ANIMAL BEHAVIOR

CONCEPTS, METHODS, AND APPLICATIONS

SECOND EDITION

SHAWN E. NORDELL
THOMAS J. VALONE

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Animal Behavior

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For

Buck, Ernie, Kirby, Grace, Max, and Louie



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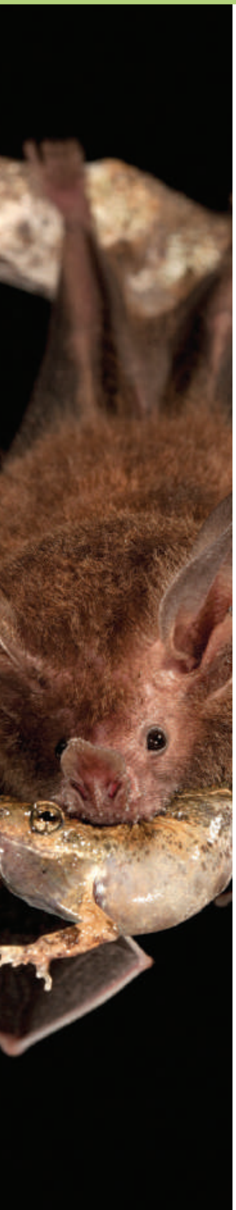

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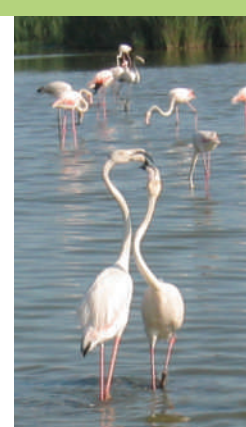

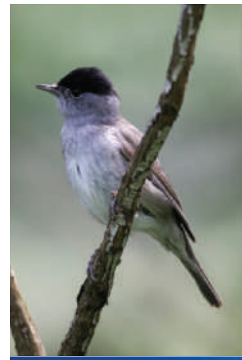

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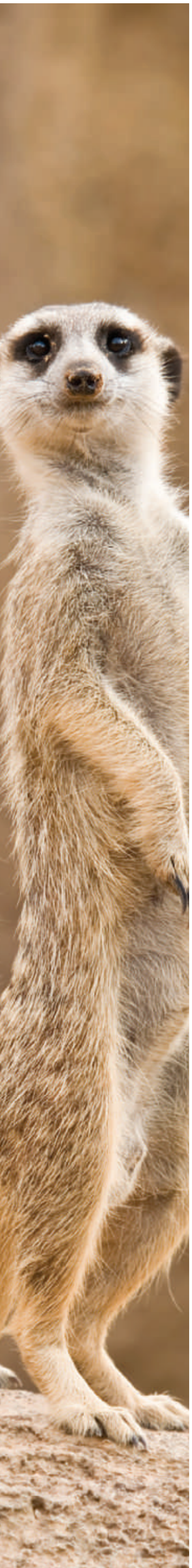

Features

Preface

Our love of science grew out of our own undergraduate experiences, when we were first immersed in the research process. We learned to develop interesting questions and testable hypotheses, read and reference the associated primary literature, collect and analyze data, and present and discuss our conclusions. In writing this book, our goal was to share that excitement and that process in order to inspire and guide new generations of students in animal behavior research.

The book's framework is based on developing mandates that aim to shift science education from a memorization-based pedagogy to a conceptual approach that promotes scientific inquiry. Both the National Academies of Science and the American Association for the Advancement of Science[1] have called for teaching approaches that stimulate curiosity about the natural world, emphasize experimental design, and foster a conceptual understanding of biological systems. In addition, these bodies have underscored the importance of developing students' quantitative reasoning and communication skills. This book responds to all of these important mandates by taking a ***conceptual approach that highlights the process of science and the real-world applications of animal behavior research***.

The Approach: Concepts, Methods, and Applications

Our approach involves three major components:

- Each chapter is organized around four to six major concepts.
- Each chapter emphasizes the process of science by deconstructing research studies to show the experimental design and methodology that drives the science of animal behavior.
- Each chapter contains one or more examples of how the major concepts are being applied to societal issues.

Throughout the book, we use an accessible, question-driven style to engage students. Incorporating Tinbergen's four questions to show the diverse nature of animal behavior research, we infuse proximate and ultimate examinations of behavior throughout each chapter.

