

# Behavior and conservation: a bridge too far?

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**Formal efforts to connect animal behavior and behavioral ecology to conservation biology and management began ten years ago, time enough to assess their impact on stopping species decline and extinction. After outlining the rationale for applying behavior to conservation, and the links that were originally proposed between them, I argue that theoretical advances in our understanding of behavior have made little practical contribution to conserving animal populations over the past decade. More optimistically, descriptive behavioral information has sometimes augmented solutions to specific conservation problems. I suggest several ways in which behavioral studies and researchers themselves could be more useful for conservation. Such changes will be necessary if the contribution of behavior to conservation is to move from intellectual wishful thinking to practical solutions for reversing the decline of small populations.**

## Crossing the divide

Conservation biology originally combined principles of ecology [1], population biology [2] and genetics [3] to study how populations and their habitats respond to anthropogenic change, and now applies this knowledge through protection, restoration and political leverage. Given that conservation biology is concerned with populations, whereas animal behavior is concerned with individual variation in behavior, there was little natural connection between them. Nonetheless, during the 1980s and 1990s, captive breeding institutions began to use behavioral knowledge informally to construct social and architectural environments that would foster breeding species, and managers of reintroduction programs began to understand the necessity of monitoring the behavior of animals following their release. During the mid-1990s, academic biologists studying animal behavior and behavioral ecology thought that they too could apply their knowledge to conservation. This was because the populations that they worked on were disappearing, habitats were changing, their colleagues were embarking on careers in conservation rather than academia, society was actively discussing conservation issues, and there was a perception that money was available for conservation efforts. This interest generated four edited books [4–7] and a special edition of *Oikos* (77: 1996) with over 100 contributing authors that touted the idea that behavioral expertise could make an

important contribution to conservation. These, together with review articles (e.g. [8–16]), explored the potential for behavioral ecology and animal behavioral knowledge to contribute to conservation.

Nevertheless, there are impediments to applying such knowledge and it seems appropriate, ten years on, to assess whether theoretical advances in understanding behavior, especially in relation to functional and evolutionary questions, but also less theory-driven understanding, have helped save populations from extinction or at least slowed population decline or facilitated population recovery. More specifically, has such knowledge changed our understanding of the way that a specific population responds to anthropogenic change and, as a result, has management action taken new steps that have successfully bolstered the population? This is a tough two-part question but a reasonable one, because this is surely one of the key goals of conservation. I argue here that theory-driven behavior has yet to become integrated into conservation, certainly less than ecology or genetics in the early days of conservation biology, or economics and sociology more recently [17], but that descriptive behavior (sophisticated natural history) does have a part to play in solving conservation problems.

## Designing the bridge

Historically, proposed links between behavioral research and conservation began with behavioral concepts rather than with conservation problems (Table 1).

## Mating systems

As illustrations, mating systems and mate choice were predicted to make contributions to the conservation arena because they influence effective population size ( $N_e$ ), a measure of the ability of a population to maintain genetic diversity. When mating systems deviate from monogamy to increasing degrees of polygyny or polyandry,  $N_e$  declines because fewer males (polygyny) or females (polyandry) contribute genetically to the next generation. Conversely, increased promiscuity can lead to a larger  $N_e$  than would be expected under monogamy, because members of the more abundant sex might have a greater opportunity to breed [18]. Knowing the outcome of these effects, however, does not suggest immediate management action, as it is difficult to alter the mating system of a species. With respect to mate choice, if females have a threshold for mates below which they will not accept a partner and if reductions in the expression of male traits occur through reduced food intake or disease, as might arise in a fragmented or polluted

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**Table 1. Proposed links between behavior and conservation biology<sup>a</sup>**

