Revisiting Old Questions Through Phylogenetic Models: Bone Mineral Content in Arboreal Primates

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Introduction

H1: «Optimal performance» minor adjustments in bone mineral content have significant structural consequences, bone mineralization is expected to remain stable across taxonomic levels (Currey & Alexander, 1985; Currey, 2003). *First long bones which dated back to 475 million years ago, conserved throughout evolution* (Erikson et al., 2002).

H2: Against «optimal performance» Weinans and Prendergast (1996), Nowland and Prendergast (2005), Jepsen (2011) and Blob et al. (2014)

Research Question:

To what extent is primate bone mineralization driven by phylogenetic inertia versus life history and locomotor ecology?

Biological Context
How do **Age** (Ontogeny), **LifeSpan, Sex, Bone side** and **Bone type** influence mineralization?

Ecological Context
Does **Home Range** size or **Canopy Height** dictate the metabolic cost of maintaining dense bone?

Biomechanical Context
Does **Locomotor Habit** and the **Humerofemoral Index** (log_humFem) drive site-specific changes?

Material:

- Non-pathological humeri and femora from 14 arboreal primate species (*n: 180*)
- **Mineralization**: Bone mineral density or bone tissue present (Allen & Burr, 2019)
- Infant: 9, Juvenile: 42, Subadult: 50, Adult: 79

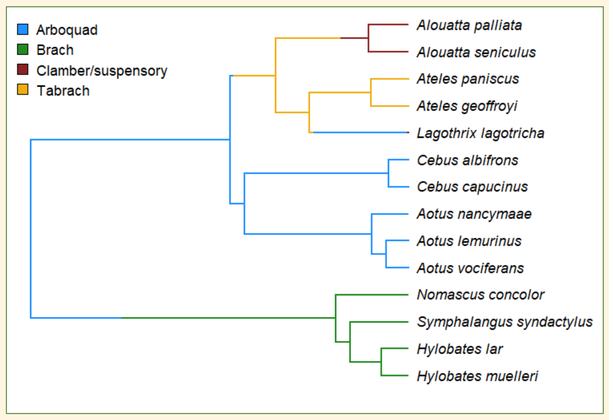


Fig.1: Stochastic mapping of a locomotor mode along branches (*make.simmap*)

Methods:

- **Scanning Parameters**: Voltage: 100kV, Current: 200 µA, Power: 20W
- **Mineral density calibration** is done in 1200 mg HA/cm3 on micro-CT phantom



- CT reconstructions are done in VGStudio Max. 3D Slicer is used for 3D model creation. Analysis is done in R
- A linear regression equation was derived from the mean grey-scale values of the phantom inserts in 3DSlicer and applied to the specimens to convert attenuation values (Hounsfield Units) into mgHA/cm³ (Bouxsein et al., 2010; Schlecht & Jepsen, 2013; Kim et al., 2021)

Analysis:

- **Phylogenetic signal (λ)** in locomotion mode and mineralization level: *geiger* package (Harmon et al., 2008), *ape*, *phytools* (Revell, 2025)
- **Phylogenetic generalized linear mixed models (PGLMM)**: *phyr* (Dean et al., 2018)
- **Bayesian Statistics**: *MCMCglmm* (Revell & Harmon, 2019)
- **Model comparison**: *AICc* and DIC (*geiger)*
- **Timetree**: Craig, Hedges, Kumar 2024

Results

Phylogenetic signal (λ)

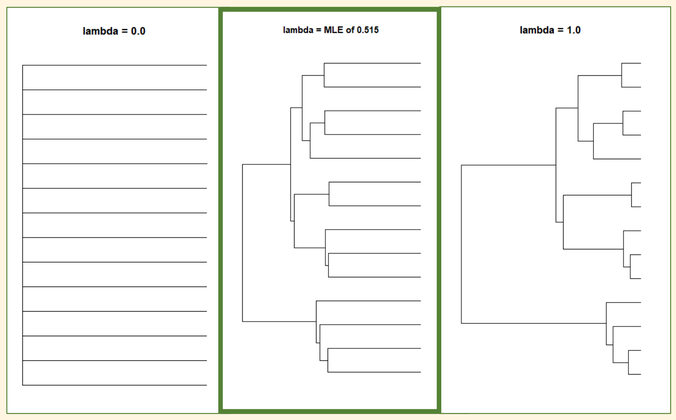


Fig.2: A Pagel's lambda (λ) test on the species-averaged residuals revealed no significant phylogenetic signal in bone mineralization (**λ = 0.50**, *p = 0.19*) (increasing phylogenetic signal from left to right).

