Animal Behavior

How and Why Animals Do the Things They Do

Volume 1 | History, Causation, and Development

Ken Yasukawa and Zuleyma Tang-Martínez, Editors

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Preface

Most people are interested in the behavior of animals, but the scientists who study animal behavior, exemplified by the authors of the volumes of this book, use time-honored methods of hypothesis testing in their attempts to understand why and how animals do the things they do. As stated in many of the chapters in this book, the scientific study of animal behavior owes a tremendous debt to Niko Tinbergen, who turned his boyhood naturalist's curiosity about the world of animals into a career that was both highly productive and extremely influential. This book is dedicated to Tinbergen.

Tinbergen proposed his famous four questions in his 1963 paper "On Aims and Methods in Ethology" (*Zeitschrift für Tierpsychologie*, 20, 410–433). Tinbergen noted that a full understanding of behavior must include both "proximate" and "ultimate" explanations. "How" questions are answered by proximate explanations of the developmental history and mechanisms that control behavior. "Why" questions are answered by ultimate explanations for the adaptive value and evolutionary history of behavior. Taken together, this approach has produced a tremendous amount of research and lots of answers, but also even more questions. The chapters in this book have been written to demonstrate the dynamic nature of the scientific study of animal behavior. We hope that you will find each chapter an informative and enjoyable glimpse into the curious minds of behavioral scientists.

As behavioral scientists, we have been inspired and influenced by many who came before us. To paraphrase Sir Isaac Newton, we have seen a little further by standing on the shoulders of giants. But we have also benefitted from many contemporaries, some of whom have recently passed away much too soon. We could name many of them, but a few who stand out to us are Val Nolan, Devra Kleiman, Penny Bernstein, Al Dufty, and Chris Evans. We should note that Chris died while writing a chapter for Volume 3, and we are therefore proud that one of his last contributions to animal behavior will appear in this book. We also dedicate this book to Val, Devra, Penny, Al, and Chris, our friends and colleagues.

SPECIAL FEATURES

Each chapter is written by active researchers who are experts in the subjects they cover. Because science tends to read like a foreign language, we have included some special features to help you understand what our contributors are telling you. First, our contributors try to explain why they are interested in their topics and how they go about asking and answering the questions they consider. Second, the technical terms (vocabulary) are listed in ***bold italics*** and are defined in the glossary at the end of each volume. Finally, each chapter also includes a list of the references cited within it. If you are interested, you can try to read some of these research papers. Some can be found using a computer search—Google Scholar is one way to find some of them. Another way is to use the name of the author to search for the author's website—many authors provide PDF copies of their papers on their websites. One last way is to visit a university library and ask to do a computer search using their electronic data bases. You will probably need to get special permission to do so, however.

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This Is How We Do It: The Scientific Study of Animal Behavior

Ken Yasukawa

INTRODUCTION

Interest in animal behavior is at an all-time high. Animal behavior is the subject of documentaries (e.g., *March of the Penguins*), animated children's adventures (e.g., *Finding Nemo*), TV shows (e.g., *Dog Whisperer*), TV series (e.g., *Shark Week*), and entire cable networks (e.g., *Animal Planet*). But *where does the information come from?* Information about the behavior of animals comes from scientific study, and the field of animal behavior is now well established. In this chapter I will briefly describe the three major methods (observations, experiments, and modeling) that researchers use to study animal behavior, and I will organize it around the process by which research is designed. My goal is a general introduction with some examples and suggestions for further reading rather than an exhaustive discussion with endless references. I write this chapter in honor of my role model, Niko Tinbergen, who established the framework for the study of animal behavior (see Chapter 2). Figure 1.1 shows some of the animals he studied.

WHO DOES RESEARCH IN ANIMAL BEHAVIOR?

