

Preface

THE TRAIN from Balboa Station moved slowly at first, making its way past the warehouses, military bases, and red-tiled roofs of Canal Zone houses, past the locks of Miraflores and Pedro Miguel, and alongside the Gaillard Cut. There it picked up speed, traveling parallel to the Panama Canal and eventually reaching stretches of tropical rainforest, dotted with small farms and banana fields. As I gazed out the window at the ponds and lakes that lay alongside the tracks, I thought about all the frogs that must be out there, feeding, calling, defending territories, laying eggs, avoiding snakes, and otherwise going about their lives. I couldn't see them, of course, nor could I hear them at night over the din and clatter of the train, but I knew they were there. On some nights, arriving on the 11:00 o'clock train at Frijoles Station on the way to Barro Colorado Island, I could hear the last few squeaks and clicks of the small treefrogs along the shore, or the last plaintive whines of túngara frogs finishing up a night of calling.

I had come to Panama in 1976 as a postdoctoral fellow of the Smithsonian Tropical Research Institute. Fresh out of graduate school, I had little experience in the tropics, but I knew of the great diversity of frogs to be found there, sometimes with more species breeding at a single pond than can be found in the entire northeastern United States. I am not sure when I first thought of writing a book on the ecology and behavior of amphibians, but certainly ideas began to germinate as I took those long train rides along the Panama Canal and my many boat rides across Gatun Lake to the jungle island of Barro Colorado.

I actually began writing this book in the early 1980s, so to say it has had a long gestation period would be a gross

understatement. Indeed, at times the project seemed to take on a life of its own, like one of those never-ending scholarly endeavors usually associated with the humanities, such as editing the correspondence of Charles Darwin or writing the definitive multivolume biography of Herman Melville. Much has changed in the intervening years, both in my life and in the study of amphibian ecology and behavior. I began the book as a young assistant professor and now find myself one of the most senior members of my department. I got married, raised two young daughters, bought and remodeled a house, taught classes, supervised graduate students, conducted field research, and served on more departmental and university committees than I can remember.

At every opportunity, I continued working on the book, sometimes for months at a time, sometimes in fits and starts as time allowed. I spent many fulfilling hours in libraries, not only at the University of Connecticut, but also at the Smithsonian Tropical Research Institute during summer trips for field research. Over the years, much of the technology associated with book writing has changed. The initial version of the first chapter I wrote was composed on a portable electric typewriter, and from there I graduated to an IBM Selectric, a mainframe computer terminal, and a succession of desktop computers. Frequent trips to the library to fill notebooks with handwritten notes have largely been replaced by access to electronic journals and the printing of thousands of pages of recent journal articles. Figures drawn by hand with a lettering set have given way to computerized graphics, while the tedious developing of black and white photographs in the darkroom has been replaced by digitally scanned images.

What also has changed over the years is the amount of information available on the ecology and behavior of amphibians, which has increased at an exponential rate, as has the number of researchers studying amphibians. When I began this book, the most recent scholarly treatment of amphibian biology was G. K. Noble's *Biology of the Amphibia*, published in 1931 and reprinted by Dover Publications in the 1950s. Since then, we have seen the publication of Duellman and Trueb's *Biology of Amphibians* (1986); the multi-volume Australian series *Amphibian Biology*, edited by Harold Heatwole (and others), which began in 1994; and volumes dealing with the environmental physiology of amphibians (Feder and Burggren 1992), amphibian hearing and acoustic communication (Fritzsche et al. 1988; Ryan 2001; Gerhardt and Huber 2002; Narins and Feng 2006), reproductive biology (Jamieson 2003; Sever 2003a), tadpole biology (McDiarmid and Altig 1999a), salamander ecology (Hairston 1987; Bruce, Jaeger, and Houck 2000), amphibian distribution (Duellman 1999c), and amphibian conservation (Beebe 1996; Semlitsch 2003a; Lannoo 2005). There also have been many other books and monographs dealing with specialized aspects of amphibian biology, or geographic treatments such as Petrunka's *Salamanders of the United States and Canada* (1998) and Savage's *The Amphibians and Reptiles of Costa Rica* (2002). Meanwhile, the explosion of journal literature dealing with amphibian ecology and behavior over the last 25 years often left me feeling like Lewis Carroll's Red Queen, always running faster and faster just to keep up. At some point, the search for that last key paper must come to an end. For this book, that point essentially was reached in the fall of 2005, although a few papers from 2006 did find their way into the references. The impossibility of being completely up-to-date is illustrated by the appearance of a 370-page monograph on the phylogeny and classification of amphibians (Frost et al. 2006) just as I was making final preparations to send this book to the publisher (see chapter 1).

