

## Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles.

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## Fall Focus on Books

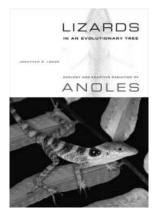
## LIZARDS REVISITED

Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. Jonathan B. Losos. University of California Press, 2009. 528 pp., illus. \$75.00 (ISBN 9780520255913 cloth).

During the past 50 years, the sub-set of squamate reptiles popularly known as "lizards" has risen to nearly star status among vertebrates as model organisms for understanding evolutionary, ecological, physiological, and behavioral processes. Among the approximately 7200 named species of squamates, about 4450 are typically called lizards (a taxonomic misnomer), and among these, about 365 are anoles. Almost everyone who has visited the Caribbean islands, Central America, or Florida has seen colorful anole dewlaps flashing in response to other anoles. Lizards in an Evolutionary Tree, by Jonathan B. Losos, centers on the use of these remarkable lizards to place major ecological principles in an evolutionary context. Losos is a Monique and Philip Lehner Professor for the study of Latin America, professor of organismic and evolutionary biology, and curator of herpetology in the Museum of Comparative Zoology at Harvard University.

Lizards in an Evolutionary Tree succeeds on all fronts. First, it is readable. Losos writes in an engaging and storylike fashion, readily transmitting scientific discovery to the reader. Second, a wealth of information is summarized—one cannot help but find these lizards fascinating. Third, clearly written natural histories of anoles draw the reader deep into conceptual biology this book could easily be used to teach an evolution or ecology course. Every discussion challenges the reader with new unanswered questions.

I particularly like the structure of the book. Losos first tells us what he plans to do, and why, in an engaging introduction to his scientific approach. He then leads a tour of anole diversity



followed by a logically clear discussion of the advantages and limitations of phylogenetic perspectives by asking questions about behavior and ecology. Chapters on behavior, ecology, life history, community ecology, microevolution, and functional capabilities are filled with detailed examples that read like mystery stories. These chapters are followed by a discussion of speciation and adaptive radiation of anoles in which all that came before is put into historical perspective. The final section of the book discusses anoles from a broad perspective and compares adaptive radiations in anoles with those of other groups of organisms.

The reasons anoles are ideal models for evolutionary and ecological studies include their high evolutionary diversity, spectacular and repeated radiations, a large range in body sizes, assemblages of varying sizes and origins, diurnality, and high ecological diversity. Their high densities on islands in the West Indies make them particularly suitable for experimental manipulations. And last, but certainly not least, they are easy to capture! As Losos correctly points out, the enormous amount of literature on nearly every aspect of the biology of various Anolis species, combined with relatively recent, well-supported phylogenetic hypotheses, has brought anoles to center stage when it comes to testing conceptual hypotheses with lizards.

The overriding theme of *Lizards in an Evolutionary Tree* is that interspecific interactions—primarily competition—have been and continue to be primary determinants of community structure in Anolis lizards. A combination of fossil (dating) and phylogenetic (relationships) data tell part of the story. Hypotheses generated from historical data can be tested as more data become available. The power of a phylogenetic approach is clear in a reconstruction of the evolution of ecomorphs in the Greater Antilles. Ecomorphs originated independently on different islands, and several ecomorphs evolved independently multiple times on single islands. The end result is convergent community structure on different islands.

The challenge, of course, is measuring evolutionary change. We know what occurred (convergent evolution of assemblages), we know the likely mechanism (interspecific interactions), but can we demonstrate a measurable evolutionary response? After all, lizards are not fruit flies with high reproductive rates and short generation times. We presume that microevolution in lizards happens so slowly that detectable changes might not occur during the lifetime of an investigator, but this may not be so. Measurement of selection gradients on populations of anoles on different islands, some with and some without the predatory curly-tailed lizard (Leiocephalus), revealed that larger female Anolis sagrei are favored on islands with predators. Males are also affected, but a number of interacting factors complicate the results, including a relationship between island size and selection acting on male hindlimb length. Particularly interesting is a shift in microhabitat use by anoles in response to predators. Predators outrun shorter-legged anoles more easily, but shorter-legged anoles are better at using arboreal perches and thus escaping the terrestrial curly-tailed lizards. After only six months, not only does a significant microhabitat shift occur (terrestrial to arboreal) in A. sagrei but population hindlimb length decreases accordingly, thereby suggesting natural selection in the predicted direction.

