

Integrating ontogeny into ecological and evolutionary investigations

As far as morphological change is concerned, evolution acts by altering development.

Liem & Wake (1985)

Given that resource utilization abilities and predation risk are generally related to body size, many species will undergo extensive ontogenetic shifts in food and habitat use. Such shifts create a complex fabric of ecological interactions in natural communities.

Werner & Gilliam (1984)

The field of 'integrative biology' utilizes multidisciplinary approaches to establish a more complete and, therefore, insightful interpretation of an organism's biology. Certainly there is nothing unprecedented about integrative strategies in seeking to understand the natural world. In fact, the major structuring of Western science 2500 years ago by Aristotle and others involved those simultaneously interested in a wide range of topics from gross anatomy, physiology, chemistry, classification of organisms, astronomy, philosophy, and earth sciences. Even as late as the 18th and 19th centuries, integrative biology was alive and well and most investigators saw little need for establishing hard boundaries between subdisciplines. For example, Darwin was a master of integrative biology who, in forming his dynamic view of life, embraced studies in embryology, paleontology, functional morphology, animal husbandry, heredity, biogeography, ecology, earth sciences, and even physics. The 20th century witnessed the establishment of strong subdisciplinary boundaries that effectively compartmentalized biology into numerous factions whose investigators rarely collaborated. Despite this divisive trend, some biologists continued to seek interdisciplinary connections.

The 'Grand Synthesis' was ushered in by Fisher (1930) and others who sought to bridge the artificial schism between genetics and evolutionary theory. Evolution and genetics were united into the field of population genetics which allowed unprecedented insights into microevolutionary change. More recently, the fusion of ecology and functional morphology into the field of ecomorphology has garnered significant support in recent treatments by Ricklefs & Miles (1994), Wainwright and Reilly (1994), and others. Analogously, ecology and physiology were fused into the field of ecophysiology. The beauty of such an integrative approach is that it elucidates the evolutionary underpinnings of present ecological patterns by quantifying morphological correlates of niche space under the presumption that natural selection favors character displacement over competition, and that this displacement is measurable.

Our overall goal in this volume is to add to the growing body of integrative approaches to biological research by presenting a variety of works that incorporate ontogenetic data into studies of systematics, functional morphology, ecology, and evolution. We maintain that integrating an ontogenetic perspective into investigations of complex systems provides a more insightful and balanced interpretation because 1) it is selection on developmental variation that produces phenotypic variation among adults in populations, 2) commonality in developmental patterns may indicate common ancestry (and lack thereof may be indicative of convergence), and 3) preadult individuals directly influence the dynamics of populations and communities through time.

Discussions concerning the theoretical and empirical relationships between ontogeny and evolution have a long history that is both broad and deep (see reviews by Gould 1984; Hall 1992). Clearly, variation in developmental programs may generate novel adaptive character states upon which natural selection may act, i.e., diversity among adult forms begins with divergent developmental patterns (Müller 1990; Raff 1996; McNamara 1997; Klingenberg 1998). Genetic variation is subsequently translated through the process of ontogeny where selection may favor novel morphologies that, in turn, are inherited as evolutionary changes within populations. Thus, natural selection is manifest along the continuum from organogenesis to adulthood; morphogenetic variability is filtered throughout the developmental/adaptive program.

The pervasive force behind the evolution of morphological innovation lies in developmental plasticity and the ability of morphogenetic systems to accommodate change, while simultaneously maintaining functional relationships among subcomponents. The morphological, physiological, and behavioral results of ontogeny, as manifested in adults,

