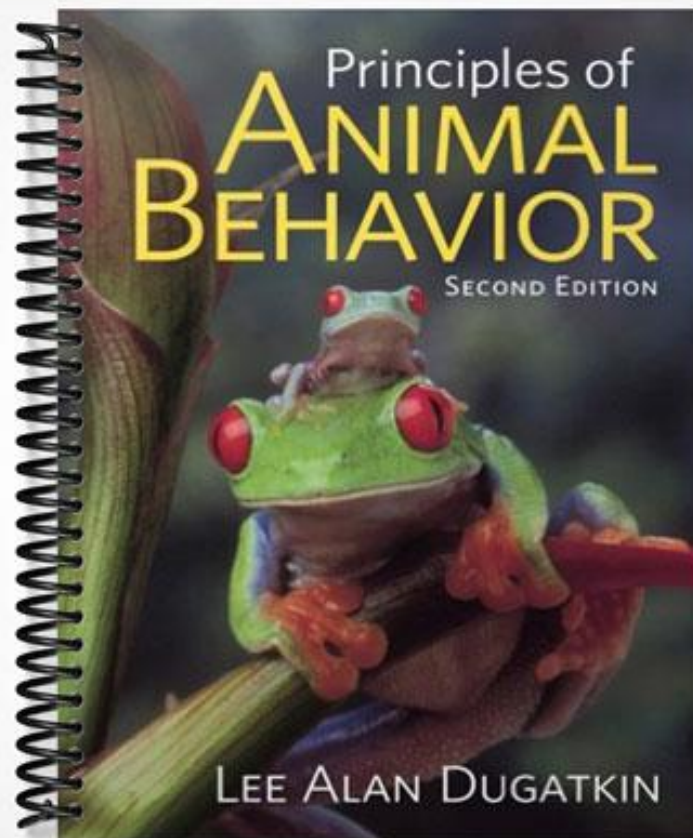


SOLUTIONS MANUAL



Principles of
**ANIMAL
BEHAVIOR**

SECOND EDITION

LEE ALAN DUGATKIN

INSTRUCTOR'S MANUAL

Lee Alan Dugatkin's
Principles of Animal
Behavior

SECOND EDITION

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Lee Alan Dugatkin's

Principles of Animal Behavior

SECOND EDITION

Ryan L. Earley

DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF ALABAMA



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Preface

“The whole art of teaching is only the art of awakening the natural curiosity of young minds.”

—Jacques Anatole François Thibault (1881)

As an undergraduate, I was at first overwhelmed by the integrative nature of animal behavior, with its roots in mathematics and game theory, evolutionary biology, neurobiology, endocrinology, and molecular genetics. After absorbing the literature for a couple of years, however, proximate and ultimate causation (and the powerful fusion of the two) began to make sense, and I grew more comfortable with the many mechanisms underlying animal behavior. Today, research in animal behavior and behavioral ecology has progressed in many significant ways, some unimaginable just fifteen years ago. The field of animal behavior has become even more integrative and sophisticated, and the stacks of articles reporting clever experimental designs, innovative theory, or noteworthy results climbs closer to the ceiling seemingly every day. From a student’s perspective, the advances in animal behavior translate into a vast amount of introductory material that needs to be covered in a relatively short period of time. This new edition of Dr. Lee Alan Dugatkin’s *Principles of Animal Behavior* captures many of these advances with fluid text, fabulous examples, and a stress on the interplay between ultimate and proximate causation.

