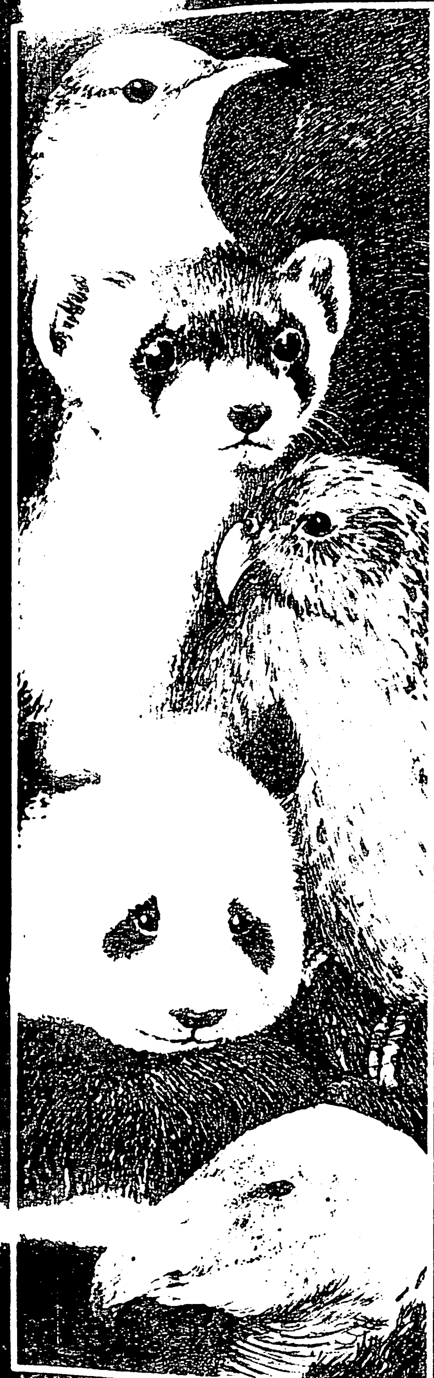
A PRIMER OF CONSERVATION BEHAVIOR



[illegible]lumstein and Esteban Fernández [illegible]uricic

www.[illegible]sinauer.com

A PRIMER OF CONSERVATION BEHAVIOR Blumstein and Fernández-Juricic

1 What Is Conservation Behavior?

Conservation behavior, the application of knowledge of animal behavior to solve wildlife conservation problems, is a relatively young, integrative field. Biologists using conservation behavior apply theoretical and methodological insights from animal behavior, ethology, and behavioral ecology to conservation biology and wildlife management (**Box 1.1**). While conservation biology was created in the 1980s as a "crisis discipline" aimed at conserving biodiversity (Soulé & Wilcox 1980), it has matured into a genuinely integrative discipline (see Box 1.1). By contrast, conservation behavior formally emerged as a discipline with the publication in 1997 of Clemmons & Buchholz's edited proceedings of a workshop held at the 1995 Animal Behavior Society meeting in Lincoln, Nebraska. This edited volume was the first of four (Caro 1998; Gosling & Sutherland 2000; Festa-Bianchet & Apollonio 2003). It was joined by several substantive reviews (Strier 1997; Sutherland 1998a; Reed 1999; Anthony & Blumstein 2000), along with special issues of journals that were devoted to how the fields of behavior and conservation biology can be integrated (*Oikos* Volume 77, 1996; *Environmental Biology of Fishes* Volume 55, 1999; *Applied Animal Behavior Science* Volume 102: 3–4, 2007).

Despite this academic interest, recent critics have noted that behavior has little to offer to conservation biology, and that there have been only a few successful applications of behavioral knowledge to conserve or manage species (Caro 2007). Conservation behavior typically focuses on the conservation and management of single species. In a perfect world, we would preserve habitat and ecosystems and we would have no single-species management problems. However, the world is far from perfect and single-species management is an unfortunate fact of conservation. Many governments have legislation that focuses on single-species management (e.g., the United States Endangered Species Act; see Box 1.2), and sometimes the public demands it (e.g., consider public interest in pandas, whales, and elephants).

In this *Primer* we hope to show you specifically *how* behavioral knowledge is used (and can be used) to help conserve and manage threatened or vulnerable species, as well as control overabundant species, and how knowledge of the behavior of groups of single species may also be useful for multi-species management. The goal is to develop a toolkit that provides new approaches when facing conservation and management problems. We provide worked examples to illustrate precisely how biologists can apply behavior to solve management problems. Our audience includes both students of animal behavior and conservation biology as well as professional wildlife managers.

BOX 1.1 Some Important Definitions

Animal behavior is the formal study of non-human behavior. It seeks to develop general principles of behavior and predictive models.

