Natural History Note

Natural History Constrains the Macroevolution of Foot Morphology in European Plethodontid Salamanders

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abstract: The natural history of organisms can have major effects on the tempo and mode of evolution, but few examples show how unique natural histories affect rates of evolution at macroevolutionary scales. European plethodontid salamanders (Plethodontidae: *Hydromantes*) display a particular natural history relative to other members of the family. *Hydromantes* commonly occupy caves and small crevices, where they cling to the walls and ceilings. On the basis of this unique and strongly selected behavior, we test the prediction that rates of phenotypic evolution will be lower in traits associated with climbing. We find that, within *Hydromantes*, foot morphological traits evolve at significantly lower rates than do other phenotypic traits. Additionally, *Hydromantes* displays a lower rate of foot morphology evolution than does a nonclimbing genus, *Plethodon*. Our findings suggest that macroevolutionary trends of phenotypic diversification can be mediated by the unique behavioral responses in taxa related to particular attributes of their natural history.

Keywords: evolutionary rates, phenotypic evolution, convergence.

Introduction

Understanding the forces that alter the pace of evolution is essential for deciphering how phenotypic diversity is generated and maintained. Because adaptive evolution is the product of natural selection, changes in ecological selection pressures are expected to affect the evolution of phenotypic traits that enable organismal survival in those habitats. Not surprisingly, then, changes in habitat or ecological regime can result in changes in phenotypic evolutionary rates (Hoffman and Hercus 2000; Hendry et al. 2008). For example, evolutionary rates are frequently higher in populations that face ecological shifts or novel environments than in those found in more typical or undisturbed habitats (Reznick et al. 1997; Hendry et al. 2008). Likewise, species invading new habitats or those introduced to new geographic localities can display elevated rates of evolution (McPeek 1995; Clegg et al. 2002; Revell et al. 2007; Herrel et al. 2008). These and other examples (e.g., Franssen et al. 2013; Caruso et al. 2014; Cureton and Broughton 2014) demonstrate how alterations in ecological selective regimes can have a profound effect on the rate at which phenotypic diversity accumulates.

Current evidence suggests that rates of phenotypic evolution frequently vary among lineages, and they often do so as a response to differing selective pressures that these lineages face (e.g., Gingerich 1983, 2001; Hendry and Kinnison 1999; Harmon et al. 2003; Hendry et al. 2008; Mahler et al. 2010). Likewise, rates of evolution can also differ among traits within the same lineage, particularly when different traits within species experience distinct selective regimes, thereby affecting the pace at which their evolution occurred (Martin and Pfennig 2011; Klaczko et al. 2015). Indeed, some have suggested that certain types of traits evolve at higher rates than others (Gittleman et al. 1996; Blomberg et al. 2003), and a number of empirical studies have shown that traits can evolve at different rates (e.g., Hone et al. 2005; Ackerly 2009). For example, cold tolerance in some lizards evolves at a faster rate than does heat tolerance, because behavioral thermoregulation buffers organisms from selection attributable to the latter environmental pressure but not the former (Munoz et al. 2014). Likewise, sex-specific responses to environmental effects can generate dramatic differences in the rate of evolution in sexually dimorphic traits (e.g., Kaliontzopoulou et al. 2015). Thus, there is emerging evidence suggesting that rates of phenotypic evolution can differ among traits, even within the same lineage and measured from the same individuals (see also Gvozkik 2015; Wheatcroft and Price 2015).

The European salamanders of the genus *Hydromantes* display a unique natural history and suite of associated be-