Behavioral category	Example
<b>Methodological topics</b>	
Measures of behavior	Methods of recognizing individuals enable population size to be calculated
Demography and life history	Patterns of age-specific mortality enable population viability models to be constructed
<b>Topics principally covered in behavioral ecology<sup>b</sup></b>	
Mating system	Polygyny and polyandry reduce effective population size compared with monogamy
Mate choice	Mate choice by females can reduce effective population size
Breeding system	Infanticide can increase the impact of male exploitation
Foraging and patch choice	Knowledge of habitat or feeding preferences might prevent individuals being caught in unsuitable ecological traps
<b>Topics principally covered in animal behavior<sup>c</sup></b>	
Ontogeny	Development of sexual preferences will affect how individuals are raised in captivity
Mechanisms (cues)	Attraction to light can cause individuals to go to the wrong place or become disoriented
Antipredator behavior	Failure to recognize novel predators results in collapse of a reintroduction program
Dispersal/ranging/movement	Wide-ranging species require large or connected reserves
<b>Other topics</b>	
Human behavior	Models of prey choice predict difficulties in conserving vulnerable age/sex classes

<sup>a</sup>Adapted from [49].

<sup>b</sup>Behavioral ecology is a discipline centered on functional and evolutionary questions about behavior and morphology. It tries to interpret behavior in an ecological and phylogenetic context. It has a strong theoretical framework based on game theory, optimality tradeoffs and kin selection, and uses elegant experiments and long-term demographic data sets.

<sup>c</sup>Animal behavior classically encompasses Niko Tinbergen's four questions about behavior — its development, its causation, its function and its evolution — and gives equal weight to each. It investigates hormonal, neural and cognitive mechanisms in adult and young behavior, as well as its adaptive significance. It uses experiments and observations, but also includes simple descriptive studies.

environment, this could lead to a smaller proportion of males being seen as 'acceptable' to females. As a consequence, there might be fewer males mating and an exponentially decreasing  $N_e$ , leading eventually to population extinction [19]. However, showing that free-ranging females reject suitors and cajoling females to lower their standards are no easy tasks.

### Breeding systems

Another case of how some of the proposed conceptual links are difficult to translate into management action concerns breeding systems. Models show that the removal of certain age/sex classes from a population differentially affects population growth rates depending on the breeding system and, hence, suggest that appropriate hunting quotas could be formulated [20]. Thus, in those species that exhibit sexually selected infanticide, such as lions *Panthera leo*, the removal of males results in incoming males killing the offspring of deceased or ousted males, which leads to a further reduction in population size [21]. Yet, compelling hunters to shoot only those males that have already fathered independent offspring will require sensitive observations before pulling a trigger and independent verification to determine whether the hunters comply with the rules.

### Antipredator behavior

Yet another potential bridge concerns how development of predator recognition might affect populations faced with novel predators. This is of interest when captive-reared animals lack experience of native or introduced predators, and are reintroduced to the wild. It was believed that studies that explore and mitigate these conditions could be useful in predicting and enhancing reintroduction success. For example, tamar wallabies *Macropus eugenii* were taught to recognize novel predators in captivity [22]. Also, wild prey might succumb to reintroduced predators, so effort was devoted to understanding how Yellowstone moose *Alces alces* respond to cues of reintroduced

wolves *Canis lupus* [23]. Although these studies are intellectually intriguing, they and other antipredator manipulation projects have still made little practical contribution to the management of wild prey populations.

### Realities

Based on these and other examples, I surmise that, where theoretical concepts were suggested to be useful for solving conservation problems, they were not done so convincingly because they lacked practicality in application. Ideas proposed by theory-driven academics working outside the conservation arena are generally not solutions to specific practical conservation problems, but notions about what might matter under a set of hypothetical conditions. For example, what might happen to a population if a given fishing net size caught only males; and how might groups hunt or defend themselves if they were each reduced to a handful of individuals? By contrast, wildlife managers trying to save specific populations and habitats need help with actual problems rather than generalized principles, especially those principles that can be summarized as 'it depends on...'. Thus, it is unsurprising that you do not hear participants at conservation biology meetings extolling the methods, theory and findings from animal behavior studies. The match between behavior and conservation biology was poor in the past, as measured by published papers [12] and behavior textbooks [24], and still is, as evidenced by joint membership of behavior and conservation societies (Angeloni, L. and Crooks, K.R., personal communication) and current research interests (Table 2). At recent society meetings, for instance, behavioral ecologists focus on sexual selection, life histories, mating strategies and signaling, whereas contemporary conservation concerns centre on marine conservation, biogeography, and invasive and wide-ranging species, completely different subject matter. Conservation projects typically use behavior only as a tool to solve a problem on a case-by-case basis: for example, where do individuals move in relation to land use, where do they settle, and how

