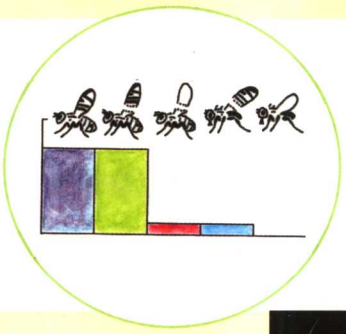
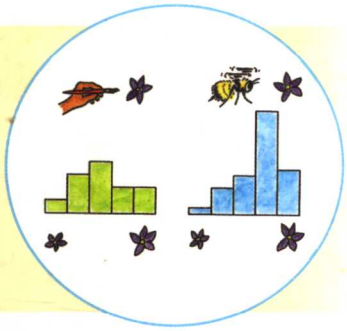
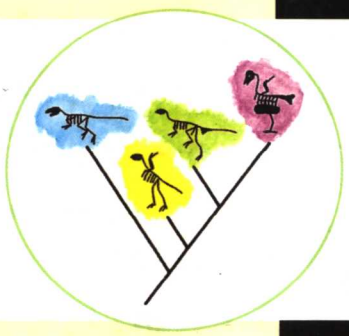
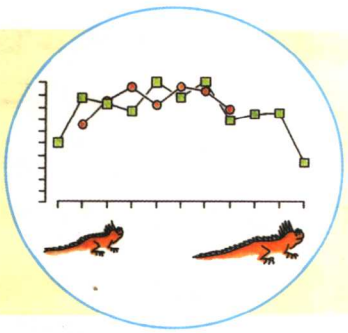
Evolutionary Analysis

Scott Freeman ✦ *Jon C. Herron*









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Preface

Evolutionary Analysis is a text for undergraduates majoring in biology and related fields. We assume that readers have completed their introductory coursework and are studying evolution, among other topics, to prepare for careers in human and animal healthcare, environmental management and conservation, primary and secondary education, science journalism, and biological and medical research. We hope this book will be a valued addition to your course. Our goal is to help students learn to:

- Ask interesting questions about evolution;
- Design experiments and plan observations that would answer those questions;
- Read and critically evaluate papers from the primary literature; and
- Contribute to an informed conversation about evolution between specialists and the lay public.

In short, we hope to help readers learn to think like evolutionary biologists.

This approach is inspired by the movement to reform undergraduate science education and its theme of teaching science as a process of discovery. Presenting science as science is done, instead of as a body of facts, is laudable and exciting. But what does this concept actually look like in practice? Can a textbook cover the foundations of a scientific field—its conceptual framework, classical results, and current research topics—in the context of exploring questions? Can instructors motivate students of biology with the same spirit of curiosity and investigation that motivates practicing scientists?

We wrote *Evolutionary Analysis* because we believe that the answer to these questions is yes. Instead of surveying facts, the book introduces each major organizing theme in evolution through a question. How has HIV become drug-resistant? Why did the dinosaurs, after dominating the land vertebrates for 150 million years, suddenly go extinct? Are humans more closely related to gorillas or to chimpanzees? Next we develop the strategies that evolutionary biologists use for finding an answer. Often a theoretical treatment helps to focus the question, frame hypotheses, and make predictions. Then we consider observations and experiments that test the predictions made by competing hypotheses, and discuss how the data are interpreted. Frequently, the conclusions prompt a new round of questions. Throughout the exposition our objective is to present evolutionary biology as a dynamic field of inquiry.

This investigative framework, and the theme of thinking like evolutionary biologists, unifies the book's four parts. These chapter groupings are intended to support several different approaches to organizing a course on evolution.

- Part I, Darwinism and the Fact of Evolution, demonstrates the relevance of evolution to real-life problems, establishes the fact of evolution, presents natural selection as an observable process, and introduces some of the major approaches and methods used by contemporary researchers.
- Part II, Mechanisms of Evolutionary Change, develops the theoretical under-

pinnings of the Modern Synthesis by exploring the mechanisms of evolution and speciation, the nature of adaptation, and molecular evolution.

- Part III, The History of Life, emphasizes phylogenetic analysis and contemporary inquiry, with chapters devoted to methods for reconstructing phylogenies, the origin of life and early evolution, the Cambrian explosion, and mass extinctions.
- Part IV, Current Research—A Sampler, provides in-depth coverage of other issues inspiring contemporary investigations, including human evolution, sexual selection, life histories, and conservation.

Most chapters include boxes that cover special topics or methods, provide more detailed analyses, or offer derivations of equations. All of the chapters end with a set of questions that encourage readers to review the material, apply their understanding to new issues, talk to their peers and instructors, and explore the current literature.

Studying evolution should be relevant to readers' personal and professional lives, and interesting to students new to the field. As a result, we include discussions of the evolution of drug resistance in pathogens, evolution and human health, the evolution of senescence, sexual selection, social behavior, eugenics, and biodiversity and conservation.

In partnership with the book, the text-specific website *Evolution in Action* provides a forum where professors and students can interact with their colleagues and peers at other campuses. The site includes research postings, virtual experiments and simulations, current hyperlinks, book updates, and additional questions to test students' knowledge. *Evolution in Action* is located at

http://www.prenhall.com/freeman

To access the site enter the username **beagle** and the password **galapagos.**

Like the science, this book and the website are a work in progress. If we have left things out that interrupt the flow of your course, if there are examples that would illustrate concepts better than the ones we use, if sections prove confusing, or if we have done something right, please let us know. We will do our utmost to improve future editions of the book based on your input. Please contact us through the website.