Behavioral ecology is the economic study of animal behavior that focuses on behaviors' costs and benefits. It emerged in the late 1960s and initially focused on the study of the adaptive utility of behavior and developed "optimality models." Modern behavioral ecologists use a remarkable variety of tools and ask both proximate and ultimate questions (see Box 1.3) in their quest to understand the diversity of behavior.

Conservation biology emerged in the 1980s to conserve biodiversity (Soulé & Wilcox 1980). It has evolved into a mature and interdisciplinary discipline that combines "principles of ecology, biogeography, population genetics, economics, sociology, anthropology, philosophy, and other theoretically based disciplines to the maintenance of biodiversity" (Groom et al. 2006).

Ethology is the naturalistic study of animal behavior pioneered by European behavioral biologists in the middle part of the 20th century. Its initial focus was on causation and development, but modern ethologists ask both proximate questions—those about development and immediate causation—as well as ultimate questions—those about current adaptive utility and evolution (see Box 1.3).

Wildlife management is the application of scientific principles to conserve and manage wildlife populations. It has a long history of applying population biology tools and, more recently, to applying population genetic tools.

Why Is Conservation Behavior A Unique Field?

One might initially think that conservation biology explicitly integrates behavior into it and therefore it is not necessary to formally define conservation behavior. However, a formal recognition of animal behavior as being a valid component of conservation biology is important because it allows us to narrow down the questions conservation behavior can answer, which leads to the development of more specific methods and tools. Of course, maintaining animal biodiversity is only a subset of the biodiversity and

ecosystem processes that conservation biology aims to conserve. With respect to managing single species (the realm of conservation behavior), population biology and population genetics are described as disciplines that have important insights. While ex-situ conservation (e.g., captive breeding), reintroduction (moving animals from captivity to the wild to restore or rescue a population), and translocation (moving animals from one wild location to another to restore or rescue a population) are discussed in conservation biology books, understanding the behavioral aspects of these tools can improve the effectiveness of conservation interventions.

Probably the closest daily practitioners of conservation behavior are wildlife biologists who deal with a multitude of very specific problems affecting single or multiple species. Wildlife biologists have formidable empirical knowledge of the behaviors of species they work with. Interestingly, wildlife managers are not typically trained in behavioral biology. To be a "certified wildlifer" (www.wildlifesociety.org), one must take 36 semester hours of Biological Science courses such as wildlife management, wildlife biology, ecology, zoology, and botany (as well as other requirements). Interestingly, a behavior course is only one of many possible options. By contrast, most people formally trained in behavior, are Ecology and Evolutionary Biology majors who take a lot of chemistry, physics, and biology, but are typically not required to take wildlife management. Although behavioral biologists may have received a more conceptual animal behavior training, they do not necessarily have a good understanding of field biology. Creating opportunities for conversations between wildlife biologists and behavioral biologists should lead to a fruitful integration of ideas. One example is population viability, which is to an extent mediated by behavior: fecundity by mating behavior, survival by foraging behavior and antipredator behavior, etc. Our aim in writing this *Primer* is to help foster these insights and conversations.

We should note that this simplistic view of training traditions (wildlife biologists and behavioral biologists) is not always that clear, and that there are many biologists that actively use behavior and many that do not. But, if you are interested in behavior or if you are passionate about the conservation of biodiversity, why not integrate conservation and behavior when appropriate? Since there are some challenges to integrating conservation and behavior, we will explore two answers to this question.

I am too busy doing cutting-edge behavioral research to think about conservation behavior

Many academics believe that by focusing on academic research they are unable to also think about conservation behavior or work with endangered species. To some extent, the same argument was used in the 1980s about why ecologists could not think about conservation biology. Fortunately, we now have many academic biology departments that embrace conservation biology, and many academic biologists are engaged in important conservation projects.

The arguments then, and now, often boil down to noting that since there is limited time to work, one must focus on what they need to do to get hired and promoted. It can also be argued, that to conduct cutting-edge research one needs to work with common "model" species and manipulate them to identify causality. Such options are sometimes not available with endangered species, which may be exceedingly rare, and may have additional constraints on experimentation. If sample sizes are small (because of rarity) it may be difficult to produce unambiguous answers. Moreover, some argue that when it comes time to search for a job in a non-applied discipline, or be promoted in a more theoretically-focused department, work with endangered species will be counted against them because they have taken the time to do this rather than publish another paper in a top-ranked theoretical journal.

However, conservation behavior embraces a variety of academically exciting topics. In this *Primer* we aim to show you how fundamental knowledge of behavioral mechanisms and evolution can provide useful information that can be used to maintain biodiversity. We hope to show you how theoretical discoveries in the fields of habitat selection, foraging, and antipredator behavior, communication and environmental acoustics, individuality and personalities, social behavior, and sexual selection have important implications and lessons for species management. And we hope to show you how some of these discoveries were made with no particular applied problem in mind but that does not prevent them from potentially being useful to solve conservation and management problems.