Animal behaviorists are a diverse lot. They range in age from elementary school children (Blackawton et al., 2010) to retirees (several chapters in this book). Those with advanced degrees come primarily from biology,

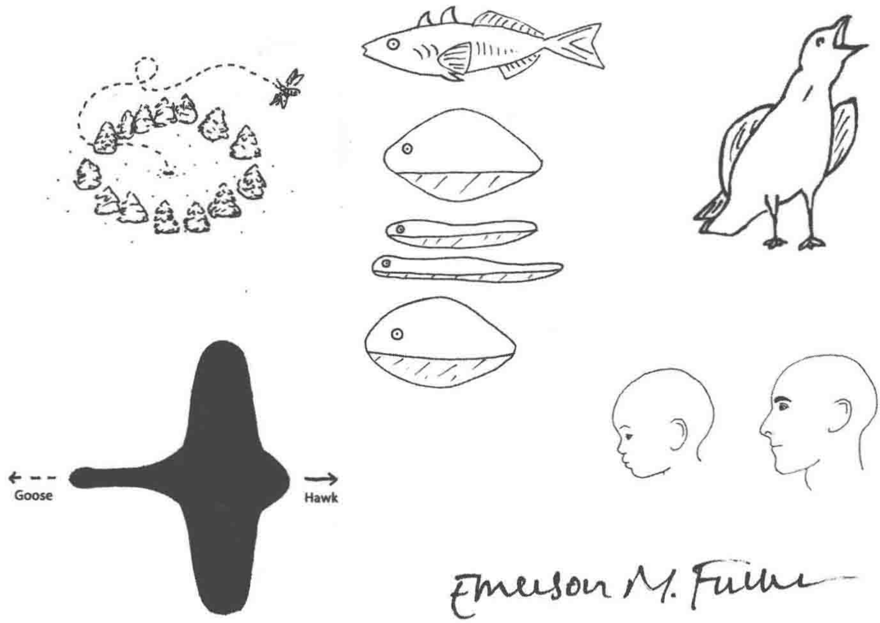

Figure 1.1. Drawings of some of the animals studied by Niko Tinbergen. (Redrawn by Emmerson Fuller)

psychology, and anthropology, but disciplines such as mathematics, physics, sociology, economics, and philosophy are also represented. And they reside throughout the world, although North America, Europe, and Australia are disproportionately represented.

FUNDING FOR RESEARCH

Some research projects require few financial resources. My doctoral thesis study of red-winged blackbirds (*Agelaius phoeniceus*), for example, required travel to my study site, a few items of equipment (a telescope, which I borrowed; binoculars; a stop watch; and a clipboard), and a few supplies (data sheets, pencils, coffee, and Snickers bars). In contrast, however, before most animal behaviorists can conduct their research projects, they must secure funding to pay for travel, housing, personnel, equipment, supplies, and animal care. Authors published in a single recent issue of *Animal Behaviour*, a highly respected, international journal, acknowledge funding from a variety of governmental and nongovernmental sources, including the National Science Foundation and National Institutes of Health (USA), Natural Science and Engineering Research Council (Canada), Consejo Nacional de Ciencia y Technología de México, Biotechnology and Biological Sciences Research Council, and Natural Environment Research Council (UK), Northern Ireland Environment Agency, Centre National de la Recherche Scientifique (France), Fundação para a Ciência e a Technologia (Portugal), Max-Planck-Institut für Verhaltensphysiologie (Germany), Austrian Science Fund, Hungarian National Science Foundation, Swedish Research Council, Swedish Environmental Protection Agency, Academy of Finland, Netherlands Organisation for Scientific Research, Swiss National Science Foundation, Commission of the European Communities, Agency for Innovation by Science and Technology (Lithuania), Israel Science Foundation, National Research Foundation (South Africa), Australian Research Council, New Zealand Marsden Fund, Fujian Province Nature and Science Project (China), National Geographic Society, Volkswagenstiftung, Birds Australia, Canadian Society of Ornithologists, and the Leverhulme Trust. This listing of funding sources also emphasizes the worldwide reach of animal behavior and the variety of foundations and government agencies that support animal behavior research.

