Instructor's Manual

CARL T. BERGSTROM • LEE ALAN DUGATKIN

evolution

SECOND EDITION

Matthew E. Gruwell

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Carl T. Bergstrom and Lee Alan Dugatkin's

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Instructor's Manual by
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Chapter 1

An Overview of Evolutionary Biology

Chapter Summary and Discussion Points

Introduction

Charles Darwin evolved biology when he theorized that all organisms share a common ancestry and that an organism's fitness within its environment is the result of natural selection. Darwin's evolutionary theory led to a natural explanation for the diversity of life and, thus, a paradigm shift in biological thought that now reaches every subdiscipline of biology. For example, when anatomy students now study the structure of bones in the human wrist, it is possible to extrapolate their understanding of skeletal structures to other tetrapods and find bones of the same origin being used in similar or very different ways.

Section 1.1: A Brief Introduction to Evolution, Natural Selection, and Phylogenetics

As a primer to the ensuing chapters, this section explains the idea of descent with modification as being the way in which all organisms change over time due to natural or artificial selection, leading to the premise that all life is subject to the principles of evolution. For example, to truly understand a species such as *Homo sapiens*, one must study and understand primates, their closest relatives. This section offers students a refresher on some of the basics of genetics, which sets the stage for defining selection. Artificial selection is covered using multiple examples of crops, including a detailed figure of human selection of many different food crops over thousands of years, as well as a more specific example involving strawberries. These examples are then contrasted with an example of natural selection involving pesticide resistance in insects. Antibiotic resistance also is explored as a problem that will be solved only by using the principles of evolutionary biology. Lastly, to help students see that evolutionary principles aid in the study of conservation biology, the authors introduce the concept of tree thinking using the phylogenetic tree of life and extinction. This section concludes with the Key Concept Question (see Key Concept Question 1.1): Can you think of other ways that evolutionary thinking might affect studies in conservation biology?

Discussion Points:

- What two things did Darwin originally notice and how did that lead to his theory? What are some examples from the natural world that confirm Darwin's idea?
- How do artificial and natural selection differ? How does artificial selection demonstrate the reality of evolution? When are examples of human influence

causing change in a system still considered natural selection?
- Why is antibiotic resistance a serious threat to modern medicine? How will the principles of evolutionary biology help control this problem?

Section 1.2: Empirical and Theoretical Approaches to the Study of Evolution

This section divides the types of research conducted in evolutionary biology into two major methods: empirical and theoretical. Empirical research is further divided into observation or manipulation of a natural system. Observation studies involve gathering data from a system without manipulating it and include studies such as research on the fossil record, inferring phylogeny from genetic sequences, or observing behavior. This is demonstrated by comparing similarities between chimps and humans in anatomy and genomics to show common ancestry and determine what separates them genetically. Manipulation of natural systems is explained by a second example of empirical study, which involves breeding systems and testes size in 33 species of primates. Theoretical biology is introduced as a major discipline in evolutionary biology through the work of Ronald A. Fisher and William D. Hamilton, in which they utilized mathematical models to predict and understand sex ratios. This is followed by an actual example of changing sex ratios in the blue moon butterfly on the Samoan islands.

Discussion Points:
- Of the two research methods discussed, which would be most useful in testing specific hypotheses?
- What is the usefulness of theoretical studies in evolutionary biology?

Answers to Review Questions

1. Paradigm shifts represent fundamental changes in the way we think about and study nature from a scientific perspective.

2. (1) All species are descended from one or a few ancestral life-forms. (2) A process Darwin dubbed *natural selection* explains the fit of organism to environment.

3. This evidence includes, but is not limited to, molecular genetic, anatomical, physiological, behavioral, developmental, and hormonal data. Such data can be amassed from fossils or contemporary organisms.

4. Artificial selection is the human-driven analog to the process of natural selection. In artificial selection, we selectively breed individuals with traits that are beneficial to us.

5. Bacteria reproduce extremely rapidly—as fast as hourly or even faster. Bacterial population sizes are enormous, providing a vast supply of genetic variation. Natural selection imposed by antibiotic resistance is very strong.

For all of these reasons mutations conferring antibiotic resistance can quickly arise and rapidly spread through bacterial populations.