result from two factors: 1) those that are intrinsic – character states that are inherited unchanged from ancestors, or are the distinctive products of emergent properties generated from tissue interactions and/or heterochrony (Klingenberg 1998), and 2) those that are extrinsic – characters generated by and strongly influenced by environmental forces (Lauder 1982). Intrinsic and extrinsic factors interact in myriad ways during ontogeny, resulting in morphological variation among juveniles. This variation is then filtered by natural selection and what remains become adults. The crucial point here is that natural selection acts upon successful integration and function during development in essentially the same way as it selects for adaptive morphologies in adults. Furthermore, it can be argued that selective pressures are greatest during development and, therefore, the key to evolutionary changes in morphology are best understood by the study of preadult organisms (Raff 1996; McNamara 1997). *Unfortunately, it is the dynamic nature of morphogenesis in relation to ecological and evolutionary theory that is so frequently overlooked.* Indeed, the adult is often considered as an immutable construct into which all of the various organ systems must somehow be packaged during development. In kind, juveniles typically are presented as prefunctional, preadult forms, rather than portrayed as evolutionarily important, adaptive stages that manifest their own niche, known as the ontogenetic niche (Werner & Gilliam 1984; Coppinger & Smith 1990).

The intuitive kinship between ontogeny and evolution has a historical partnership as represented in some of the earliest naturalistic writings (Gould 1984). Recent attempts have been made to integrate morphology, developmental, evolutionary biology, and phylogenetics into a unified theory of the evolution of biological form (Klingenberg 1998). Publications by Nitecki (1990), Raff (1996), and McNamara (1997) reignited an interest in the intrinsic power of ontogeny as an instigator of evolutionary novelty. What remains underappreciated, however, is how the interrelationship between juveniles and adults affects population/community dynamics as well as ecosystem evolution.

Because emphasis is placed mostly upon juvenile survivorship to a reproductive age, little attention is given to character differences between juveniles and adults. Furthermore, variation among juveniles, and the role that these differences play in the ‘ecological theater’ are frequently ignored. This is, in part, because the juvenile period is often an ephemeral component of the life cycle, and therefore hard to measure and is easily omitted from traditional theory. Most telling in this regard is the implied, if not formally defined, distinction given to adult form as *the significant unit of a species’ niche*. Ostensibly, an understanding of the

full mosaic of an organism's niche is crucial in interpreting the rules that govern population, assemblage, and community structure (Werner & Gilliam 1984; Liem & Wake 1985). Typically, little or no consideration is given to the juvenile niche, its adaptive nature, or its place in understanding ecological and evolutionary patterns (Werner & Gilliam 1984; Werner 1999). Indeed, resource partitioning among juveniles results in niche fragmentation often to the extent that each age-class functions as an ecological species (Tchumy 1982). We are not suggesting that adult-biased measures of natural history are in any way invalid, but we consider the inclusion of the ontogenetic perspective essential to understanding fully the many aspects of evolutionary and ecological theory.

Darwin, the master of synthesis, would probably applaud recent attempts to resynthesize the major subdisciplines of biology – the intended scope of this book. This volume is unique in that we have brought together a diverse group of bat biologists and asked them to discuss the importance of investigating the underlying developmental patterns of form, function, ecology, evolution, and systematics within the context of their own specialized fields. We have tried to present the current state of research and understanding of chiropteran development. For example, several of the authors provide insights into the ongoing mono- versus diphyletic origin of bats debate by integrating developmental data with patterns observed in morphology, genetics, and fossils. Readers of this volume will, in some cases, be provided with empirical approaches to studies in ecology and evolution from an ontogenetic perspective. In other cases, the reader will find an update on our current understanding in that field and a wealth of suggestions for further research that should help provide insights into some of the more vexing questions in bat biology. We view this compendium as a broadly based contribution to the field of bat biology, and we encourage integration of an ontogenetic framework into all studies of evolution and ecology.

STRUCTURE AND OVERVIEW

In this volume, we provide an up-to-date account of ontogenetic studies of the Chiroptera, and how these studies relate to the ecology and evolution of this diverse and highly successful group. In addition, we reassert the importance of ontogenetic data in studies of systematics, evolutionary diversity, and ecological patterns. We promote ontogeny as a fundamental link between the vastly different time scales of ecological and morphological change.