Thus, by doing cutting edge behavioral research, and particularly research that has demographic consequences, a broader impact of your work is that you are generating knowledge that could be used by a biologist working in conservation. To really help, focus on what you know best and think outside the immediate box. Then ask yourself, what are the demographic consequences of your behavior of interest? This is an essential step in developing individual based models (discussed in Chapter 2). Clearly write these implications in your academic publications. Persuade your editors to allow you to include these comments. By doing so, you are playing an important role of creating and disseminating knowledge that may be used in the future.

But, there are more things you can do. We suspect that you got interested in studying behavior because you are excited about animals and nature. Well, this may be your opportunity to contribute to saving the nature we value. To do so, you may take a few more steps.

For instance, have an honest discussion with those working in the front lines of protecting and managing wildlife about the problems they face. Learning about wildlife management needs is essential because there are problems that must be solved. By clearly understanding conservation and management needs, you might be able to build intellectual links between your area of behavioral expertise and a particular management solution. You may get excited about a particular national or international conservation topic or species of conservation concern and may wish to contact people in charge of that program and talk with them.

Actively seek collaborations with biologists working in wildlife management and conservation. These collaborations could take the form of research projects or even education projects. Bringing behavior into the picture can easily engage people as they generally enjoy learning about animals. Keep in mind that simply because you are working with a conservation question does not necessarily mean that money to fund the research suddenly appears. Often, it does not.

What about the question of where to publish conservation behavior research? Sometimes, conservation actions and management procedures create experimental situations that can be used to test important theoretical ideas. For instance, a conservation intervention on Seychelles warblers (*Acrocephalus sechellensis*) was used to test habitat saturation models and was ultimately published in the journal *Nature* (Komedeur 1992). Many other conservation behavior papers are published in top-ranked journals and we discuss a number of them in this *Primer*.

For all of the above reasons, we believe that theoretically inclined biologists who want to contribute to conservation behavior can do so. If we do not work to conserve the biodiversity we study, there will not be anything left to study.

I am too busy conserving to think about conservation behavior

In some circles, there is stigma about the role of animal behavior in conservation as having little or no value. Animal behavior is sometimes considered too academic or too elitist. The obvious implication is that some behavioral biologists are sometimes seen as disconnected from conserving and managing species in the real world. This may be true in some cases (see above). However, it is also true that often the reality of dealing with a species does call for knowledge of animal behavior.

Consider this example: During their long migration routes, migratory species travel across different landscapes, including urban areas. When crossing downtown areas with tall buildings, some birds collide with the windows and die. This source of mortality is estimated to be as high as 1 billion birds per year, and could reduce the local abundance of many species of conservation concern (Klem 1990). Despite the population level consequences, this can be seen as an animal behavior problem. Why can't birds avoid colliding with the buildings? Is it a problem with the ability of the bird to detect the building? Or perhaps the building is easily detected but the animals are attracted to it? Answering these fundamental questions requires using animal behavior concepts and tools (e.g., sensory biology, preferences, etc.). More importantly, answering these questions may bring a novel approach to reducing or eliminating this problem (e.g., making buildings more distinctive to birds, reducing night lighting to decrease attraction, etc.).

The key is thinking about the core of your conservation problem. Many problems may not point towards behavior at all. But, as you will see from the examples in this *Primer*, behavior is at the root of many problems. Identifying a fundamental animal behavior question that underlies your conservation problem may provide new insights on solving the problem because the field of animal behavior has a wide conceptual breath. This means that you can use animal behavior to put the observations you have already made in the field in an alternative, conceptual framework that can provide some guidance on how to manipulate experimental factors that will attract or repel a species, for instance. Using any kind of conceptual framework (be it behavior, or population ecology, or genetics) can lead you to the solutions more quickly than going through a trial-and-error process, which can sometimes be expensive, of what to modify. For instance, the framework of giving-up densities can be used to improve the suitability of patches for some species by reducing three types of costs that animals face: metabolic, missed foraging opportunities, and predation risk (see Chapter 6).

So, you may have seen the importance of behavior in some conservation problems and have identified a fundamental animal behavior question underlying your conservation problem. Does this mean you need to start reading books about animal behavior and behavioral ecology? You may do that, but you may also communicate with behavioral biologists. You would be surprised by how many academics started their careers studying behavior, but at a later stage in their professional career become deeply involved in conservation and management. These are the people who would be more willing to talk to you about your conservation problem. Google them, email them, phone them.

Your communication with behavioral biologists may begin as a source of gathering useful information about your problem (e.g., do birds colliding with windows perceive colors? Are birds attracted or repelled to certain colors?). However, cultivating these relationships may also end up being a source of collaboration. Many of the examples cited in this book started with phone calls or emails between wildlife biologists and behavioral biologists, and evolved into key contributions to the field of conservation behavior.