6. Phylogenetic diversity is a measure of diversity that takes into account how much of the evolutionary history of the group being studied is preserved.

7. The two basic ways to gather empirical evidence to test hypotheses are observational and experimental studies.

8. Neutral mutations are mutations that do not affect fitness.

9. Sex ratio measures the ratio of females to males in a given population.

10. Regardless of whether empirical work precedes theoretical work or vice versa, each of these informs the other, and this (ideally) leads to the generation of new, testable hypotheses.

Answers to Key Concept Application Questions

11. We can apply the exact same reasoning we used for the case of the evolution of antibiotic resistance in bacteria to the cases of antiviral resistance evolution by viruses and antifungal resistance evolution by fungi. Similar arguments also apply in agriculture to the evolution of herbicide-resistant weeds and pesticide-resistant insects.

12. Answers will vary, but the theory of continental drift and plate tectonics represents one such paradigm shift. The theory of continental drift proposed that continents are drifting landmasses that move over geological time and therefore even the large-scale geography of the earth is dynamically changing. The theory of plate tectonics provided us with a mechanistic understanding of how continental drift takes place. Together, these theories provide an explanation of why surface of our planet looks the way that it does now, how large landmasses are created and destroyed, and so much more.

13. The study of descent with modification is the conceptual glue that unites all of the life sciences. Without adopting an evolutionary approach in the biological sciences, we have many potentially important, disparate facts, but no common theoretical perspective to unite them.

14. By selecting for traits that are either aesthetically pleasing or in some sense practical, humans have shaped everything from the size (think miniature poodle to Great Dane) to the behavior (herding, hunting, retrieving) of domesticated dog breeds.

15. Now that the molecular genetic techniques associated with studying gene expression are widely available, evolutionary biologists can study not just how differences between species in protein-coding DNA sequences are associated with evolutionary change, but also how differences in when genes are turned on and off are associated with evolutionary change.

16. As we noted in the chapter, a 1 female to 1 male sex ratio is so common that it is hard to imagine any other sex ratio, but what we want to understand is *why* a 1:1 sex ratio is so ubiquitous in the first place. To do that, we need to consider other possible sex ratios, and then examine which sex ratio is favored by natural selection and under what conditions. Once we make clear our assumptions, mathematical models give us the power to do exactly that.

Suggested Readings

This list of suggested readings is printed at the end of this chapter in the student textbook and reprinted here for your convenience and planning.

Birkhead, T. R., and T. Pizzari. 2002. Postcopulatory sexual selection. *Nature Reviews Genetics* 3: 262–273.
• This paper will give you a better understanding of the sperm competition and sperm allocation work we discussed in this chapter.

Engelstädter, J., and G. D. D. Hurst. 2009. The ecology and evolution of microbes that manipulate host reproduction. *Annual Review of Ecology, Evolution and Systematics* 40: 127–149.
• A detailed review on issues we discussed in the *Wolbachia*/blue moon butterfly sex ratio example.

Huxley, T. H. 1863. *Evidence of Man's Place in Nature*. D. Appleton, New York.
• Huxley—Darwin's colleague—presented evidence for human evolution in this book.

Kuhn, T. 1962. *The Structure of Scientific Revolutions*. University of Chicago Press, Chicago.
• In this volume, a classic in the philosophy of science, Kuhn outlines the idea of a paradigm shift.

Varki, A., D. H. Geschwind, and E. E. Eichler. 2008. Explaining human uniqueness: genome interactions with environment, behavior, and culture. *Nature Reviews Genetics* 9: 749–763.
• An interesting discussion of how to understand what molecular genetic comparisons tell us (and don't tell us) about similarities and differences between humans and other primates.

Chapter 2

Early Evolutionary Ideas and Darwin's Insight

Chapter Summary and Discussion Points

Introduction

Understanding how people perceived the natural world prior to Darwin enables better comprehension of how and why Darwin came to his conclusions and why his determinations were so groundbreaking. By showing how people tried to make sense of the natural world, sometimes failing and sometimes succeeding, this chapter aims to help students improve their scientific thinking. The idea is: Science moves forward by building on what other people already know. Pre-Darwinian scientists had many questions about the natural world, as outlined on page 30. Instructors may want to go through these questions with students and have them think critically about how the questions can be answered without using the principles of evolution.

