola *et al.*, 2011; Duya *et al.*, 2011; Rickart *et al.*, 2011, 2013, 2016; Heaney *et al.*, 2013a, b). 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 (Supporting Information, Appendix S4). Additional details of localities and trapping methods can be found in the citations above. We calculated a climbing probability for each species as follows:

$$\text{Climb index} = (\text{AC}/\text{AT}) / [(\text{AC}/\text{AT}) + (\text{GC}/\text{GT})]$$

where AC is 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 zero (terrestrial only) to one (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 one. Although not recorded in the citations above, *Apomys gracilirostris* is currently known only from terrestrial captures (Ruedas, 1995; L.H.R., field notes) and was given a score of zero. For non-Philippine species, which generally lack detailed trapping data, we scoured the literature for information on climbing behaviour and scored each species qualitatively into one of three groups: 'Terrestrial', 'General' and 'Arboreal' (Supporting Information, Appendix S4). Here, 'Arboreal' means that climbing is an integral life-history trait for the species, 'General' refers to species that are known to climb opportunistically but are not thought to require climbing for survival, and

'Terrestrial' indicates species that are not thought to climb owing to habitat, behavioural or dietary niche.

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.*, 2013a; Pagés *et al.*, 2015; Supporting Information, Appendix S5). Sequences were aligned with MAFFT (Katoh and Standley, 2013) and inspected visually using Geneious v.7.1 (<https://www.geneious.com>). We found no ambiguous regions of the alignment. We selected the best-fitting 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 BEAST2 v.2.4.3 (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 BEAST2 v.2.4.3 were run for 200 million generations. Convergence was evaluated using Tracer v.1.6.0 (Rambaut *et al.*, 2018) to confirm that effective sample sizes were > 1000, that the trace of the log-likelihood had plateaued and that each chain reached the same plateau. We used TreeAnnotator v.2.4.3 (Bouckaert *et al.*, 2014) to discard the first 20% of trees as burn in and to generate a time-calibrated maximum clade credibility tree (Fig. 2).

BAYESIAN GENERALIZED LINEAR MULTILEVEL MODELLING

We modelled the relationship between morphology and climbing using phylogenetic Bayesian multilevel models, with the climb index as our response and the morphological indices as our predictors. Multilevel models have several advantages over other methods, because they can incorporate both intraspecific morphological variation and phylogenetic relationship as group-level effects. Intraspecific 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' means, 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