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Relative hindlimb length in anoles is an ideal trait with which to examine form and function because of its correlation with microhabitat use. As a result, macroevolutionary forces can be examined by tying phenotypic variation to ecological causes; basically, the phenotype  $\rightarrow$  performance  $\rightarrow$  fitness paradigm.

The discussion of island and mainland anoles in Chapter 16 ("The Five Faunas Reconsidered") especially caught my attention because it is both speculative and thought provoking. The compelling argument is that differences in density and diversity of predators on island and mainland habitats affected the course that evolution may have taken. Alternatively, one might wonder whether frequent (evolutionarily speaking) catastrophic events (such as hurricanes) on West Indian islands have repeatedly affected anole populations such that the ability to rapidly respond to habitat change in itself has been favored. "Evolvability" is addressed in the last chapter. Anoles show greater variability in morphology and thermal physiology than other lizard clades. It might be instructive to conduct laboratory experiments to determine whether island and mainland anoles differ in their ability to change limb length or thermal physiology in response to habitat characteristics. A long history of predictably high predator diversity and abundance may have had a lesser impact on evolutionary rates in mainland anoles than a long history of catastrophic events has had on island anoles.

The overall layout of the book, with a single column of text on each page, is appealing. I particularly like the creative use of annotations, which allows the text to flow while giving the interested reader additional detailed information (and some very entertaining anecdotes). Color photographs and graphics throughout complement the presentation. Only one rather minor inconsistency in the text comes to mind: Following a convincing defense of the phylogenetic species concept, Losos emphasizes "reproductive isolation as an appropriate framework for consideration of the nature of anole species" (p. 22). Yet the entire book emphasizes a phylogenetic approach to understanding the evolution and diversity of anoles. That aside, errors are rare (e.g., listing "Pianka and Vitt 2003" as "Vitt and Pianka 2003" in the literature cited).

Although Losos targets the book to "those deeply interested in anoles and those interested in general questions of biodiversity, evolutionary biology and ecology" (p. 8), I would broaden that to include all students of the natural sciences interested in discerning how inquisitive scientists reconstruct the history of life. A good reading of Lizards in an Evolutionary Tree will most likely result in "field envy" by laboratory experimentalists. For Jonathan Losos, the laboratory is the West Indies, his Petri dishes are the many islands teeming with Anolis lizards, and his experiments are real-world demonstrations that natural selection has produced an astounding diversity of life on Earth.

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## **HOW CREATURES WORK**

Glimpses of Creatures in Their Physical Worlds. Steven Vogel. Princeton University Press, 2009. 328 pp., illus. \$35.00 (ISBN 9780691138077 paper).

Steven Vogel has written a number of books on biomechanics, from the diverting and amusing *Life's Devices* (1988) and *Cats' Paws and Catapults* (1998) to the scholarly, insightful, and amazingly useful *Comparative Biomechanics* (2003). The success of these works has been so great that Vogel has been largely immune from the rat race of the research grants system, and instead has been able to pursue his interests in such areas as the flowinduced ventilation of sponges and prairie-dog burrows, or the responses of leaves and trees to wind.

Vogel is part of the school of physiology and biomechanics, fostered by the legendary Knut Schmidt-Nielsen, at Duke University, and his eclecticism and inventiveness are remarkable. He has a good knowledge of both the animal and plant kingdoms, plus a knowledge of physics, engineering, and physical chemistry, and thus is able to apply principles used in, for example, commercial chemical engineering to the problems of gaseous exchange or water loss by leaves. He also has the ability to sense a problem and an enviable knack for explaining what is happening.



Glimpses of Creatures in Their Physical Worlds is a reworking of essays published in the Journal of Biosciences between 2004 and 2007 that approximately form the chapters of this book. In the reworking, these articles have been edited to allow cross-referencing, and the older material has been updated to account for more recent findings. Vogel admits to retreating from optics or acoustics and toward an abiding interest in the behavior of fluids and solids. What we have then are 12 chapters, loosely interrelated, covering topics in physical chemistry, fluid dynamics, the dynamic and static behavior of structures, and the solutions of living organisms to everyday physical problems.

In his earlier works, Vogel has shown a fondness for alliteration, double entendre, and puns, but in this

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