I am already practicing conservation behavior

If you are a wildlife biologist or behavioral biologist already engaged in conservation behavior, we do thank you for your hard work. It is likely that some of your published work is already cited in previous edited volumes on conservation behavior or in this *Primer* (however, keep in mind that our purpose in writing this book was not to conduct a comprehensive literature review, but rather illustrate applications with examples). You will hopefully find that our *Primer* contains new ideas or methods that you may find useful in solving some of your conservation problems. But, if you have additional novel insights, please, do not hesitate to share them with us so that we can learn more and potentially include them in subsequent editions. As a conservation behavior practitioner, we encourage you to promote the use of the discipline, when appropriate, to your peers, to your bosses, and to the community in general. Given the severity of our biodiversity crisis, we think that the more diverse our toolkit is, the higher the chances of telling success stories.

Adaptive Management: The *Key* to Conservation Behavior

The best management decisions come from the best science, or so scientists are taught. These days we use "active adaptive management" (Walters & Holling 1990), whereby management plans are modified based on the results of well-designed experiments that collect data on factors or variables that are demonstrably important for conservation or management (e.g., Ministry of Forest and Range 2001). We believe that we must take an empirical approach to demonstrating the utility of integrating behavioral science into wildlife management. Our goal is that in the future, the term conservation behavior will no longer be necessary because behavioral tools will be routinely used and combined with other tools to solve many conservation and management problems. However, we are also very pragmatic. If a behavioral approach does not help solve a problem, it is probably not that useful. After all, properly quantifying and integrating behavior into wildlife management will inevitably add more work for wildlife managers. Time is money. And money not spent on unnecessary work can be used for more necessary tasks or less work by making strategies work better the first time.

For instance, if the goal is to increase breeding success in a captive breeding program, an active adaptive management approach would be to design an experiment whereby one or more factors (such as cage size, diet, duration of daylight, etc.) is manipulated and compared to control groups. Determining what to manipulate would emerge from a good working knowledge of how animals behave in their cages. Thus, simply observing animals and their behavior may provide many insights that can generate formal tests. A second use of active adaptive management might be to increase reintroduction success. If pilot trials suggest that recently introduced animals are killed by predators, or are inefficient hunters, a properly designed adaptive management approach would do something to mitigate predation or starvation risk. For instance, we could provide cover in a "soft-release" pen (Kleiman 1989), provide pre-release predator training (Griffin et al. 2001), introduce animals socially (Shier 2005), or engage in predator harassment to reduce the likelihood that recently introduced animals will encounter predators, and then compare the fate of individuals in such treatments to control groups where no mitigation was employed.

By contrast, "passive adaptive management" occurs when biologists use historical data or data from uncontrolled experiments to come up with "best guess" management recommendations, the fate of which may be studied. It is clear that the inferences made under passive adaptive management are weaker because the approach is either correlational, or the experiments are not properly controlled. Nevertheless, the emphasis is on acquiring knowledge by conducting experiments and collecting data, and this may be the best that can be done under many circumstances.

We believe that it is essential to work within the context of adaptive management, ideally active adaptive management (Blumstein 2007), and that conservation decisions be based on evidence (Sutherland et al. 2004). Expert judgement is important to narrow the context upon which active adaptive management can be applied, because experimental evidence on every behavioral facet is not available and conservationists sometimes cannot wait. We are empiricists; therefore, the application of behavioral knowledge must be both cost-effective and help manage or recover populations. We hope this book demonstrates how we can develop this knowledge and incorporate it into current conservation and management methods.

Examples of How Conservation Behavior Can Solve Wildlife Management and Conservation Problems

Of the many areas where animal behavior can contribute to management and conservation, we emphasize four throughout the *Primer*: improving captive breeding success, improving the success of translocations and reintroductions, managing anthropogenic impacts on wildlife, and managing wildlife in urbanizing environments. We provide a brief introduction to each of these themes.

Captive breeding

The IUCN recommends that captive breeding programs be started when it is likely that a population will become critically endangered or extinct (IUCN 2002). Captive breeding requires that animals are brought into captivity and managed in a way to increase the population size (in captivity) while retaining genetic variation. Ideally, captive breeding is integrated with a re-introduction program (see below). Captive breeding is a difficult and expensive proposition, but it is often required once a species is listed under the Endangered Species Act in the United States of America (**Box 1.2**).

Black-footed ferrets (*Mustela nigripes*) almost went extinct. Individuals from the last-known, relict population were brought into captivity in 1985 to begin a captive-breeding reintroduction program. Unfortunately, canine distemper caused the wild and captive populations to crash. By 1987, the population had dropped to 18 ferrets, so all known ferrets were brought into captivity. Despite these setbacks, captive breeding and reintroduction have been moderately successful so far. The current black-footed ferret recovery plan (USFWS 2006) expects to spend at least an additional $12 million for captive breeding alone in order to recover the species to a level at which it can be de-listed by 2030. In total, an estimated $72 million is required to de-list the species.

