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Ecology, Evolution, and Plate Tectonics

Jonathan Roughgarden

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Preface

Anolis lizards are the colorful green, gray, or brown lizards readily seen around houses, gardens, and woods in the West Indies. Anoles are active mainly during the day, as contrasted with the geckos also seen in and near houses, which are active primarily at night. Male anoles have a yellow, red, or white throat fan used in territorial displays and courtship; they extend and retract this fan in a special sequence to communicate with one another. Both males and females have toe pads, a sign of their arboreal habit. Together with students and colleagues, I have studied these animals on the islands of the eastern Caribbean during the last 20 years. This book offers a summary of why these animals have held our interest for so long and what we have learned.

Anoles typically perch on trees or bushes scanning the ground for insects. When a desirable insect appears, an anole runs and captures it, and hence an anole is called a "sit-and-wait" predator. Anoles occupy a niche filled by birds in North America and Europe. The West Indies lack most ground-feeding insectivorous birds such as robins, blue jays, and so forth; these are replaced by anoles. Birds are warm-blooded, which means they use metabolic energy to maintain the high body temperature required for effective locomotion. Lizards, in contrast, are cold-blooded, which does *not* mean they are cold but does mean they attain a high body temperature in a more elegant way—by basking directly in sunlight. Hence, an anole does not waste food to stay warm but uses all its food directly for maintenance, growth, and reproductive activities. Lizards are thus more efficient than birds, and a given food supply supports as many as 100 more lizards than birds. As a result, the abundance of lizards in the West Indies is phenomenal—one lizard per m^2 is typical. The total population size on a typical 400 km^2 island in the eastern Caribbean is therefore on the order of 10^8. This abundance implies that anoles are big players in the ecological communities found on Caribbean islands, and much of the ecosystem's energy and carbon flow through their populations.

Anoles are also big players in the zoological kingdom. The genus, *Anolis*, contains about 300 species, which makes it one of the largest genera of vertebrates.[1] These 300 species are distributed throughout Central America, northern South America, and the Caribbean islands, including the Greater Antilles (Puerto Rico, Hispaniola, Jamaica, and Cuba) and the Lesser Antilles (the small islands at the eastern margin of the Caribbean). Anoles are also found throughout the Bahamas. About half of the anole species occurs on Caribbean islands, the other half in Central and South America. These 300 species of anoles are about 5-10% of the entire present-day lizard fauna of the world.

The Greater and Lesser Antilles contain species unique to each island. For

[1]The official Latin name for a species consists of two words, the genus, which is capitalized, followed by the species itself, which is not capitalized, and both are italicized. The word "anole" is an informal common name for these animals.

example, the 11 *Anolis* species of Puerto Rico and its nearby cays are found only there. Hispaniola, adjacent to Puerto Rico on the west, has more than 35 *Anolis* species of its own, and none in common with Puerto Rico or Cuba. Closest to Puerto Rico on the southeast are the islands of Anguilla, St. Martin, and St. Barths. These are considered as a single "bank" because they are separated by shallow water. These three islands were united during the last glaciation period 15,000 years ago when the sea level was much lower. This bank has two species of anoles. These two species are found only there and nowhere else; they are not shared with Puerto Rico to its north or with the small islands still farther south. In this sense, then, the fauna on each of the Greater and Lesser Antillean islands is unique to the island.

A slight exception is that Jamaica has six native species, plus one invader from Cuba. Cuba itself, however, has a large native fauna of over 35 species that are not otherwise shared with Jamaica. In contrast, the Bahamas differ from the Greater and Lesser Antilles in *not* having any native species. The entire Bahamas appear to be under water occasionally and are recolonized anew from the adjacent Greater Antilles whenever they reappear.

From a scientific standpoint, the Caribbean islands with their *Anolis* lizards comprise a *system*. The islands offer miniature laboratories to study ecology and evolution. Indeed, this system is especially suited for the interdisciplinary subject of evolutionary ecology—the study of how an ecological context supplies the natural selection that drives evolution and of how evolutionary change among species in turn affects their ecological situation. Furthermore, it also appears that anoles may be used as "living strata" to aid in reconstructing the plate-tectonic origin of the Caribbean region, and perhaps also Central America. Together with other reptiles, lizards have a history that extends back over 100 million years, which is the period during which much of the Caribbean formed and major tectonic motion has occurred. These, then, are the scientific motivations for working with anoles on Caribbean islands.

Both our field studies and theoretical models have been directed mostly to the Lesser Antilles, simply because they are smaller and easier to understand than the Greater Antilles. Hence, this book is mostly about the small islands dotting the eastern margin of the Caribbean and, even more specifically, often aimed at the northeastern corner of the Caribbean where we have had the most experience.

Much of the research discussed in this book has been published previously in peer-reviewed scientific books or journals, sparing the need to reprint gory detail. Instead, the aim here is to synthesize, to compare what we thought we'd find with what we really did find, and to indicate where our understanding is still fragile. The theoretical aspects of Chapter 1, however, are new and not published elsewhere.

The computer programs developed in this book are written in a relatively new dialect, Scheme, of the venerable computer language, Lisp. Programs about an animal's ability to learn, to remember and to innovate are easy to express in this dialect. Also, web and tree-like data structures are found throughout biology, and all dialects of Lisp easily represent these data structures. Programs for all the calculations in the book are supplied on a diskette that can be purchased for a nominal price from the publishers. The programs are written in Scheme, with a few extras tossed in written in C and Pascal. Hopefully the interpretative nature of Scheme, together with the availability of the programs, will encourage a hands-on attitude to the theory presented in the book. Not only can the numerical value of a constant be changed on the fly but so can the actual structure of a model.

I am especially grateful to David Heckel, Steve Pacala, and John Rummel for

their efforts during the initial period of this work, and to Steve Adolph, Roman Dial, Andy Dobson, Eduardo Fuentes, Lloyd Goldwasser, John McLaughlin, Ken Naganuma, Warren Porter, and Sharoni Shafir for important contributions at other stages. I acknowledge the efforts of students and others who have helped in the lizard censuses and related field activities. I also thank Mme. Flemming of St. Martin for allowing work to be carried out on her land for over 12 years, Vikki and Carl Leisegang for their excellent seamanship during the Anguillita experiments, and Mr. Bryan of West End, Anguilla for allowing the Anguillita experiments on his property. I am grateful to Ernest Williams for introducing me to *Anolis* many years ago, to Tom Schoener for valuable discussions, and to Bob and Judith May for hospitality during sabbatical visits to Princeton and Oxford. I am indebted to Jonathan Losos for an exquisitely detailed and thoughtful review of the entire manuscript. Finally, I thank my colleagues at Stanford for their interest and support over the years.

The field research reported here has been funded by the National Science Foundation, and the theoretical research primarily by the Department of Energy. Recently, research on the relation between adaptive computation and animal behavior has been supported by the Interval Research Corporation of Palo Alto.

This book is dedicated to the peoples of the Caribbean. It highlights biological treasures that are their inheritance.

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