Section 2.1: The Nature of Science: Natural versus Supernatural Explanations

The beginnings of scientific thinking are introduced in this chapter as methodological naturalism, defined as a natural and methodical way of looking at the world. Anaximander, an ancient Greek philosopher, often is cited as the first to use methodological naturalism, with the first natural explanation of the Solar System in 600 B.C. This thought process led to some hypothesis formulation, an idea that is solidified by the useful Key Concept Question 2.1 on page 32. Aristotle believed in hypothesis testing to ensure that principles and facts do not contradict each other, though he did not always use such methods (refer to the quote by Aristotle on page 32). It took time before scientific thinking became the norm, but logic alone did not provide the entire framework required to produce the eventual breakthroughs of evolutionary biology.

Discussion Point:

- How important an advancement was scientific thinking in the history of science?

Section 2.2: Time and a Changing World

It has taken a long time for man to understand that changes over a vast expanse of time were required for the world to arrive at this stage of geological time. Ancient Greeks mostly believed the world to be unchanging, though some, such as Empedocles and Xenophanes, recognized evidence to the contrary. Before Darwin, biblical scholars placed the creation of the world at around 4000 B.C.; however, some

scientists grasped the idea of an ancient Earth, which prompted Charles Lyell's theory of uniformitarianism in contrast to catastrophism. Lyell's *Principles of Geology*, published in three volumes in 1830–1833, profoundly impacted Darwin.

Discussion Point:

- Why are an understanding of geology and the law of uniformitarianism important background of the theory of evolution?

Section 2.3: The Origins and Diversity of Life

The ancient Greeks made many contributions to understanding the natural world, some of which were discredited over time. Aristotle classified species according to their complexity of structure and function, with each organism becoming more complex as it moved down the chain. Aristotle's theory, however, held two misconceptions that had to be disproved before evolutionary thought could proceed: The first misconception was that organisms could be ranked based on complexity; the second, that organisms are fixed and unchangeable. Spontaneous generation is another notion proffered by the ancient Greeks, who were attempting to use natural rather than supernatural explanations. This theory also was disproven, by Francesco Redi, but was not accepted as disproven due to the invention of the microscope and the seemingly spontaneous generation of microbes.

Indeed, there were many influences on Darwin and his work, including his grandfather, who in the late eighteenth century offered ideas for the origin of life similar to the theory of evolution. Erasmus Darwin hypothesized that all life was related, and that humans once walked on four legs and were descended from primates. He also recognized the struggle for existence, but failed to put together the entire theory of evolution by natural selection. He also incorrectly believed in some ideas, such as the inheritance of acquired characteristics. Robert Chambers and two of his contributions to the field—the principle of progressive development, and thinking in populations—also are discussed in this section.

Discussion Points:

- How did Redi's experiment disprove the idea of spontaneous generation?
- How did Chambers' contributions influence future discovery?

Section 2.4: Organisms Are Well-Suited to Their Environments

This section highlights three pre-Darwinian scientists who noted that organisms were well adapted to their environments and came up with theories about these trends. William Paley attributed all to God as the watchmaker designing precise instruments, with which Darwin disagreed. Jean-Baptiste Lamarck used methodological naturalism in his inheritance of acquired characteristics theory, which was the first truly evolutionary theory for transformation of one species into another (the inheritance of acquired characteristics). Patrick Matthew outlined a theory of evolution by natural selection very similar to Darwin's, and Darwin acknowledged him. Matthew, however, did not include common descent, had scant evidence in comparison to Darwin, and published in a very obscure location—the

endnotes of a work titled *On Naval Timber and Arboriculture*. The last paragraph in this section (see page 41) discusses five major developments that preceded and facilitated Darwin's theory.

Discussion Points:

- Why is it unfair to remember Lamarck only by his faults in being wrong about inheritance? What if Mendel had come first?
- Why is Matthew not recognized for the theory of evolution by natural selection?

