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SYMPOSIUM

A Bigger Picture: Organismal Function at the Nexus of Development, Ecology, and Evolution: An Introduction to the Symposium

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Synopsis Over the past 40 years of research, two perspectives have dominated the study of ecomorphology at ontogenetic and evolutionary timescales. For key anatomical complexes (e.g., feeding apparatus, locomotor systems, sensory structures), morphological changes during ontogeny are often interpreted in functional terms and linked to their putative importance for fitness. Across larger timescales, morphological transformations in these complexes are examined through character stability or mutability during cladogenesis. Because the fittest organisms must pass through ontogenetic changes in size and shape, addressing transformations in morphology at different time scales, from life histories to macroevolution, has the potential to illuminate major factors contributing to phenotypic diversity. To date, most studies have relied on the assumption that organismal form is tightly constrained by the adult niche. Although this could be accurate for organisms that rapidly reach and spend a substantial portion of their life history at the adult phenotype (e.g., birds, mammals), it may not always hold true for species that experience substantial growth after one or more major fitness filters during their ontogeny (e.g., some fishes, reptiles). In such circumstances, examining the adult phenotype as the primary result of selective processes may be erroneous as it likely obscures the developmental configuration of morphology that was most critical to early survival. Given this discrepancy—and its potential to mislead interpretations of how selection may shape a taxon's phenotype—this symposium addresses the question: how do we identify such ontogenetic "inertia," and how do we integrate developmental information into our phylogenetic, ecological, and functional interpretations of complex phenotypes?

Introduction

The symposium *A Bigger Picture: Organismal Function at the Nexus of Development, Ecology, and Evolution* (January 2016, Society for Integrative and Comparative Biology, SICB) focused on a fundamental question in integrative biology: what links the ontogenetic stability and instability of phenotypes with the patterns of morphological diversity seen across the tree of life? Comparative anatomists have traditionally approached this question from one of two perspectives. For anatomical complexes critical to survival (e.g., feeding apparatus, locomotor systems, sensory structures), ontogenetic changes in morphology are often interpreted in terms of their ecological significance and linked to their putative importance for fitness. Across evolutionary time scales, morphological transformations in these complexes are examined through character stability or mutability during cladogenesis (Schwenk et al. 2009). Because ontogenetic changes in size and shape must enable the survival and reproduction of organisms, it is predicted that addressing such transformations at different time scales, from life histories to macroevolution, would create a deeper understanding of the major factors contributing to phenotypic diversity. This expectation is partly rooted on the assumption that the adult niche tightly constrains adult form (Norton et al. 1995; Loreau 2000; Pocheville 2014). Although this could be accurate for organisms that rapidly reach and spend a large portion of their life history at the adult phenotype (e.g., birds, mammals), it may not always hold true

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for species that experience substantial growth after one or more major fitness filters during their ontogeny (e.g., predation pressures prior to size-based refugia in some fishes, performance limitations on access to prey in reptiles). In such circumstances it may be erroneous to make adaptive interpretations based on the adult phenotype, as it likely obscures the developmental configuration of morphology that was most critical to early survival (Carrier 1996; Herrel and Gibb 2006).

The potential for morphological canalization as a result of developmental processes was noted by Frazzetta (1975) and described experimentally by Burggren (1992), but it was Carrier (1996) who provided the most tangible insight with his studies of locomotor development. Carrier noted that performance traits can be critical for survival immediately after birth or hatching (also see Heers et al. 2016). Neonates, however, are often "handicapped" by their small size, requisite coordination due to differentially immature anatomical and neurological structures, and naiveté about their environment. Altogether, these features can result in higher mortality rates for early life-history stages. Thus, he argued, the immense benefits of performance improvements in neonates and juveniles would result in adult phenotypes that specifically reflect selection on pre-adult forms (Carrier 1996). The logical extension of this argument is that adults may exhibit performance capabilities that exceed the demands of the adult niche (i.e., "over performers"; Gignac and O'Brien 2016; Herrel et al. 2016).