This manual was created with the interests of both students and instructors in mind and with the intent of stimulating student-student and student-teacher interactions. Each chapter begins with detailed answers to the discussion questions posed at the end of the text chapter, with special emphasis on recent work in the area. As should be clearly evident from the first page of the manual, the answers to these questions are directed at future animal behaviorists in the hope of *awakening the natural curiosity of young minds*. Dr. Dugatkin challenges students to color outside the lines in the sense that his questions are geared toward familiarizing students with topics and/or studies that were not, on the whole, covered in

great detail in the text. The answers provided in this manual do not simply revisit the *Principles of Animal Behavior* text verbatim. Rather, I hope that the answers will serve as templates (or even targets) for within-class and extramural discussion sessions, group projects, or lively debates. Furthermore, the discussion questions provided in *Principles of Animal Behavior* would certainly be useful as mock essay exams for students, and the answers I have provided may help to get students' ethological gears turning. Another potential use for this manual would be as a supplemental, in-classroom resource for students, particularly given that the answers are tailored toward individuals who might be having some trouble wrapping their minds around certain concepts. Lastly, I hope that the answers to the discussion questions provide a useful resource for instructors. Many of the answers cite recent related literature, the references for which are located at the back of the manual. These additional citations may also serve as fuel for discussion groups, exam questions, or assignments related to hypothesis testing, experimental design, critical thinking, and so forth.

The second part of each chapter in this manual contains a set of ten multiple-choice questions and five “review and challenge” questions. The multiple-choice questions are derived directly from the chapters of *Principles of Animal Behavior* and should be useful for testing students' knowledge of the text. The review and challenge questions either ask students to elaborate on the concepts that they learned in each chapter or require students to conduct further research on selected topics in animal behavior. These questions are in essay format and some might be useful as exam questions, depending on the length of the class period. In addition, the review and challenge questions can be used as student-led discussion pieces, individual presentations, or group research projects.

I extend my sincere gratitude to those who awakened my inner-ethologist and to those whose insights were invaluable in the completion of this manual. First and foremost, I thank Lee Alan Dugatkin—a central figure in my development as an experimental biologist, a dear colleague, and an extraordinary mentor—for providing me with the opportunity to collaborate again on this textbook-manual fusion. I thank Matthew Freeman, Mike Wright, and Sandy Lifland at W.W. Norton & Company for their patience and significant comments and correspondence regarding this manual. I am also indebted to Larry Wolf (Syracuse University) and Yuying Hsu (National Taiwan Normal University) for encouraging me, as an undergraduate, to pursue a career in animal behavior and for igniting my passion for discovery in the field of ethology. Kristin Bonnie (Beloit College), Varenka Lorenzi (Georgia State University and Center for Behavioral Neuroscience, GSU/CBN), Matthew Grober (GSU/CBN), and Gordon Schuett (GSU) offered precious advice on the contents of this manual. And I thank my beloved family—Richard Earley, Barbara Scavotto-Earley, and Angela Earley—for their perpetual encouragement, support, and understanding. This manual is dedicated to my students—Janet Campbell, Alex Cheah, Donald Copeland, Heidi Dunbar, Mark Dykstra, Mark Garcia, Marcel Garcia, Whitney Janzen, Michelle Lennox, Bryan Levay, Rosemary Luzania, Jacqueline Ma,

Farzad Marzlom, Swapna Medichetti, Kelly Miller, Heather Nuanes, Margarita Ortiz, Laura Paiva, Nasir Sadeghi, Boopathy Sivaraman, Haley Stephenson, Max Stephenson, Sina Tuy, and Stephanie Wong. They taught me just how rewarding it can be to engage curious minds. Their work has exemplified the truly integrative nature of animal behavior!

Ryan L. Earley

DISCUSSION QUESTIONS

1. Take a few hours one weekend day and focus on writing down all the behavioral observations you've made, as well as any, even indirect, behavioral hypotheses you have constructed. Think about your interaction with both humans and non-humans. How has your very brief introduction into ethology reshaped the way you observe behavior?

