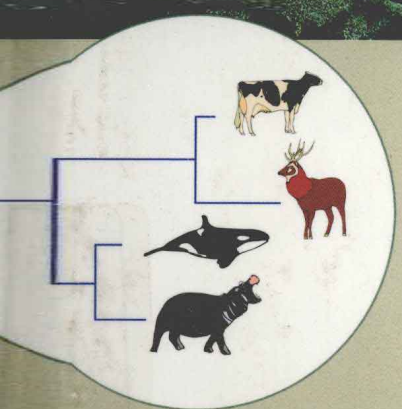
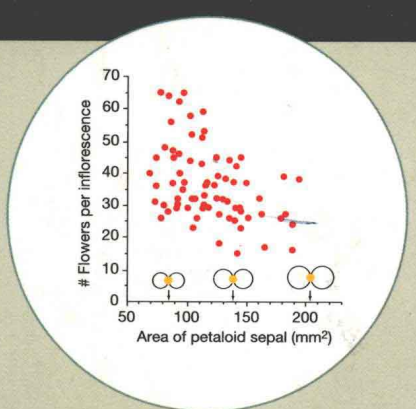
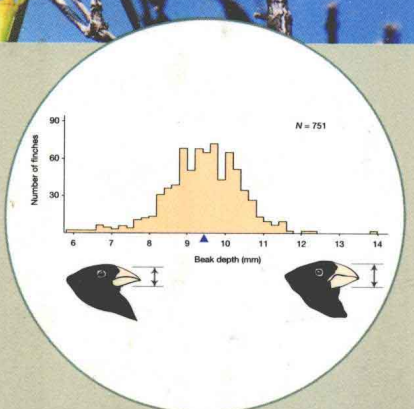
Evolutionary Analysis

SECOND EDITION







Scott Freeman Jon C. Herron

EVOLUTIONARY ANALYSIS

SECOND EDITION

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PRENTICE HALL
Upper Saddle River, NJ 07458

Library of Congress Cataloging-in-Publication Data

FREEMAN, SCOTT,
Evolutionary analysis / Scott Freeman, Jon C. Herron.—2nd ed.

Includes bibliographical references
1. Evolution (Biology) 2. Evolution (Biology)—Research. I. Herron, Jon C. II. Title
QH366.2.F73 2001 576.8—dc21 00-034663
ISBN 0-13-017291-X

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Cover photos (from left to right): Two color morphs of Northern Water Snake, *Nerodia sipedon*, in cypress swamp near New Orleans, Louisiana, May, 1988 by Photo Researchers, Inc.; cast of trilobite fossil, *Cryptolithoides ulrichi*, Viola Limestone, Ordovician, Murray County, Oklahoma, May, 1998 by A. Graffham/Visuals Unlimited; four-winged fly by Edward B. Lewis; bottlenose dolphins, *Tursiops truncatus*, captive, Waikaloa Hyatt, Hawaii by Flip Nicklin/Minden Pictures; *Begonia involucrata*, two inflorescences, male & female flowers by Douglas W. Schemske; finch (*Geospiza fortis*) by T.J. Ulrich, Academy of Natural Sciences of Philadelphia.
Cover illustrations: Jon C. Herron; Robin S. Manasse

Published by Prentice-Hall, Inc.
Upper Saddle River, New Jersey 07458

Printed in the United States of America
10 9 8 7 6 5 4 3 2 1

ISBN 0-13-017291-X

Prentice-Hall International (UK) Limited, *London*
Prentice-Hall of Australia Pty. Limited, *Sydney*
Prentice-Hall Canada, Inc., *Toronto*
Prentice-Hall Hispanoamericana, S.A., *Mexico*
Prentice-Hall of India Private Limited, *New Delhi*
Prentice-Hall of Japan, Inc., *Tokyo*
Pearson Education Asia Pte. Ltd.
Editora Prentice-Hall do Brasil, Ltda., *Rio de Janeiro*

Preface

The aims and audience of *Evolutionary Analysis* have not changed from the first edition to the second. Our goal is still to help students learn how to think like evolutionary biologists. The presentation is intended for undergraduates who are majoring in the biological sciences in preparation for careers in medicine, conservation, education, science journalism, or research. We assume that our readers have finished their introductory coursework and are ready to explore how a course in evolutionary biology can enrich their personal and professional lives.

