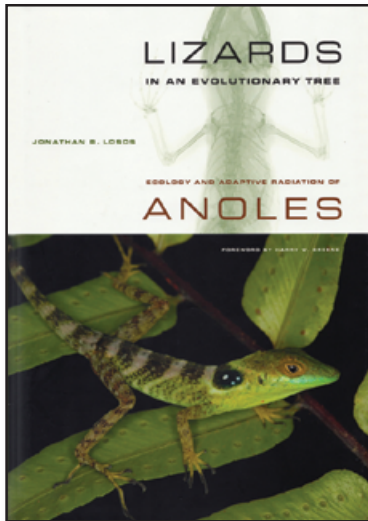


Herpetological Review, 2011, 42(2), 314–316.
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Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles

By Jonathan B. Losos. 2009. University of California Press (www.ucpress.edu). xx + 527 pp. Hardcover. US \$95.00. ISBN 978-0-520-25591-3 (Paperback US \$49.95. ISBN 978-0-520-26984-2).



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The history of evolutionary theory is tightly linked to vertebrates and islands. The year of evolution (2009) has reminded biologists and non-biologists that finches

in the Galapagos Archipelago inspired some of the most provocative thoughts in Charles Darwin's mind. Since then, these ecologically diverse birds have gained a privileged place as promoters of one of the deepest revolutions in human thought. Far away from the Galapagos and from Darwin's itinerary, another group of vertebrates on another group of islands quietly awaited their own opportunity to gain a privileged place in the history of science. In *Lizards in an Evolutionary Tree*, Jonathan Losos tells the story of Caribbean anoles and their contributions to evolutionary biology. For over five decades anoles, particularly the genus *Anolis*, have been the subject of an extraordinary wealth of research dealing with most aspects of the fields of ecology and evolutionary biology. These lizards have not only been useful model systems, anoles are special because they have been instrumental in the development and refinement of theories that have shaped our view of ecological and evolutionary dynamics, contributing greatly to our understanding of major theories such as adaptive radiation and speciation. Anoles, therefore, deserve a great deal of attention from those interested in ecological and evolutionary processes as they occur in nature. However, to read and assimilate the monumental amount of literature on anole evolutionary ecology would require a large part of one's career. The good news is that Losos has done just this, achieving an extraordinary synthesis in a single, solid, entertaining, and comprehensive volume.

The book is impeccably well-organized and its 17 chapters cover the entire diversity of primary theoretical and technical fields relevant to understanding the evolution of adaptations and the origin of new species. While the many footnotes (477 on 409 pages) can be somewhat distracting, they typically contain important relevant information and are worth the pause from the main text. After a couple of pages these footnotes become pleasing distractions because they often also contain entertaining stories that tend to be absent from scientific books of this quality.

In the first three review chapters (2–4, Chapter 1 is a general introduction to the problem of evolution), Losos provides a fine account of the most important aspects of anole diversity. Information in these chapters covers themes as varied as species concepts, competition, key traits involved in sexual and ecological performance, biogeography, reproductive isolation, and arguably one of the most comprehensive treatments about anole ecomorphs (and non-ecomorphs) available in the literature. In these chapters, the reasons why these lizards are excellent model organisms for evolutionary and ecological research become apparent. Losos also makes the case for how critical species-specific natural history information is for understanding evolutionary processes. Clear maps and astonishing color pictures contribute to making these chapters accessible and enjoyable to read.

In chapters 5–7, the book turns to phylogeny. Of particular interest for all comparative biologists are timely discussions of the application of phylogenetic approaches to evolutionary questions (Chapter 5), a field in which the author himself has made important contributions. From this chapter, it becomes clear that not all phylogenetically based analyses can be taken at face value. For example, Losos shows why ancestral reconstructions (widely used in the mainstream scientific literature) under several circumstances should be interpreted with caution. Chapter 6 discusses the phylogeny of anoles, and explains how this information has unravelled the biogeographic history of the group. In this phylogenetic framework, evolutionary changes that accompany the selective challenges encountered in newly colonized areas can be appropriately interpreted. This information is used to discuss the roles of divergent and convergent adaptation that have shaped anole morphologies, and remarkable historical scenarios emerge. For example, a well-established observation in biogeography is that colonization between mainland and islands is typically unidirectional, from the former to the latter. Colonization in the other direction is thought to be less likely because island species are regarded as weak competitors if placed in continental ecological arenas. However, phylogenetic evidence suggests that anoles have not only recolonized the continent from the Caribbean islands several times, but also that these adventurous colonizers have been remarkably successful establishing an extraordinary lineage of almost 130 species. Patterns of dispersal and speciation