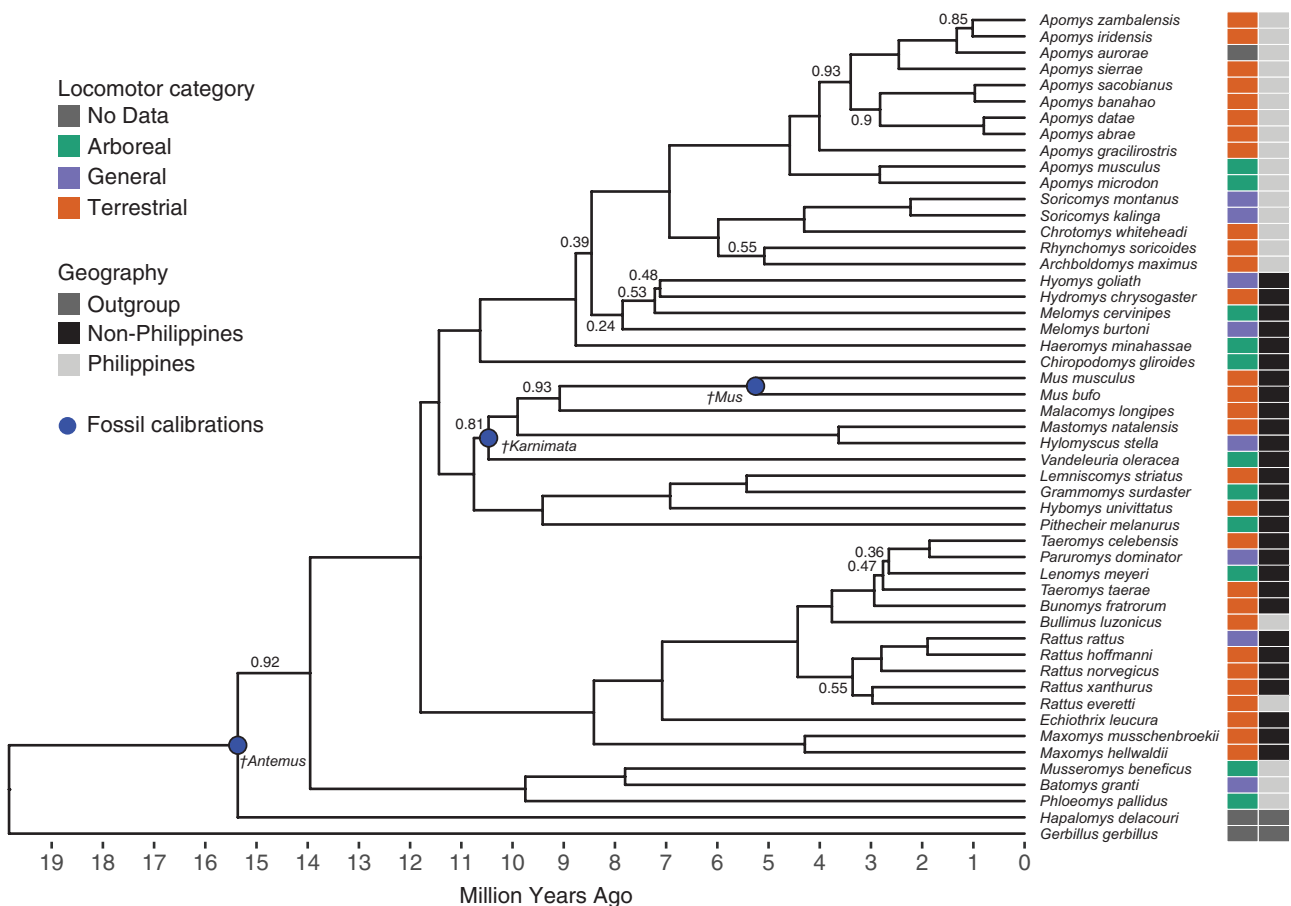


Figure 2. Maximum clade credibility tree, showing posterior probabilities < 0.95, the position of fossil calibrations, and the tip states for locomotor category and biogeographical origins.

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 centre-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 bounded the climbing probability estimates between zero and one. To avoid increased variance owing 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 resulted in 100 models for each of the 17 indices. Our model is as follows:

$$\text{logit}[\text{Pr}(Y = 1)] = \alpha + \beta_N x_N + R_p + R_s + \epsilon,$$

where Y is a vector of climbing probabilities, α is the intercept, β_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 χ^2 prior (de Villemereuil *et al.*, 2013; Carter & Worthington, 2016), and ϵ represents residual variance and is fixed to one for binary data (Hadfield *et al.*, 2013). A significant relationship between the climbing index and a morphological index is shown by a posterior probability (β_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 behaviour for other species of murines that lack detailed observational data (see Climbing Behaviour 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 (Supporting Information, Appendix S4; Fig. S1).

We fitted 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 as follows:

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

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 θ_j is the intercept or threshold for the j th cumulative probit, i.e. $\text{probit}[P(Y_i \leq j)]$. 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 λ ; 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 whether the trait is strongly associated with phylogenetic relatedness. We used the `pp_check` function from brms to validate our model by comparing observed data with simulated data from the posterior predictive distribution. We compared the predictive ability of each model using k -fold cross-validation using subset number $k = 10$. This method divides the data into ten subsets (default in brms), then validates the results of the nine subsets for each missing subset.

RESULTS

The general time reversible with a proportion of invariant sites and gamma distributed rate variation (GTR+I+ Γ) model of sequence evolution was found to be the best fit for all five gene partitions of the alignment. All four BEAST2 v.2.4.3 runs converged, and every run led to estimated sample size 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.*, 2013b; Rowe *et al.*, 2016; Aghova *et al.*, 2017; Rowsey *et al.*, 2018). Posterior probability of clade support was largely > 95%, although a few nodes were poorly supported (Fig. 2).