Our approach and philosophy are also unchanged. Our tack is to present the topics that form the core of evolutionary biology in the same spirit of inquiry that drives research. Wherever possible, we motivate the material with the types of questions that evolutionary biologists ask. Are humans more closely related to chimpanzees or gorillas? If people with the *CCR5-Δ32* mutation are resistant to infection by HIV, will this allele increase in frequency in populations afflicted by the AIDS epidemic? Why did the dinosaurs suddenly go extinct, after dominating the land vertebrates for over 150 million years? Often a theoretical treatment will help to focus these questions, generate hypotheses, and make predictions that can be tested. After introducing the experiments and observations that biologists have used to test competing hypotheses, we analyze the data that resulted and consider what work remains to be done. Throughout the book, our objective is to present evolutionary biology as a dynamic and increasingly interdisciplinary enterprise.

Although the fundamental premise and approach of the book have not changed, its organization has. To align the sequence of chapters more closely with the way that most professors teach the course, we have reorganized the chapters into five units:

- **Part I, Introduction**, demonstrates why evolution is relevant to real-world problems, establishes the fact of evolution, and presents natural selection as an observable process.
- **Part II, Mechanisms of Evolutionary Change**, develops the theoretical underpinnings of the Modern Synthesis by exploring how mutation, selection, migration, and drift produce evolutionary change. The population genetics coverage is dramatically expanded from the first edition, but simplified by the placement of most algebraic treatments in boxes. These chapters have also been enriched by an increased focus on how population and quantitative genetic models can be applied to real-life problems in medicine and conservation.
- **Part III, Adaptation**, is a new unit that begins by introducing methods for studying adaptation, and follows up by offering detailed investigations into sexual selection, kin selection, and selection on life history characters.

- **Part IV, The History of Life**, starts with an analysis of speciation and phylogeny inference methods. Subsequent chapters focus on Precambrian evolution, the Phanerozoic, and human evolution.
- **Part V, Current Research—A Sampler**, includes a chapter treating classical and recent topics in molecular evolution. The unit also contains two new chapters. One of these focuses on evolutionary insights that have emerged from advances in developmental genetics; the other explores applications of evolutionary biology in epidemiology, medical physiology, human behavior, and public health.

As in the first edition, most chapters include boxes that cover special topics or methods, provide more detailed analyses, or offer derivations of equations. All chapters end with a set of questions that encourage students to review the material, apply concepts to new issues, and explore the primary literature.

Website and Transparencies

The companion website for Evolutionary Analysis has been revised and expanded. Each unit now includes two case studies. These tutorials challenge students to pose questions, formulate hypotheses, design experiments, analyze data, and draw conclusions. A tutorial for population genetics features problems students can solve using a downloadable simulation. The website also provides answers to selected end-of-chapter questions, guides to exploring the literature, links to other evolution-related sites, and an opportunity to email us with suggestions and comments.

The website for Evolutionary Analysis is accessible through the book's homepage at

http://www.prenhall.com/freeman

Prentice Hall's commitment to a four-color format for this edition of Evolutionary Analysis has enabled us to make the diagrams, data graphics, and photographs easier to interpret and the overall presentation brighter and more accessible. In response to requests from professors using the first edition, a set of 100 full-color overhead transparencies has been developed for the second edition. All transparencies are labeled with large, boldface type for easy reading in the classroom. Professors can get the transparency set by contacting either their local Prentice Hall representative, or Prentice Hall faculty services at (800) 526-0485.

Acknowledgments

We'd like to extend our heartfelt thanks to all of the colleagues who have helped this book serve students better by contributing published reviews, commissioned reviews, emailed suggestions, packets of reprints, and conversations with us at meetings. In particular, the additions and revisions in this edition were inspired by a series of thoughtful and constructive critiques provided by the following colleagues:

Leticia Aviles, *University of Arizona*
Loren E. Babcock, *The Ohio State University*
David Begun, *University of Toronto*
Andrew Berry, *Harvard University*
Keith A. Crandall, *Brigham Young University*
W. Ford Doolittle, *Dalhousie University*
Jerry F. Downhower, *The Ohio State University*
Scott Edwards, *University of Washington*
Gary M. Fortier, *Delaware Valley College*
Glenys Gibson, *Acadia University*
Lonnie J. Guralnick, *Western Oregon University*
Werner G. Heim, *Colorado College*
Joel Kingsolver, *University of Washington*
Andrew H. Knoll, *Harvard University*
Robert A. Krebs, *Cleveland State University*
Catherine S. McFadden, *Harvey Mudd College*
Andrew Martin, *University of Colorado*
Arnold I. Miller, *University of Cincinnati*
Nancy A. Moran, *University of Arizona*
Stephen W. Schaeffer, *Pennsylvania State University*
Robert Sinsabaugh, *University of Toronto*
Maureen Stanton, *University of California, Davis*
Daniel B. Thompson, *University of Nevada, Las Vegas*
Sara E. Via, *University of Maryland, College Park*

It would be difficult to overemphasize how much this edition has benefited from the care and creativity of these reviewers. In a very real sense, this book is a product of a community that is passionate about the study of evolution and devoted to teaching.