This financial support was absolutely necessary, but funding is extremely competitive—most research proposals are not funded. Professional animal behaviorists constantly deal with the stress of securing funding.

HOW DO ANIMAL BEHAVIORISTS GET STARTED?

Every journey must start with the first step, but that step can be very difficult. Paul Martin and Patrick Bateson (2007) suggest that the first step is to ask a question about behavior. Anything from a very general "What does this animal do?" to a narrow and more hypothetical "Do females prefer conspicuous male behavior?" will do. In many cases, research tends to generate more and more specific questions, and the questions emerge from earlier observations, questions, and potential answers.

Here is an example. Early observations of the behavior of my study species, the red-winged blackbird, showed that males defend territories (i.e., they try to keep other males out of small portions of nesting habitat). So, an initial question might be, "How do male red-winged blackbirds defend their territories?"

With the first step taken, a next step would be to gather more information. Typically, this next step involves doing some background reading or making preliminary observations and then using this information to propose some possible answers, which we call ***working hypotheses***.

For our initial question, doing a computer search, reading classic papers (Nero, 1956a, 1956b; Orians & Christman, 1968), and observing males at a marsh in spring would be helpful. Our reading and observation would tell us that males scan the habitat constantly from prominent perches, frequently produce a song that sounds like "o-ka-lee," and show the red-and-yellow wing patches (***epaulets***) for which the species is named. At this point we have at least two potential answers to our question: (1) Song is used to defend the ***territory***. (2) Epaulets are used to defend the territory. To make it easier to talk about these two hypotheses, we give them names. Although it might be tempting to name each one after the person who proposed it, it is more helpful to give them descriptive names such as the "song hypothesis" and the "epaulet hypothesis" for territory defense.

These potential answers are working hypotheses because each one is a testable explanation (answer to our question), and having more than one possibility means we are using the method of ***multiple working hypotheses*** (Chamberlin, 1890). Once we have working hypotheses, we must test their ***predictions***, but *what does that mean*? In our context, a prediction has nothing to do with telling the future. Each working hypothesis must predict the results of research that someone could perform. We then do the research to see whether we get the predicted results or some other results. This ***hypothesis testing*** is critical to designing research in animal behavior or any other scientific discipline.

But *what predictions do our two hypotheses make*? One suggestion to identify predictions is to use the "if–then" construction.

1. *If* red-winged blackbird song is used to defend territory (hypothesis), *then* males should sing when they are on territory but not when they away from the territory, and males that are unable to sing should be unable to hold their territories (predictions).
2. *If* red-winged blackbird epaulets are used to defend territory (hypothesis), *then* males should show their epaulets when they are on territory but not when they are away from the territory, and males that lack epaulets should be unable to hold their territories (predictions).

Once testable predictions have been identified, the next step is to choose a research design, including a statistical method, to test the predictions. Research design and statistical analyses are both very large and complex topics well beyond the scope of this chapter.

HOW DO ANIMAL BEHAVIORISTS TEST HYPOTHESES?

You were probably taught that the scientific method involves making observations, formulating hypotheses, and testing them with experiments. Although this description is correct in its broad outline, it does little to explain what happens in actual practice. Note that, despite what you learned about the scientific method, hypothesis testing is not limited to experiments—observations and modeling can also be used to test hypotheses. The key aspect of hypothesis testing is whether the research design is appropriate to test a specific prediction and whether the prediction, and therefore the hypothesis itself, can be ***rejected*** (Popper, 1959). According to this view, tests of hypotheses are attempts to falsify them. In other words, when we design tests of predictions, we always choose designs that could produce results that are contrary to the hypothesis and its prediction. Although it will be tempting to design research to confirm hypotheses, such research will not provide strong or rigorous support for the hypothesis. Instead, it is important to understand that only a study with the potential to falsify a working hypothesis has the ability to generate rigorous results that add to our knowledge of animal behavior. I offer a simple thought experiment to illustrate the process of hypothesis testing.

