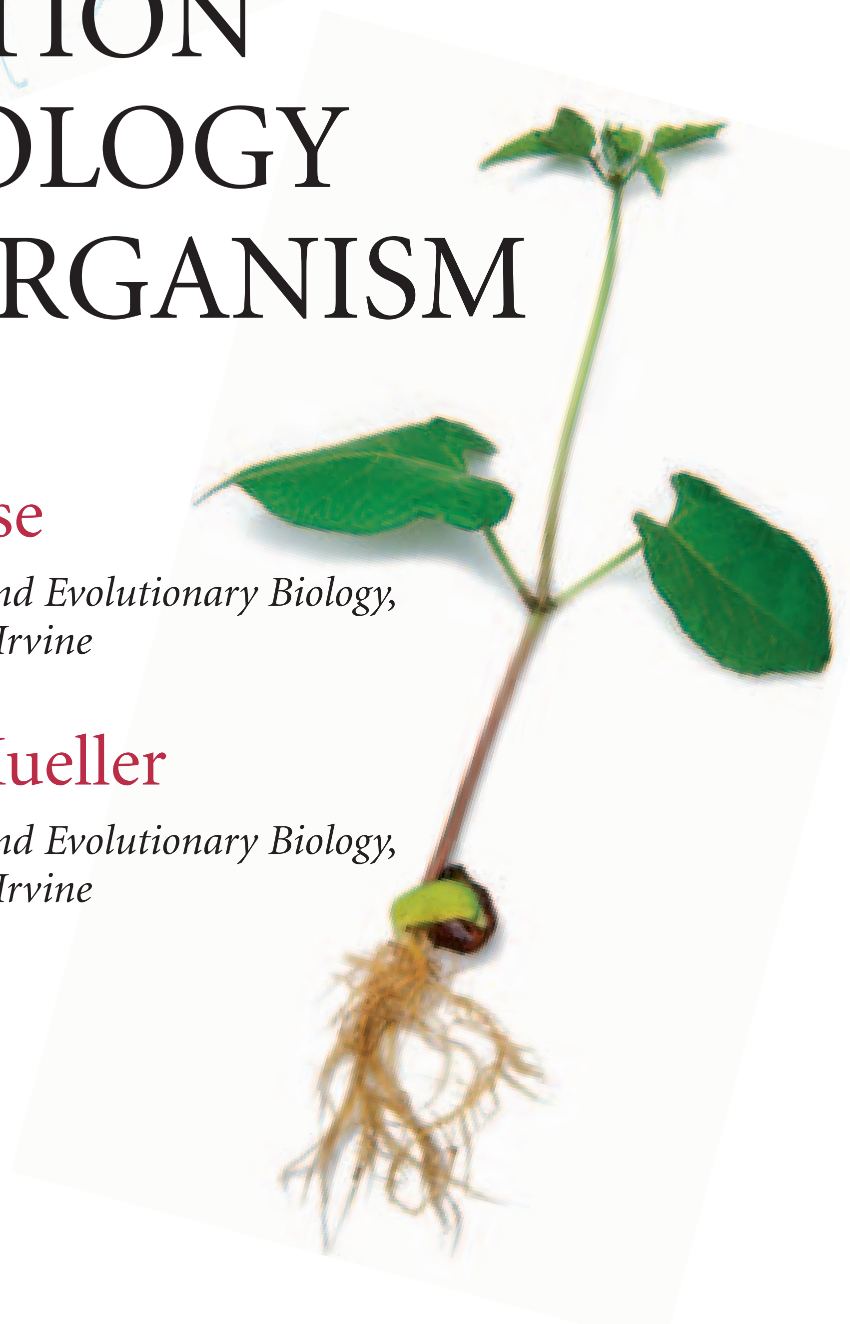
# EVOLUTION and ECOLOGY of the ORGANISM



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*To the Mueller, Krieks, Parla, Horsey, Metal, and Rose Families,*
*Near and Far*