Of course, the amphibians themselves have changed as well. Several species have gone extinct since I began writing this book, and many more are in decline or threatened by assaults on their environment. Consequently, many researchers have shifted their focus from investigating the basic biology of amphibians to research programs aimed at understanding the decline of many amphibian populations and identifying ways to prevent it. Yet a clear understanding of the basic physiology, ecology, and behavior of amphibians remains central to any successful conservation effort, and my hope is that this book will contribute to this body of knowledge.

Although I wrote this book myself, it would not have been possible without the encouragement and assistance of many family members, friends, and colleagues. In acknowl-

edging these people, it seems appropriate to start at the beginning. I owe a tremendous debt to my parents, W. Willeroy Wells and Leora Wood Wells, who unfortunately did not live to see this book completed. My father, having been a Rhodes scholar with a keen interest in history, instilled in me a love of research on all sorts of subjects. My mother, a voracious reader, a writer, and an accomplished editor, conveyed to me her love of books and her sense that writing is the essence of communicating both facts and ideas. My parents never questioned my desire to become a naturalist, or to fill our basement with tanks and cages full of frogs, salamanders, and snakes, to major in zoology in college, or to pursue a PhD in the obscure field of frog behavior. They provided love and financial support, without which this book would not have been possible. I am saddened that they did not get to see the final product.

Next to my parents, perhaps the greatest influence on my development from boy naturalist to college professor has been my teachers, starting with my high school biology teacher, Richard Ailstock, who often accompanied my friends and me on expeditions to various swamps, presented me with my first copies of *Copeia*, and invited me back to his classroom for years after I was a student to show slides of frogs to the next generation of students. At Duke University, I got my first taste of real field research in an ecology class taught by Dan Livingstone, and encouraged by him and the late Joe Bailey, I continued my class project and eventually published two papers from the work. My development as a biologist continued in a PhD program at Cornell University, a wonderful center for research in ecology and behavior. I benefited especially from the guidance, encouragement, and criticism of my major professor, F. Harvey Pough, who taught me the importance of integrating studies of physiology, ecology, and behavior to understand the biology of organisms. Steve Emlen, an inspirational teacher and pioneer in the study of vertebrate social behavior, encouraged me in every aspect of my research with frogs by his sheer enthusiasm for all things behavioral. Kraig Adler gave me access to his incredible library as I was writing my first review of frog mating systems, which was the key to getting my career as a scientist underway. Interactions with other faculty members, graduate students, and postdocs at Cornell enriched my experience and shaped my development as a biologist. There are too many of these people to mention individually, but especially influential were Jack Bradbury, Will Provine, Carl Gerhardt, Peter Narins, John Heiser, Tom Wiewandt, Bill Mautz, Gene Helfman, Gary McCracken, and the late Jasper Loftus-Hills. My formal education was completed with the postdoctoral fellowship that took me to Panama, where I benefited from interactions with many graduate students, postdocs, and staff members at the Smithsonian Tropical Research Institute. Especially important was the

influence of my postdoctoral advisor, Stan Rand, field naturalist and tropical herpetologist extraordinaire, who unfortunately also did not live to see this book completed.

During the long gestation of this book, many friends and colleagues have provided me with information, unpublished manuscripts, Master's theses, PhD dissertations, and comments on various drafts of chapters, in some cases so long ago that the final version may not be recognizable. I hope I have not forgotten to acknowledge anyone: Kraig Adler, Stevan J. Arnold, David Bickford, Andrew Blaustein, Ron Brandon, Janalee P. Caldwell, Adão Cardoso, Tun-Yu Dave Chen, Martha Crump, Sharon Emerson, Martin Feder, Robert Gatten, H. Carl Gerhardt, Harry Greene, Tim Halliday, Mark Hayes, Lynne Houck, Richard D. Howard, Victor H. Hutchison, Robert Jaeger, Michael Jennions, Murray J. Littlejohn, Horst Lüddecke, Ralph Mac Nally, Peter Morin, Peter Narins, Carlos Navas, Kiisa Nishikawa, Jim O'Reilly, Neville Passmore, John Phillips, Ken Prestwich, Michael J. Ryan, Andreas Schlüter, Joshua J. Schwartz, Ray Semlitsch, Roger Seymour, Cynthia Kagarise Sherman, Vaughan Shoemaker, Martin P. Simon, David Skelly, Margaret M. Stewart, Stephen G. Tilley, Catherine A. Toft, Daniel S. Townsend, C. Richard Tracy, Joe Travis, Paul Verrell, David Wake, Marvalee Wake, Bruce Waldman, Richard Wassersug, Earl Werner, Henry Wilbur, and Larry Woolbright. Two of my graduate students, Patrick C. Owen and Noah Gordon, did yeoman service one summer in checking all of the references in the text and reference list for the first 15 chapters, finding many errors and omissions.

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Finally, very special thanks go to my wife, Marta Lucía Martínez Wells, and my two daughters, Camila (who thinks frogs are kind of slimy) and Gabriela (who will grab any amphibian she sees), for enhancing my life in every possible way. This book is dedicated to them.

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