As described at the beginning of this chapter, almost everyone has asked questions about animal behavior—sometimes due to interest and other times due to sheer necessity—and this, technically, makes us all ethologists. Nevertheless, understanding the foundations on which ethology was built and the ways in which ethological questions are asked makes a world of difference in how inquiries related to animal behavior are posed and interpreted. My first exposure to ethology as an undergraduate student was nothing short of revolutionary. Short flower photography sessions on the banks of a pond turned into extended observation sessions of the animals inhabiting its murky edges. What were once just droves of dragonflies became populations in which there existed individual variation in coloration patterns, choice of locations to deposit eggs, territorial prowess, and so on. An understanding of ethology triggered a greater appreciation for the many facets of individual variation (e.g., behavior, morphology) and also prompted questions about the causes (e.g., development, genetic variation) and the ultimate consequences of variation (e.g., differences in reproductive success or survival). Of course, introductions into ethology may have different impacts on different people in terms of the ways they observe behavior. This first chapter emphasizes natural selection, individual learning, and cultural transmission as separate, but certainly intertwined, foundations of animal behavior. With an introductory understanding of these three foundations, you are equipped to ask questions about how natural selection could have shaped behavior across generations, how learning can modify

behavior within a lifetime, and how cultural transmission can intensify the spread of behavioral traits through a population. In addition, the examples of song production in Hawaiian crickets and xenophobia in common mole rats clearly demonstrate that environmental conditions (e.g., the presence of parasites, mesic vs. arid) constitute an important piece of the puzzle in studies of animal behavior. Thus, you should now also be more aware of the environmental theater in which animals behave and how this could affect behavior in the short term or over many generations. Having a basic introduction to ethology and its underlying principles should be like putting on panoramic glasses that expand your appreciation for the complexities of animal behavior and foster the development of rigorous ethological questions and testable hypotheses.

2. Why do we need a science of ethology? What insights does this discipline provide both the scientist and the layperson?

Ethology draws on the principles of a diverse array of fields, from neurobiology to ecology, in order to address questions about how and why animals behave the way they do. Whether questions are tackled observationally or experimentally, the insights gained by studying animal behavior permeate the lives of scientists and nonscientists alike. An exhaustive description of the many reasons why we need a science of ethology would require something akin to a multivolume encyclopedia, but several reasons are highlighted here (Caro, 1998; Dell’Oro, 2002; Price, 2003). Veterinary and farming practices are a testament to applied animal behavior in action. The growth and welfare of livestock depend in large part on the implementation of proper housing conditions and feeding regimes, a task that hinges on understanding, for instance, how group size and dominance relationships within the group affect feeding behavior and growth rates. The well-being of your pet depends on your ethological skills (e.g., detecting abnormal behavior) and then on the expert diagnosis of your veterinarian, who must be able to assess and treat behavioral disorders (e.g., stress, excessive aggression). This information is also often disseminated to animal control personnel and may be used in deciding which animal is appropriate for certain tasks—for example, in screening for seeing-eye dogs (see Chapter 17). In addition, trainers draw on the tenets of classical psychology (e.g., positive reinforcement, conditioning) to mold the behavior of household pets. Animal behavior also plays an integral role in field and zoo conservation efforts, recreational fisheries practices, and the development of national and/or state parks. For instance, understanding reproductive and courtship behavior may facilitate captive breeding programs in zoos, while knowledge of feeding behavior and competitive prowess may provide clues as to why non-native species (e.g., zebra mussels in the waterways of the United States) decimate native fauna (e.g., other bivalve mollusks and filter feeders). Changes in the behavior of stream-dwelling animals or the mere presence of some species and absence of others can tell much about water quality, pollutant levels, and ecological disturbances. Familiarity with aggressive behavior and how captive rearing programs and artificial selection

influence behavior is essential for the successful integration of fisheries-reared sport fish (e.g., salmonids, centrarchids) with natural populations. Similarly, understanding the home range size, diet, migratory patterns, and social structure of animal species within a community is an important consideration in the design and development of national and/or state parks. Lastly, the interaction of the discipline of animal behavior with neurobiology, endocrinology, and genetics is essential for understanding the molecular underpinnings of certain behavioral disorders (e.g., depression, generalized anxiety disorder, post-traumatic stress disorder) and in developing more effective treatments. All of these examples show that the insights gained by studying ethology are far reaching, impacting progress in scientific fields as different as conservation biology and medicine and influencing the daily lives of nonscientists (e.g., pet owners).