Concepts

- Each chapter is built around ***broad organizing concepts***. We present the concepts up front, at the beginning of each chapter, to provide a framework for understanding and evaluating the empirical research examples presented.
- These organizing concepts represent ***higher-order critical thinking*** and allow students to see the "big picture" of how research has led to our understanding of behavior. For example, rather than titling a section

[1]National Research Council Committee on Undergraduate Biology Education to Prepare Research Scientists for the 21st Century, *BIO2010: Transforming Undergraduate Education for Future Research Biologists* (Washington, D.C.: National Academies Press, 2003); C. A. Brewer & D. Smith, *Vision and Change in Undergraduate Biology Education: A Call to Action* (Washington, D.C.: American Association for the Advancement of Science, 2011).

"Evolution," we offer a complete concept: "Evolution by natural selection favors behavioral adaptations that enhance fitness." This clear presentation of concepts synthesizes and summarizes the information provided on complex topics, allowing students to make connections, see the broader implications of those connections, and apply their learning.

Methods

- We use carefully selected ***Featured Research*** studies from the primary literature to demonstrate the ***experimental designs and methods scientists use to address research questions***. Our selection of studies includes both classic and contemporary work that aims to highlight the global diversity of researchers who are contributing to the study of animal behavior. In our selection process, we paid particular attention to the seminal and growing contribution of women and underrepresented groups to the science of animal behavior.
- We ***deconstruct each research example*** to allow students to become immersed in the process of animal behavior research as a ***rigorous quantitative science***. We use a ***hypothesis-testing model*** to illustrate the scientific process and incorporate sufficient detail into our presentation of the methodology for instructors and students to comprehend and critically evaluate the rationale, process, and results of the given research.
- We create opportunities for students to ***develop their quantitative skills*** by interpreting graphs from ***actual data***. We present or summarize actual data in the "Results" figures and include either individual data points or error bars so that students can see the variation in behavior.

Applications

- We relate the major concepts presented to real life through the ***Applying the Concepts*** feature, which shows how animal behavior research is applied to various societal issues, as well as human behavior. For example, we demonstrate how animal behavior findings are used in conservation or outside of academia, as in the manipulation of predation risk to mitigate crop damage.

NEW to This Edition

Each chapter from the first edition has been revised using the extremely constructive suggestions offered by many reviewers and adopters. Throughout the textbook, we have better integrated the major concepts with their associated featured research studies, increased our coverage of proximate questions, and updated our empirical examples.

- **New chapter—Sensory Systems and Behavior (Chapter 5).** This new chapter examines how animals gather information from their environment and how that information influences their behavior. This chapter greatly enhances the coverage of proximate research in behavior studies and allows students to better appreciate the diversity of sensory systems found in different taxa.
- **New "Applying the Concepts" features on human behavior.** These examples expand the applications of animal behavior research to human behavior, reinforcing the relevance to students of the major concepts in animal behavior.

- **New "Evaluate" questions and exercises.** These additions, which appear at the end of each Scientific Process box, are designed to more fully engage students in the research described, allow students to develop their quantitative skills, and promote in-class discussions of the material.
- **New photos throughout the book.** These additions enhance the visual presentation of the research and illustrate the diversity of species discussed.
- **Enhanced supplements program.** For the Second edition, we have expanded and improved upon the already robust ancillary package that accompanies the text. Enhancements include an expanded test item file, refined and expanded PowerPoint Lecture Notes slides for each chapter, and an updated interface for the Video Library and Guide.

Changes by Chapter

Chapter 1—The Science of Animal Behavior: We moved the history of animal behavior to the first chapter, along with a discussion of proximate and ultimate research studies and Tinbergen's four questions. These changes better set the stage for how knowledge in the field has developed.

Chapter 2—Methods for Studying Animal Behavior: This chapter has been moved up to improve the continuity from Chapter 1. We also moved the section on hypothesis testing to this chapter to better introduce experimental design and scientific literacy in our explanation of how research is disseminated and communicated. Finally, we expanded the coverage of mathematical models to better demonstrate how these are used to generate hypotheses.

Chapter 3—Evolution and the Study of Animal Behavior: This chapter was relocated to follow the chapter on methods and precede the chapter on behavioral genetics, providing a more logical flow. In addition, we have expanded our coverage of frequency-dependent selection, game theory modeling, and individual and group selection.

