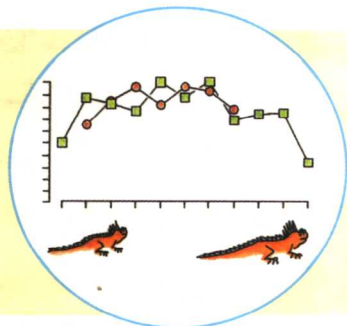
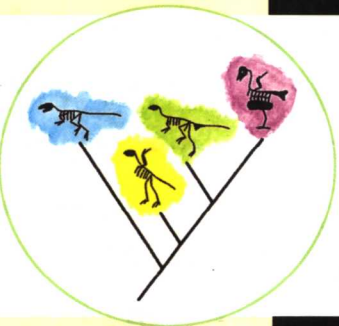
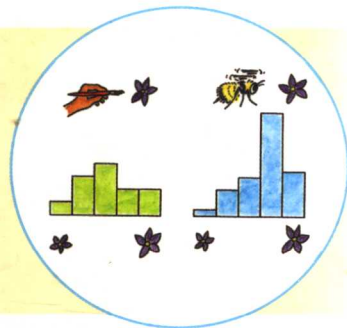
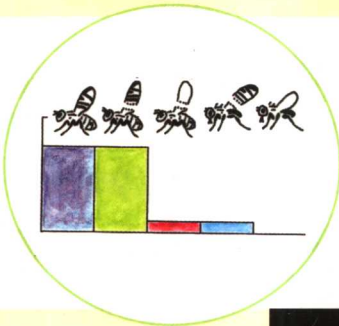


Evolutionary Analysis

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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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Scott Freeman
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Brief Contents

P A R T I

Darwinism and the Fact of Evolution 1

- CHAPTER 1 A Case for Evolutionary Thinking: Understanding HIV 3
CHAPTER 2 Darwinism and the Fact of Evolution 27
CHAPTER 3 Methods of Evolutionary Analysis 67

P A R T II

Mechanisms of Evolutionary Change 101

- CHAPTER 4 Mutation: The Origin of New Genes and Alleles 103
CHAPTER 5 Mendelian Genetics in Populations: The Mechanisms of Evolution 121
CHAPTER 6 Evolution at Multiple Loci: Linkage, Sex, and Quantitative Genetics 179
CHAPTER 7 Molecular Evolution 225
CHAPTER 8 Agents of Selection and the Nature of Adaptations 267
CHAPTER 9 Mechanisms of Speciation 313

P A R T III

The History of Life 361

- CHAPTER 10 Estimating and Using Phylogenies 363
CHAPTER 11 The Origin of Life, and Precambrian Evolution 399
CHAPTER 12 The Cambrian Explosion and Beyond 443
CHAPTER 13 Mass Extinctions and Their Consequences 491

P A R T IV

Current Research—A Sampler 527

- CHAPTER 14 Human Evolution 529
CHAPTER 15 Sexual Selection 569
CHAPTER 16 Social Behavior 611
CHAPTER 17 Aging and Other Life History Characters 645
CHAPTER 18 Evolution and the Human Condition 685
CHAPTER 19 Biodiversity and Conservation 729

Contents

Preface xi

P A R T I Darwinism and the Fact of Evolution 1

CHAPTER 1 A Case for Evolutionary Thinking: Understanding HIV 3

- 1.1 The Natural History of the Epidemic, HIV, the Immune System, and AIDS 4
- 1.2 Why Does AZT Work in the Short Run, but Fail in the Long Run? 11
- 1.3 How Does HIV Defeat the Immune Response? 14
- 1.4 Why is HIV Fatal? 16
- 1.5 Where Did HIV Come From? 19
- 1.6 What, if Anything, Does Evolutionary Biology Have to Say About Ways to Stem the AIDS Epidemic? 21

Summary 22 • *Questions* 22 • *Exploring the Literature* 23 • *Citations* 24

CHAPTER 2 Darwinism and the Fact of Evolution 27

- 2.1 The Fact of Evolution 27
- 2.2 Natural Selection: Darwin's Four Postulates 33
- 2.3 The Evolution of Beak Shape in Galápagos Finches 36
- Box 2.1 Issues that complicate how heritabilities are estimated 40
- 2.4 The Nature of Natural Selection 44
- 2.5 The Importance of Time 48
- 2.6 On the Origin of Species 49
- Box 2.2 A closer look at dating with radioisotopes 50
- 2.7 The Evolution of Darwinism 51
- 2.8 The Debate over Scientific Creationism 55

