

The Emergence of Conservation Behavior

Conservation biologists have begun to apply general principles of animal behavior to solve conservation problems. Four major edited volumes and a number of reviews published in the last decade have proposed theoretical and empirical links between behavior and conservation (see the Animal Behavior Society's Conservation Committee website: www.animalbehavior.org/ABS/Conservation/). To strengthen this multidisciplinary collaboration, it is essential for conservation biologists to understand the types of questions addressed by the field of animal behavior (proximate and ultimate) and the implications of these questions for conservation biology, the conservation literature, and recovery teams. Conservation biologists may be unfamiliar with the jargon of behavioral biologists, but lack of knowledge is no excuse to ignore animal behavior. We believe that behavioral biologists have much to contribute to conservation biology and that by involving conservation behaviorists too late in conservation plans or recovery teams, we will continue to suffer avoidable setbacks, waste precious funds, and lose priceless animals.

The Nobel Prize-winning ethologist Nikko Tinbergen first outlined two main types of questions that could be asked about any behavioral phenomenon. Proximate questions focus on behavior's development or immediate causation. Ultimate questions focus on behavior's evolutionary history or current adaptive utility. Thus, by definition, conservation behavior should be viewed as a field of study that encompasses multiple levels and incorporates a variety of disciplines, including genetics, physiology, behavioral ecology, and evolution.

Understanding social relationships that lead to fitness (ultimate questions) has clear links to conservation. For instance, infanticide by males is an adaptive reproductive strategy that needs to be considered in the management of some species, such as bears and African lions. Managers typically view males as superfluous and model populations based on the number of breeding females. However, in species where males kill offspring sired by other males to encourage females to come into estrus and mate with them, any subsequent social disruption has a large effect on population size. Normally adaptive reproductive strategies have other consequences when individuals encounter anthropogenic changes. For instance, as water quality declines, it becomes more difficult for fish

that use visual signals to make adaptive mate-choice decisions. As a result, fish may hybridize and suffer reduced individual fitness and the population itself may decrease.

Some argue that ultimate questions are most important for conservation because they link variation in behavior with fitness. However, understanding how proximate processes affect survival is also crucial. For example, we know that training captive-reared animals to recognize predators may increase post-release survival. Yet further studies on the developmental contexts, presence of sensitive periods, and types of experiences required may yield more efficient and effective training programs.

From a management perspective, searching for the fitness consequences of behavioral responses may provide insights into the impacts of certain human activities on wildlife, but this does not necessarily translate into conservation gains. We believe that mechanistic research will increase the predictive power of our conceptual and mathematical models. In general, by searching for mechanisms, we search for a deeper understanding of how animals make adaptive decisions. And by taking this sort of uniquely behavioral approach, we may gain important information about how to better manage populations.

For instance, a strategy to better manage the effects of tourists on wildlife is to understand the proximate mechanisms underlying the response of animals to humans. We recognize the importance of documenting population-level responses to human disturbance. However, to reduce negative effects on wildlife and increase the number of species that can be viewed by tourists, managers must know how to control rates of human visitation to protected areas. To predict habitat use in areas with different levels of human visitation, we need to determine the number of tourists per unit time and area that do not negatively affect the frequency of resource use (e.g., feeding, nesting, and roosting sites) by target species. In due course, we must identify behavioral indicators of disturbance and develop an understanding of the behavioral mechanisms that explain the tolerance of some, but not all, species to human disturbance. It is essential to recognize these qualitatively different questions along with their applied implications when assessing the value of conservation behavior.

Habitat loss is a huge threat to biodiversity, yet habitat improvements are often made without regard to how

species perceive the habitat (a proximate question) or the behavioral consequences of such intervention. For instance, adding nest boxes (i.e., increasing nesting habitat) is often done to increase reproductive success for cavity-nesting birds. If the artificial nest boxes are too close together, however, there may be unintended social consequences. Clumped nest boxes lead to an increased rate of egg dumping and conspecific brood parasitism, both of which reduce reproductive success. Hence, without attention to behavioral details, such well-intentioned habitat "improvement" programs may waste valuable funds and have detrimental effects on the population under recovery.

To develop more effective programs, conservation biologists must fully recognize the value of integrating proximate and ultimate behavioral studies. In recent years, this lack of integration has generated resistance toward increasing the diversity of the conservation behavior literature and has constrained the use of behavioral data by recovery teams.