Carrier (1996) did not name this phenomenon, but we do so here as ontogenetic inertia. Ontogenetic inertia is the physiological, morphological, or performance consequence of developmental trajectories required to overcome one or more major selective filters acting on early life-history stages, but which specifically imbue adults with exaggerated physiologies or morphologies and cause them to over perform for their specific ecological niche. The primary value of identifying cases of ontogenetic inertia is that it helps researchers focus on the life-history stages that likely have the greatest impact on a species' phenotype. When ontogenetic inertia operates, adult phenotypes may loosely fit the resources they exploit and this may, in turn, open up new opportunities for more diverse resource exploitation.

Is ontogenetic inertia a universal phenomenon? Taxa with substantial parental care (e.g., placental mammals; see Santana and Miller 2016) are largely capable of successfully shepherding their offspring through early life-history stages when mortality would otherwise be high. In such cases, the mechanism thought to underlie ontogenetic inertia—fitness filters for phenotypic traits in early ontogeny—would be expected to play a lesser role in shaping a taxon's phenotype. Instead, developmental trajectories leading to phenotypes that specifically facilitate occupation of the adult niche would be more important (reviewed in Herrel and Gibb 2006). This mechanism is better understood as a major contributor to morphological diversifications across deep time (Marriog and Cheverud 2001, 2005) via heterochrony (Goswami et al. 2016; Urban et al. 2016), shifts in allometry (O'Brien et al. 2016), many-to-one mapping (Olsen and Westneat 2016) and terminal addition (Camacho et al. 2016), among other developmental processes. The role(s) of ontogenetic inertia in shaping organismal diversity, on the other hand, may be more complex and nuanced, requiring cross-disciplinary approaches that integrate data from organismal, life-history, and taxonomic levels.

A major consequence of failing to identify ontogenetic inertia, when present, is that we may erroneously attribute the conformation of adult phenotypes to a presumed adult niche. This can lead to spurious interpretations of how selection on physiology or performance may drive patterns of morphological, behavioral, or ecological diversification. Thus, we directed the symposium toward important questions at the interface of ontogeny and macroevolution that have yet to be fully addressed:

(1) How do we identify cases of ontogenetic inertia in biological systems, and what are the general patterns characterizing this phenomenon?
(2) How does the integration of developmental information change our phylogenetic, ecological, and functional interpretations of complex phenotypes?

The symposium

We aimed the symposium at addressing the import and magnitude of the above questions primarily through the study of ontogenetic shifts of functional traits within macroevolutionary frameworks. Our goals were, (1) to advance an interdisciplinary dialog about ontogeny–function–evolution relationships with researchers who span a diverse range of taxonomic and disciplinary interests; (2) to identify and frame forefront questions about these relationships; and (3) to spur collaborations examining how life-history patterns relate to macroevolution along morphological and performance axes. We sought out speakers who would represent the breadth of diversity across vertebrates. Through the detailed study of living and fossil chondrichthyians (Wilga et al. 2016), bony fishes (Baliga and Mehta 2016; Hulsey et al. 2016; Wainwright 2016), reptiles (Gignac and O'Brien 2016; Herrel et al. 2016), birds (Bhullar 2016; Heers 2016), and mammals (Goswami et al. 2016; Santana and Miller 2016), the research presented at the symposium examined issues of functional redundancy, innovation, modularity, performance, and morphological transformations across developmental and evolutionary timespans. The studies presented in this volume include both paleontological and neontological perspectives, often combined to gain reciprocal insights into the patterns and processes that have shaped organismal diversity. To address practical considerations about the time and effort required to collect data on developmental and comparative series of organisms, we also recruited speakers to present on new tools-of-the-trade in ecomorphology research. These laboratory and field studies should provide insights to others still developing their own research programs. By organizing studies with both overlapping and unique perspectives, we hope to spur conversations about the role of ontogeny and function in macroevolutionary processes and for these discussions to continue well beyond the questions posed, and insights offered, herein.

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