**Table 2. The current match between behavior and conservation is poor<sup>a</sup>**

ISBE	SCB
Sexual selection (6)	Marine conservation and practice (7)
Evolution of life histories (5)	Spatial ecology (4)
Mating strategies (5)	Conservation biogeography (3)
Signal evolution and communication (5)	Invasive species (3)
Acoustic signaling (4)	Conservation of wide-ranging taxa (3)
Predator–prey interactions (4)	Ecological restoration (2)
Social behavior and grouping (4)	Conservation genetics (2)
Maternal effects (3)	Adaptive management (2)
Multiple mating (3)	Land-use planning (2)
Sexual conflict (3)	Community-driven conservation (2)
Parental care (2)	Urban ecology (2)
Recognition (2)	Predictive conservation ecology (2)
Conservation (2)	Conservation Geographic Information Systems (2)
Hormones (2)	Protected area design (2)
Dispersal (2)	Environmental sociology (2)
Habitat use (2)	Other categories (13)
Foraging (2)	
Sperm competition (2)	
Other categories (9)	

<sup>a</sup>The most up-to-date summary of research interests in two biological disciplines, as shown by the topics covered in sessions at the International Society for Behavioral Ecology (ISBE) meeting in July 2006 in Tours, France, and the Society for Conservation Biology (SCB) meeting in San Jose, USA, in June 2006. Brackets show the number of sessions (there were five talks per session). Overlap between ISBE and SCB interests is low.

do they respond to disturbance and change? These are rather atheoretical questions, unrelated to reproductive skew theory, optimality, cooperation or game theory, or debates about animal culture. So do more atheoretical behavioral studies have more to offer conservation?

### Where do we stand?

Here, I discuss nine practical enterprises in which animal behavior, mostly of a descriptive nature, appears to be important and could help to solve certain conservation problems [25].

#### Response to human activities

Many wildlife management studies have examined the effect of human activities on the behavior of animals [26]. For example, noise and light pollution disrupt animal communication systems. As illustrations, in Leiden, the Netherlands, the minimum frequency of the songs of male great tits *Parus major* increases as the amplitude of traffic noise increases. Birds in noisy territories try to overcome background noise by singing notes that reach higher frequencies [27]. Similarly, killer whales *Orcinus orca* off the coast of Washington State, USA, increase their call duration in the presence of whale-watching boats; whales try to counteract anthropogenic noise when it reaches a critical level [28]. In these and other examples (e.g. [29]), investigators began with an obvious conservation issue and looked for behavioral responses (Step 1; Box 1). It is clear that an understanding of such behavior will be important in the highly politicized controversy over sonar testing and its effect on marine mammals.

#### Response to land-use change

To investigate the effect of changing land use on populations, conservation biologists try to understand patterns of movement and mortality in areas affected by urbanization and fragmentation. For example, radio collars on 50 bobcats *Lynx rufus* and 86 coyotes *Canis latrans*

in the Santa Monica mountains, west of Los Angeles, USA, showed that home ranges were larger in more urbanized landscapes, that individuals principally ranged through developed areas at night and that males used urban areas more than females, but that there were no differences in survival rate between urban and rural habitats [30]. By understanding basic behavior and patterns of mortality, we can assess the effects of habitat disturbance (Step 2; Box 1). Because such species are valued by city dwellers, this information is likely to be used in environmental impact assessments of urban expansion.

### Box 1. Seven steps to making behavioral research contribute better to conservation<sup>a</sup>

#### 1. Begin with a conservation problem

First, talk to conservation biologists, zoo managers or park wardens, assuring them that the work will be relevant.