emerge, and Chapter 7 covers the exciting topic of ecomorphological evolution in great detail. The predictability of body size and shape evolution are explored, with interesting accounts of phylogenetic patterns of ecomorphs and the debated, but intriguing, idea of evolution by character displacement. These chapters make a strong case for how autonomous the process of adaptation can be, and how crucial the effect of selection is to shaping the functional, causal, and dependent linkages between environmental pressures and phenotypes (see Hurst, 2009, for a discussion of the genetics of selection effects). As Williams (1966) vividly argued in his famous book, adaptation should be accepted as an explanation when other alternatives have failed. This imposes a difficult challenge as alternative hypotheses often offer appropriate mechanistic pathways to explain organismal features. However, as Losos shows in his book, the adaptive explanation for Caribbean *Anolis* evolution is strongly supported from a number of empirical angles, including replicated associations between ecological demands and morphological traits and functional capabilities. Losos also emphasizes that not all *Anolis* are the same, and that this idealized evolutionary story is much more complex on other islands and on the mainland. The field of ecomorphology is, in summary, richly presented in this section.

Losos broadly reviews the biology of anoles in the next section of the book (chapters 8–13), covering all aspects of anole interactions, from causes to consequences, and from ecology to sexuality. These broad discussions even touch on topics that lizard biologists rarely mention, including potential intelligence and sleeping habits. Chapter 8 includes a diversity of topics that are rarely known in such detail in any single genus, such as reproduction, growth, lifespan, parasites, predators, diet and other forms of ecological interactions. Chapter 9 focuses on one of the most exciting fields in evolutionary biology, the origin and impact of intraspecific interactions to determine social and sexual dynamics, with a clear review of the main principles of sexual selection theory. The discussion includes the unavoidable phenomenon of sexual dimorphism, a remarkable and debated outcome of evolutionary diversification within species. Losos presents a clear, unbiased and comprehensive review of the problem of phenotypic differences between the sexes. The chapter gives deserved weight to the two main explanations proposed by Darwin (1874), natural selection on ecological preferences or sex roles, and sexual selection. The focus of the analysis is primarily on the evolutionary forces that determine the direction of patterns of sexual dimorphism and the outcome. However, no particular detail is given to the complex genetic factors that allow or constrain divergence in alternative, sex-specific directions in the first place, once selection has provided the evolutionary impetus for the expression of this phenotypic divergence (Fairbairn et al. 2007). Chapter 10 presents a particularly informative review on how

temperature, humidity, light and other factors govern the ways anoles exploit common areas by means of micro- and macro-environmental segregations. Once again, the pivotal role of anoles in the establishment of current theories and models is highlighted, as Losos reminds us how these lizards have been instrumental in the development of the field of thermal biology.

From Chapter 11, the book turns into a fascinating and dynamic synthesis of information from previous chapters and the focus shifts to the broad fields of adaptive radiation and speciation, which represent the real essence of evolution. In chapters 11–13, the theory of adaptive radiation is introduced from the multiple angles required to understand how evolutionary mechanisms (essentially, natural selection) ultimately drive evolution. A brief but clear theoretical background to adaptive radiation is presented, in which Losos emphasizes that this process is important because it results in the evolution of disparate ecological and phylogenetic diversity from single ancestors, whereas the timing of diversification (the well known “early burst”) is simply one of the features of the process, rather than a crucial concept involved in its definition. These three chapters offer a complete review of the anole adaptive radiation, where studies of community ecology (from predators to parasites), field manipulation of free-ranging lizards, and phylogenetics provide evidence of the effects of divergent natural selection on adaptation and cladogenesis. Interesting syntheses of field evolutionary genetic experiments across generations and of geographic variation as an encouraging avenue to investigate adaptive radiations are presented.