Chapter 4—Behavioral Genetics: We added a new concept on heritability and reorganized the discussion and examples of gene expression and quantitative trait loci (QTL) mapping. We also updated and expanded the discussion of fire ant genetics and social organization and greatly expanded the coverage of animal personalities. New material includes an additional empirical example on spiders and a discussion of a meta-analysis of research that relates to a mathematical model explaining the evolution of personalities.

Chapter 5—Sensory Systems and Behavior: NEW to the second edition, this chapter focuses on proximate research that examines a variety of sensory systems, including chemoreception, mechanoreception, and photoreception. It also covers the detection of electric and magnetic fields and the co-evolution of sensory systems in a predator–prey system.

Chapter 6—Communication: This chapter has been moved up to enhance the continuity from sensory systems to communication. We also added new studies on environmental influences on signals, including research on ant chemical pheromone trails and fish visual signals, and the new concept of extended phenotype signals, with empirical examples, for more complete coverage of communication.

Chapter 7—Learning, Neuroethology, and Cognition: We have added a discussion and empirical examples of animal teaching to bolster understanding of the social learning concept. In addition, we updated and improved our treatment of cognition with new examples that better reflect recent developments in the field. Finally, we expanded our coverage of brain and behavior research with examples of research on brain size and cognition in fish.

Chapter 8—Foraging Behavior: We have added a new concept that deals with individuals obtaining food from other individuals, focusing on kleptoparasitism and producer–scrounger models, and have provided relevant empirical studies.

Chapter 9—Antipredator Behavior: We expanded our proximate coverage of links between stress hormones and behavior and predation risk. This chapter also offers new coverage of evasive actions animals use once attacked by a predator, including an empirical example of a startle display in butterflies.

Chapter 10—Dispersal and Migration: We have expanded our coverage of the evolution of migratory behavior, including the addition of an empirical example of heritability of migratory behavior in birds.

Chapter 11—Habitat Selection, Territoriality, and Aggression: We have greatly expanded our discussion of game theory by adding a new section on self-assessment and mutual assessment models. We have also expanded our coverage of proximate work on hormonal influences on aggression by including associations between juvenile hormone and wasp aggression.

Chapter 12—Mating Behavior: We have expanded the discussion of Fisher's runaway process.

Chapter 13—Mating Systems: We have added an examination of human mating systems.

Chapter 14—Parental Care: We have reorganized this chapter so that parent-offspring conflict theory provides a theoretical framework for understanding variations in parental care exhibited by individuals in a population. We have also added the new concept of co-evolution involving interspecific brood parasitism and egg rejection behavior.

Chapter 15—Sociality: This chapter has undergone a substantial revision. We have expanded our coverage of kin selection with the addition of empirical proximate work on kin discrimination and have revised concepts relating to cooperative reproduction to emphasize kinship and ecological constraints (e.g., habitat saturation) with several new empirical examples. We have also expanded our coverage of the division of labor hypothesis and the evolution of sterile castes.

Teaching and Learning Features

Scientific Process boxes: To further emphasize the process of science, each chapter contains one or more Scientific Process boxes. These features present detailed descriptions of research within a scientific framework, clearly and concisely laying out each step of the process: research question, hypotheses, predictions, methods, results, and conclusions. Students can thus easily follow the research example at a glance, from its conception (the original research question) to the use of the scientific method (the creation of testable hypotheses, the experimental protocol, and the evaluation of data) and ultimately the findings of the work (conclusions of the study). The details contained in these examples illustrate and reinforce the rigorous nature of animal behavior research.

Applying the Concepts: Each chapter contains examples showing how animal behavior research is being applied to real-life situations, including applications to human behavior. This allows students to understand the importance and relevance of "pure" scientific research to larger societal issues. By including these features in every chapter, students have the opportunity to see the broader implications and importance of research.

Toolboxes: These boxes explain essential skills or complex terms in the field of animal behavior research with the aim of building students' intellectual and practical toolkit. They do not appear in every chapter but are included as needed and can provide students who lack essential knowledge typically acquired in prior courses, such as how to construct and interpret phylogenies, with the additional ***background information*** needed.

Chapter Summary and Beyond: At the end of each chapter, we provide a brief summary of the concepts covered. In doing so, we also point students to recent papers that further develop the ideas presented in the chapter. No textbook can be exhaustive, and so these papers are ideal for students or instructors seeking additional information about a concept.

Chapter Questions: At the end of each chapter, we provide critical thinking questions and assignments designed to foster class discussions. Answers to even-numbered questions are provided in the textbook, while answers to odd-numbered questions can be found online in the Instructor's Support Package (see below). These answers provide explanations in response to chapter questions, as well as background information that can aid in leading class discussions.

