Pearson International Edition

Evolutionary Analysis

Fourth Edition

Scott Freeman Jon C. Herron

EVOLUTIONARY ANALYSIS

FOURTH EDITION

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Pearson Education International

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Preface

Evolutionary Analysis is for undergraduates majoring in the life sciences. We assume that readers have completed much or all of their introductory coursework and are beginning to explore in more detail particular areas of biology that are relevant to their personal and professional lives.

We expect our readers to pursue careers in a diversity of fields, including medicine, education, environmental management and conservation, journalism, biotechnology, and research. We therefore attempt, throughout the book, to show the relevance of evolution to all of biology and to real-world problems.

Our primary goal is to encourage readers to think like scientists. We present evolutionary biology not as a collection of facts but as an ongoing research effort. When exploring an issue, we begin with questions. Where did HIV come from? Why did prairie chicken populations continue to decline despite successful efforts to restore their habitat? How closely related are humans and chimpanzees? We use such questions to motivate discussions of background information and theory. These discussions enable us to frame alternative hypotheses, consider how they can be tested, and make predictions. We then present and analyze data, consider its implications, and highlight new questions for future research. The analytical and technical skills readers learn from this approach are broadly applicable, and will stay with them long after the details of particular examples have faded.

Consistent with our presentation of evolutionary biology as a dynamic research enterprise, we have tried to keep our coverage as up-to-date as possible. This has made the fourth edition as exciting to work on—and as daunting—as the first three. Many of the fields we cover are advancing at a rate we would not have dreamed possible just a few years ago. More than once our editors have had to tear chapter manuscripts from our hands while there were still more changes we wanted to make.

There is something new in every chapter. Among the new examples we are most excited about are these:

- Evidence that disease progression in HIV patients results, in part, from evolution of the viral population toward greater competititve fitness (Chapter 1).
- Population-genetic data indicating that heterozygotes survived an epidemic of spongy brain disease at a higher rate than homozygotes (Chapter 6).
- A demonstration that the substitution of one allele for another at a single locus can dramatically alter a flower's appeal to different pollinators (Chapter 9).
- Data suggesting that the frequency of Apert syndrome in human populations reflects selection at the level of stem cells in tissues acting in oppostion to selection at the level of individuals in populations (Chapter 10).
- Results showing that female crickets scent-mark their mates to avoid copulating twice with the same male (Chapter 11).

- Common-garden experiments revealing that an invasive plant evolved greater weediness when released from a life-history trade-off (Chapter 13).
- Documentation that a change in the phenotype of a plant resulted from a change in gene regulation (Chapter 15).
- Phylogenetic evidence that viruses played a key role in the transition from RNA World to DNA world, and in the origin of the three domains of life (Chapter 17).
- New insights into the evolution of the tetrapod limb from both developmental genetics and a recently discovered transistional fossil (Chapter 19).

We encourage readers to check the literature for new developments that have been reported since the book went to press; there are sure to be many.

Two trends we have witnessed since the first edition are reflected in changes to the table of contents. First, phylogenies have grown so central to research in evolution that we felt we had to introduce tree thinking much earlier in the book. We have therefore moved Estimating Evolutionary Trees into Unit 1, where it has become Chapter 4. Second, the Human Genome Project and the technologies it fostered have ignited an explosion of genomic data. Comparative analyses of whole genomes have yielded startling insights into the evolutionary process. To convey some of the excitement of this new frontier, we have added a chapter on Phylogenomics and the Molecular Basis of Adaptation. As Chapter 15, it concludes Unit 3.

There are four units in all:

- **Part I, Introduction**, shows that evolution is relevant outside books and classrooms, establishes the fact of evolution with a mixture of classical and recent evidence, presents natural selection as an observable process, and develops modern methods for reconstructing evolutionary trees.
- **Part II, Mechanisms of Evolutionary Change**, develops the theoretical underpinnings of modern evolutionary biology by exploring how mutation, selection, migration, and drift produce evolutionary change.
- **Part III, Adaptation**, introduces a variety of methods for studying adaptation, and offers detailed accounts of research in sexual selection, kin selection, life history evolution, and Darwinian medicine.
- **Part IV, The History of Life**, begins with an analysis of speciation. It then considers the origin of life, the universal phylogeny, and major events in the history of multicellular organisms. Because of its importance for understanding macroevolution, our chapter on Development and Evolution is part of this unit. The unit and book end with human evolution.