The integration becomes still stronger in chapters 14–16, where the evolutionary diversification of anoles is reviewed in great detail. In these chapters, as in the rest of the book, no theoretical biases or biased speculations are found. All major theories of diversification are incorporated into the discussion, including the largely demonstrated fact that natural selection is a prominent driver of speciation. However, several controversial views, such as founder effect speciation (Coyne and Orr 2004), are also included in the discussion. As can be expected for an island adaptive radiation, due weight is also given to geographical models of speciation (allopatry, sympatry, parapatry). Some fascinating explanations of selection-based speciation are presented, such as the potential impact of head-bobbing and variation of dewlaps on the breakdown of gene exchange between diverging species. Phylogeny, rates of evolution, sexual dimorphism and niche expansion as agents of diversification, key innovations, island biogeography theory, ecomorphs, and the adaptive landscape approach, among others, are dynamically recalled in these final chapters. The book concludes with Chapter 17, in which an overview touching on other adaptive radiations elegantly summarizes the extensive information presented in the preceding chapters.

Throughout the book, Losos provides responsible and unbiased discussions and interpretations of the available evidence, and still better, maintains the tendency to complement certain ideas with novel speculations about the factors involved in anole lizard evolution. Although many scientists often feel reluctant to take intuitive speculations into account, it cannot be denied that scientific progress relies importantly on the freedom of imagination to suggest alternative explanations for phenomena. Some of these speculations may be proven incorrect, but they inspire the reader to think freely about possible explanations for evolutionary questions.

Finally, an important question that many potential readers of Losos's book may be asking is whether this is primarily about anole lizards or about evolutionary ecology. Many might immediately argue that this book is about evolutionary ecology. However, I believe one of the greatest achievements of Losos is the integration of fields he provides in this book. Losos, more than most evolutionary biologists, makes a strong case that species-level natural history is critically important to fully understand a complex multi-phenomena process like evolution. Hence, Losos has managed to write a book that will serve a broad audience. It represents one of the best and most comprehensive synthetic treatments of the theories of adaptive radiation and speciation based on the empirical context of a specific model system, but it also

provides a thorough review of the diversity and natural history of anoles. It has to be said, however, that this is a decidedly scientific book, and clear understanding of theoretical concepts is paramount to the story it tells. For example, despite the enormous diversity of theories encompassed by Losos in this book, the introductory text for each of these ideas is generally brief. Hence, the author implicitly assumes that readers are familiar with the main concepts. However, in this book jargon and simple language are balanced, making it accessible to a broad audience, while maintaining a consistently high level of scholarship. This book is, therefore, a true representation of Einstein's quote "everything should be made as simple as possible, but not simpler."

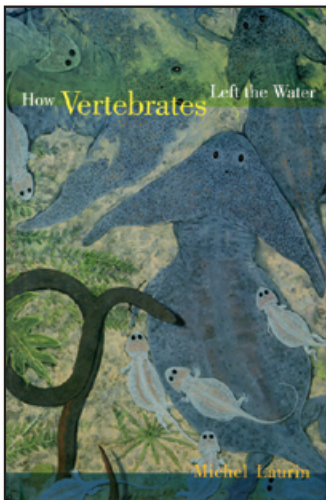
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PUBLICATIONS RECEIVED

How Vertebrates Left the Water

By Michel Laurin. 2010. University of California Press (www.ucpress.edu). Hardcover. xv + 199 pp. US \$34.95. ISBN 978-0-520-26647-6.



This is an English translation, with minor updates, of Laurin's original French book of 2008. It is concise, clear, and well written. The book serves both as a summary of the important changes that took place in this most important of vertebrate transitions and as an argument for parsimony and phylogenetic nomenclature. It begins with a critique of rank-based nomenclature and offers phylogenetic nomenclature as a solution to aspects of instability in the prevailing system. This is followed by an explanation

of parsimony-based methods of phylogenetic reconstruction and a discussion of molecular and paleontological dating. The introductory chapter is rounded out by brief treatments of homology, the geological time scale, and paleogeography. Laurin then considers what living taxa can tell us about the conquest of the land before addressing such topics as the evolution of limbs, the diversity of Paleozoic stegocephalians, and the adaptation of the skeleton, respiratory system, skin, and sensory organs to life on land. The slender volume closes with a glossary of more than 50 terms, a bibliography of more than 150 entries, and a combined subject/taxon index. The book draws heavily on the author's works from the early 1990s onwards and unabashedly promotes his views on a number of topics. At the same time, it does a remarkable job of distilling down each of the subjects addressed to just a few clear, concise, information-packed pages. The book ably succeeds in the author's desire to make the material accessible to those with little prior knowledge in the field and, indeed, offers even novices a succinct view of how modern vertebrate paleontologists test hypotheses about the evolution and biology of extinct organisms. It may be especially useful for herpetologists, systematists, and anatomists whose work