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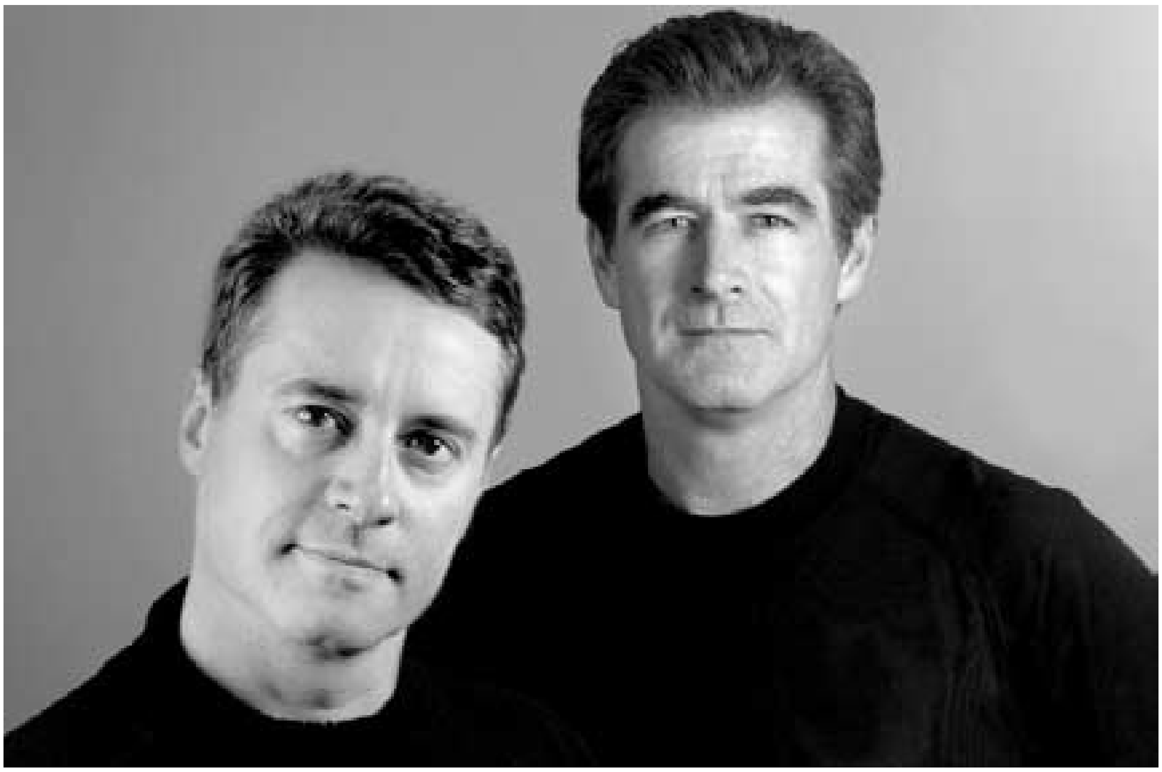

**Michael R. Rose**

Michael Rose went to the University of Sussex in 1976 for doctoral studies with Brian Charlesworth on the fruit fly *Drosophila melanogaster*. There he began his work on the evolution of aging and created fruit flies with genetically postponed aging. In 1991, his book *Evolutionary Biology of Aging* appeared, offering a view of aging that was a complete departure from the views that had dominated the aging field since 1960. Rose received the Busse Research Prize from the World Congress of Gerontology. Among his other honors is a teaching award from the School of Biological Sciences at the University of California, Irvine. He has written popular articles for *Technology Review* and *Scientific American*, as well as a general-audience book, *Darwin's Spectre: Evolutionary Biology in the Modern World*. He has published a total of more than 200 scientific publications of all kinds. The 2004 book *Methuselah Flies* assembles selected articles from the last 25 years of work in the Rose laboratory. He is Professor of Ecology and Evolutionary Biology at the University of California, Irvine and the Director of the University of California Intercampus Research Program on Experimental Evolution.

**Laurence D. Mueller**

Larry Mueller received his Ph.D. in 1979 from the University of California, Davis, where he studied under Francisco Ayala. Mueller then went on to do postdoctoral research in theoretical population genetics with Marcus Feldman at Stanford University. He was an Assistant and Associate Professor at the Washington State University before assuming his current position of Professor of Ecology and Evolutionary Biology at the University of California, Irvine. Mueller has published over 70 research papers in the fields of evolution, population genetics and population ecology. He is also the author of *Stability in Model Populations* with Amitabh Joshi. In his current research, Mueller uses experimental evolution to study problems like density-dependent natural selection and the evolution of late-life demographic patterns in *Drosophila*.