BOX 1.2 The United States Endangered Species Act

Initially developed in 1966, the US Congress strengthened the Endangered Species Act (ESA) in 1973. Any species in the US as well as in other countries can be listed. Listing and subsequent management is the responsibility of the US Fish and Wildlife Service. Once listed, all Federal agencies are required to develop recovery plans to conserve threatened or endangered species and are prevented from engaging in activities that would harm such species. Importantly, critical habitat gets designated and protected, and landowners are prevented from killing or injuring individuals of a listed species. Subsequent amendments in 1978, 1982 and 1988 have modified, but not substantially changed, the ESA (www.fws.gov/endangered/esasum.html).

Once a species is listed, the USFWS is supposed to develop a *recovery plan*, which is a plan to recover a species to the point of "de-listing." Many species, though listed, do not have formal recovery plans. Some species have been successfully de-listed, but de-listing often takes many years, and the controversy over the wolves in Yellowstone National Park (www.yellowstonenationalpark.com/wolves.htm) illustrates that de-listing may be more of a political decision than a biological one. The politics of conservation are essential to understand, but are beyond the scope of this book.

In addition to the ESA there are a number of other national and international laws, conventions, and programs to conserve biodiversity (e.g., The Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES], the Convention on Biological Diversity [CBD], and the Marine Mammal Protection Act [MMPA]. See Groom et al. [2006] pages 104–108 for a discussion of these and others).

California condors (*Gymnogyps californianus*) almost went extinct. Urbanization, conflicts with ranchers, and the use of lead shot by hunters reduced the 1987 population to 22 individuals—all in captivity. An aggressive captive-breeding reintroduction program was started in 1987, and by 2005, the population rose to almost 300 birds, with more than 125 reintroduced to the wild. In the past 20 years, the California condor recovery program has cost between $35–40 million (www.fws.gov/hoppermountain/cacondor/FAQ.html). The Condor population has not been de-listed and de-listing will cost many more million dollars (e.g., to further increase the population size, cover legal costs, etc.).

These are two examples of captive-breeding reintroduction programs that underscore their extremely expensive costs. Fundamental knowledge from behavioral biology can help improve the successes of both captive breeding and reintroduction programs, given the costs of intensive recovery. In some cases, greater behavioral knowledge may help alleviate concerns people have with a particular conservation solution (e.g., reintroduction). These concerns could be about how animals may fare upon release. The Colorado lynx (*Lynx canadensis*) introduction attracted considerable criticism because lynx starved upon release (Bekoff 1999). The red wolf (*Canis rufus*) recovery program provides another example where being able to reintroduce animals hinged on public perception. In this case, people were concerned about the animals' ability to avoid getting killed by cars and there were concerns about the welfare of the animals before and during the reintroduction process (USFWS 2007). In both cases, studies of animal behavior provide information vital for planning and successfully executing a reintroduction.

For a given species, there are many husbandry considerations that must be identified (Kleiman et al. 1997). For instance: How should animals be housed—alone or socially? How much space is required? What should the temperature be in the captive environment? What should the light cycle be? What sorts of food are required? Should any of these parameters vary seasonally? While it may be possible to generalize from what is known from species' close relatives, species may also differ substantially in adaptive ways.

Understanding the unique adaptations that a species has might influence husbandry. For instance, some species show sexually-selected infanticide, a behavior where a male moves into a females home range or takes over another males' harem, kills the offspring sired by the previous male so as to induce the females to cycle sooner and therefore allows him to reproduce rather than caring for the offspring of another male (Ebensperger & Blumstein 2007). If a captively bred species engages in this behavior, it would not be prudent to move males around while females have potentially vulnerable young (Anthony & Blumstein 2000). Thus, a fundamental knowledge of natural behavior may shed light on these and other factors and, by doing so, we may breed animals more efficiently in captivity.

Translocation and reintroduction

When a species or population becomes extinct, recovery depends on taking animals either from another wild location and translocating them to the area for recovery, or taking animals from captivity and reintroducing them to the wild (Kleiman 1989). Unfortunately, many reintroductions fail (Wolf et al. 1996, 1998). This is both an ethical issue (a failed reintroduction means that animals have died; Bekoff 1999, 2002), and a management one (it is expensive to rear up and release animals for them only to die). Nonetheless, translocation and reintroductions remain important tools in the recovery of threatened or endangered populations or species (Seddon et al. 2007), and they may be relevant if we are to restore ecosystem function in communities in which species have been lost (e.g., Smith et al. 2004).

Another use of translocations is to remove problem animals (Linnell et al. 1997; Conover 2002). Typically, these focus on carnivores (wolves and bears), but many homeowners trap and translocate "problem" possums, squirrels, and raccoons. There may also be ethical issues in these translocations if translocated animals die (as many do) because they are moved into unfamiliar habitat.