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. 3). These four indices are MANUS (length of third proximal phalanx of hand/length of third metacarpal; a measure of relative finger length), PES (length of third proximal phalanx of foot/length of third 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. 3; Table 2). The GI index coefficient had a negative credible interval that did not overlap zero (Table 2). However, because the intercept value did overlap zero and the credible interval of the regression coefficient was large, we excluded this measurement from future models. Additional ordinal models were fitted using the four variables MANUS, PES, IM and TAIL.

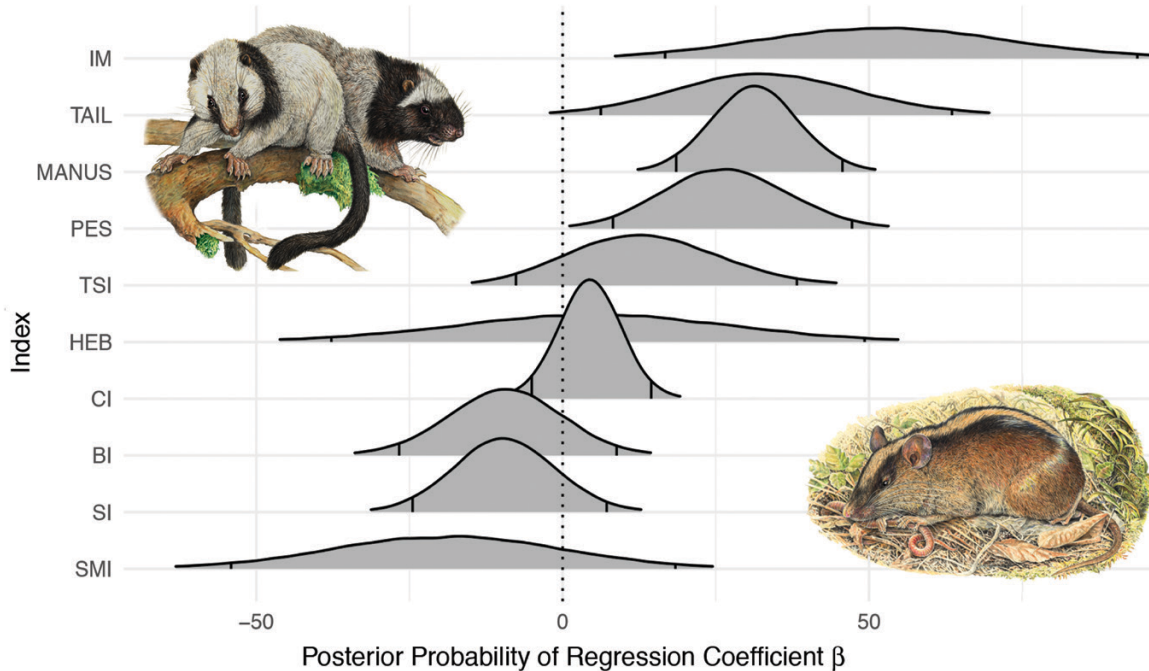


Figure 3. Results of logistic regression models in MCMCglmm. Density plots display the posterior probability of the β regression coefficient for each morphometric index, with 95% credible intervals delimited by vertical bars. Eight variables with large variance are not shown (see Table 2). Two Philippine 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.

Table 2. Results of MCMCglmm logistic regression of morphological index vs. arboreality.

Index	α HPD	α 95% credible interval	β HPD	β 95% credible interval
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)
MANUS	-22.50	(-32.89, -12.43)	31.3188	(17.36, 45.57)
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)
PES	-12.35	(-21.35, -3.10)	26.4282	(6.46, 47.04)
IM	-38.40	(-67.13, -10.09)	52.4149	(13.17, 92.99)
TAIL	-16.51	(-32.06, -2.29)	32.1920	(3.63, 63.20)
SI	6.23	(-6.40, 18.71)	-9.7533	(-25.89, 7.06)

α is the intercept, and β is the regression coefficient of the index. HPD represents the highest density of the posterior distribution. Coefficients that do not overlap zero are in bold.