Section 2.5: Darwin's Theory

The two major insights that were the basis of Darwin's theories are also the framework for the textbook, so students must master these concepts: (1) the conditions of existence within the environment determine how traits help or hinder all living and nonliving organisms and allow for natural selection; and (2) the common ancestry of all living things. The history of Darwin's scientific journey also is explored, including his collection of data and authorship of *On the Origin of Species*. While Alfred Russel Wallace simultaneously conceived the idea of evolution by natural selection, Darwin's work eventually became the authority due to his extensive coverage and data.

As a means to understand and eventually explain modification in organisms, Darwin surmised that agriculture and the domestication of animals by selective breeding processes was artificial selection by humans acting as a natural environment to sculpt the organisms. A specific example of artificial selection in pigeons illustrates this idea. Darwin continued down this road to explain the formation of new species. In Darwin's time, the idea of new varieties was acceptable but of new species was not, so he had to show significantly different organisms on the path to becoming new species.

Discussion Points:

- What are the conditions of existence and common ancestry? Why are these ideas key to understanding evolution?
- Why was a discussion of artificial selection in pigeons necessary in *On the Origin of Species*?

Section 2.6: Darwin on Natural Selection

This section outlines Darwin's transition from artificial (human-imposed) selection to natural (environment-imposed) selection. Darwin noted that the key differences between artificial and natural selection are the selective agent and the traits being selected. He explained that natural selection was a long and powerful process, and that small changes that cause differential reproductive success make a large difference in evolutionary time. The power of natural selection lies in its constancy, working all the time and for a long time frame. It also can work only if there is a limiting resource so that not all survive. Thomas Malthus provided a limiting resource when he wrote that humans could not sustain agricultural growth at the

rate of population growth and would be selected against through disease, war, or famine. The discussion on natural selection ends by showing how natural selection works as a variational process (not considered prior to Darwin) rather than a transformational process (see Figure 2.21). This section has multiple important quotes by Darwin that demonstrate his thorough understanding of evolution.

Discussion Point:

- What is natural selection? What is the time frame in which it operates?

Section 2.7: Darwin on Common Ancestry

The main point students should understand from this section is that Darwin used common ancestry to answer the question, "Where do species come from?" From this idea, Darwin created the first tree of life, or phylogenetic tree. The science behind systematics is introduced with a clustering example using the major groups of vertebrates and smaller groups of similar animals within the larger groups, in other words deer, related to squirrels in the mammal group, are less closely related to frogs. Systematics looks at clusters of species and hierarchical patterns of similarity (see Figure 2.25 on page 55). As the idea of descent with modification developed, Darwin and Wallace noted phylogeographic patterns in the species they studied.

Discussion Point:

- How does a phylogenetic tree explain the hierarchical pattern of clustering organisms together, as seen in nature?

Section 2.8: Problems with Darwin's Theory

When Darwin put forth his theory of evolution, three flaws were unexplainable at the time: (1) an understanding of the evolution of complex structures, (2) vestigial organs and/or structures, and (3) source of variation. These flaws have been eliminated now by additional work; for example, the last "flaw" we now know to be mutation as explained by genetics, while the other two are covered in detail in later chapters.

Discussion Point:

- How have the problems with Darwin's theory been overcome with our current understanding of evolution?

Section 2.9: The Reaction to Darwin and Early History of the Modern Synthesis

Students will learn how scientific and religious leaders first perceived Darwin's ideas. Religious leaders took issue with his theory, while scientists did not have the understanding to accept natural selection and gradual change. It was a long time, post-Darwin, before his ideas became universally accepted among evolutionary biologists. Eventually, evolutionary biologists, who were split between Mendelians and biometricians, came together to form the modern synthesis, or evolutionary synthesis, that is outlined in this section.

Discussion Point:

- Outside the realm of science, how does the world around you perceive Darwin? Are these views informed? Are they opinions of people who do not understand science?

Answers to Review Questions

1. Methodological naturalism refers to the set of methods and procedures that seeks to explain the physical world through natural rather than supernatural causes. It is an important foundation for science because it focuses explanatory efforts on observable phenomena and testable predictions about the physical world.

2. The discovery of fossils in mountain ranges by Greek philosophers such as Xenophanes suggested that those mountain ranges were once below water. This led the philosophers to conclude that the physical world is not unchanging and static, but constantly changing.