The Numbers Game

In this game your task is to guess the rules used to choose the next number in a series. We will start with the numbers 1, 2, and 4. Your first task is to design experiments to gather data by proposing numbers to test potential rules (hypotheses). I have used this exercise in many of my classes and even with the faculty at my college. In every case, students (and my colleagues) pick an obvious rule and then propose numbers that *fit* it. So, they propose 8, 16, 32, and so on to test the rule "double the previous number." *What are my students doing?* In one respect, they are testing hypotheses. They have a particular rule (hypothesis) in mind, and they are proposing numbers (making predictions) that can be tested (they fit or not). Unfortunately, they will never get any closer to identifying the rule because they are attempting to confirm their hypothesis instead of trying to disprove it. *What's the difference?* All of their numbers *fit* their hypothesis and will do so to infinity (or until the class ends). To illustrate this point, suppose someone else believes that the rule is "a number larger than the previous one." The predictions 8, 16, 32, and so on also fit that hypothesis, so *which one is correct?* Unfortunately, attempts to confirm either hypothesis do not allow us to choose one over the other.

To test the hypothesis critically, you must propose a number that *does not fit* the hypothesis. *Why does that help?* Because if the proposed number does, in fact, fit the rule, then you have showed that the hypothesis is *incorrect*—you have disproved the hypothesis. In contrast, even if you double the last number 100 times, you still have not proven the doubling rule because the predictions fit lots of other rules (e.g., "a number larger than the last"). It is only by eliminating some possible hypotheses that we learn something. So, in our example, if you want to test the doubling hypothesis, then you should propose a number that is *not* double the last number. For example, after 32, you could propose 63. *What happens when you find out that 63 fits?* Obviously, the rule is not "double the last number."

Testing the Epaulet and Song Hypotheses

Let us return to our two working hypotheses for territory defense in male red-winged blackbirds. *How have predictions of the epaulet hypotheses been tested?* Andrew Hansen and Sievert Rowher (1986) observed that male red-winged blackbirds conceal their epaulets while they trespass on other territories and when they are first establishing their territories, but once ownership is established, they show their epaulets during encounters with other males. In addition, Frank Peek (1972) found that males whose epaulets are blackened with hair dye are more likely to lose their territories than males treated similarly but whose epaulets were not changed. These tests have the potential to disprove the hypothesis, but both the observations and experiments support the predictions of the epaulet hypothesis.

What about the song hypothesis? Gordon Orians and Gene Christman (1968) observed that song is the most common and conspicuous vocalization male red-winged blackbirds give on their territories, and that trespassing males do not sing. Douglas Smith (1976) showed that males that are surgically prevented from singing have much more difficulty holding their territories than males that are given sham operations. These observational and experimental studies also have the potential to disprove the song hypothesis, but the results support the hypothesis. Before describing observations and experiments in more detail, it is important to discuss the advantages and limitations of observations and experiments.

EXPERIMENTS AND OBSERVATIONS: DIFFERENT KINDS OF VALIDITY

Many people believe that ***experimental studies*** are better than ***observational studies*** and that experimental researchers are more rigorous (scientific) than those who rely on mere observations. Fortunately for animal behavior, this viewpoint is misinformed. Marian Stamp Dawkins (2007) offers a thorough discussion of the value of observational studies, and Alan Kamil (1988) cogently discusses this issue in his explanation of ***validity***.

Research in animal behavior (and in science in general) that involves gathering data can be broadly divided into experimental and descriptive work, but empirical research is really a continuum, with purely descriptive, observational study in the animal's natural habitat (fieldwork) at one end and tightly controlled laboratory experiments at the other. Between the extremes are other kinds of empirical research including ***natural experiments*** and ***quasi-experiments***. Kamil (1988) asserts that no one kind of research is inherently better than another because each has advantages and limitations. The critical feature is not where or how data are gathered but the implications of the results. The study of animal behavior has always used a combination of methods.