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havioral adaptations that provide an interesting backdrop upon which to evaluate the influence of ecological selection on rates of phenotypic evolution. Unlike most other plethodontid salamanders, European *Hydromantes* spend significant time in caves and subterranean crevices (Lanza 1991; Salvidio 1992, 2006; Lanza et al. 1995, 2006), where they are often found clinging to the walls and ceilings (fig. 1). Additionally, they exhibit this behavior even when in terrestrial environments, clinging to rock faces and walls as well as trees (Salvidio et al. 1994; Casali et al. 2005; Lanza et al. 2006). Morphologically, adult *Hydromantes* display considerable webbing on their hands and feet (Lanza 1991; Adams and Nistri 2010; Salvidio et al. 2015), which, in other salamander lineages (e.g., *Bolitoglossa*), generates the suction required for adhesion during climbing (see Alberch 1981). Furthermore, recent morphometric investigations in *Hydromantes* have demonstrated that adult foot morphology is highly convergent across species (Adams and Nistri 2010), a pattern consistent with the hypothesis that foot morphology is under strong selection due to the biomechanical constraints associated with climbing. If this hypothesis is correct, other morphological traits not associated with climbing would not be affected by these ecological challenges. Therefore, when morphological patterns are considered in light of natural history observations for the genus, a clear macroevolutionary prediction emerges: that evolutionary variation in foot morphology should be restricted due to the strong selection pressures elicited as a result of the biomechanical requirements of climbing. If this hypothesis is correct, one can therefore predict that the evolutionary rate of phenotypic traits associated with climbing in *Hydromantes*—namely, aspects of foot morphology—should be lower than rates of evolution for other phenotypic traits not associated with this behavior. Likewise, one may predict that rates of phenotypic evolution in foot morphology should be lower in *Hydromantes* than in other salamander lineages that do not



Figure 1: *A* and *B*, *Hydromantes strinatii* found in its native habitat. Photographs courtesy of F. Crovetto. *C*, D. C. Adams in a Tuscan cave, having recently retrieved an adult *Hydromantes italicus* from the cave wall.

exhibit extensive climbing. In this natural history note, we test these predictions explicitly.

Material and Methods

We obtained phenotypic measurements from 198 adult salamander specimens from all eight species of Italian *Hydromantes* from the collections of the Museo di Storia Naturale (Sezione di Zoologia), Universitá di Firenze (mean specimens per species [range] = 25 [15–33]). Only specimens from a single geographic locality per species were utilized to minimize among-locality variability. From each specimen, we measured several morphological traits related to general body proportions as well as several foot traits that were related to climbing. Specifically, the following phenotypic traits were measured (fig. 2*A*): head length (HL), forelimb length (FLL), hindlimb length (HLL), foot area (FA), middle toe length (MT), and sinuosity (Sin; a measure of the degree of foot webbing; Jaekel and Wake 2007; Adams and Nistri 2010). HL, FLL, and HLL were measured in millimeters using Mark IV digital calipers (Brown and Sharpe), whereas FA (mm^2), MT (mm), and Sin were quantified from digital images using TpsDig2 (Rohlf 2013). In addition to the above data for *Hydromantes*, we also obtained FA measurements from 510 adult individuals from 45 species of salamander from the genus *Plethodon*. For both species, FA was square-root transformed, so that all traits were in similar units and scale for subsequent analyses (see Adams 2013). Species mean values for each trait were then obtained.

To test the predictions described above, we compared rates of phenotypic evolution among traits in the following manner. First, we estimated rates of phenotypic evolution for all traits under a Brownian motion model of evolution using a multigene, time-calibrated molecular phylogeny for amphibians (Pyron 2014). To match our data to the tree, we pruned the original phylogeny, which contained over 3,300 species, so that only the relationships among the eight species of Italian *Hydromantes* were retained (fig. 2*B*). Next, the fit of each trait to the phylogeny was obtained under Brownian motion, and from this fit, we estimated both the rate of phenotypic evolution (σ^2) for the trait and its 95% confidence intervals (obtained from the Hessian matrix; e.g., Adams 2013). In like manner, we estimated the rate of phenotypic evolution and 95% confidence intervals for FA in *Plethodon*. Comparisons of phenotypic rates of evolution were then accomplished by examining the overlap of 95% confidence intervals across traits. Finally, for FA in *Hydromantes*, we compared the fit of a single-peak Ornstein-Uhlenbeck (OU) model to that of Brownian motion (BM) using standard likelihood procedures. Data underlying the results are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.4cs45 (Adams et al. 2017). All analyses were performed in R 3.2.0 (R Core Team 2016) using scripts written by the senior author.