In addition, we'd like to extend our sincere thanks to students who emailed suggestions for improvement. Especially helpful were the formal written critiques contributed by Dr. Peter Wimberger's class at the University of Puget Sound, and many comments and suggestions from our own students at the University of Washington.

We owe a special debt to three colleagues who contributed revisions of key chapters and to Dr. Kathleen Hunt, who contributed revised versions of the end-of-chapter questions. We are tremendously fortunate to have had such talented contributors involved in the preparation of this edition. Specifically, Dr. Michael Hart of Dalhousie University revised the chapters on life history, phylogeny inference, and the Phanerozoic and originated the chapter on evolution and development. His command of the literature and enthusiasm for evolutionary biology were a tremendous asset during the revision process, and his ingenuity and excitement about science made him an absolute joy to work with. Dr. Niles Lehman of the State University of New York, Albany, revised the chapter on the origin of life and Precambrian evolution. His creativity, passion, knowledge, and rapid work were vital in bringing students a fresh and accurate read on this dynamic topic. Dr. David Begun of the University of Toronto updated the chapter on human evolution. His expertise was an invaluable contribution to our coverage of this fast-moving field, and his willingness to work to a tight deadline was greatly appreciated.

This book would not exist without the skill, professionalism, and dedication of the editorial and production team at Prentice Hall. Paul Corey's leadership and commitment as Editorial Director of Science and Mathematics have been instrumental. Senior Production Editor Debra Wechsler did a superb job managing the thousands of details required to make a book as free of errors and omissions as is humanly possible. Art Editor Karen Branson assembled and managed a talented group of artists to create the four-color figure program. Robin S. Manasse did most of the new biological illustrations, including the animals on the cover. Art Directors Anne France, Joe Sengotta, and Jon Boylan created an attractive design and cover

for the book. Andrew Stull was responsible for expanding and improving the website. Executive Marketing Manager Jennifer Welchans is supplying the drive and tools necessary to ensure that professors throughout the world have an opportunity to consider the book for their course.

Finally and most, we thank Editor in Chief of Biology Sheri Snavely, whose vision and energy are the wellspring of this book. Her passion for publishing, infallible instincts, humor, and devotion are a constant source of inspiration.

Scott Freeman
Jon C. Herron
Seattle, Washington

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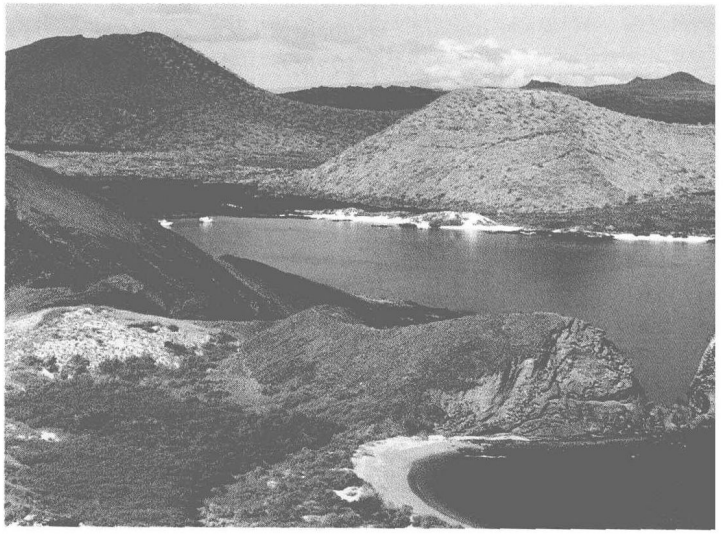