Data: We include data summaries as they typically appear in the primary literature (with individual data points plotted on line graphs and the inclusion of means and standard error bars in bar graphs) rather than the typical cartoon summary often found in textbooks. Thus, students can see that variation in behavior is ubiquitous in research.

Images: The book contains research examples from all over the world, covering a diverse range of taxa. We have strived to include ample representation from major taxa (invertebrates, amphibians and reptiles, fish, birds, and mammals) in each chapter. Because most students have a limited knowledge of animal diversity, we have included an image of each featured species in addition to brief natural history descriptions of that species. The textbook's website (www.oup.com/us/nordell) includes over 300 additional images provided by researchers that illustrate research protocols, habitat features, and study organisms.

Support Package

Oxford University Press offers a comprehensive ancillary package for instructors who adopt *Animal Behavior: Concepts, Methods, and Applications*, Second Edition. The Ancillary Resource Center (ARC), located at www.oup-arc.com/nordell, contains the following teaching tools:

- **Video library and guide:** To help students better understand animal behavior research and visualize the science in each chapter, and to provide instructors with an easy-to-use resource for videos tied directly to the concepts covered in the text, we have assembled links to three types of short videos:
    1. Natural history videos that illustrate specific behaviors of the study organisms in the featured studies

2. Process-of-science videos that illustrate the methodology described in featured research
3. Interviews with the scientists whose research is featured in the book

- We have carefully selected these videos because even though animal behavior is a visual endeavour, students often have little experience with the diversity of taxa studied or these species' behavior. Each video link is accompanied by a brief description of its content and information on the video's length. We hope that instructors will incorporate these videos into their classes to help students better understand animal behavior and research on that behavior.
- **Digital image library:** The image library includes electronic files in PowerPoint format of every illustration, graph, photo, figure caption, and table from the text, in both labeled and unlabeled versions. Images have been enhanced for clear projection in large lecture halls. The library also includes more than 300 additional photos from researchers depicting study organisms, research protocol set-ups, data collection, and habitats. We provide these photos and a guide to their content for each chapter so that instructors can easily incorporate them into their courses.
- **Lecture notes for each chapter:** Editable lecture notes in PowerPoint format make preparing lectures faster and easier than ever. Each chapter's presentation includes a succinct outline of key concepts and featured research studies, and incorporates the graphics from the chapter. New to the Second Edition, in the PowerPoint lecture notes, we have written inquiry questions for each chapter that create opportunities for students to assess their critical thinking skills. These graphically based questions allow students to develop and practice their quantitative and cognitive skills. Additionally, each chapter's presentation includes links to relevant videos from the video library and guide to make it easier for faculty to incorporate these materials into their lectures.
- **Test bank:** The authors have created a test-item file that includes over 350 exam questions in multiple-choice and short-answer formats. The test-item file now also includes in-class activity questions and short-answer questions that faculty can use to foster an active learning classroom.
- **Suggested further readings:** To assist instructors in identifying classic, contemporary, and relevant readings from the primary literature, we have assembled a list of over 25 suggested further readings taken directly from the journal *Behavioral Ecology*. These readings, like the video library, are tied directly to the concepts covered in the text. In addition, we provide a pedagogical outline to help students develop their ability to critically evaluate the primary literature.

Contact your local OUP sales representative or visit www.oup-arc.com/nordell to learn more and gain access to these instructor resources.

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Animal Behavior

Chapter 1

The Science of Animal Behavior

We can observe animal behavior everywhere. In backyards and parks, squirrels collect and bury nuts to eat later. Each spring, birds, frogs, and crickets sing to attract mates. Under the eaves of houses and other buildings, wasps make nests, where the queen lays eggs and workers care for offspring. Farther from our home, male giraffes in Africa exchange blows by swinging their heads and necks against one another in competition for females (Figure 1.1), while fish in the Great Barrier Reef form large schools to minimize predation (Figure 1.2). And each fall and spring, millions of birds migrate between temperate and tropical regions.

This book will introduce you to the wonders of animal behavior. In this chapter, we begin by exploring the ways that animals and their behaviors are an important part of the world. We then introduce the science of animal behavior and the scientific method. We'll see how scientists test hypotheses to learn about the natural world and examine a fundamental characteristic of animal behavior research: it looks at both the proximate mechanisms that generate that behavior as well as the ultimate reasons for why it evolved. We'll examine the varied approaches and perspectives used to study animal behavior. Finally, we discuss that although most scientific hypotheses about behavior are developed in the context of evolution, many nonscientists try to explain animal behavior based on the idea that animals possess human emotions.