#### 2. Choose a study area wisely

Work in threatened habitats or disturbed habitats where results will be relevant to conservation decisions.

#### 3. Work on several species at the same time

Reserve design or habitat restoration involves knowing the response of many species that live there, not just one.

#### 4. Work on high-profile species

You get the attention of the public and politicians.

#### 5. Avoid using surrogate species

Work on threatened rather than on common species. Much behavioral research has shown that even closely related species respond differently to the same environmental perturbation; therefore results from one species are difficult to extrapolate. Moreover, some managers are not comfortable or willing to draw comparisons between different systems.

#### 6. Get information to managers quickly

Many wildlife managers do not read academic journals. They respond best to face-to-face conversations and clear, rapidly produced reports.

#### 7. Popularize your work

Put time into writing popular articles not just dry science. Spread the

<sup>a</sup> See also <http://www.animalbehavior.org/ABS/Conservation/thirteen.html>.

### Use of corridors

As habitat fragmentation is such a widespread problem and can disrupt dispersal, dozens of studies try to understand how animals perceive and use regions of the landscape that facilitate movement [31]. For instance, macroinvertebrates such as hard clams *Mercenaria mercenaria* live at lower abundance on intertidal oyster reefs connected to salt marshes by corridors of sea grass because predatory blue crabs *Callinectes sapidus* readily move along these corridors without being detected and preyed on by birds [32]. In another study, eastern bluebirds *Sialia sialis* were tracked after they had been seen feeding on wax myrtle *Myrica cerifera* seeds [33]. Edges of experimental corridors channeled the flight paths of the birds between patches and a resulting model predicted the observed pattern of seeds collected from bird faeces. This observational study provides evidence that corridors promote tree regeneration and hence habitat integrity.

### Avoidance of roads

Another type of study of management significance looks at how wildlife negotiates roads that fragment their habitat [34]. Overpasses made famous because of their size (50 m wide) have been built over the Trans-Canada Highway in Banff National Park, along with underpasses (<12 m wide). Over almost three years, elk *Cervus elaphus*, deer *Odocoileus virginianus*, grizzly bear *Ursus arctos* and wolves were found to prefer the exposed overpasses, whereas cougars *Puma concolor* and black bears *Ursus americanus* preferred constricted underpasses [35], and microtine rodents completely avoided overpasses [36]. This research helps solve the problem of the best way to facilitate population and gene flow in species whose habitats are fragmented by roads, and addresses these issues for several species simultaneously (Step 3; Box 1).

### Reserve design

For reserves with hard boundaries, their effectiveness is related to the movement of species within them. Large carnivores range widely and suffer high levels of human-induced mortality when they venture outside protected areas [37]. The critical reserve size that is necessary to maintain different carnivore species was calculated using a logistic regression to predict the reserve size at which populations persisted with a probability of 50%. Critical reserve size correlates positively with female home-range size after accounting for phylogeny and population size. Thus, patterns of ranging are an important predictor of effective reserve size and the findings of this study carry public relations weight because species are charismatic (Step 4; Box 1).

### Response to exploitation

In some populations that are subject to exploitation, the reproductive behavior of individuals is affected. For example, researchers monitored endangered saiga antelope *Saiga tatarica* populations in Kalmykia, Russia, from 1992 to 2002, a period during which they witnessed a 95% population collapse initiated by hunting [38]. As time went on, the proportion of young and adult females that were fecund decreased. When the adult male:female ratio

reached a 1:36 threshold, many females did not reproduce. At this point, harem defense broke down and dominant females aggressively excluded subordinate females from access to males. Here, a combination of reproductive and behavioral data shows that hunting of males is driving the population to final extinction. Such findings could not have been extrapolated from other species with potentially different mating systems or female dominance hierarchies (Step 5; Box 1).