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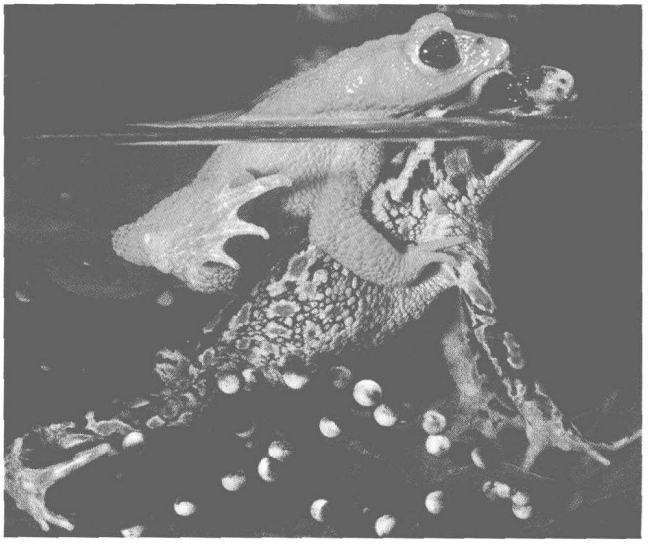

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The Galápagos islands have served as a laboratory for evolutionary studies for over 160 years. (Frans Lanting/Minden Pictures)

INTRODUCTION

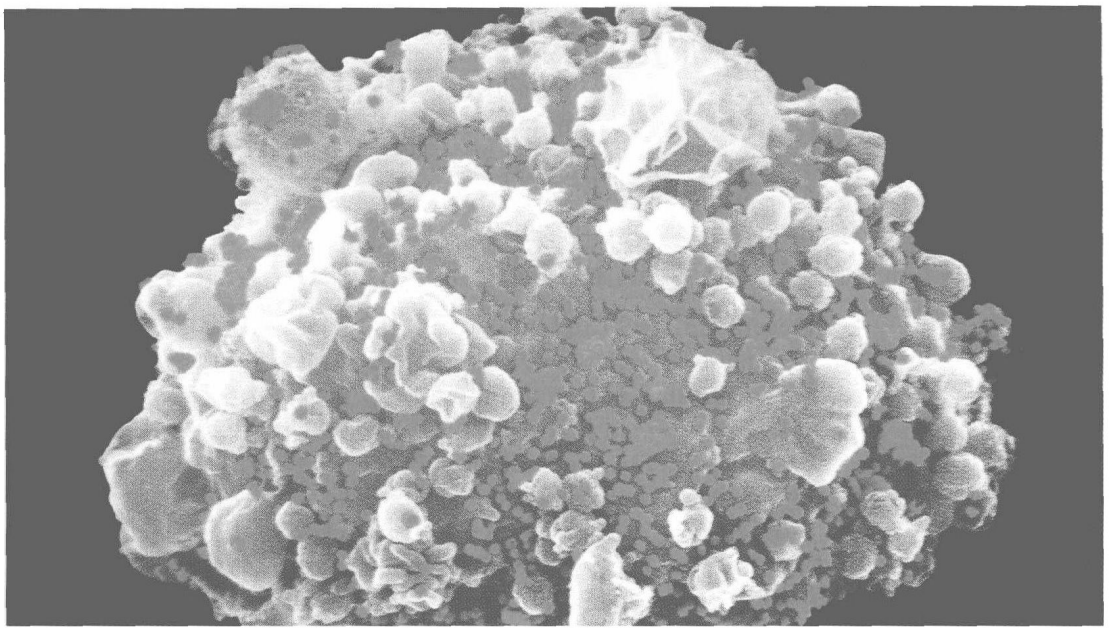
AMONG THE ATTRACTIVE ASPECTS OF EVOLUTIONARY BIOLOGY IS THAT IT IS ROOTED in a single, organizing mechanism. This mechanism is natural selection. Gaining a thorough understanding of natural selection is thus the first challenge for anyone studying evolution. Natural selection is simple in concept, but widely misunderstood. Understanding how the process works requires moving beyond slogans like "survival of the fittest."

Our primary goal in Part I (Chapters 1–3) is to introduce natural selection as an agent of evolutionary change. Our exploration of the process begins with a chapter devoted to understanding the human immunodeficiency virus (HIV) and the AIDS epidemic. Chapter 2 expands on this presentation by reviewing evidence that all organisms have changed through time, or evolved, throughout the history of life—much as HIV has evolved over the past half century. In Chapter 3 we explore how natural selection works in more detail. This sequence of chapters lays the groundwork for exploring the other mechanisms that cause change through time, in Part II.

Our secondary objective in these chapters is to introduce the experimental and analytical methods used by researchers in evolutionary science. These methods are a prominent theme throughout the text. We emphasize them to help readers learn how to ask questions, design experiments, analyze data, and critically review scientific papers, in addition to mastering facts. The detailed examples we present not only make the general concepts of evolutionary biology clear but also provide insight into how we know what we know.

CHAPTER 1

A Case for Evolutionary Thinking: Understanding HIV



The red particles emerging from this human T cell are HIV virions. (National Institute for Biological Standards and Control, England/Science Photo Library/Photo Researchers, Inc.)