Ordinal mixed models were used to estimate how well the four variables fitted with predicted categorical locomotor modes in species that lacked quantitative

climbing assessments. All models converged properly; each parameter had a high effective sample size (> 1000), and posterior-predictive checks showed

good model fit (Supporting Information, Fig. S2). We fitted regularizing normal priors on the group-level effects $N(0, 1.5)$ to prevent Markov chain Monte Carlo (MCMC) chains from searching unreasonable areas of parameter space (Gelman, 2006; McElreath, 2016). Each of the four variables had a positive effect on locomotor mode in murines (Table 3), but marginal effects plots demonstrated that both TAIL and IM had large credible intervals, which diminished their value for inferring locomotor state (Fig. 4). These results were confirmed with k -fold cross-validation, which showed that MANUS was the best-fitting model for climbing in murine rodents (although the standard errors of MANUS and PES overlapped; Table 4), and that TAIL was the poorest fitting of the four ordinal models.

There was high variance in the posterior distribution of Pagel's λ values for all indices owing 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 the phylogenetic signal of MANUS (Fig. 5; Table 5). Similar values were estimated for PES and IM, but TAIL produced a higher Pagel's λ (Fig. 5).

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 the ecological traits of these species. 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 assign other murine species accurately 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 β values and intercept values that do not overlap zero. MANUS and PES also effectively predicted the 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 behaviour in murines. Given the high predictive ability (Fig. 4) and low phylogenetic signal, we conclude that the MANUS index is a simple and effective way to infer climbing behaviour 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.

The observed relationship between finger length and climbing is not new, as having long having long fingers relative to hand size is thought to increase grasping ability, a crucial 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 test quantitatively the assumption that hand proportions and climbing behaviour 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 might 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 an ecomorphological signal that might be obscured by forcing naturally continuous life-history traits into categories.

Skeletal features previously associated with climbing in rodents and other small mammals include equally proportioned limbs (IM of approximately one), 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).

Table 3. Results from brms ordinal regression for four indices

Index	α [1] mean	α [1] 95% credible interval	α [2] mean	α [2] 95% credible interval	β mean	β 95% credible interval
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)

" α " values [1] and [2] represent the two estimated thresholds between the three categorical locomotor modes.

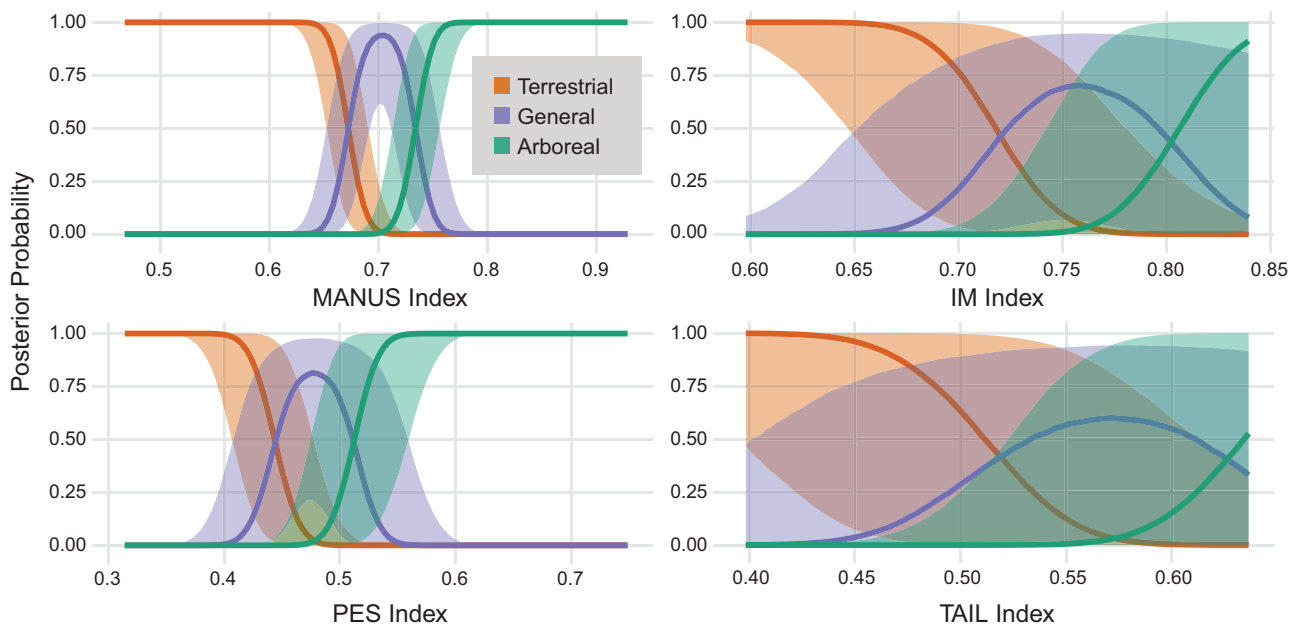


Figure 4. Marginal effect plots of ordinal models for the four strongest predictors of locomotion. The 95% credible intervals are displayed around the mean trend lines. The x -axis scales are bounded by the observed values for each of the four indices.