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 readers to review the material, apply concepts to new issues, and explore the primary literature.

Additional Resources for Instructors and Students

The new edition of *Evolutionary Analysis* offers an Instructor Resource Center on CD containing all of the line art, tables, and all photos from the book in both JPEG and PowerPoint® files. All presentation art has been carefully modified for optimal visibility when projected. An unlabeled version of the line art is also included to facilitate customization.

The student Companion Website for *Evolutionary Analysis* has again been revised and updated. This website is accessible through the book's homepage at:

www.prenhall.com/freeman

It features carefully crafted chapter study quizzes that offer elaborate instructional feedback. These quizzes are designed to increase understanding of the underlying concepts of each chapter as well as prepare students for taking tests. Activities such as simulations and case studies challenge students to pose questions, formulate hypotheses, design experiments, analyze data, and draw conclusions. Many of these activities accompany downloadable software programs that allow students to conduct their own virtual investigations. The Companion Website also offers the answers to the end-of-chapter questions and weblinks to other evolution-related sites.

Acknowledgments

We owe the effectiveness and success of *Evolutionary Analysis* to the generosity, creativity, energy, and support of the many colleagues and students who have helped us write a better book. They have reviewed chapters, shared their data and photographs, answered our questions, emailed us with suggestions, sent us reprints, and talked with us at meetings. It is a privilege to spend time with this remarkable community, and we thank them for their collaboration.

In preparing the fourth edition we have been guided by thoughtful, detailed, and constructive critiques by:

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Paul Wilson, *California State University*

If deficiencies remain, the fault is ours for not following more closely their excellent advice.

The following colleagues read chapters in proof. Their keen eyes and thoughtful feedback applied considerable polish to the manuscript:

Lynda Delph, *Indiana University*
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Tamra Mendelson, *Lehigh University*
Sara Via, *University of Maryland*
Helen Young, *Middlebury College*

RMBlue Studios helped develop the figure program, prepared the beautiful new illustrations, and revised the existing art. Kathleen Hunt revised the thought-provoking end-of-chapter questions and exploring the literature items. Brooks Miner assisted with library research, helped plan chapter revisions, and made invaluable suggestions on the manuscript.

The editorial and production team at Pearson Prentice Hall have been, as ever, superb. We thank them for their guidance, support, collaboration, and friendship. ESM President Paul Corey has been steadfastly committed to this project from the beginning. Editorial Assistant Lisa Tarabokjia arranged for the reviews. Senior Media Editor Patrick Shriner and Assistant Editor Jessica Berta developed the media components. Art Director Kenny Beck designed the book. Jacqueline Ambrosius oversaw the formatting and composition of the text. Prentice Hall's remarkable team of sales representatives are, even as we put the final touches on this edition, disseminating the book to professors everywhere.

