Limb Evolvability in *Pan troglodytes*

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IMPORTANT TERMS

Trait Covariance: the degree to which changes in one trait may influence the development and/or evolution of another trait (can be measured as **integration**)

Evolvability: how easy it is for a trait to evolve in response to selective pressures (less integration = more evolvability)

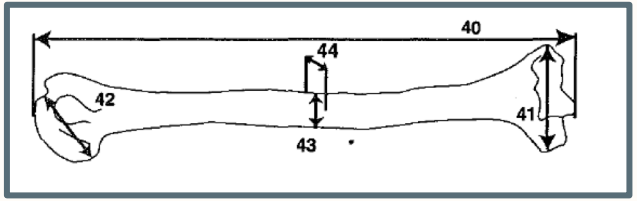
BACKGROUND

In primates, trait evolution is affected by the relationship between traits. Bones of the arm and legs tend to be highly integrated, displaying significant covariance. This integration appears to be due to functional demands – bones that work together need to fit well together.

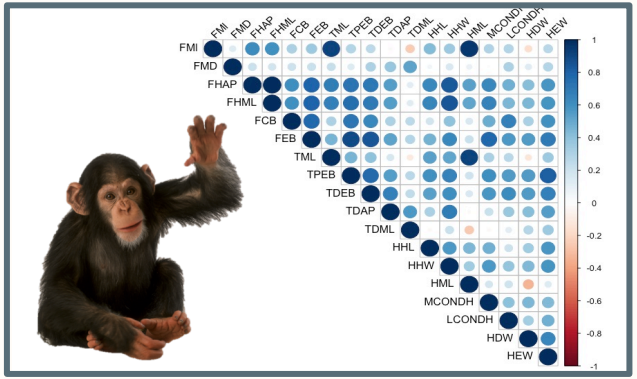
Unlike quadrupedal monkeys who use all four limbs to walk, chimps (*Pan troglodytes*) are partially bipedal and appear to have less integration between traits in their upper and lower limbs. This decrease in trait covariance may have resulted in increased evolvability among these traits - allowing for the upper and lower limbs to respond differently to evolutionary pressures and drive changes in limb function.

HYPOTHESES

1. Covariance will exist between the humerus, femur, and tibia of *Pan troglodytes,* shaping evolvability.
2. Traits of the upper limb will be less integrated and more evolvable than traits in the lower limb.



Figures 1 & 2. Above**:** Example **l**inear measures collected from chimp humerus, *Standards*, Buikstra J. & Ubelaker D. 1994
Below: Plot of trait covariances across humerus, femur & tibia.



	e(β)	*r(β)*	*Integration*	*a(β)*
Humerus	0.0056*	0.0077	0.5686*	0.4314
Femur	0.0029	0.0046	0.8401	0.1599
Tibia	0.0030	0.0045	-1.1548	2.1548

Table 1. Estimates of evolvability, respondability, integration, and autonomy. Asterisk (*) indicates high evolvability and low integration of humerus when compared to lower limb bones.

MATERIALS & METHODS

Osteometric data: 21 adult chimpanzees from the Mammal Collections at the American Museum of Natural History.

Measurements: standard & adjusted length, distal & proximal epiphyseal breadth, anterior-posterior diaphyseal diameter, medial-lateral diaphyseal diameter for humerus, femur, & tibia (**Figure 1**). Measures collected using osteometric boards and sliding digital calipers.

Methods: After controlling for sex, measures of evolvability were estimated using equations calculated by Hansen & Houle 2008, Bolstad et al. 2014 (See below)

Statistic	Symbol	Equation
Evolvability	$e(\beta)$	$\beta' P \beta$
Respondability	$r(\beta)$	$\sqrt{\beta' P^2 \beta}$
Autonomy	$a(\beta)$	$\frac{c(\beta)}{e(\beta)}$

RESULTS

Results support our hypotheses. These traits demonstrate the expected pattern of positive covariance between limbs (Figure 2), and the humeral traits are considerably less integrated and more evolvable than those of the femur or tibia (Table 1). These findings suggest that this sample of *Pan* follows the expected pattern of primate limb evolvability.

Abstract:

In primates, trait covariance is common among limb segments and bony structures. Trait covariance signifies the changes in one trait that may influence the development and/or evolution of another trait. Evolvability refers to this influence, meaning trait covariance can affect an organism's ability to evolve when exposed to selective pressures. Covarying traits may limit a trait's ability to respond to selective pressures, indicating that traits with high covariance have low evolvability. When observing these differences in the humerus, femur, and tibia, it is essential to account for the measures of evolvability: the evolvability, respondability, autonomy, and integration of traits. In this study, we analyze how the measures of evolvability affect limb segments of chimpanzees, *Pan troglodytes*. We hypothesize that covariance between the humerus, femur, and tibia will affect evolvability, and the humerus will be less integrated than the femur or tibia. After controlling for sex, results indicate that the humerus is less integrated than the femur or the tibia. These findings support our initial predictions, further suggesting that covariance between structures effects evolvability and that humeral traits are significantly less integrated and more evolvable than those of the lower limb.