



# Digest: Microhabitat use and developmental timing shape anuran limb evolution\*

Peishu Li<sup>1,2</sup>

<sup>1</sup>Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois 60637

<sup>2</sup>E-mail: [peishu@uchicago.edu](mailto:peishu@uchicago.edu)

Received May 5, 2020

Accepted June 16, 2020

**Do frog limb shapes reflect microhabitat use against the backdrop of shared ancestry, body size variation, and developmental constraints? Stepanova and Womack found that when phylogeny and body size are controlled, microhabitat use is a key factor in explaining anuran limb evolution. The shape of distal limb elements in anuran limbs also evolves at a higher rate than proximal elements, suggesting that a relaxation of developmental constraints in distal elements may be shared across tetrapod limb development.**

A holistic understanding of morphological evolution requires consideration of both extrinsic and intrinsic factors (Goswami et al. 2014). Extrinsic factors, often in the form of similar selective pressure from the environment, are frequently invoked to explain phenotypic convergence between lineages (Losos et al. 1998). In contrast, intrinsic factors, such as allometry and trait covariation, may direct patterns of phenotypic variation without apparent adaptive significance (Goswami et al. 2014).

The tetrapod limb skeleton offers an ideal system to disentangle the relative contribution of extrinsic versus intrinsic factors in shaping morphological evolution. Given their proximity to external substrate, limbs have been a key character in studying the ecomorphological diversification of both extant and extinct lineages (e.g., Van Valkenburgh 1987). On the other hand, even with ecological specializations, limb morphology may still reflect the influence of allometry and phylogenetic history (Van Valkenburgh 1987). Moreover, in recent years, developmental processes are increasingly recognized as another major driver of morphological variation in the limb skeleton (Kavanagh et al. 2013). Differences in developmental timing may shape divergent patterns of morphological integration in the limb skeletons of closely related groups (Goswami et al. 2014). It has been postulated that in mammals, more distal, late-developing limb elements may be

more variable and susceptible to selection than proximal elements (Young and Hallgrímsson 2005). However, whether this constituted a common pattern observed in tetrapod limb development in general remained poorly understood.

In this issue, Stepanova and Womack (2020) examined the covariation of limb shape with phylogeny, body size, microhabitat use, and developmental timing in 236 living anuran species. Using three-dimensional geometric morphometrics and phylogenetic comparative methods, the authors found that both forelimb and hindlimb shapes showed a significant relationship with both phylogenetic history and body size. When phylogeny and body size were controlled, microhabitat use drove limb shape differentiation among anurans, and an evolutionary model with individual optima for each microhabitat best explained the pattern of anuran limb evolution. Moreover, species utilizing different microhabitats exhibited divergent evolutionary rates and morphological disparity in limb skeletons. Burrowers stood out with higher evolutionary rates in both forelimbs and hindlimbs than all the other microhabitat ecomorphs. Lastly, in both forelimbs and hindlimbs, distal elements with late developmental timing had higher evolutionary rates than proximal elements. Distal elements also appeared more susceptible to changes associated with or related to body size and microhabitat use.

While previous analyses presented conflicting results on the relationship between anuran limb morphology and microhabitat, Stepanova and Womack (2020) demonstrated that both anuran forelimbs and hindlimbs exhibit similar adaptive responses to

\*This article corresponds to Stepanova, N. and Womack, M.C. (2020), Anuran limbs reflect microhabitat and distal, later-developing bones are more evolutionarily labile. *Evolution*. doi:10.1111/evo.13981. <https://onlinelibrary.wiley.com/doi/10.1111/evo.13981>

microhabitat variation, once the effect of phylogeny and body size were controlled. Future studies may further investigate the pattern of morphological integration between anuran forelimbs and hindlimbs. Moreover, within-limb differences in evolutionary rates and morphological disparity observed in anurans corroborate previous results on mammalian limb development (Young and Hallgrímsson 2005). This supports the hypothesis that relaxed developmental constraints on distal limb segments may characterize tetrapods as a whole. The structure of the underlying gene regulatory network that may explain this shared pattern in tetrapod limb development merits further investigation.

#### LITERATURE CITED

- Goswami, A., J. B. Smaers, C. Soligo, and P. D. Polly. 2014. The macroevolutionary consequences of phenotypic integration: from development to deep time. *Proc. R. Soc. B Biol. Sci.* 369:20130254.
- Kavanagh, K. D., O. Shoval, B. B. Winslow, U. Alon, B. P. Leary, A. Kan, and C. J. Tabin. 2013. Developmental bias in the evolution of phalanges. *Proc. Natl. Acad. Sci. USA* 110:18190–18195.
- Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279:2115–2118.
- Stepanova, N., and M. C. Womack. 2020. Anuran limbs reflect microhabitat and distal, later-developing bones are more evolutionarily labile. *Evolution* <https://doi.org/10.1111/evo.13981>
- Van Valkenburgh, B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. *J. Vertebr. Paleontol* 7:162–182.
- Young, N. M., and B. Hallgrímsson. 2005. Serial homology and the evolution of mammalian limb covariation structure. *Evolution* 59:2691–2704.

Associate Editor: K. Moore  
Handling Editor: T. Chapman

#### SUBMIT A DIGEST

Digests are short (~500 word), news articles about selected original research included in the journal, written by students or postdocs. These digests are published online and linked to their corresponding original research articles. For instructions on Digests preparation and submission, please visit the following link: <https://sites.duke.edu/evodigests/>.