3. *Imagine you are out in a forest, and you observe that squirrels there appear to cache their food only in the vicinity of certain species of plants. Construct a hypothesis of how this behavior may have been the result of (a) natural selection, (b) individual learning, and (c) social learning.*

Caching is a behavior in which animals store provisions for future use. There may be many hypothetical reasons why squirrels cache their food near certain species of plants. Thus, the answers provided here should be considered as only some of the many possibilities. First, let us examine how this type of caching behavior could arise as a result of natural selection. Let us assume that at some time in the past substantial variation in caching behavior existed between individuals of this population: some squirrels stored their food in open areas, some cached near grasses, and still others cached near well-foliated plants. You discover that some social animals exhibit cache-raiding behavior—that is, astute observers within the social group will watch where others store their food and subsequently raid the cache for a free meal or for free stores of their own (Bugnyar and Kotrschal, 2002). Suppose that squirrels live in social groups within which individuals have ample opportunity to observe the caching forays of their groupmates. Individuals that cache in open areas or near grasses that provide little cover are easily seen by their cache-raiding conspecifics. Thus, these animals lose much of their food to the thieves and experience low rates of food retrieval. In contrast, squirrels that store provisions near well-foliated plants are able to evade cache-raiders, maintain the secrecy of their cache location, and retrieve a large proportion of the stored food. If squirrels that retrieve a large proportion of their cache survive better over winter, grow faster, and experience competitive or reproductive advantages, then the different caching strategies (e.g., in open areas, among grasses, or near well-foliated plants) have associated fitness consequences. Animals that cache out of view of conspecifics may survive to reproduce multiple times or may be capable of producing many offspring, while animals that cache in the open or near grasses either die early or cannot invest as much energy in offspring. Thus, natural selection favors the caching behavior in which food is stored near well-foliated plants (i.e.,

these animals contribute more offspring to future generations). What you are observing while hiking through the forest is the result of natural selection acting on the different caching strategies; natural selection has shaped behavior such that most animals in the group cache near well-foliated plants. This interpretation assumes that natural selection acted on caching behavior rather than on the ability to learn where to cache food.

If individual learning is responsible for the observed caching behavior, then the squirrels' current caching decisions are based on past caching experiences. At a young age, squirrels may store their food in several different locations—in open areas, near grasses, and near well-foliated plants. But, since cache-raiders are present, only the stores located near well-foliated plants will provide a high return. Perhaps the squirrels are able to keep track of how profitable each cache site is in terms of the proportion of provisions retrieved from each location. With experience, squirrels will learn that caching in the open or near grasses is less profitable than caching near well-foliated plants. Thus, the returns of past caching experiences alter future caching decisions. It is important to note that if individual learning mediates caching behavior, all squirrels will not cache near well-foliated plants. Younger or less experienced animals will be more prone to make “mistakes” (e.g., caching in open areas) than older, more experienced squirrels. In this situation, behavioral variation will exist between individuals based on experience, and caching behavior will vary within each individual, depending on its age and experience. As stated in the chapter, invoking learning as an explanation does not preclude natural selection; natural selection could favor the ability to learn, while learning itself produces the observed caching behavior.

Lastly, if social learning (or cultural transmission) is responsible for caching behavior, then squirrels will observe where conspecifics are storing food and might copy this choice when caching their own food. The propensity to cache food or to learn the location of superior storage sites could have been shaped by natural selection, but rapid transmission throughout the population of information about new caching locations could be achieved through social learning. At one time, the squirrels in this group could have all cached food in open areas, but one squirrel might have deviated from this pattern and stored its food near well-foliated plants. Observer squirrels with no past experience caching near well-foliated plants might copy this behavior and begin to store food in the same manner as the first “demonstrator.” In this situation, information is transmitted passively from one individual to the next. It is also possible that the location of caching sites could be transmitted via social learning from parents to offspring in an active fashion analogous to teaching (Chapter 5). Here, one might predict consistent caching behavior within kin groups, but not between different kin groups (thus, all individuals in the population would not necessarily cache near well-foliated plants). Crossing kin boundaries, novel food storage behavior could spread through the population quickly. Without emigration from the group, however, this behavior would be unlikely to reach adjacent squirrel populations. Nonetheless, different populations of the same squirrel species living in habitats with similar structures might cache food in sim-

ilar characteristic locations. With the appropriate empirical tests, one could determine whether population-specific caching behaviors were shaped by cultural transmission or by environmental factors.