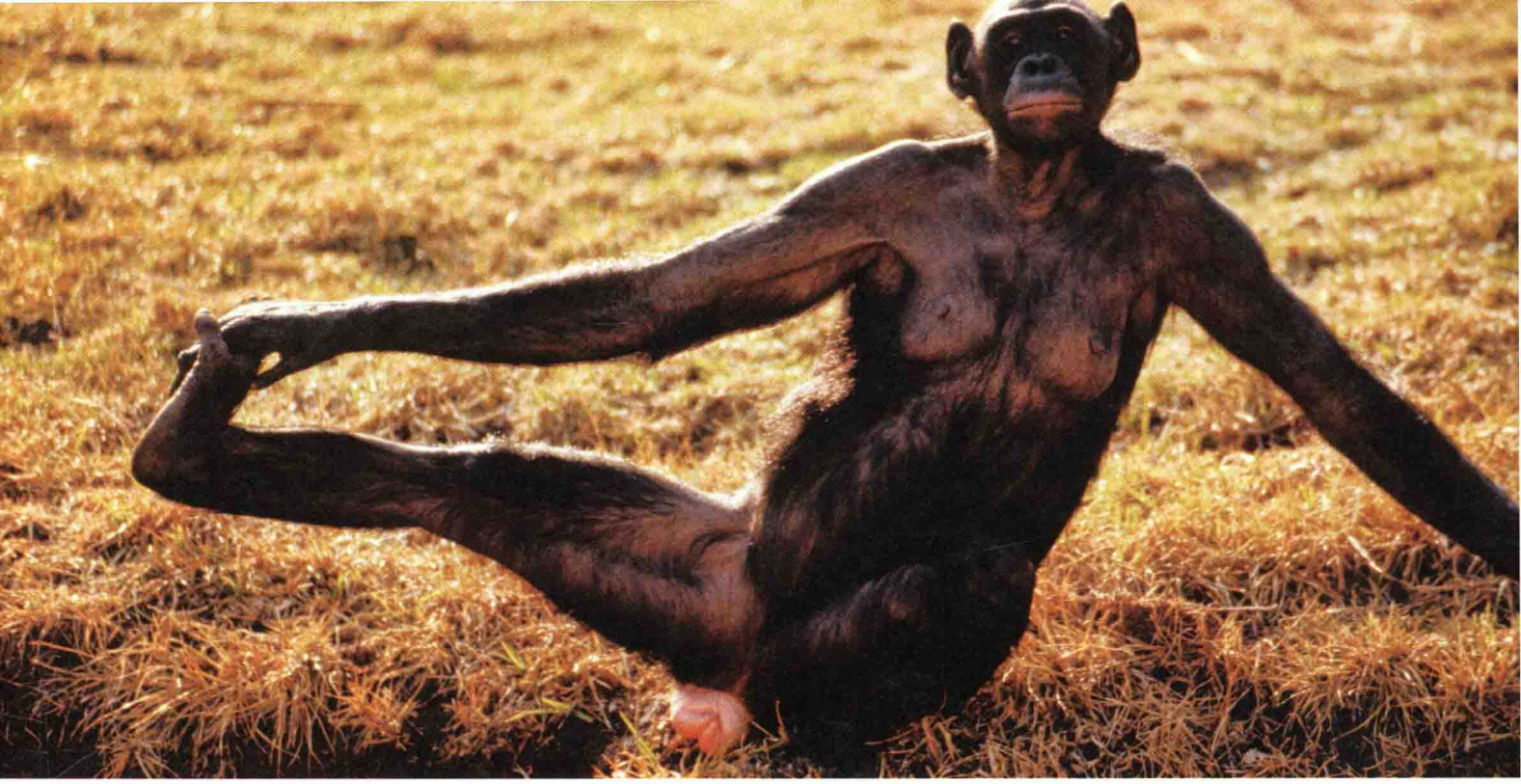
Production Editor Debra Wechsler is outstanding at her job and a joy to work with. How she has put up with us, in the midst of overseeing a million last-minute details, we do not understand. We cannot thank her enough.

Finally, we thank the two extraordinary editors with whom it has been our great fortune to collaborate. Former Publisher Sheri Snavely willed this project into existence and devoted herself wholeheartedly to its success through its first three editions. It will always be her book. After getting us started on the fourth edition she passed the project into the highly capable hands of Acquistions Editor Andrew Gilfillan. He has been a pillar of wisdom and support. Now it is his book too.

Jon C. Herron
Scott Freeman
Seattle, Washington

Brief Contents

Contents



Bonobos are, along with common chimpanzees, our closest living relatives. Here, a female stretches.

PART I

INTRODUCTION

Where did Earth's organisms come from? Why are there so many different kinds? How did they come to be so apparently well-designed? These are the fundamental questions of evolutionary biology. The answers are found in both the pattern and mechanism of evolution. The pattern is descent with modification from common ancestors. The primary mechanism is natural selection.

Our first goal in Part I (Chapters 1–4) is to introduce the pattern and process of evolution. In Chapter 1 we explore an example, the evolution of HIV. In Chapter 2 we look at the pattern of evolution and at evidence of common ancestry. In Chapter 3 we focus on the mechanism of evolution. Natural selection is evolutionary biology's organizing principle; its simplicity is among the discipline's charms. Natural selection is widely misconstrued, however. Understanding it requires moving beyond slogans like "survival of the fittest." In Chapter 4 we cover methods for reconstructing evolutionary history.