Results

Comparisons of evolutionary models found little support favoring an OU process over Brownian motion ($\log L_{BM} = -6.65$; $\log L_{OU} = -6.55$). This result was not surprising, however, because there were only eight species in the group, and the power to detect an OU process with such small sample sizes was exceedingly limited (see fig. 6 in Boettiger et al. 2012). When comparing evolutionary rates among

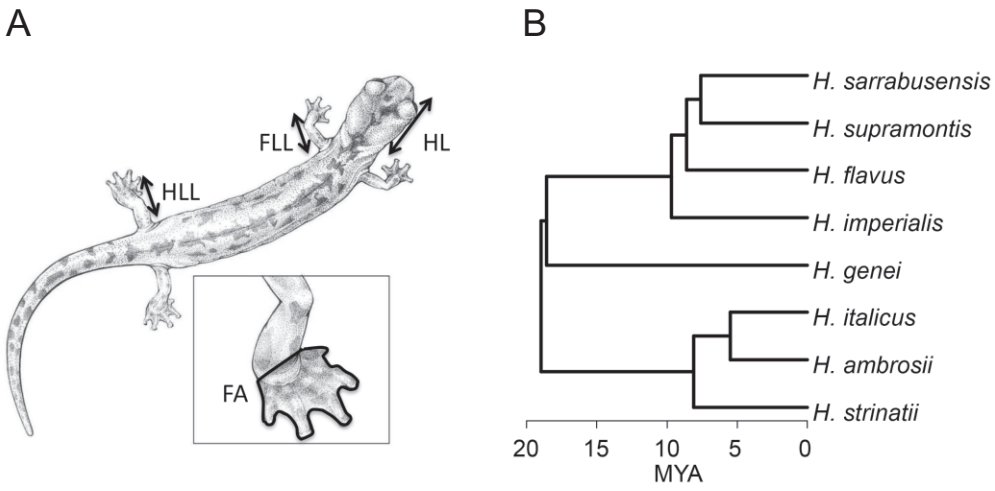


Figure 2: *A*, Locations of primary phenotypic measurements obtained from adult *Hydromantes* salamanders (FA = foot area, FLL = forelimb length, HL = head length, HLL = hindlimb length). Drawing by J. Gassman. *B*, Time-calibrated molecular phylogeny displaying the estimated phylogenetic relationships among European *Hydromantes* salamander species (adapted from Pyron 2014).

traits within *Hydromantes*, we found that FA evolved significantly more slowly than did the phenotypic attributes that were not related to climbing (HL, HLL, and FLL), a pattern consistent with our predictions (fig. 3). Likewise, the other foot-related traits (MT and Sin) also evolved more slowly than the general body measures (fig. 3), corroborating the hypothesis that foot traits associated with climbing evolved more slowly than did other traits. Importantly, we found that the rate of foot evolution in the nonclimbing genus (*Plethodon*) was similar in magnitude to rates of phenotypic evolution of body traits in *Hydromantes* but was significantly higher than rates of evolution of foot traits in *Hydromantes* (fig. 3). This finding was consistent with the prediction that rates of phenotypic evolution for traits related to climbing are lower in lineages that climb (*Hydromantes*) than they are in lineages that do not extensively display this behavior. Taken together, these observations are consistent with biological predictions, based on natural history, that foot morphology in *Hydromantes* is under strong ecological selection due to the biomechanical constraints of climbing, which results in a lower rate of evolution of foot morphology at the macroevolutionary level.