Table 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

Although 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 attributable to the large phenotypic variation across murine rodents. The Philippine species in the present 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 predict climbing behaviour effectively. Perhaps other measurements are important in more phenotypically conserved groups,

although our results demonstrate that MANUS effectively predicts climbing behaviour 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 for one experimental example, see Horner, 1954). Our results support a positive relationship of tail length with climbing in Philippine murines, but we find large variance (Supporting Information, Fig. S1) and low predictive ability (Fig. 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 5; Fig. 5) and, without additional research, we caution against using this single metric to infer climbing in mammals.

Although not without variance, phylogenetic signal in the MANUS index is low. Low signal may be interpreted in a variety of ways (Kamilar & Cooper, 2013), but we suggest that a Pagel's λ HPD of 0.021 (Table 5; Fig. 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). Although our understanding of locomotory styles of extinct species will always require inference, our findings here suggest that relative finger length is

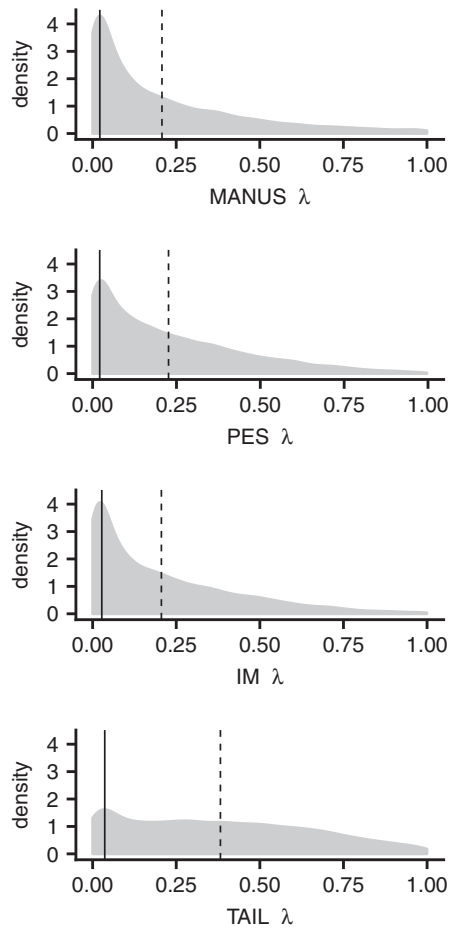


Figure 5. Posterior distribution of Pagel's λ for each of the four morphometric indices that predict locomotor category. Vertical lines indicate mean (dashed) and highest posterior density (continuous).

Table 5. Estimated Pagel's λ values for four indices

Index	Highest posterior density	Mean	95% credible interval
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)

a simple and effective way to infer climbing behaviour in murines and, perhaps, in mammals more generally.

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AUTHOR CONTRIBUTIONS

J.A.N. designed the study, with suggestions from J.A.E. and L.R.H. J.A.N. collected measurement data and developed statistical models. L.R.H., T.C.D., A.S.A., K.C.R. and J.A.E. collected specimens for this study. J.A.N. wrote the manuscript, with input from all authors. We have no competing interests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Raw linear measurements of Philippine murines.

Appendix S2. Morphological indices of Philippine murines.

Appendix S3. Morphological climbing indices of Philippine and non-Philippine murines.

Appendix S4. Climbing indices and trapping records of Philippine murines.

Appendix S5. GenBank accession numbers.

Figure S1. Density plots of murine climbing indices.

Figure S2. Posterior predictive checks of ordinal models.

SHARED DATA

Data and R code are currently available at: https://github.com/jonnations/Murine_Morphology