Figure 1.1. Giraffe behavior. An aggressive interaction between two males.

CONCEPTS

FEATURES

Scientific Process

Applying the Concepts

Figure 1.2. Schooling fish. Snapper form schools to minimize predation.

1.1 Animals and their behavior are an integral part of human society

Understanding the behavior of animals has always been important to people. Beginning in prehistoric times and continuing for tens of thousands of years, humans painted images of animals on cave walls all over the world. These drawings are detailed enough to allow us to identify different species (both extinct and extant), and many images depict animals exhibiting behaviors such as eating, sleeping, and engaging in acts of aggression. Recent research indicates that these paintings were likely intended to present realistic depictions of animals and their behavior rather than to evoke symbolic connotations (Pruvost et al. 2011). Because humans in prehistoric times relied on animals for food, knowledge about animal behavior was important for survival (Shipman 2010).

Animals and animal behavior are still an integral part of society. Millions of people live and interact with animals daily. The American Veterinary Medical Association reports that in 2011, in the United States alone, over 80 million households contained a pet (American Veterinary Medical Association 2012). This number includes approximately 139 million freshwater fish, 90 million cats, 73 million dogs, 18 million other small mammals, 16 million birds, and 11 million reptiles. Most owners value their pets for companionship: we, for example, enjoy both watching our pets behave and interacting with them.

Figure 1.3. Police working dogs. Dogs are used as trackers and substance detectors.

Many people work with animals. Cattle, chickens and turkeys, hogs, and sheep are important agricultural products; horses are used by ranchers, law enforcement officials, and the horse-racing industry; and dogs have long been used in both police work and the military (e.g., Ensminger 2012) (Figure 1.3). In all of these cases, people manage animal behavior to accomplish a task. In a different way, the behavior of animals is also integral to medicine. It helps researchers assess and learn about sensory, motor, and cognitive functions. For instance, behavioral changes often reflect the effects of neurochemical agents, neurotoxins, or hormonal changes, which can be more easily studied in animals than in humans. Research on memory, cognitive function, and learning often involves measuring and recording animal behavior.

In addition, animals provide entertainment for millions of people. According to the World Association of Zoos and Aquariums, more than 700 million people visit zoos and aquariums worldwide each year (Gusset & Dick 2011). Many movies and popular television shows feature animal behavior, and entire television networks, such as Animal Planet and National Geographic Wild, are dedicated to animals.

Yet the study of animal behavior involves much more than interacting with pets, working with animals, or watching animals in movies or on television. Rather, animal behavior researchers use the scientific method to understand the behaviors we observe. So what exactly do we mean by *behavior*?

Figure 1.4. Lizard thermoregulation. Ectotherms, like this chuckwalla (*Sauromalus varius*), move to cool locations as their body temperature rises.

Recognizing and defining behavior

We define **animal behavior** as any internally coordinated, externally visible pattern of activity that responds to changing external or internal conditions (Beck, Liem, & Simpson 1991; Levitis, Lidicker, & Freund 2009). Let's examine each part of this definition in turn.

animal behavior Any internally coordinated, externally visible pattern of activity that responds to changing external or internal conditions.

Internally coordinated refers to internal information processing such as endocrine signaling, sensory information processing, or the action of neurotransmitters. When two male giraffes meet during the breeding season, such processes coordinate their aggressive behavior. However, when a lion's mane moves away from its body because of a gust of wind the animal is *not* exhibiting a behavior, because it has no control over this movement.

Externally visible activity refers to patterns that we can observe and measure. For example, we can observe a squirrel eating an acorn and can quantify this behavior. We cannot externally observe the variation in a lizard's heart rate.

We can, however, observe an animal's *behavioral response to changing conditions*. For example, male crickets, frogs, and birds vocalize in response to changes in day length, temperature, or moisture at specific times of the year. Similarly, during a summer day, a desert lizard moves from the top of a hot rock to the underside of a cool ledge to reduce its body temperature (Figure 1.4). Lizards are ectotherms; as such, they cannot regulate their body temperature internally but can do so behaviorally.