### Captive breeding

Many of the early connections between behavioral research and conservation were forged in zoos, and opportunities still exist to help species breed in captivity. Behavior in the wild might also be important for behavior in captivity [39]. Across 35 species of carnivore, there was a positive correlation between home-range size and two outcome measures that are important to captive breeding institutions: infant mortality in captivity and pacing – a form of stereotypic behavior. This was true even after differences in overall activity, body size and phylogeny had been accounted for. Polar bears *Ursus maritimus*, with their huge home ranges, were particularly badly affected. Again, there is a clear conservation outcome applied to a specific problem in zoological institutions: species with large home ranges are unlikely to flourish in captivity; thus, it is vital that such information be conveyed effectively to zoo curators (Step 6; Box 1) because investment made in breeding these species would have small returns.

Sex allocation theory has also helped captive breeders of the flightless and endangered kakapo *Strigops habroptilus* to modulate chick sex ratio. Kakapos taken from the wild and fed generously in captivity produce a preponderance of sons, as predicted for species for which male competition for mates is intense. Reducing the quality of food to a level at which mothers still lay but produce both daughters and sons has increased the viability of the captive population [40].

### Reintroduction and restoration

Many rehabilitation projects demand some behavioral knowledge to be successful. For instance, at one point, all California condors *Gymnogyps californianus* were confined to captivity and their survival depended on increasing the captive population before reintroduction began. Chicks were fed by condor-head-shaped puppets, so that they would not imprint on humans and be attracted to people following release; this proved successful. Similarly, whooping cranes *Grus americana* have been raised by people disguised as cranes, who direct them to good feeding locations and mimic their alarm calls in the face of danger [41]. Retaining natural behavior and preventing habituation to people facilitated smooth release in both species.

In a mammalian example, black-tailed prairie dog *Cynomys ludovicianus* translocations were more likely to be successful if they were moved in family groups than in non-family groups; because families stayed together in groups, they suffered lower predation rates and enjoyed greater survival. Despite greater initial costs of capture, moving family groups was more cost effective in the end [42].

### Monitoring

Monitoring is central to conservation and behavior can be of help. As a case in point, individual differences in corncrake *Crex crex* song can be used to count numbers of these secretive birds that would otherwise be impossible to census [43]. In a second example [44], of nine large mammal species living at significantly lower densities in a hunted area than in an adjacent fully protected area in Tanzania, individuals from seven species living in the hunted area watched or fled from the observer more often. Of three species found at similar densities, none were more wary. Given that hunting data, especially illegal hunting data, are difficult to collect, behavior provides a shortcut to identifying which populations are under illegal pressure [45].

### Closing the gap

To summarize, theoretical advances in understanding behavior over the past 30 years, personified by the growth of behavioral ecology, have proved rather irrelevant in helping to solve the biodiversity crisis. Theoretical questions are not of great use to conservation (but see [46]), but the information gathered in the process of working on them can sometimes help solve specific conservation

problems, especially if simple guidelines are followed (Box 1 and Figure 1).

First and most important, if you are interested in applying behavior to conservation, begin with a conservation issue. Start by talking to those on the front line of conservation to discover their specific concerns, assuring them that your work will be of some relevance. Second, tackle a conservation problem by working in a threatened habitat, or compare populations in disturbed and undisturbed areas. Simply working in a well-protected national park gives little insight into how individuals respond to threat. Third, try to work on several species or, better still, several taxa simultaneously. Think about a corridor. Conservation biologists do not want to know whether one species crosses a corridor between two patches, but how many species in the community do [47]. Fourth, consider working on a flagship species because it gets people's attention; it could galvanize political will to benefit sympatric species. Fifth, work on threatened and endangered populations and avoid using surrogate species. There is an increasing trend for graduate students in behavior to work on common species that are somehow thought to be similar to a species of conservation concern. This is because rare species are difficult to locate and inevitably result in small sample



**Figure 1.** Examples of how behavioral studies can be made more relevant to conservation. **(a)** Contact stakeholders before starting on a conservation project. In a study of behavioral and demographic responses to poaching, talk to local butchers about meat prices first. **(b)** Work in disturbed habitats, such as this grassy verge, as this is a front line of conservation. **(c)** Work on several species simultaneously, as they might show different responses to the same anthropogenic perturbation. **(d)** Choose to work on flagship species, as they attract the attention of the public and politicians. **(e)** Work on threatened populations, as conservation findings will be directly relevant to helping them. **(f)** Make time to have face-to-face conversations with people who affect the populations that you work on. **(g)** Practice public speaking; you need to broadcast your findings or no one will listen. (All photos by Tim Caro.).