As we discuss in Chapter 7, applying knowledge of animal behavior may have profound effects on the success of reintroductions. For instance, if animals live socially, they may benefit from being introduced in their social groups (Shier 2005). Even animals that aggregate to reduce predation risk, but do not form complex social relationships, might benefit from being introduced socially (Blumstein 2000).

Captive breeding has risks. Among them are the risks to individuals who do not develop in their natural environment. Many species learn about their predators through experience living in their natural environment. If individuals are reared in a predator-free environment and then reintroduced into a predator-rich environment, it is no wonder that many die. Pre-exposing prey to their predators in such a way that they can acquire experience with them prior to their release into the wild may be an important conservation behavior management tool (Griffin et al. 2000).

Anthropogenic impacts

Recreational activities have been encouraged in recent decades as a way of connecting humans with the natural environment, encouraging local economies, and supporting environmental education efforts. The downside, however, is an increase in the rate of human visitation to pristine areas that could trigger negative effects, particularly when species do not have alternative habitats. Although studying behavioral responses to human disturbance is not the way of establishing whether a species is threatened due to recreational activities, it can provide insights into the mechanisms underlying human-wildlife interactions by analyzing them with the theoretical context of anti-predator behavior. The assumption, empirically corroborated, is that wildlife react to humans in similar ways as they do to predators. Mechanisms explaining anti-predator behavior (e.g., the risk-disturbance hypothesis [Frid & Dill 2002]) can now help us predict the outcome of human-wildlife encounters. For instance, species responses to recreationists are usually aggravated after certain thresholds of visitation, which are likely to be species specific. Understanding these relationships can help us manage recreational activities that focus on wildlife viewing, without eroding biodiversity. In addition, this understanding helps reduce cases of conflicts or incidents affecting human health and safety. Clearly, these benefits can address some of the political components of conservation.

Urbanization

More than 50% of the human population now lives in urbanized environments. This creates environmental problems within cities for species that live on remnant fragments of suitable habitat. For instance, in Southern

California native chaparral birds have higher chances of surviving in large patches where coyotes are present because the abundance of domestic cats decreases due to coyote predation (Crooks & Soulé 1999). In smaller remnant patches, coyotes tend to be absent, which thanks to the overabundance of cats associated with humans, increases local predation on native birds. Predatory behavior is the key to regulating interactions in this human dominated habitat. However, the forefront of the urbanization problem lies at the edge of urban sprawl, as new housing developments enhance habitat attrition, fragmenting and restricting the distribution of wildlife. A deep understanding of the behavioral patterns of dispersion, avoidance–attraction to humans, and habitat selection allows us to develop methods of reducing the negative effects of urbanization, while maintaining certain ecological processes.

Questions Conservation Behavior *Cannot* Answer

As Caro noted in the Epilogue to his 1998 edited volume, conservation behavior cannot answer many conservation or wildlife management questions. In part, this is because conservation biology works at a larger scale than single species. For instance, developing strategies for landscape-level habitat protection is not in the realm of conservation behavior (Caro 1998; Buchholz 2007). However, establishing the definition of appropriate (preferred, required) habitat from the species' perspective, and how connected remnants need to be considered with respect to the species' mobility is in the realm of conservation behavior. Managers often need answers quickly, but conservation behavior studies may take a while. However, there are a lot of conservation behavior questions that may be answered more quickly by using the extensive literature on animal behavior that already exists. For those questions that conservation behavior can address, we believe that the toolkit presented in this book may be useful.

Our Approach in This Primer

We adopt a multidisciplinary approach and the Tinbergian approach, which uses insights, approaches, and tools from different levels of behavioral analysis (**Box 1.3**), to solve applied problems in wildlife management. In the following chapters we illustrate how, we believe, applying conservation behavior principles can be productive.

DEFINE A CONSERVATION PROBLEM Depending upon the nature of the problem, this may be relatively focused: Why do the captive bred offspring of southern white rhinos (*Ceratotherium simum simum*) not reproduce? (Swaisgood et al. 2006); or rather diffuse: What is responsible for the disappearance of reintroduced Vancouver Island marmots? (Bryant & Page 2005). As with all research, the more precisely defined the problem, the easier it is to study it. In the case of the rhinos, they breed well regardless of if they are in the wild,

BOX 1.3 Tinbergen's Four Questions

In 1963, Niko Tinbergen wrote *On the Aims and Methods of Ethology* and proposed what are now referred to as Tinbergen's Four Questions. These questions, based in part on previous suggestions by Ernst Mayr, helped guide behavioral research for the past four decades. These four logically distinctive and mutually exclusive types of questions about causation, development, adaptive utility, and evolutionary history can be profitably applied to any behavioral phenomenon. Importantly, by asking questions at multiple levels of analysis, our knowledge about behavior is enriched. Broadly, a behavioral question can focus on *how* something works, or *why* it is as it is.