Measuring behavior: elephant ethograms

Featured Research

Behaviors must be measurable—that is, we must be able to quantify our observations with numbers according to specific rules (Martin & Bateson 1993)—and different people must be able to recognize a behavior independently. Often, such characterization begins when a trained observer completes an **ethogram**, which is a formal description or inventory of an animal's behaviors. Ethograms typically list or catalogue defined, discrete behaviors that a particular species exhibits.

ethogram A formal description of an animal's behaviors.

Figure 1.5. Captive Asian elephant. Ethograms are often constructed to describe and quantify the behavior of captive animals.

time budget A summary of the total time and relative frequency of different behaviors of an individual.

Researchers can use an ethogram and measure how many times a behavior occurs (its frequency), the length of time of a behavior (its duration), the frequency of the behavior per unit time (its rate), or the vigor or forcefulness of the behavior (its intensity). Sometimes only certain behaviors, such as social behaviors (e.g., grooming self, grooming others, chasing others), are quantified. Typically, a more complete list of behaviors that occur over a specific time period is recorded (e.g., sleeping, grooming self, grooming others, walking, climbing tree, eating food, drinking). From these observations, a researcher can then determine both the total and the relative time that an animal engaged in each behavior—in other words, the measure of the behavior divided by the overall time spent observing the animal. The resulting **time budget** indicates the total time and relative frequency of each behavior.

Ethograms are commonly constructed for animals in captivity and can be used as a baseline for healthy behavior. Paul Rees created an ethogram for captive Asian elephants (*Elephas maximus*) (Figure 1.5) at the Chester Zoo in the United Kingdom (Rees 2009). When elephants were in their outdoor enclosure, he recorded their behavior every five minutes for an entire day once a week for 11 months. His ethogram contains 15 behaviors, including feeding, standing, and digging (Table 1.1). In addition, he measured stereotypic behavior, or captivity-induced behavioral anomalies that are used as an index of the welfare of captive animals (Mason 2010). These behaviors often include repetitive behaviors that lack an apparent purpose, such as head bobbing or pacing. Rees found that captive elephants spent about a quarter of their time feeding, and that stereotypic

TABLE 1.1 Elephant ethogram. This ethogram describes the behavior of captive elephants (*Source:* Rees 2009).

BEHAVIOR	DESCRIPTION
High-frequency behaviors	
Dusting	Collecting soil and throwing it over the body/rubbing it onto the skin (while standing still or walking), including digging into the soil for this purpose
Feeder ball	Feeding or attempting to feed at a metal feeder ball containing small quantities of food
Feeding	Collecting food with the trunk and placing it in the mouth while standing still or walking (does not include suckling or activity at the feeder ball)
Locomotion	Walking (except feeding or stereotyping)
Playing	Chasing another elephant/mock fighting with another elephant (but not as a result of an antagonistic encounter or as part of courtship)
Standing	Standing motionless (not while stereotyping or dusting)
Stereotypy	Repetitive behavior with no obvious purpose: weaving, head bobbing, pacing backward and forward or in an arc, walking in circles
Suckling	Calf suckling from mother or other female (measured separately from feeding)
Low-frequency behaviors	
Aggression	Hitting/pushing as a result of an antagonistic encounter (but not as a part of play)
Bathing	Standing/lying in pool/squirting water from pool over body with trunk
Digging	Digging in soil using the foot (but not as a part of a dusting behavior)
Drinking	Collecting water in the trunk and squirting it into the mouth
Lying down	Lying down on the ground (on side or prone)
Rolling	Rolling in soil or mud (but not as a part of playing with another individual)
Sex	Courting or being courted/mounting another elephant or being mounted by another elephant of either sex

behavior was negatively correlated with feeding behavior; in other words, the more time spent feeding, the less time spent pacing or head bobbing. Rees suggests that using widely spaced feeders to supply food slowly and at random times could reduce the frequency of stereotypic behavior.

We turn next to a discussion of the scientific method: the process scientists use to understand the behaviors they observe.

1.2 The scientific method is a formalized way of knowing about the natural world

When you think of science, you may think first of an impressive body of knowledge—the facts that you are asked to learn in class. Have you ever considered where that knowledge came from? It was obtained by human beings seeking to understand the natural world. Scientists engage in the **process of science**, which involves observing events, organizing knowledge, and providing testable explanations (Mayr 1982). The process of science is fundamental to our understanding of the natural world.

process of science Observing events, organizing knowledge, and providing explanations through the formulation and testing of hypotheses.