3. Lyell proposed that geological processes, for example the process of sedimentation, operate in a slow, gradual manner. Darwin, who knew Lyell's work well, proposed that the process of natural selection also usually operates in a slow, gradual manner.

4. In the Middle Ages, people believed that Earth was only a few thousand years old. The primary source of evidence for this belief in the Western world was the Bible and its purportedly historical record of events since the creation of Earth, Adam, and Eve.

5. Spontaneous generation is the idea that fully formed, complex life-forms arise from nonliving matter. Early microscopes revealed bacterial colonies and fungal cells appearing seemingly out of nowhere, and scientists assumed that they must have arisen through spontaneous generation.

6. The inheritance of acquired characteristics is the idea that traits that are acquired during the lifetime of an organism are inherited by its offspring.

7. (1) Over time, natural selection makes organisms better and better suited to their environments. (2) All species have descended from one or, at most, a few common ancestors: Species that share more recent common ancestry tend to resemble one another more than do species that share more distant common ancestry.

8. The selective agent and the traits selected are the two most salient differences between these processes. Humans are the selective agent in artificial selection, whereas "nature"—environmental conditions—is the

selective agent in natural selection. In artificial selection, breeders choose the trait being selected based on some personal interest: aesthetic, economic, and so forth. The process of natural selection selects traits that increase reproductive success and/or longevity.

9. Wallace concluded that new species must arise from previous ones.

10. During transformational change, a lineage changes over time because new traits acquired during the lifetime of individuals within it are passed down to the next generation. In a variational process, preexisting variation is sorted within a population, and this sorting produces the changes seen over time.

11. Darwin's theory provides an explanation for the hierarchical patterns of similarity between organisms. Aristotle's *scala naturae* arranges all living things on a single linear hierarchy from least to most developed. Darwin's theory replaces this with a branching pattern of common ancestry in which all currently living forms are descended from the same ultimate ancestor. In Darwin's model, we cannot place mice below humans, for example, because both species share a common ancestor and each has evolved from this ancestor for the same duration of time.

Answers to Key Concept Application Questions

12. Darwin needed to demonstrate that the world was not static and unchanging. The discovery that species went extinct was one piece of evidence that he could use to demonstrate this.

13. Sarah's records underwent a transformational process here that affected each one individually rather than sorting among them. The gradual decline in their quality is similar to that seen when each mountain in a mountain range slowly erodes, wearing down the entire mountain range over time.

14. Natural selection maximizes reproductive success, not survival per se. A lizard can drop its tail and grow a new one—or even reproduce successfully without one. A beaver, by contrast, would not have further reproductive success after shedding its testicles, and therefore this behavior would not be favored by natural selection.

15. Given that his readers were familiar with artificial selection, Darwin hoped that once he explained how the process of natural selection was similar to the familiar process of artificial selection used to create new dog breeds and pigeon varieties, his readers would, by force of logic, accept the idea of natural selection.

Suggested Readings

This list of suggested readings is printed at the end of this chapter in the student textbook and reprinted here for your convenience and planning.

Burkhardt, R. W., ed. 1984. *The Zoological Philosophy of J. B. Lamarck*. University of Chicago Press, Chicago.
• An edited volume on the work of Lamarck, with special reference to his theories of transformation.

Costa, J. T. 2014. *Wallace, Darwin, and the Origin of Species.* Harvard University Press, Cambridge, Mass.
• An interesting read on both Darwin and Wallace's ideas on evolution.

Darwin, C. 1859. *On the Origin of Species*. John Murray, London.
• Here Darwin lays out his grand theory of descent with modification.

Glick, T. F., ed. 1988. *The Comparative Reception of Darwinism*. University of Chicago Press, Chicago.
• An excellent cross-cultural discussion of the reaction to Darwin's ideas.

Malthus, T. 1798. *An Essay on the Principle of Population, As It Affects the Future Improvement of Society*. J. Johnson, London.
• For insight into why overpopulation and competition play a role in Darwin's theory of natural selection.

Mayr, E. 1991. *One Long Argument*. Harvard University Press, Cambridge, Mass.
• A short, but wonderful book on Darwin and evolutionary biology.