Internal and External Validity

Validity has two distinct meanings in scientific research. ***External validity*** describes how well results of a study can be generalized to other situations or conditions. ***Internal validity***, in contrast, is the extent to which an effect can be attributed to a specific cause. In an ideal world, we would want to know what causes a particular behavior and how the cause-and-effect relationship works in all other situations. In the real world, however, we cannot have it both ways.

It should be clear that a descriptive field study has external validity because it is conducted in the situations and conditions normally experienced by the animals being studied. Field researchers want as many different conditions as possible to see a full range of behavior, so they make no attempt to control conditions. Observations of red-winged blackbird behavior by Robert Nero (1956a, 1956b) and Orians & Christman (1968) are well-known examples. The conditions that make such studies externally valid, however, also prevent us from knowing with complete confidence what causes a particular behavior to occur.

In contrast, a well-controlled laboratory experiment achieves the ***rule of one variable*** because control and experimental groups are identical in all ways but one (the ***experimental variable***), so any difference between them must occur because of the experimental manipulation. Ideally, in the perfect experiment, there are no ***confounding variables*** (other things that might explain the differences), so controlled laboratory experiments have high internal validity. William Searcy's (1988) study of male red-winged blackbird song approaches the rule of one variable. Searcy played recorded songs of males to captive females in a laboratory and found that four different song types (a repertoire) are more stimulating to the female than a single song type. The control necessary to achieve internal validity, however, makes it impossible to generalize the results because we have no idea what would happen if other things also varied.

A natural experiment, in which the researcher takes advantage of some change in the environment, falls between the extremes but is closer to descriptive field study. There is a weak sense of control in that the researcher compares behavior before and after some natural event. A spectacular example is the eruption of Mount St. Helens, which was used to study the behavior of male red-winged blackbirds (Orians, 1985). Prior to the eruption, males rarely fed their nestlings, but they did so in the next breeding season, perhaps because there were fewer females than usual for them to attract as mates or because the volcanic ash that "fertilized" the insect supply improved the food supply.

A quasi-experiment is closer to the other extreme. Here the researcher manipulates a variable while attempting to control some conditions, but because not all possible confounds are controlled, the researcher cannot say with complete confidence that a difference between control and experimental groups is caused by the experimental manipulation. I tested predictions of the song hypothesis by conducting an experiment in the field in which I compared the ability of "singing" and silent loudspeakers to defend otherwise empty red-winged blackbird territories (Yasukawa, 1981). Singing speakers were more effective than silent ones in discouraging trespassers, but uncontrolled confounds included time of day, day of the season, territory quality, age and experience of the removed male red-winged blackbirds and their neighbors, and many others.

Although no one method can produce both internal and external validity, a combination of methods can produce great confidence in explaining a particular behavior. Taken together, the many studies of red-winged blackbird song and epaulet function are a good example.

PRELIMINARY CONSIDERATIONS IN TESTING BEHAVIORAL HYPOTHESES

Once we have a question, some preliminary information, at least one working hypothesis, and predictions, we can begin hypothesis testing. Behavioral data can be used to address Nikolaas Tinbergen's (1963) four central questions of animal behavior.

1. What causes the behavior to occur? (causation)
2. How does the behavior develop? (development)
3. How does the behavior affect survival, mating ability, and reproductive success? (function)
4. What is the evolutionary history of the behavior? (evolution)

Before any observations are done or behavior measured, it is very important to make a series of decisions (Martin & Bateson, 2007). The level of analysis must be chosen to provide enough detail to be worthwhile but not so much that it is overwhelming. A species with sufficient background information and appropriate life history and social characteristics that is reasonably available, easy to observe, and tolerant of human observers must be identified. Finally, a good location, whether in the field, zoo, aquarium, farm, or laboratory, must be found and appropriate times to do the research chosen. With these decisions made, observer effects, anthropomorphism, and ethics must also be considered.