Scientific discoveries continue to occur today at a tremendous pace. Every week, new discoveries appear on television, in magazines, and on the Internet. As instructors, we look back at our courses from just five years ago and marvel at how much has changed in so short a time. You and your instructors may be involved in new discoveries yourselves.

Why does scientific progress occur so rapidly? What is different about scientific knowledge compared with knowledge in the humanities? As we see next, the process of science means constructing hypotheses that make testable predictions.

The importance of hypotheses

Some disciplines—like English, history, and philosophy—are part of the humanities. Others, like anthropology and sociology, are social sciences. Still others, like biology and chemistry, are natural sciences. In all these disciplines, scholars seek to gain a better understanding of the world. In the humanities, researchers are interested in understanding the human experience. The social sciences involve knowledge of human behavior and societies. And in the natural sciences, researchers strive to understand the natural world.

You may have noticed differences between your courses not only in the information presented but also in how you are expected to think about that information. For example, the humanities discuss art, literature, and how humans think and act. You might be expected to present your own perspective while critically evaluating the perspectives of others. Often, two people may arrive at very different perspectives using similar evidence.

Historians, for example, strive to understand why certain events happened by interpreting personal journals, letters, government publications, and newspaper articles. A historian forms a thesis, or narrative, to explain events and then interprets relevant documents to support that thesis (Hult 2002). For instance, a historian might be interested in what motivated Thomas Jefferson, John Adams, James Madison, and other founding fathers of the United States to declare independence from England and form their own system of government. Were economic considerations, such as preservation of individual wealth, the primary motive (Beard 1913), or did convictions about individual liberty and rights play a larger role (McDonald 1958)? By examining the Declaration of Independence,

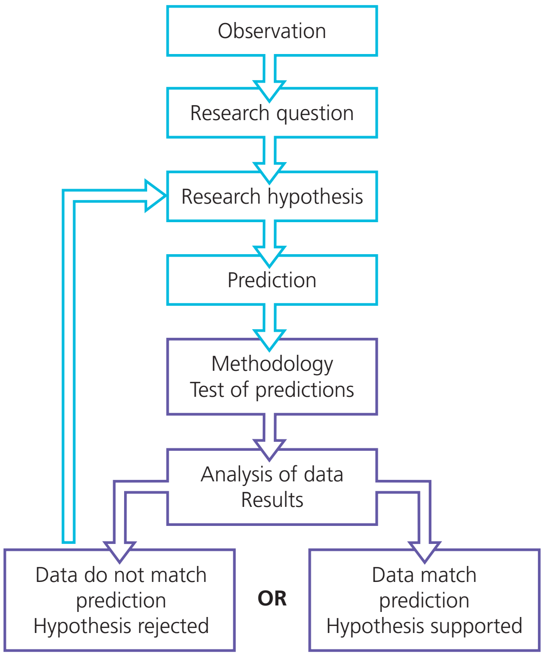

Figure 1.6. The scientific method. This flowchart summarizes the scientific method.

the U.S. Constitution, the *Federalist Papers*, and letters written by key figures, historians have developed these and other interpretations. In each case, research involves discovering, reevaluating, and interpreting the evidence.

Scientists, like other scholars, begin with questions, but they formulate these questions into hypotheses. Hypotheses are explanations that make predictions that can be tested. Because these tests can be repeated and confirmed by other scientists, their results are much less subject to debate. This is why science sometimes seems like just an accumulation of facts. Yet these facts are the results of scientific studies that have been confirmed repeatedly by the scientific community over many years.

The scientific method

Scientists use the scientific method to learn about the natural world. The scientific method is a formalized process that involves the testing of hypotheses (Figure 1.6). This process often begins with an observation of a single event or pattern that requires explanation. This observation forms the basis of a **research question**—a brief statement of something that we would like to understand. For example, suppose you were walking through your neighborhood and observed that some yards had many American robins (*Turdus migratorius*) feeding in them, while other yards had very few. Robins, common songbirds found on lawns throughout North America, feed on invertebrates such as earthworms and beetle grubs. This observation might lead to the following research question (Scientific Process 1.1):

research question A formal statement of an unknown that begins the scientific method.

Research question: Why is there variation in the number of robins feeding in different yards?

The identification of patterns like this can be accomplished with careful observation and mere human curiosity. Throughout this book, you will see how researchers have identified different behavioral patterns that have led to a variety of research questions.