Bayesian Mixed Models

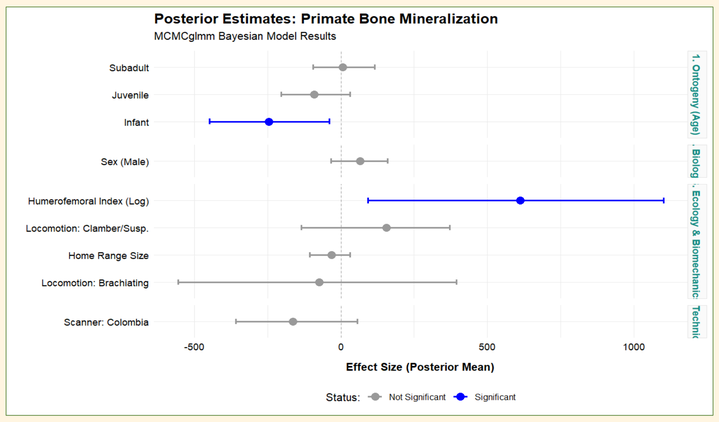


Fig.3: The best supported model selected via DIC: fixed effects account for **55.6%** of total variation ($R^2_{marginal}$), while the full model captures **95.5%** ($R^2_{conditional}$). Age (Ontogeny) (*pMCMC: 0.02*); log_humFem (Biomechanics) (*pMCMC: 0.01*).

Variance Partitioning of the best supported Bayesian model

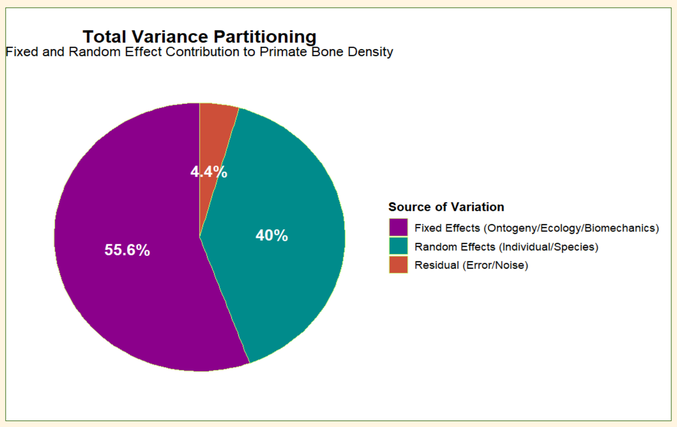


Fig.4: Fixed effects (ontogeny, ecology, and biomechanics) explain the majority of the variation (55.6%). Of the remaining variance, the vast majority is attributed to individual-level plasticity (37.22%), and species accounted for (0.86%) variation.

Phylogenetic generalized linear mixed model (PGLMM)

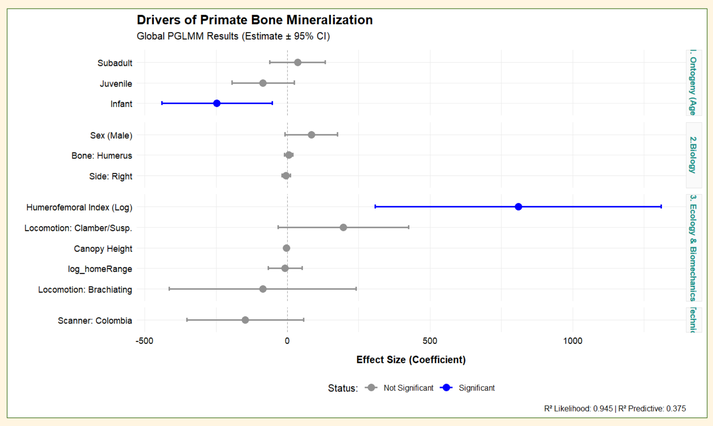


Fig.5: The comprehensive global model (AIC = 1960.3) was the best-supported model, outperforming the baseline model (ΔAIC = 71.7) and single-context models (Locomotor ΔAIC = 20.7; Spatial ΔAIC = 44.2). Results indicate that biomechanical proportions (log_humFem, *p < 0.001*) show a significant positive relationship with bone mineralization, while infant status (*p = 0.025*) negative.

Discussion

Key-Takeaways

X	«Optimal performance
√	Against «Optimal performance»

- Mineralization is not strictly dictated by deep evolutionary history (phylogeny). Instead, it varies between individuals based on their age, locomotor behavior, and spatial ecology.
- Both models strongly agree that:

Biomechanical Context: The intermembral index (log_humFem) is a highly significant predictor of bone density (PGLMM *p = 0.001*; MCMCglmm *pMCMC = 0.01*)

Ontogeny (Age): Infants have significantly lower bone mineralization than adults (estimate - ~245 mg/cm³, *p < 0.02* in both models)

- In PGLMM, clambering/suspensory (*p = 0.092*) and being male showed marginal positive effect on bone density (*p = 0.07*). They lost its strict significance in Bayesian model selection (*pMCMC = 0.2*).
- In PGLMM, canopy height is marginally significant negative predictor (*p = 0.094*), while it is not in Bayesian model selection.

Methodological Limitation

Checking the selection of the Ornstein-Uhlenbeck (OU) model was not a statistical artifact of tree topology (Cooper et al., 2016):

- A parametric bootstrap (n = 1000 simulations) was performed to generate traits under a pure Brownian Motion process.
- False positive rate of 7.8% at the maximum, false Delta AICc generated by the null simulations was 8. Because my empirical Delta AICc (2.28) was exceeded, **I cannot statistically reject a Brownian Motion (BM) model in favor of OU**.

Therefore, while adaptive signals are present in the fixed effects, the underlying mode of evolution remains equivocal.

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