# PREFACE

This book introduces biology students to the basic concepts of the spectrum of fields that we call Darwinian biology, a spectrum that includes population genetics, population ecology, community ecology, macroevolution, physiological ecology, systematics, and functional morphology. Charles Darwin first brought this type of science to fruition and all these fields owe their foundations to his pioneering work, directly or indirectly. Our primary goal in the book is to elicit the students' interest. Secondarily we want to prepare undergraduate students for more advanced specialist courses in Darwinian biology as they pursue their degrees. We have adopted the following means to achieve these ends:

- Evoking Darwinian theory using stepped-out equations and concrete graphics to foster quantitative intuition.
- Using examples illustratively rather than exhaustively, to support and sharpen the student's understanding.
- Using evocative text to give the student an appreciation for the drama of the science and the color of its material.
- Using a magazine format that allows text and graphics to combine synergistically, with close juxtaposition.
- Consistently emphasizing concepts over details and scientific reasoning over terminology.

We want to help students over the hump that keeps them from understanding state-of-the-art texts in evolution, ecology, physiology, and cognate fields. Our hope is that using this book will make students more interested in Darwinian science, and faculty more willing to teach it. For two decades biology curricula have been dominated by cell and molecular biology, with Darwinian biology relegated to passing mention in introductory courses or to small advanced courses taken by few students. This is ironic at a time when the abundance of sequence data from molecular biology pointedly confronts biology with its need for Darwinian theories and analytical tools. Yet that toolkit has mostly fallen into disuse, poorly understood even by many biology faculty. The time for the rediscovery of this other half of biology has arrived.

The general theme of the book is the interconnectedness of organism, environment, and evolution. In studying the book, students should develop an integrated understanding of the organism that is founded in evolution and ecology. Just as biochemistry and molecular biology provide the foundation for our understanding of the cell, we use evolutionary biology and ecology here to construct a foundation for understanding the organism.

With this in mind, *Evolution and Ecology of the Organism* (henceforth *EEO*) integrates the component Darwinian disciplines. Instead of three separate sections for Evolution, Ecology, and Organismal Biology, thematic interconnections have been developed that combine elements of all these areas throughout the text. In so doing, *EEO* follows the precedent of contemporary research, in which ecologists, for example, use molecular genetic data and phylogenetic analysis.

## Level

One of the most important issues for any textbook is that of level. There are a number of excellent advanced textbooks in ecology, evolution, and organismal biology. They are not going to be displaced by *EEO*. Each of those books already approaches 1000 pages in length. In order to achieve a comparable scope and replace three of these advanced disciplinary books, *EEO* would then need to be 2200 pages long. As you can see, it is not such a weighty tome.

In addition, *EEO* does not compete with general biology texts, which introduce students to the diversity of life-forms, cells, and habitats. Such books are the factual starting point for biology degrees, and have only rudimentary introductions to the conceptual content and empirical results of evolutionary biology or ecology. *EEO* will be best comprehended and utilized by students who have already taken a good introductory biology course.

The content of *EEO* is primarily aimed at the biology major in the second or third year of the college or university curriculum. However, students who have taken AP biology can begin their university education with courses based on *EEO*. At the other end of the spectrum, graduate students, post-docs, and faculty from other areas of biology may find *EEO* a helpful source of basic information about Darwinian biology as well. But these qualifications aside, we would expect *EEO* most often to be assigned to second and third year biological science majors as part of their core curriculum. Such text adoptions might be for courses called "Ecology, Evolution, and Organism" or "Integrative Biology." Or it might be assigned in a sequence of courses called "Ecology," "Evolutionary Biology," etc. In the process of sending out the text for review and talking to our colleagues, we have heard of a number of variations on these themes.