sizes. But results from common species might not generalize [48]. Moreover, managers and funders will typically have interest only in those species that are actually at risk. Note, however, that esoteric questions applied to endangered species are not enough; they need to be of conservation significance. Sixth, those accustomed to disseminating their findings in high-quality scientific journals need to change tactics and put time into workshops and face-to-face conversations with managers, and produce clear and simple reports rapidly. Although we should strive for rigorous science in conservation, political realities sometimes demand uncomfortably rapid recommendations. Currently, the academic system of merit increase does not reward such activities and our colleagues conducting more basic research are not ready to change it. Seventh, all biologists, of whatever stripe, should popularize their findings better through public speaking and popular writing. If those who value nature are not willing to address the issue of diminishing biodiversity publicly, decisions will be made by those who are less informed. I urge biologists interested in behavior to address real conservation issues head on and deflect accusations by future generations that we failed to deliver.

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<http://www.endocytobiology.org/>

### 11–14 September 2007

High Latitude Terrestrial and Freshwater Ecosystems: Interactions and Response to Environmental Change, Abisko, Sweden  
<http://www.emg.umu.se/circ/workshop>

### 13–14 September 2007

Systems Biology and the Biology of Systems: how, if at all are they related? Buxton, Derbyshire, UK  
<http://www.newphytologist.org/systems/default.htm>

### 19–21 September 2007

11th Evolutionary Biology Meeting, Marseilles, France  
<http://www.evolutionary-biology.org>

### 20–21 September 2007

Mathematical Models in Evolution and Ecology, Brighton, UK  
<http://www.maths.sussex.ac.uk/MMEE2007>

### 22–26 September 2007

Evolutionary Genetics of Host-Parasite Relationships, Roscoff, France  
[http://www.cnrs.fr/sdv/cjm/cjmprog\\_e.html](http://www.cnrs.fr/sdv/cjm/cjmprog_e.html)

### 7–10 October 2007

6th International Zoo & Wildlife Research Conference: Behaviour, Physiology & Genetics, Berlin, Germany  
<http://www.izw-berlin.de/>

### 17–20 October 2007

67th Annual Meeting of the Society of Vertebrate Paleontology, Austin, TX, USA  
[http://www.vertpaleo.org/future\\_meetings.htm](http://www.vertpaleo.org/future_meetings.htm)

## 2008

### 20–25 January 2008

GRC Origin of Life, Ventura, CA, USA  
<http://www.grc.org>

### 3–8 February 2008

GRC Molecular Evolution 2008, Ventura, CA, USA  
<http://www.grc.org/programs.aspx?year=2008&program=molecevo>

### 24–29 February 2008

GRC Genes & Behavior, Lucca (Barga), Italy  
<http://www.grc.org>

### 7–8 April 2008

BES Annual Symposium: Ecology of Industrial Pollution - Remediation, Restoration and Preservation, University of Birmingham, UK  
<http://www.britishecologicalsociety.org/articles/meetings/current/2008annualsymp/>

### 5–8 June 2008

SMBE 2008 Annual Meeting, Barcelona, Spain  
<http://www.smbc.org/meetings.php>

### 6–11 July 2008

GRC Metabolic Basis of Ecology, Biddeford, ME, USA  
<http://www.grc.org>

### 13–18 July 2008

Society for Conservation Biology 2008, Chattanooga, TN, USA  
<http://www.conbio.org/Activities/Meetings/>

### 3–8 August 2008

93rd ESA Annual Meeting, Milwaukee, WI, USA  
<http://www.esa.org/meetings/upcomingmeetings.php>

### 15–18 October 2008

68th SVP Annual Meeting, Cleveland, OH, USA  
<http://www.vertpaleo.org/meetings/future.htm>