Summary 60 • *Questions* 62 • *Exploring the Literature* 63 • *Citations* 63

CHAPTER 3 Methods of Evolutionary Analysis 67

- 3.1 Experimental Approaches 67
- Box 3.1 A primer on statistical testing 73
- 3.2 The Comparative Method 78
- 3.3 Reconstructing History 83
- 3.4 Strategies for Asking Interesting Questions 94

Summary 95 • *Questions* 96 • *Exploring the Literature* 97 • *Citations* 98

P A R T II Mechanisms of Evolutionary Change 101

CHAPTER 4 Mutation: The Origin of New Genes and Alleles 103

4.1 Where New Alleles Come From 103

4.2 Where New Genes Come From 109

4.3 Chromosome Alterations 114

Summary 117 • *Questions* 118 • *Exploring the Literature* 119 • *Citations* 120

CHAPTER 5 Mendelian Genetics in Populations: The Mechanisms of Evolution 121

5.1 Mendelian Genetics in Populations: The Hardy-Weinberg Equilibrium Principle 122

Box 5.1 Combining probabilities 123

5.2 Selection 128

Box 5.2 A general treatment of selection 131

Box 5.3 Generating expected values using the Hardy-Weinberg Principle, and comparing observed and expected values using the χ^2 (Chi-square) test 136

5.3 Mutation 140

Box 5.4 Equilibrium allele frequency under mutation-selection balance 144

5.4 Migration 145

Box 5.5 Selection and migration in Lake Erie water snakes 149

5.5 Genetic Drift 151

5.6 Nonrandom Mating 157

Box 5.6 Mechanisms of inbreeding avoidance 166

5.7 The Adaptive Landscape 168

Summary 172 • *Questions* 172 • *Exploring the Literature* 174 • *Citations* 175

CHAPTER 6 Evolution at Multiple Loci: Linkage, Sex, and Quantitative Genetics 179

6.1 Evolution at Two Loci: Linkage Equilibrium and Linkage Disequilibrium 180

6.2 The Adaptive Significance of Sex 191

Box 6.1 John Maynard Smith's model of sexual versus asexual reproduction, and the twofold cost of sex 194