We begin with Simmons's review (Chapter 2) of chiropteran systematics to establish a taxonomic foundation for the book. She starts with a discussion concerning the range of data sets and analyses used to construct phylogenies of bats, and explains the analytical methods as well as the strengths and weaknesses of each. Simmons comments on the difficulties faced by systematists in discerning the relationships among taxa and proposes the integration of data from fossils, ontogeny, morphology, and molecular biology in systematic investigations, especially some of the more vexing questions in bat biology such as the 'monophyly versus diphily' debate. By summarizing the literature of the current state of understanding of the relationships within families of microchiropterans, she discusses the inferences of evolutionary patterns as derived from bat phylogenies. Following Simmons's review, the text is arranged roughly in developmental order. Karim & Bhatnagar (Chapter 3) review the literature and compare patterns of implantation, placentation, and early development among extant bat species representing many families, and discuss the wide variation present. Beginning with a discussion of what is known about ovum maturation, fertilization, and preimplantation of the embryo, the authors complete this chapter with a discussion of phylogenetic considerations of fetal membrane characters. In Chapter 4, Reep & Bhatnagar tackle questions of the role that neuronal connections play in discussions of bat evolution and emphasize the importance of developmental data to this debate. New data are presented on layer VII of the cerebral cortex, as an example of an adult trait whose variation has specific developmental connotations. Reep & Bhatnagar also incorporate what is known about brain development in bats with comparative analyses of similarities and differences among other mammalian groups. Underlining the role that developmental studies can play in elucidating the apparently convergent visual pathways in pteropodids and primates, they also assess the role of developmental studies in understanding differential enlargement of particular brain regions in taxa of differing foraging strategies, and the relationship of these patterns to general trends in mammals. Vater (Chapter 5) begins with a brief note on biosonar and after describing the basic anatomy and evolution of the bat cochlea, she discusses the ontogeny of echolocation and the developmental and functional feedback link between the larynx and hearing system in a section entitled 'Who is leading development?' Vater also relates the ontogeny of hearing and vocalization with what is known of cochlear and neurological development and function in bats. Pedersen (Chapter 6) describes the morphogenesis and anatomy of the chiropteran skull from the perspective that it has evolved first and foremost to function as an acoustical horn

adapted for echolocation. He provides compelling statistical support for how the origin and evolution of nasal- versus oral-emitting taxa was driven by divergent developmental pathways early in ontogeny. Pedersen argues that the evolutionary divergence between emission types is most likely a result of selective forces acting upon the form and function of the pharynx during echolocation rather than selection on cranial shape or head posture *per se*. He casts his data into a developmental landscape model depicting divergent developmental pathways between nasal- and oral-emitters. Wible & Davis (Chapter 7) use *Megaderma lyra* as a model to provide new data on the ontogeny of the chiropteran basicranium and show how important ontogenetic studies are for understanding the details of adult basicranial anatomy, especially in identifying the components of the tympanic floor and roof. They highlight how developmental phenomena (sequence, number, pattern) are underutilized and potentially very important taxonomic characters. By using basicranial ontogeny, Wible & Davis provide information for a dynamic interpretation of static adult morphology and for assessing the interrelationships among taxa. They also discuss differences and similarities in form of the basicranium between micro- and megachiropterans. In Chapter 8, Phillips begins with the premise that mammalian dental morphology is a direct reflection of an animal's diet and evolutionary history. He utilizes dental eruption patterns to decipher evolutionary mechanisms and pathways and compares the evolution of dental morphology in micro- and megachiropterans. Phillips concludes that whereas microchiropterans have retained an evolutionarily conserved morphology, megachiropterans are relatively unconstrained evolutionarily and have lost the detailed coronal morphologies of their ancestors. He goes on to assert that biochemical studies of oral environment and the digestive tract are important in understanding dental morphology and evolution. Adams (Chapter 9) describes the ontogeny of the handwing in bats and provides analysis of previously unpublished data for both micro- and megachiropteran handwing development, including comparative growth trajectories. He also incorporates postnatal development of the wing and flight ability into an age-specific model of resource partitioning and survivorship among juveniles and adults. He demonstrates the ontogenetic niche for *Myotis lucifugus* by quantifying shifts in niche dimensions with changes in wing-loading and aspect ratio. These data are integrated and displayed in the form of an adaptive landscape model illustrating when the strongest selective pressures on juveniles may occur, challenging survivorship at the transition points among juvenile niche spaces. In Chapter 10, Adams & Thibault provide previously unpublished data on the growth and devel-