The next step in the scientific process is the formulation of a hypothesis, or, more formally, a research hypothesis. You may think of a hypothesis as an educated guess, but this definition is far too simplistic. Rather, a research **hypothesis** is an explanation that is based on assumptions and produces a testable prediction. Research hypotheses are evaluated using two statistical hypotheses that reflect the two possible outcomes. One outcome is that the proposed explanation for the observation *does* have a significant effect; this is the **alternate hypothesis**, or $\mathbf{H_a}$. The other possible outcome is that the proposed explanation does *not* have a significant effect; this is the **null hypothesis**, or $\mathbf{H_0}$, the hypothesis of no effect. These terms were coined by Sir Ronald Fisher (1966), a British geneticist, evolutionary biologist, and statistician. Together, the null and alternate hypotheses are known as statistical hypotheses.

hypothesis An explanation based on assumptions that makes a testable prediction.

alternate hypothesis The statistical hypothesis that the proposed explanation for an observation does significantly affect the behavior of the organism.

null hypothesis The statistical hypothesis that an observation results from chance. Also called the hypothesis of no effect.

For example, to explain why more robins feed in some yards than in others, you might hypothesize that the quantity of food varies between yards and that this variation affects robin abundance. This leads to two statistical hypotheses:

Alternate hypothesis: The amount of food in a yard determines the number of robins feeding there.

Null hypothesis: The amount of food in a yard does not determine the number of robins feeding there.

SCIENTIFIC PROCESS 1.1

Robin abundance and food availability

RESEARCH QUESTION: *Why is there variation in the number of robins feeding in yards?*

Hypothesis: The amount of food in a yard determines the number of robins feeding there.

Prediction: Yards with more food will have more robins.

Methods: The researchers:

- Counted the number of robins at the same time of day in each of 30 yards
- Quantified the amount of food (earthworms) available to robins in each yard by examining several 900 cm^2 sampling areas
- Mixed 40 g of yellow ground mustard seed into 4 L of water and then poured the mixture into each sampling area so that it was absorbed into the soil
- Counted the number of earthworms that emerged in each sampling area over a period of 10 minutes

Results:

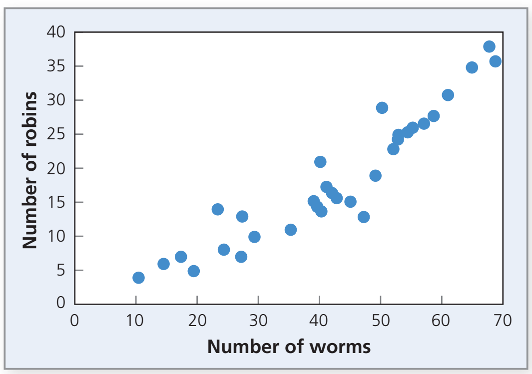

Figure 1. The greatest numbers of robins were found in yards with the most worms.

OR

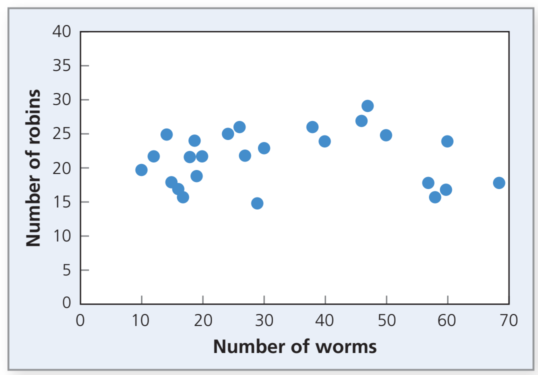

Figure 2. There is no relationship between the number of robins and the number of worms in yards.

Conclusion 1: The hypothesis is supported. Yards with more earthworms have more robins.

Conclusion 2: The hypothesis is not supported. Yards with more earthworms do not have more robins.

EVALUATE

Design a sampling protocol for counting the number of robins in yards. Draw a graph that shows a negative relationship between the number of robins and the number of worms in yards.

The alternate hypothesis assumes that the amount of food in a yard is the only factor that determines the number of robins feeding there. Both the alternate and null hypotheses make predictions, although they are different:

Alternate hypothesis prediction: Yards with more food will have more robins.

Null hypothesis prediction: There is no relationship between the amount of food in a yard and the number of robins in the yard.

The last step in the scientific process is to evaluate the research hypothesis by testing the prediction of the null hypothesis. One way to do this is to make new observations by collecting data from many different yards on the number of