Based on our experiences and those of many of our colleagues, it is difficult to publish papers on conservation behavior, a problem not restricted to any particular journal. When manuscripts on conservation behavior are submitted to conservation journals, negative reviews may highlight a lack of immediate applicability or a lack of a direct link between behavioral responses and fitness (e.g., reproductive output, survival rates). Yet general questions about proximate behaviors that affect survival, mortality, or population size are all topics that are explicitly relevant to conservation biology.

When conservation behavior manuscripts are submitted to behavior journals, they may be rejected because of an apparent lack of theoretical framework, or, if they are accepted, authors are asked to remove most references to conservation. However, conservation behavior itself can be theoretical. For example, predicting the behavioral mechanisms underlying the vulnerability of a species to human impacts and predicting how long antipredator behaviors persist following isolation from predators are behavioral considerations that are explicitly, theoretically motivated.

A far greater threat to species survival than the difficulties of publishing conservation behavioral findings is the tendency of recovery teams to wait too long to integrate behavioral biologists into their efforts. Such oversights appear to be related to a lack of understanding of how behavioral studies are conducted. For instance, an exciting and promising line of conservation behavior research seeks to increase reintroduction success by evaluating the antipredator abilities of animals prior to release and then following their fates. If individuals with inferior antipredator behavior are preyed upon more frequently than those with superior abilities, then pre-release training may be used to prepare animals for release. For years, ethologists have used simple models, tax-

dermic mounts, and playback of sounds through speakers to study the perceptual and assessment abilities of a variety of species. Through the use of simple stimuli, these techniques allow one to learn about how animals assess risk.

Although managers must make tough decisions about what can be done with animals prior to release, they must think critically about how much they can learn from these studies to improve success rates. The recovery programs for black-footed ferrets (*Mustela nigripes*) and golden lion tamarins (*Leontopithecus rosalia*) provide evidence that fully integrating behavioral biologists into the recovery process can make a difference. In both cases, paying attention to the environment these species were reared in and providing pre-release behavioral enrichment was essential for ultimate success. In the long run, it may be more cost-effective to incorporate behavioral biologists at the outset of captive breeding and reintroduction programs rather than to wait until a "problem" emerges, animals die, and precious funds are spent.

Conservation behavior will not provide the solutions to all conservation problems, but we conservation behaviorists need to show how useful a behavioral perspective can be. By understanding the type of questions conservation behavior can address, one can better evaluate how and when wildlife conservation could benefit from behavioral knowledge. Addressing both proximate and ultimate questions of conservation behavior is essential to improving our management decisions. Two research areas in particular will not only help bridge the gulf between conservationists and behaviorists but will also help research on conservation behavior to produce specific conservation outcomes.

First, we must develop predictive models of behavior that are accessible to wildlife managers. Advances have been made in foraging theory and modeling habitat selection, wherein animal decisions have been modeled with increased sophistication. However, the sophistication that comes with deeper understanding may impede application by its complexity. Behavioral biologists should strive to make their models accessible to others by identifying specific behavioral mechanisms. These mechanisms should be the basis of bottom-up models that predict the behavior, movement, habitat use, and distribution of species of conservation concern.

Second, we must develop an ultimate understanding of how and why species are vulnerable to human impacts. Study of conservation behavior is much more than simply documenting whether or not humans affect wildlife. The explosion in comparative biology and macroecology in the past decade offers a framework for future advances in predictive evolutionary models. Future studies should examine how variation in life history and natural history explains variation in proneness to extinction, tolerance to human disturbance, and tolerance to invasive species at local scales.

Ignoring the diversity and methods of modern behavioral biology places conservation-dependent animals at peril. Although we are excited that some wildlife managers and conservation biologists appreciate the expertise offered by behavioral biologists, we believe that many still fail to appreciate the importance of proximate mechanisms. Some pigeonhole behavioral research as too species-specific and fail to recognize that behavioral biologists can produce generalizable and predictive models. With an increased appreciation of what conservation behaviorists have to offer, and a fundamental integration of them into recovery teams, we believe that future recovery efforts will be more successful and cost-effective, and

that the exciting integrative field of conservation behavior will prosper.

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