Proximate questions are those employed to explain how something works or how it develops. For instance, studies of functional morphology (e.g., which muscles and bones are used when animals perform a certain behavior) tell us how behavior is patterned and its structural basis. Studies of behavioral genetics identify the degree to which genes are responsible for behavior and the exciting new field of genomics identifies those genes. And studies of behavioral endocrinology tell us about hormonal control or regulation of behavior. These three examples illustrate *causal* questions. By answering them, we learn about how behavior works. A logically distinct type of proximate question focuses on the *development* (or ontogeny) of behavior. Ontogenetic questions might ask about the degree to which a particular behavior requires specific individual experiences to be properly performed, and address the time course of development.

Ultimate questions are those employed to explain why we see the diversity of behavior. For instance, studies that focus on the evolution of behavior tell us how or when a particular behavior evolved. They might also tell us how many times a behavior evolved. To do so, evolutionary biologists construct phylogenetic trees (hypotheses about the relationships between species) and then "optimize" (i.e., map) behavioral traits on these trees. A logically distinct type of ultimate question focuses on the *current adaptive utility* of a trait. Only traits that increase the fitness of individuals will evolve or be maintained by natural selection. For instance, if long legs aid in escaping predators, we expect natural selection for leg length and running speed to evolve. Importantly, these four types of questions (or levels of analysis) produce questions that are mutually exclusive only within a level. Consider bird song.

We can ask about the evolutionary history of song learning. Song learning has evolved in parrots, hummingbirds, and passerine birds. Among passerines, it is seen in a broad group called the oscine birds.

We can also ask about the current adaptive utility, or function, of bird song. Male birds may sing to attract females and to defend their territories from other males. In some species, males that sing more songs have more mates and therefore have higher fitness. It would be illogical to suggest that because male birds sing to defend territories (a finding that emerged from the study of the adaptive significance or function of a behavior), song learning has evolved only once (a finding that emerged from the study of the evolutionary history of song). Questions within each of these four levels of analysis are

(continued on next page)

mutually exclusive only with other questions within that level. Thus, song learning could have evolved once, twice, or three times, or bird song may function as a form of intra- or inter-sexual display, but the number of times it evolved does not bear on its function.

We can ask proximate questions about bird song as well. For instance, recent work on the genetics of song has discovered that humans and birds both express the *FoxP1* and *FoxP2* genes. In birds, these genes are specifically expressed during song learning. A set of neurons, called the higher vocal center (HVC), seems to be responsible for the neural control of song learning. In some species, the size of the HVC is correlated with the number of songs they produce, while in other species, the size of the HVC changes seasonally and becomes largest when song learning is required.

Finding evidence that the HVC does not change seasonally has no direct bearing on whether or not *Fox* genes are expressed during song learning. Nor does it directly bear on hypotheses about the evolution of song learning abilities, or about whether or not males that have larger repertoires have higher fitness. Again, these questions are mutually exclusive.

The beauty of taking a Tinbergian approach to studying behavior is that it forces us to examine qualitatively different sorts of questions. By doing so, we generate considerable knowledge about the diversity of behavior. Recognizing these are qualitatively different questions is essential as well to ensure that arguments about explanation are contrasting different hypotheses at the same level of analysis.

on protected ranches, or brought into captivity from the wild. However, the captive-born offspring of rhinos fail to reproduce. Swaisgood and colleagues (Swaisgood et al. 2006; Swaisgood 2007) have systematically studied rhino reproductive endocrinology. They refuted the hypothesis that there is something systematically wrong from an endocrinological perspective with captive-born individuals but did discover that in captivity, rhino females may have uterine infections. Based on a keeper survey they identified no differences between wild-caught and captive-born females in their reproductive behavior. The hypothesis that older females were reproductively suppressing their offspring was refuted. They found differences in the early social development: captive born females are much more social than they are in the wild. Swaisgood and colleagues continue to test hypotheses to nail down the mechanism responsible for reproductive failure of the offspring from captive-born females.

DEFINE QUESTIONS It is prudent to narrow down questions that can be answered by working at the conservation behavior interface. Wildlife management is a rich and mature discipline in its own right. There are a variety of methods to estimate the size of a population (Williams et al. 2002) and to determine the likelihood of a population persisting over some time

(Beissinger & McCullough 2002). We must identify *specifically what behavioral knowledge* may be important in helping solve a potential problem. This is key to the successful integration of behavior into conservation biology and wildlife management.

DEVELOP A FOCUSED HYPOTHESIS AND MAKE SPECIFIC PREDICTIONS If we believe that lack of exposure to predators during some critical period results in predator-naïve prey, we must specify the critical period and define precisely what sort of exposure to predators is important (the smells, sights, sounds, or actual experience interacting with a predator).