AT THE START OF A COURSE, IT CAN BE USEFUL TO STEP BACK AND ASK TWO questions: What sort of content will be covered? and How will this information help me in my professional and everyday life? To help answer these questions, we explore the evolution of human immunodeficiency virus (HIV). This is the pathogen that causes the acquired immune deficiency syndrome (AIDS).

In this chapter, we introduce the scope of evolutionary analysis through an in-depth look at a prominent contemporary issue. Our goals are to illustrate the kinds of questions that evolutionary biologists investigate, demonstrate how an evolutionary perspective can inform research throughout the biological sciences, and introduce concepts that will be explored in detail later in the text.

HIV is a compelling case study because it raises issues that are almost certain to influence the professional and personal lives of every one of our readers. As an emerging virus that rapidly evolves drug resistance, HIV exemplifies two pressing public health issues. AIDS already qualifies as one of the most devastating epidemics ever experienced by our species.

Here are the questions we address:

- Why have promising AIDS treatments, like the drug azidothymidine (AZT), proven ineffective in the long run?
- Why are some people resistant to becoming infected or to progressing to disease once they are infected?
- Why does HIV kill people?
- Could a vaccine provide protection from the diversity of HIV strains found today?

As a case study, HIV will demonstrate how evolutionary biologists study adaptation and diversity.

These questions may not sound as if they have anything to do with evolutionary biology, but evolutionary biology is the science devoted to understanding two things: (1) how populations change through time in response to modifications in their environment, and (2) how new species come into being. More formally, evolutionary biologists study adaptation and diversity. These are exactly the issues targeted by our questions about AIDS and HIV. Before we tackle them, however, we need to delve into some background biology.

1.1 The Natural History of the Epidemic

In December, 1999 the United Nations' AIDS program estimated that about 40 million people worldwide were infected with HIV (Piot 1998; Figure 1.1). The epidemic has already been responsible for more deaths than the black plague that devastated Europe in the 14th century. By the end of 2001, AIDS is almost certain to overtake the "Spanish" influenza outbreak of 1918 as the epidemic responsible for the most deaths in all of human history.

Most HIV infections result from two related but distinct epidemics that occurred during the 1980s and 1990s: one among heterosexual men and women in sub-Saharan Africa and south and southeast Asia, and the other among homosexual men and intravenous drug users in the United States and Europe. The dual epidemics are distinguished by the number of people involved and the disease's mode of transmission.

In sub-Saharan Africa, the number of AIDS cases is almost overwhelming (see Mann and Tarantola 1998; Piot 1998). Epidemiologists estimate that over 23 million Africans are currently infected with HIV-1. In most sub-Saharan cities, over 75% of

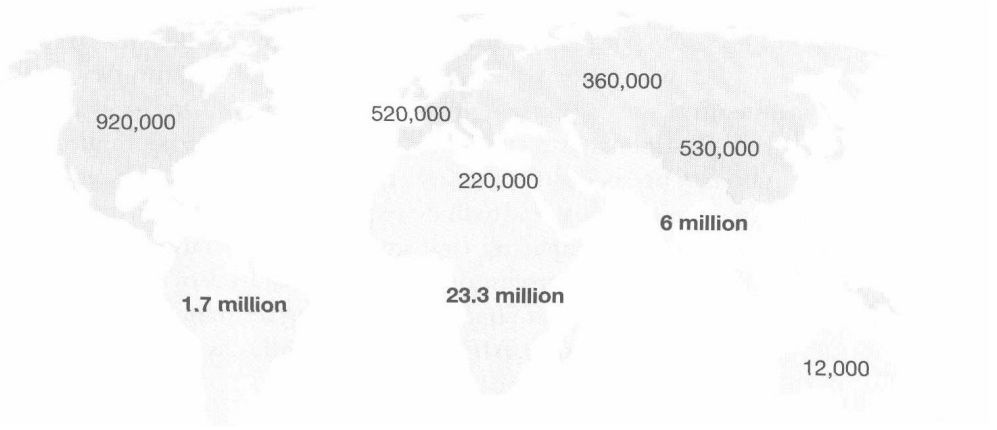


Figure 1.1 Distribution of HIV infections This map shows the geographic distribution of HIV-1 infections. The most dramatic conclusion to be drawn from this figure is that AIDS is primarily a disease of developing nations. It is estimated that over 90% of HIV-infected people live in the poor countries of the southern hemisphere. Two-thirds of these are in sub-Saharan Africa alone.