6.3 Selection on Quantitative Traits 203

Box 6.2 Additive genetic variation versus dominance genetic variation 207

Box 6.3 The bell-curve fallacy, and other misinterpretations of heritability 209

Box 6.4 The selection gradient and the selection differential 214

Summary 220 • *Questions* 221 • *Exploring the Literature* 223 • *Citations* 223

CHAPTER 7 Molecular Evolution 225

Box 7.1 Segments of the genome 226

7.1 Single-Copy Sequences 227

7.2 Duplicated Coding Sequences 236

Box 7.2 A model for the molecular mechanism of recombination 242

7.3 Highly Repetitive Sequences 244

7.4 Organelle Genomes 246

Box 7.3 Evidence for horizontal transfer of genes 251

7.5 Genomic Parasites, Selfish Genes, and Genomic Conflict 252

Summary 260 • Questions 261 • Exploring the Literature 262 • Citations 262

CHAPTER 8 Agents of Selection and the Nature of Adaptations 267

8.1 The Adaptationist Program 268

8.2 Adaptations to the Physical Environment 270

Box 8.1 Why temperature affects physiology 271

8.3 Adaptations to the Biological Environment 284

8.4 Phenotypic Plasticity 291

8.5 Trade-Offs and Constraints 297

8.6 The Maintenance of Genetic Variation 305

Summary 306 • Questions 307 • Exploring the Literature 309 • Citations 310

CHAPTER 9 Mechanisms of Speciation 313

9.1 Species Concepts 313

9.2 Mechanisms of Isolation 318

9.3 Mechanisms of Divergence 323

Box 9.1 Protein electrophoresis 327

Box 9.2 Sympatric and parapatric speciation 328

9.4 Secondary Contact 333

9.5 The Genetics of Differentiation and Isolation 339

9.6 Asexual Species 344

Box 9.3 QTL mapping 345

9.7 Rates of Speciation 348

Summary 355 • Questions 355 • Exploring the Literature 357 • Citations 357

P A R T III The History of Life 361

CHAPTER 10 Estimating and Using Phylogenies 363

Box 10.1 A field guide to evolutionary trees 364

10.1 Which Characters Are Best for Inferring Phylogenies? 366

Box 10.2 Cladistic methods 368

10.2 Optimality Criteria: How Do We Choose the Best Tree from Among the Many That Are Possible? 372

10.3 Models of Character Change 374

10.4 Algorithms for Searching Among the Many Possible Trees 376

10.5 Evaluating and Interpreting Trees 378

10.6 Using Phylogenies to Answer Questions 384

Summary 392 • Questions 393 • Exploring the Literature 396 • Citations 396

CHAPTER 11 The Origin of Life, and Precambrian Evolution 399

11.1 What Was the Most Recent Common Ancestor of All Living Things? 400

Box 11.1 Rooting the tree of life 408

11.2 When Did the Cenancestor Live? 414

11.3 Where Did the Cenancestor Come From? 419

Box 11.2 The panspermia hypothesis 422

11.4 How Did the Cenancestor's Descendants Evolve into Contemporary Organisms? 429

Summary 435 • Questions 436 • Exploring the Literature 438 • Citations 438

CHAPTER 12 The Cambrian Explosion and Beyond 443

12.1 The Nature of the Fossil Record 444

12.2 The Cambrian Explosion 450

12.3 Innovations: Developmental Genetics and Macroevolutionary Change 459

12.4 Transitional Forms 469

12.5 Macroevolutionary Patterns 474

Summary 485 • Questions 486 • Exploring the Literature 487 • Citations 487

CHAPTER 13 Mass Extinctions and Their Consequences 491

13.1 Background Versus Mass Extinction 491

13.2 The Big Five: Extinction Events in the Phanerozoic 493

13.3 End-Permian: The Mother of Mass Extinctions 496

13.4	Cretaceous-Tertiary: High-Impact Extinction	503
13.5	Are Mass Extinctions Periodic?	509
13.6	Recent: The Human Meteor	511
13.7	Consequences of Mass Extinctions	517
<i>Summary 520 • Questions 521 • Exploring the Literature 523 • Citations 523</i>		

P A R T IV Current Research--A Sampler 527

CHAPTER 14	Human Evolution	529
14.1	Relationships Among Humans and the Extant Apes	530
14.2	The Recent Ancestry of Humans	538
14.3	The Origin of the Species <i>Homo sapiens</i>	545
Box 14.1	Using linkage disequilibrium to date the divergence between African and non-African populations	554
14.4	The Evolution of Uniquely Human Traits	554
<i>Summary 561 • Questions 562 • Exploring the Literature 564 • Citations 564</i>		

CHAPTER 15	Sexual Selection	569
15.1	The Asymmetry of Sex	571
15.2	Male-Male Competition: Intrasexual Selection	575
Box 15.1	Alternative male mating strategies	581
15.3	Female Choice	584
Box 15.2	Extra-pair copulations	588
15.4	Diversity in Sex Roles	596
15.5	Sexual Selection in Plants	598
15.6	Sexual Dimorphism in Body Size in Humans	600
15.7	When Sexual Selection and Natural Selection Collide: Túngara Frogs	603
<i>Summary 604 • Questions 605 • Exploring the Literature 607 • Citations 608</i>		

CHAPTER 16	Social Behavior	611
16.1	Kin Selection and the Evolution of Altruism	612
Box 16.1	Calculating coefficients of relatedness	613
16.2	Evolution of Eusociality	621
Box 16.2	The evolution of the sex ratio	624
16.3	Reciprocal Altruism	627
Box 16.3	Prisoner's dilemma: Analyzing cooperation and conflict using game theory	629

16.4 Behavioral Genetics 633

Summary 640 • *Questions* 640 • *Exploring the Literature* 641 • *Citations* 642

CHAPTER 17 Aging and Other Life History Characters 645

17.1 Basic Issues in Life History Analysis 647

17.2 Why Do Organisms Age and Die? 648

17.3 How Many Offspring Should an Individual Produce in a Given Year? 662

Box 17.1 Is there an evolutionary explanation for menopause? 664

17.4 How Big Should Each Offspring Be? 671

17.5 Life Histories in a Broader Evolutionary Context 675

Summary 680 • *Questions* 681 • *Exploring the Literature* 682 • *Citations* 683

CHAPTER 18 Evolution and the Human Condition 685

18.1 Evolution and Human Behavior 686

Box 18.1 Is cultural evolution Darwinian? 687

18.2 Evolution and Human Health 703

Box 18.2 Genetic sleuthing solves a medical mystery 706

18.3 Evolution and Future Human Populations: Eugenics 718

Summary 723 • *Questions* 724 • *Exploring the Literature* 725 • *Citations* 725

CHAPTER 19 Biodiversity and Conservation 729

19.1 How Many Species Are There? 731

19.2 Why Is Species Loss a Problem? 738

Box 19.1 Ecological disaster on Easter Island 740

19.3 The Genetics and Demography of Small Populations 743

19.4 Systematics, Conservation, and Hard Choices 750

Summary 760 • *Questions* 760 • *Exploring the Literature* 761 • *Citations* 762

Glossary 767

Index 773

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.

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.

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

(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.

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.