DETERMINE DEPENDENT AND INDEPENDENT VARIABLES THAT NEED QUANTIFYING OR MANIPULATING To continue with our predator recognition example, are we looking to quantify changes in vigilance or some specific antipredator escape strategy (e.g., flight initiation distance)? Some species have unique responses to each of their predators; must the response be predator-specific?

IDENTIFY OR DEVELOP SAMPLING TECHNIQUES We need to employ techniques that allow us to collect data relevant to testing our hypotheses on the species of conservation concern. Behavioral biologists have a long tradition of working with model species (as do conservation biologists; Caro & O'Doherty 1999), but behavior may be species-specific. Behavioral biologists have developed a variety of methods to quantify behavior in systematic ways (Martin & Bateson 2007; Blumstein & Daniel 2007). And, behavioral biologists have developed methods to manipulate the phenotypic expression of a variety of traits (Andersson 1994). The strength of our inferences depends upon the rigor of our methods.

SELECT ANALYTICAL TOOLS Video processing, event recording software, statistical analysis, etc., enable us to answer our question. Much as population biologists use specific tools to estimate population sizes (e.g., MARK [White & Burnham 1999]), and population geneticists use specific tools to estimate genetic variation and parentage (Kinship and Relatedness [www.gsoftnet.us/GSoft.html]), behavioral biologists use event-recorders and analysis software to quantify behavior (JWatcher [www.jwatcher.ucla.edu]), sociometric programs to define social groups (SOCPROG [myweb.dal.ca/hwhitehe/social.htm]; UCINET [www.analytictech.com/] Pajek [http://vlado.fmf.uni-lj.si/pub/networks/pajek/]), and other software to quantify space use (e.g., Ranges [www.anatrack.com]). Of course the specific tools will depend upon the question to be addressed.

ANSWER THE QUESTION AND APPLY OUR ANSWER TO THE PROBLEM We believe that such questions should be designed explicitly within an active-adaptive management program. For instance, if we are testing whether pre-release predator training influences survival following reintroduction, first we want to see if there is an effect of training on predator recognition abilities and then we want to see how it influences later survival. In this instance, we must have formal controls where some individuals are not formally trained and their fate compared with those that are trained.

EXPLAIN HOW THE NEWLY GAINED KNOWLEDGE APPLIES TO THE PROBLEM When publishing the results of our work, we should explicitly address how the new behavioral knowledge that we generated can be *directly* applied to solve the conservation problem at hand. This helps strengthen the necessary integration of behavior and conservation and makes this discipline a source of novel ideas to address specific problems. And, for those that use these tools, it is important to highlight the fact that the tools and approaches are essential for successful conservation and management outcomes.

APPLY RESULTS TO REAL-LIFE PLANS Because publication does not necessarily lead to useful application, practitioners of conservation behavioral techniques should adapt their published work to actual management plans.

These nine steps assist us in finding solutions to some (not all) conservation problems, in some cases in coordination with other approaches (genetics, community ecology, etc.).

Further Reading

Clemmins & Bucholz (1997), Caro (1998), Gosling & Sutherland (2000) and Festa-Bianchet & Apollonio (2003) are book-length edited volumes on conservation behavior. Caro (2007) and Buchholz's (2007) exchange in *Trends in Ecology and Evolution* makes for stimulating reading. Pullin & Knight (2009) discuss the importance of evidence-based conservation.

2 Why Do Behavioral Mechanisms Matter?

What are behavioral mechanisms and why should we care about them? Behavioral mechanisms can be thought of as *rules* that animals follow. By studying mechanisms, we study proximate causation (i.e., we explain how animals do things). These can be rules about how hormones influence behavior, rules about how temperature influences sex determination, rules about how individuals select mates, rules about food selection, rules about how animals discriminate between signals and the background, or rules about how animals assess the risk of predation. Identifying these rules is essential because they can be used to develop predictive models. Predictive models allow us to understand how populations will respond to anthropogenic change. Once the models are built, rules can be changed to predict different scenarios, a process that makes these predictive models very useful tools. Let's start by thinking about some physiological mechanisms that underlie demographic processes.

Temperature-Dependent Sex Determination

Temperature-dependent sex determination (also called environmental sex determination) is found in a variety of reptiles (Bull 1980). A temperature difference as small as 1–2°C during incubation will influence the resulting sex of the young. In some species, females are produced at lower temperatures, while males are produced at higher temperatures; in other species, the reverse is true. It is easy to envision the consequences of climate change on offspring sex: A systematic increase in temperature can lead to a systematic bias in the sex ratio. By identifying this mechanism of sex determination in a given species, it becomes possible to manage sex ratios by manipulating incubation temperature. In captive-breeding situations this may be essential to produce animals of both sexes.