Discussion

Why rates of phenotypic evolution differ among taxa and traits is a question that has fascinated biologists for decades (Simpson 1944; Gingerich 1993; Foote 1997; Sidlauskas 2008). In some cases, elevated rates of phenotypic evolution may be observed, such as when taxa experience diversifying selection from ecological release (e.g., Millien 2006; Thomas et al. 2009) or from unique selection pressures resulting from the exploitation of novel niches or habitats (Revell et al. 2007; Hulsey et al. 2010; Mahler et al. 2010; Martin and Wainwright 2011). By contrast, lower rates of phenotypic evolution may be observed when taxa are near their adaptive peak (Collar et al. 2009) or when stabilizing selection restricts the variation in a trait at macroevolutionary scales (Wheatcroft and Price 2015). For foot morphology in European *Hydromantes*, patterns of morphological evolution appear to be a case of the latter. Specifically, we found that foot morphology evolved at a significantly lower evolutionary rate than did other phenotypic traits not associated with climbing. Furthermore, we found that the rate of evolution of foot morphology in a nonclimbing salamander lineage (*Plethodon*) was similar to that observed in general body traits but greatly exceeded the rate of evolution of foot morphology in the climbing lineage (*Hydromantes*). Together, these observations are consistent with predictions based on natural history: that foot morphology in *Hydromantes* is under strong ecological stabilizing selection due to the biomechanical constraints of climbing, which results in a lower rate of evolution of foot morphology at the macroevolutionary level.

Our findings also suggest that the phenotypic traits evaluated do not evolve in an identical manner in *Hydromantes* but instead display some degree of evolutionary independence, with foot morphology evolving separately

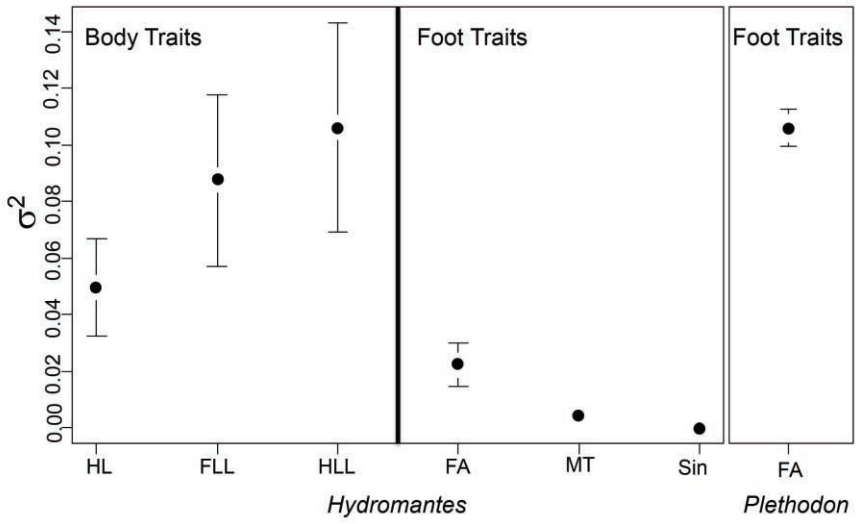


Figure 3: Estimates of evolutionary rates for the phenotypic traits used in this study (FA = foot area, FLL = forelimb length, HL = head length, HLL = hindlimb length, MT = middle toe length, Sin = foot sinuosity). For each trait other than MT and Sin, the evolutionary rate and 95% confidence intervals are shown; 95% confidence intervals for MT and Sin are too small to be viewed. The rate of phenotypic evolution in FA for *Plethodon* is displayed in the rightmost panel.

from other phenotypic traits in this group. Such a pattern is consistent with the notion of modularity, in which strong evolutionary correlations are observed within subsets of traits (modules), but where the covariation between modules is relatively weaker (Cheverud 1982; Wagner 1996; see also Klingenberg 2014; Adams 2016). Under this scenario, differing selective regimes might favor distinct patterns of covariation in different phenotypic modules, resulting in differing evolutionary trajectories at macroevolutionary scales (Wagner et al. 2007; Clune et al. 2013; Goswami et al. 2014; Denton and Adams 2015). If this hypothesis is correct, it suggests that foot morphology may represent a distinct module from other traits, where different selection pressures influence its rate of evolution. It is increasingly being recognized that modular structure can have a profound effect on patterns of phenotypic diversification. As such, whether such modular structure underlies the differing rates of phenotypic evolution observed in other organismal systems (e.g., Kaliontzopoulou et al. 2015; Klaczko et al. 2015; Wheatcroft and Price 2015) remains an important open question for evolutionary biology.

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