Our second goal is to introduce the experimental and analytical methods used by the biologists who study evolution. 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. The detailed examples we present make the general concepts of evolutionary biology clear and also provide insight into how we know what we know. ■

Prostitutes in the Songachi redlight district in Calcutta, India, learn from a health worker about the benefits of using condoms. In Songachi, an aggressive campaign to educate sex workers, madams, and pimps to distribute condoms, and to encourage condom use, has kept the prevalance of HIV among prostitutes below 12%. In other redlight districts, HIV prevalence has climbed above 50% (Cohen 2004).

1

A Case for Evolutionary Thinking: Understanding HIV

Why study evolution? Although he scarcely mentioned it in *On the Origin of Species* (1859), one of Charles Darwin's motives was that understanding evolution can help us understand ourselves. "Light will be thrown," Darwin wrote, "on the origin of man and his history." For Theodosius Dobzhansky (1973), an architect of the modern view of evolution we present in this text, the reward was that evolutionary biology is the conceptual foundation that supports all the life sciences. "Nothing in biology makes sense," he declared, "except in the light of evolution." For some readers the incentive may be that a course in evolution is required for the completion of their degree.

Here we suggest yet another reason to study evolution: The tools and techniques of evolutionary biology offer crucial insights into matters of life and death. To justify this claim, we explore the evolution of human immunodeficiency virus (HIV). HIV is the virus that causes acquired immune deficiency syndrome (AIDS).

A deep look at this prominent contemporary issue will introduce the scope of evolutionary analysis. It will illustrate the kinds of questions evolutionary biologists ask, show how an evolutionary perspective can inform research throughout the biological sciences, and introduce concepts that we will explore in detail elsewhere in the book.

HIV makes a compelling case study because it raises issues almost certain to influence the personal and professional life of every reader. HIV exemplifies pressing public health issues: It is an emerging virus. It rapidly evolves drug resistance. And it is deadly. AIDS already qualifies as one of the most devastating epidemics our species has experienced.

Here are the questions we address:

- Why did early AIDS treatments, like the drug azidothymidine (AZT), look promising when first used but prove ineffective in the long run?
- Why does HIV kill people?
- Why are some people resistant to becoming infected or to progressing to disease once they are infected?
- Where did HIV come from?

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

Some of 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 following 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 HIV and AIDS. Before we tackle them, however, we need to delve into some background biology.

1.1 The Natural History of the HIV/AIDS Epidemic

The worst epidemic in human history, judging by the number of deaths, was probably the influenza of 1918. It swept the globe in a matter of months, killing 50 to 100 million people (Johnson and Mueller 2002). The second worst was likely the Black Death, caused by a highly virulent pathogen whose identity remains controversial (see Raoult et al. 2000; Gilbert et al. 2004; Christakos and Olea 2005; Duncan and Scott 2005). It ravaged Europe from 1347 to 1352, taking 30 to 50% of the population—roughly 25 million lives (Derr 2001). More localized outbreaks over the next 300 years killed millions more. Also worthy of mention is the New World smallpox epidemic unleashed around 1520 by European conquistadores. Its death toll is harder to reckon, but over the succeeding decades it decimated Native American populations across two continents (Roberts 1989; Snow 1995; Patterson and Runge 2002).

AIDS is among the worst epidemics in human history.

The AIDS epidemic, first recognized by medical professionals in 1981, has rapidly earned a place among this grim company (UNAIDS 2005). HIV has so far infected more than 65 million people. Twenty-five million have already died of the opportunistic infections that characterize AIDS. Among the rest, many are gravely ill. And many are still spreading the disease. The Joint United Nations Programme on HIV/AIDS has estimated that by 2020 the AIDS epidemic will have claimed a total of almost 90 million lives (UNAIDS 2002a).

Figure 1.1 summarizes the global pattern of the AIDS epidemic. In the map in Figure 1.1a, regions are shaded to show the prevalence of HIV infection among adults, and labeled to indicate the total number of adults and children infected with HIV and the sex ratio among infected adults. The bar graphs in Figure 1.1b document the growth of the epidemic over time in different parts of the world.

Every day roughly 13,400 people are newly infected with HIV and 8,500 people die of AIDS (UNAIDS 2005). According to the World Health Organiza-