Without meaning to, you could have a subtle or even substantial effect on the behavior of your animals. Observer effects can be mitigated by the use of blinds (hides) in which the observer conceals him- or herself or by making a video recording of the behavior, but being restricted to a blind or using a video camera might make observing more difficult. An alternative is to spend time making the animals accustomed to your presence, but it is difficult to assess the effectiveness of such ***habituation***. Therefore, observer effects are something all animal behaviorists keep in mind and attempt to minimize in any way possible.

It is easy to misinterpret the actions of animals by assuming that they are just like us, with our thought processes and emotions. People say, "my dog is feeling guilty" or "my cat is jealous," and most movies and TV programs about animal behavior are rife with such ***anthropomorphism***. But animals are not just like us—many species differ dramatically from us in their sensory abilities, behavioral responses, and ability to learn. Using human emotions and intentions to explain the behavior of (nonhuman) animals can thus prevent us from understanding their behavior, but viewing animals as machines is not productive either. A bit of projection might lead to interesting hypotheses to test.

Any study of animal behavior should balance the information you might gain against potential harm to the animals. There are three important questions to ask when examining the ethics of behavioral research:

1. Will the research increase scientific understanding?
2. Will the research produce results beneficial to humans or to the animals themselves?
3. How much discomfort or suffering, if any, will the research inflict on the animals?

The benefits addressed by the first two questions must be weighed against the cost considered by the third. A valuable tool in determining this balance is the *Guidelines for the Treatment of Animals in Research and Teaching*, produced jointly by the Animal Behavior Society (ABS) and the Association for the Study of Animal Behaviour and published each January in the journal *Animal Behaviour*. These guidelines are also included in the *ABS Handbook*, which can be found on the website of the Animal Behavior Society (www.animalbehaviorsociety.org). In addition, colleges and universities in the United States have institutional animal care and use committees that examine and approve research protocols, and journals such as *Animal Behaviour* require potential authors to stipulate that their research conforms to ethical care and use guidelines. I should also mention that in many cases researchers must also get permission (e.g., from a property owner) and permits (e.g., state and federal) to do approved research.

Keeping your question or hypothesis in mind, you next need to make preliminary observations, identify the behavioral variables to measure, and choose suitable recording methods for making the measurements.

HOW DO ANIMAL BEHAVIORISTS PERFORM OBSERVATIONAL STUDIES?

Dawkins (2007) discusses three principles of good observational design. First, ***replication*** must be ***independent***, meaning that one observation or animal must not influence or affect another one. For example, if you observe one individual many times, each observation is not independent of the others because the same animal is involved—we would not get a good picture of the differences in behavior that can occur in this species because the one individual may, by chance, behave strangely or differently from the normal pattern of the species. Such an improper use of repeated observations is called ***pseudoreplication***, and it leads to improper statistical analysis and interpretation of results. Unfortunately, attempts to avoid pseudoreplication can also lead us astray. A hypothetical example follows (Dawkins, 2007).

Suppose we want to know whether schooling fish respond differently to large and small predators. If we use a single school of 20 fish to observe reactions to large and small predators, then obviously each animal is not an independent replicate because each school member is affected by the other fish in the school, so we end up with only one unit of replication (the school). To avoid pseudoreplication and to generate a more useful sample size (number of independent replicates), we decide to observe each fish separately, thus producing 20 independent replicates. Unfortunately, although we have generated a statistically valid design, we have also produced a biologically meaningless (invalid) one because these fish are schooling animals, so they do not encounter predators singly. Ideally, then, we would need to study enough different schools of fish to allow for valid statistical analysis.

Second, variables must not be ***confounded***. Although we mentioned confounding variables in the context of the internal validity of controlled laboratory experiments, confounds can complicate observational studies as well.