4. *Why do you suppose that mathematical theories play such a large part in ethology? Couldn't hypotheses be derived in their absence? Why does mathematics force an investigator to be very explicit about his or her ethological hypotheses?*

Theoretical approaches to ethology involve the construction of virtual mathematical worlds in which the investigator examines the influence of a defined set of parameters on, for instance, foraging decisions or dominance hierarchy formation. As described in this chapter, mathematical models often simplify the natural world and its inherent complexities to generate explicit predictions about animal behavior that are applicable across a wide variety of animal systems. Mathematical models sometimes spawn novel predictions that are not entirely intuitive or that call for a restructuring of current hypotheses. Thus, these predictions often serve as the springboard for empirical tests in ethology, as is evident throughout this textbook. The beauty of many mathematical models is their generality and testability. Are the predictions upheld when tested empirically in nature or in the laboratory? If the predictions do not generally apply to the real world, those who are mathematically savvy can revise the assumptions of the model or adjust the parameters used to generate new, testable predictions. Similarly, if a model applies to some animal systems but not to others, new mathematical theories can provide insights into why certain behavioral patterns differ among different species. Thus, although hypotheses can, and often are, developed in the absence of mathematical theory, the predictions of these models can cull the behavioral options or provide novel behavioral alternatives for empiricists to examine.

MULTIPLE-CHOICE QUESTIONS

1. Natural selection is *best* described as a process by which
 - a. the frequency of certain traits increases over evolutionary time in a random fashion.
 - b. the frequency of traits that confer reproductive and/or survival success increases over evolutionary time.
 - c. the frequency of traits that are passed on from one generation to the next increases over evolutionary time.
 - d. the frequency of traits that confer reproductive and/or survival success and that are passed on from one generation to the next increases over evolutionary time.
 - e. the frequency of traits that hinder reproductive and/or survival success and that are passed on from one generation to the next increases over evolutionary time.

2. Individual learning and cultural transmission differ in which of the following ways:
 - a. Individual learning alters the behavior of an organism within a lifetime, while cultural transmission does not.
 - b. Individual learning can lead to the rapid spread of a behavior through a population, while cultural transmission cannot.
 - c. Individual learning does not permit the transmission of information across generations, while cultural transmission does.
 - d. Individual learning involves copying the behavior of others, while cultural transmission does not.
 - e. Individual learning allows behavioral traits to spread quickly through a population both within an organism's lifetime and across generations, while cultural transmission allows behavioral traits to spread through a population only across generations.
3. Xenophobia is defined as the
 - a. fear of scarce resources.
 - b. fear of arid environments.
 - c. fear of disruption of group dynamics.
 - d. fear of living underground.
 - e. fear of unknown individuals from outside one's group.
4. Which of the following statement(s) are *not* true:
 - a. Learning and natural selection operate independently.
 - b. Past experiences can alter behavior within the lifetime of an individual via learning.
 - c. The ability to learn can be genetically encoded.
 - d. Natural selection can operate on the ability to learn.
 - e. Learning can change behavior within a generation, while natural selection can change the frequency of different learning rules across generations.
5. W. D. Hamilton's inclusive fitness hypothesis states that:
 - a. Total fitness depends only on the number of viable offspring an individual produces.
 - b. Both one's own offspring and the benefits received from helping to raise related offspring contribute to total fitness.
 - c. The number of viable offspring sired contributes less to total fitness than the number of related offspring an individual helps to rear.
 - d. Total fitness is influenced to a large extent by helping to rear unrelated offspring.
 - e. Total fitness is influenced only by the extent to which an individual helps to rear offspring of blood relatives.