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Our publisher's enthusiastic and talented team of editors, designers, and producers have been generous, tireless, patient, and good-humored while guiding this book through conception, creation, production, and launch. Editor in Chief of Prentice Hall Science Paul F. Corey has been rock-steady in his leadership and support. Executive Managing Editor Kathleen Schiaparelli kept the project on schedule. Senior Production Editor Debra Wechsler was tolerant with us and eagle-eyed with the manuscript, ensuring that the art and printed text are accurate and complete, and that a million different pieces came together in the end. Art Editors Karen Branson and Gus Vibal managed the art production and cheerfully gave emergency tutorials in electronic art preparation. Art Director Heather Scott coordinated the design of the book and the cover. Chris Thillen carefully copyedited the manuscript. Senior Marketing Manager Jennifer Welchans is providing tremendous energy and enthusiasm in marketing the book.

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Seattle, Washington

Brief Contents

Contents

PART I

DARWINISM AND THE FACT OF EVOLUTION

One of the most attractive aspects of evolutionary biology is that it is rooted in a single, general, organizing mechanism called natural selection. Gaining a thorough understanding of natural selection is thus the first challenge for anyone new to the science of evolution. Natural selection is simple in concept, but widely misunderstood. Understanding how the process works requires moving far beyond slogans like "survival of the fittest."

The primary goal of Part I (Chapters 1–3) is to introduce natural selection as the primary agent of evolutionary change. This presentation lays the groundwork for exploring the other mechanisms that cause change through time, in Part II.

A secondary objective of the first three chapters is to introduce the experimental and analytical methods used by researchers in evolutionary science. These methods are a prominent theme in Chapters 1 and 2 and are the primary focus of Chapter 3. Our goal is to help readers learn 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

At the start of a course it can be useful to step back and ask two questions: What sort of content will be covered? How will this information help me in my professional and everyday life? To help answer these questions, we explore the evolution of human immunodeficiency viruses 1 and 2 (HIV-1 and HIV-2). These are the pathogens that cause 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 of the most pressing public health issues of our time. AIDS may, in fact, become 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 AZT, proven ineffective in the long run?
- How does HIV win its battle against the immune system?
- Why does HIV kill people?
- Where did HIV come from?
- How can we best manage the AIDS epidemic?

These questions may not sound as if they have anything to do with evolutionary biology. But evolution is the science devoted to understanding two things:

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

(1) how populations change through time in response to modifications in their social, biological, and physical environments, 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. But before we tackle them, we need to delve into some background biology.

1.1 The Natural History of the Epidemic, HIV, the Immune System, and AIDS

In late 1996 the World Health Organization estimated that almost 23 million people worldwide were infected with HIV (Holden 1996; Figure 1.1). Most of these infections resulted from two related but distinct epidemics that occurred during the 1980s and early 1990s: one among heterosexual men and women in urban areas of sub-Saharan Africa, and the other among homosexual men and intravenous drug users in the United States and Europe. These two waves of infection are distinguished by the number of people involved and by the disease's mode of transmission.

The nature and size of the AIDS epidemics in Africa, North America and Europe, and Asia contrast sharply.

In sub-Saharan Africa the number of AIDS cases is almost overwhelming in magnitude (see De Cock et al. 1990; Palca 1991; Paley 1994; Piot 1996). Epidemiologists estimate that over 14 million Africans are now infected with HIV-1, and project that one-third of the workforce in some countries may eventually die of AIDS. In some African cities AIDS is already the leading cause of adult death. In this epidemic HIV is transmitted primarily through heterosexual intercourse, and men and women are about equally likely to be infected.

In contrast, the AIDS epidemic in North America and Europe is characterized by transmission via homosexual intercourse and needle sharing among intravenous drug users. Rates of infection in the general population are much lower than in Africa (Figure 1.2), and men are much more likely to be infected with HIV than women. For example, about one in a hundred men and one in eight hundred women, for a total of over 835,000 people, are now thought to be infected in the United States (Levy et al. 1994). Although rates of

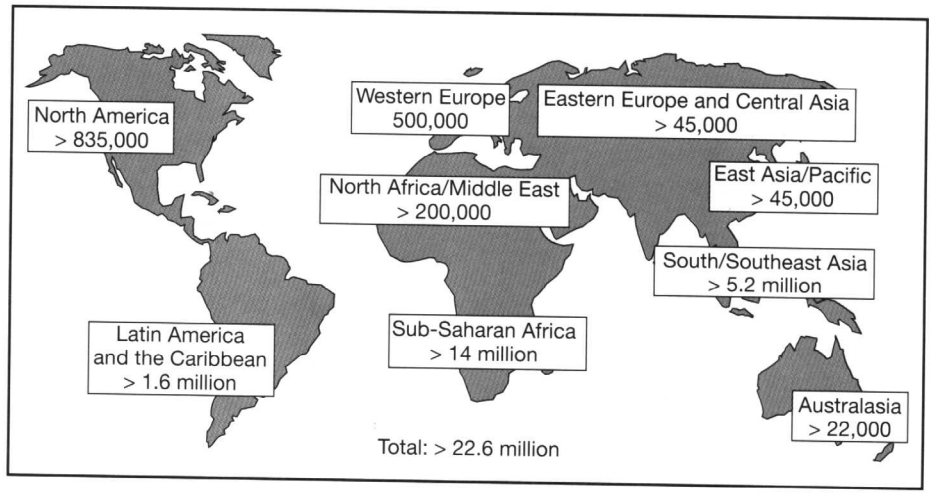

***Figure 1.1* Distribution of HIV infections** This map shows the geographic distribution of HIV-1 and HIV-2 infections. The most dramatic conclusion to be drawn from this figure is that AIDS is primarily a disease of developing nations. It is estimated that over 90% of HIV-infected people live in the poor countries of the southern hemisphere. Two-thirds of these are in sub-Saharan Africa alone.