A sensible question might be why don't these courses just use the traditional advanced texts in combination? For exceptionally well-prepared students, this may be workable. However, our experience is that the vast majority of biology majors become alienated from the study of ecology and evolution by the narrow specialization and quantitative detail of advanced texts in our disciplines. While advanced students may already understand the interconnections between population ecology, behavioral ecology, and population genetics, for example, intermediate-level students need an integrative framework within which to place the findings of these particular disciplines. We supply such an integration of Darwinian biology in a way that multiple separate texts cannot.

## Format

*EEO* breaks with tradition with respect to format as well as content, to meet its twin goals of communication and integration. In *EEO*, the concepts are the focus. Because of this, these concepts are rendered primarily in visual form. Biology research is now image-driven, meaning that most of our discussions are based on images and photographs that convey our ideas. The use of dramatic colorful illustrations is commonplace in biology seminars. *EEO* is put together with graphics and photographs as the foreground elements and detailed text content as a background element. We try to make Darwinian biology lively and appealing.

Because *EEO* assembles the material so that at least half of it is conveyed graphically—and we consider that half to be essential content—we have designed the book so that all the one- or two-page spreads are art-centered and self-contained. These spreads are designed to convey a single message. That single message is embodied by a single declarative sentence, displayed prominently at the top of the page. In this way, information is focused into distinct nuggets, which we call Modules.

We are excited about this book. It has been a very important project for us and we have devoted long hours to its creation, looking forward to the day when students would sit down with the book and be enticed, we hope, by the fascinating world of Darwinian biology. We would appreciate any suggestions you might have about the book, how it works for you in your classroom, what additional content should be added, and so on. Please contact us at mrrose@uci.edu or ldmuelle@uci.edu and let us know what you think.

## Acknowledgments

We are very grateful for the support and encouragement we have received from so many over the seven years we have been working on this book. The individuals who have directly contributed to this project are listed on the copyright page and in the acknowledgments list below. Still others contributed indirectly by supplying us with our formal and informal educations over the years, particularly our teachers, advisors, and colleagues, in many cases long before we actually started writing. Francisco J. Ayala, Brian Charlesworth, James F. Crow, Marcus W. Feldman, William D. Hamilton, Rudolf Harmsen, John Maynard Smith, and Sewall Wright have been our greatest direct influences. We know that we should have made greater use of the knowledge and the direction that we received from them, but time is running out on this edition of our book.

There are some individuals whom we would like to single out for particular thanks. Sheri Snavely, our Publisher at Prentice Hall, has stayed with us throughout this project, from her immediate enthusiasm when we first broached the project to her in Larry's office in 1997, to the last hectic days of New Year's 2005, as everything was racing toward a conclusion. Her belief in our dream saw us through the days when we wondered if we were ever going to accomplish the goals we had set for *EEO*.

Paul Corey stood behind Sheri and us, providing wisdom and sagacity in his very natural way. Teresa Ryu Chung was our principal Prentice Hall editor for years and years, and indomitably put up with our vacillations and digressions. Erin Mulligan then took over to help us prepare our final draft. In getting the book to press, Production Editor Debra Wechsler has been unbelievable in her care, diligence, and determination; the book is as close to our vision as it is thanks to her. Carol Trueheart, Editor in Chief of ESM Development was there for us through this process with helpful doses of sanity. Development Editor Annie Reid and copy editor Chris Thillen made our words smooth and eloquent when we were all too bound up in circumlocution or confusion. Sheila Norman found amazing photographs, both ap-

propriate and dramatic. The design team was led by Carole Anson. Art Director Jonathan Boylan directed the design, making so much of the book beautiful, at least in our eyes. Patricia Burns and Connie Long from Artworks created the art program, key to making the book such a visual feast. Lisa Tarabokjia actually took our desperate phone messages, and Karen Horton scrambled to get us over the final finish line during the accuracy check.

We considered more than ten publishers for this project, and most of them would no doubt have been excellent, but we have found great fulfillment with Prentice Hall as a publishing partner. We have asked for a lot of help all the way through. What we have received has consistently exceeded our expectations, sometimes even our comprehension.

Our most important academic colleague on this project was George V. Lauder, who was originally slated to be an author. Unfortunately, he was called back to his natal stream at Harvard, which prevented him from continuing with us. He contributed the first draft of Chapter 2 and was heavily involved in planning the content and format of the book.