6. Conceptual approaches to ethology involve
 - a. generating complex mathematical models of the world to establish explicit predictions about animal behavior.
 - b. combining ideas from different subdisciplines in a novel way to generate new sets of predictions about animal behavior.
 - c. conducting controlled experiments in the field to test hypotheses related to animal behavior.
 - d. conducting controlled experimental studies in the laboratory to test hypotheses related to animal behavior.
 - e. neglecting past observations and experiments in order to generate novel concepts concerning animal behavior.
7. Which of the following *best* describes the empirical approach to ethology:
 - a. Always assume that correlations between two events indicate that one event caused the second event to occur.
 - b. Design a series of controlled experiments in the field or laboratory to test an existing theory.
 - c. Avoid manipulating ethological or environmental variables in order to conduct a properly controlled study.
 - d. Observe animal behavior in a natural setting to uncover interesting trends and use controls or manipulations to determine causality.
 - e. Utilize only observational methods to test theories and concepts related to animal behavior.
8. Contemporary ethological experimentation was initiated by which of the following Nobel Prize winners:
 - a. R. A. Fisher, John Maynard Smith, and W. D. Hamilton
 - b. Niko Tinbergen, R. A. Fisher, and Konrad Lorenz
 - c. Karl von Frisch, W. D. Hamilton, and James Watson
 - d. W. D. Hamilton, Konrad Lorenz, and R. A. Fisher
 - e. Konrad Lorenz, Niko Tinbergen, and Karl von Frisch
9. The three foundations of ethology are
 - a. molecular genetics, natural selection, and learning.
 - b. neurobiology, anthropology, and psychology.
 - c. psychology, learning, and cultural transmission.
 - d. cultural transmission, natural selection, and learning.
 - e. endocrinology, developmental biology, and natural selection.
10. Marlene Zuk and her colleagues' work on the field cricket *Teleogryllus oceanicus* provided insights into how natural selection can operate in a natural setting over short periods of time. Which of the following *best* describes Zuk's work on the Hawaiian Islands:
 - a. Parasitic flies acted as a selection pressure that drove changes in the wing morphology and behavior of male crickets.

- b. All male crickets adopted a “silent calling” strategy for attracting females to avoid being detected by parasites.
- c. The researchers found no evidence that morphology and behavior would respond to strong selection pressures such as those imposed by parasitic flies.
- d. The cricket population neared extinction due to parasitic fly infestations, and many conservation biologists fear that their numbers will not recover.
- e. Male crickets adopted a new behavioral strategy to avoid parasitic infection but, surprisingly, their morphology appeared not to change over time.

REVIEW AND CHALLENGE QUESTIONS

1. What is the key difference between observational and experimental studies in ethology? What are some possible advantages to each type of study?
2. Can natural selection and learning or natural selection and cultural transmission influence specific behavioral patterns simultaneously? Provide an example demonstrating the possible interactions between natural selection and either learning or cultural transmission.
3. Based on the definitions provided in the text, what are the primary differences between individual learning and social learning?
4. Conceptual advances in ethology often mark the marriage of ideas generated in animal behavior with those of different subdisciplines or even entirely different fields. What do conceptual approaches contribute to ethology? As you become more familiar with the animal behavior literature, can you identify key interactions between different disciplines that have triggered new developments and/or novel ways of thinking about a specific set of behaviors?
5. As a student of animal behavior, you must distinguish between correlation and causation. What types of information can be gleaned from a correlation between two events? How can you establish whether the first event caused the second to occur? As an optional exercise, devise an imaginary correlation between two events relevant to animal behavior. Present this discovery to your classmates and formulate several alternative causal hypotheses (i.e., what else could have caused this event to occur)? Finally, develop an experiment or multiple experiments to test between these alternatives.

ANSWER KEY FOR MULTIPLE-CHOICE QUESTIONS

- | | |
|------|-------|
| 1. d | 6. b |
| 2. c | 7. d |
| 3. e | 8. e |
| 4. a | 9. d |
| 5. b | 10. a |