opment of the hindlimb in micro- and megachiropterans. In addition, they discuss the functional morphology, evolution and phylogenetics of the calcar as described in other studies and add a previously unpublished ontogenetic perspective to deciphering its evolutionary and systematic pathways in the diphyletic versus monophyletic argument of mega- and microchiropterans origins. Hermanson reviews the literature on what is known concerning the ontogeny of flight muscles and describes the biochemical maturation of skeletal (flight) muscle in bats in Chapter 11. He evaluates this literature in comparison with data collected by him and others on the muscle biology of locomotion in an array of vertebrates, and uses it as a springboard to advance new considerations in discussions of the evolution of flight in mammals. Hermanson re-evaluates his 'toggle-switch' hypothesis in light of new data and develops an ontogenetic model for the evolution of flight. In Chapter 12, Jones discusses the ontogeny, evolution, and phylogeny of social behavior in bats. Beginning with a discussion of social interactions among pups, he leads the reader through the significance of the many aspects of maternal care and allomaternal care. Jones reports on aspects of social learning, the ontogeny of emergence times and foraging behavior, and evidence of maternal care after weaning.

In summary, we see ontogeny as a fundamental link between the vastly different time-scales of ecological and evolutionary change and, therefore, the integration of morphogenetic analyses are essential to understanding complex biological systems. Unfortunately, as biologists we tend to become overly focused within our own subdisciplines, and readjusting our sights to integrating studies from other fields will require special attention. Perhaps this volume will be heuristic in stimulating more biologists to integrate an ontogenetic perspective into research programs.

REFERENCES

- Coppinger, R. P. & Smith, C. K. (1990) A model for understanding the evolution of mammalian behavior. In *Current Mammalogy*, ed. H. H. Genoways, pp. 335–74. New York: Plenum Press.
- Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*. London: J. Murray.
- Fisher, R. A. (1930) *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Gould, S. J. (1984) *Ontogeny and Phylogeny*. Cambridge: Belknap Press of Harvard University Press.
- Hall, B. K. (1992) *Evolutionary Developmental Biology*. London: Chapman & Hall.
- Hutchinson, G. E. (1965) *The Ecological Theater and the Evolutionary Play*. New Haven and London: Yale University Press.

- Klingenberg, C. P. (1998) Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological Reviews*, **73**, 79–123.
- Lauder, G. V. (1982) Historical biology and the problem of design. *Journal of Theoretical Biology*, **97**, 57–67.
- Liem, K. F. & Wake, D. B. (1985) Morphology: current approaches and concepts. In *Functional Vertebrate Morphology*, ed. M. Hildebrand, D. M. Bramble, K. F. Leim & D. B. Wake, pp. 366–77. Cambridge: Belknap Press of Harvard University Press.
- McNamara, K. J. (1997) *Shapes of Time: The Evolution of Growth and Development*. Baltimore: Johns Hopkins University Press.
- Müller, G. B. (1990) Novelty: a side effects hypothesis. In *Evolutionary Innovations*, ed. M. H. Nitecki, pp. 99–132. Chicago: University of Chicago Press.
- Nitecki, M. H. (ed.) (1990) *Evolutionary Innovations*. Chicago: University of Chicago Press.
- Raff, R. R. (1996) *The Shape of Life*. Chicago: University of Chicago Press.
- Ricklefs, R. E. & Miles, D. B. (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. In *Ecological Morphology*, ed. P. C. Wainwright & S. M. Reilly, pp. 13–41. Chicago: University of Chicago Press.
- Tchumy, W. O. (1982) Competition between juveniles and adults in age-structured populations. *Theoretical Population Biology*, **21**, 225–68.
- Wainwright, P. C. & Reilly, S. M. (1994) *Ecological Morphology: Integrative Organismic Biology*. Chicago: University of Chicago Press.
- Werner, E. E. (1999) Ecological experiments and a research program in community ecology. In *Experimental Ecology*, ed. W. J. Resetarits, Jr. & J. Bernardo, pp. 3–26. Oxford: Oxford University Press.
- Werner, E. E. & Gilliam, J. F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, **15**, 393–25.