Our departmental colleagues in Ecology and Evolutionary Biology, UC Irvine, have played a wide range of supportive roles in this project. At one point, we saw the book virtually as an embodiment of our Department's collective knowledge. But then we recovered our sanity, having realized that you couldn't write a reasonable textbook with ten or more authors. Other colleagues at the University of California as a whole also inspired us to keep going. Darwinian biology is somewhat like a big scary Scottish clan, with all the intellectual fistfights, theoretical afflatus, and drunken color that you might expect. But it is our home, and we love it.

Michael Rose and Larry Mueller,
Irvine, California

## Reviewers

The authors would like to thank the colleagues who reviewed the manuscript for this book at various stages of the project.

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# BRIEF CONTENTS

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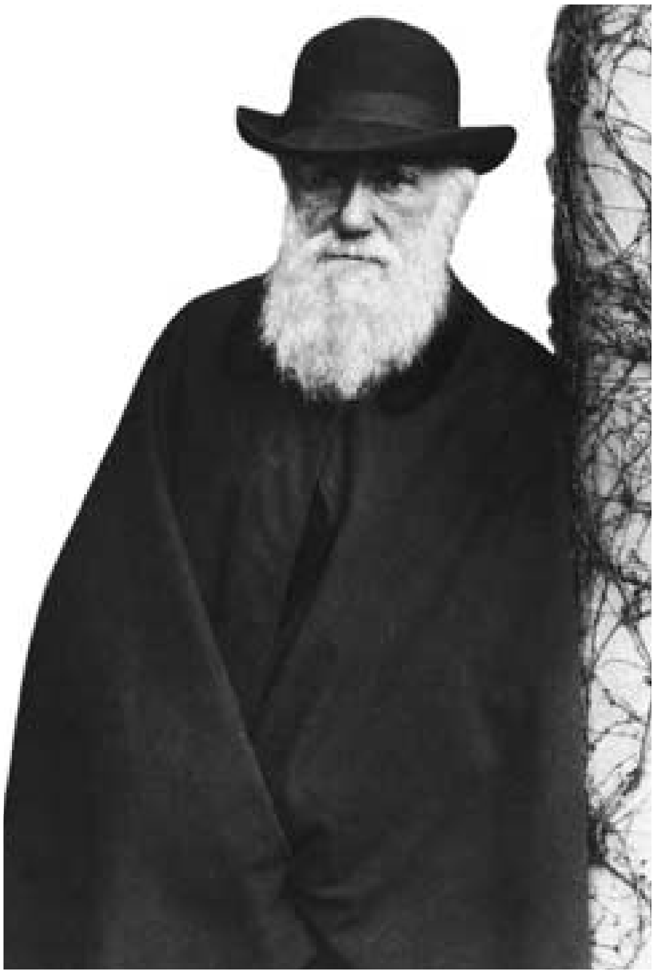

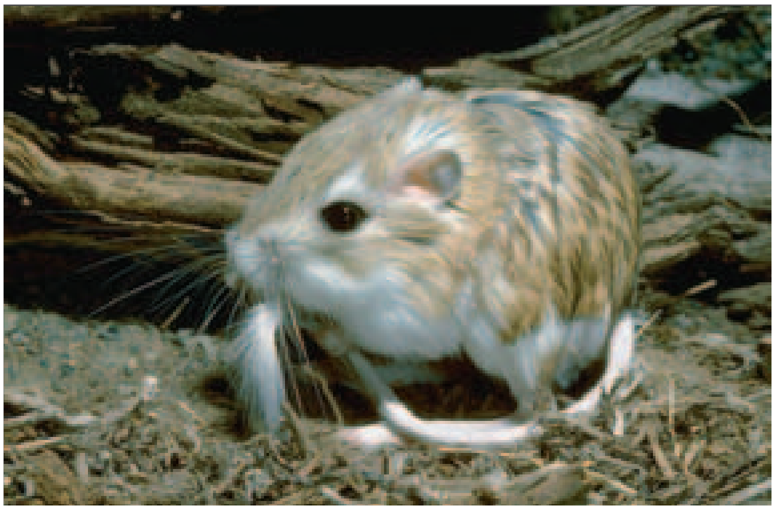

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