Chapter 2

Integrating behavior into conservation biology: Potentials and limitations

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I explore the current and potential contributions of behavioral studies to conservation biology, and clarify limitations in applying behavioral ecology and ethology to conserving biological diversity. In my opinion, behavior has played a much more important role at certain scales of conservation problems than at others. Specifically, the behavioral sciences have most influenced conservation at the relatively local scales of populations and species, while the conservation of most of the world's biological diversity will occur not at those scales but at larger scales of ecosystems, landscapes, and biomes. Thus, there appears to be a discordance between the ecological scales at which behavior is most pertinent to conservation and the scales at which conservation efforts will protect the most biological diversity. For behavior to make a larger contribution to conservation, it will have to be translated more often into 'currencies' that can be linked across scales directly to conservation.

To see how I arrived at this opinion, I examine how conservation biology has been formulated as a science and has developed 'tools' to deal with the problem of disappearing diversity. Then I review how behavior fits, or could better fit, into the repertoire of approaches that conservation biology offers for conserving biological diversity, paying particular attention to the currencies needed for translating behavior into conservation and the potential for future behavioral contributions.

The formulation of conservation biology and its tools

Conservation biology emerged as the science of scarcity and diversity (Soulé 1986) in the 1980s in response to the perception that extinction rates had become greatly accelerated (Myers 1979; Wilson 1988; Reid 1992; Smith *et al.* 1993). Conservation biology has the explicit goal of maintaining biological diversity – genetic diversity, species diversity, and ecosystem integrity (Soulé 1985; Beissinger 1990). Biological diversity has grown from the simple concept of species diversity to include genetic diversity, the evolutionary uniqueness of species or taxonomic diversity, the functional processes or interactions of species and physical environments that maintain ecosystems (functional diversity), and landscape diversity or the diversity of ecosystems in a region (Soulé 1985; Beissinger 1990; Noss 1990). This expanded definition of biological diversity emphasizes the processes (e.g., inbreeding, genetic drift, mortality, dispersal, nutrient cycling, succession, and disturbance) and interactions (e.g., coevolution, predation, and competition) that play a crucial role in maintaining or eroding biological diversity. Conservation biology only encompasses a subset of all conservation issues because of its mission to conserve biological diversity. For example, outside of the purview of conservation biology are the more traditional wildlife conservation problems of managing game and pest species, and planning landscapes where humans and wildlife can coexist (e.g., urban ecology), unless these problems directly relate to conserving rare species or ecosystems.

Conservation biology developed from the principles of evolutionary and ecological processes at different spatial and time scales (Beissinger 1990): (1) population genetics and evolutionary biology provide the framework to protect the evolutionary potential of species to adapt to changing environments; (2) demographic processes (mortality and reproduction) drive extinction probabilities and comprise the study of population ecology; (3) underlying demography is the process of individuals making choices (the study of behavior and life history); and (4) community, ecosystem, and landscape ecology provide the foundation for biogeographic distributions of organisms, and determine the potential for ecosystems to be restored or maintained in the face of natural disturbances and human development.

In examining both the sources of conservation principles and the expanded concept of biological diversity, it is clear that behavior should be an explicit part of conservation biology. It is certainly an underlying (implicit) or explicit component of each of the four knowledge areas and is important to many of the processes that are an integral part of maintaining or destroying biological diversity. The linkage between behavior and the application of conservation biology, however, has been weak. Perhaps this has occurred in part because much behavioral research attempts to develop reductionist approaches to elucidate the proximate and ultimate factors responsible for the occurrence and

Table 2.1 *Seven tools that have emerged from the development of conservation biology that can be applied to conserve biological diversity and their dominant context for use*

Dominant context	Tools
Prevent the loss of biological diversity	Reserve and Landscape Design Ecosystem Management Population Viability Analysis
Compromises between conservation and development	Sustainable Development
Recover threatened populations, species or ecosystems	Field Recovery of Endangered Species Captive Breeding and Reintroduction Ecosystem Restoration

evolution of behavioral patterns, while conservation biologists use different kinds of information in their tools designed to solve conservation problems.

Seven 'tools' or knowledge areas, with emerging principles that can be applied to conserve biological diversity at different scales, has marked the development of conservation biology (Table 2.1). These tools can be grouped into those which can be implemented to prevent the loss of biological diversity, to promote compromise between conservation and development, and to recover threatened populations, species, and ecosystems. Most tools are so new that it is too soon to assess their full potentials (Reserve and Landscape Design, Ecosystem Management, Population Viability Analyses, Sustainable Development, and Ecosystem Restoration), whereas others have now established sufficient track records that their potentials to succeed or fail in conserving biological diversity are more certain (Field Recovery of Endangered Species, and Captive Breeding and Reintroduction). Each tool has contexts for which its use is more appropriate than others, although admittedly some of these tools can be used in more than one context. I have placed them according to what I consider each tool's dominant purpose and optimal potential to achieve conservation.

In the remainder of this chapter, I examine these tools individually, assess how these tools explicitly draw upon studies of ethology in their current application, and how behavioral science might be better incorporated into them in the future.

Contribution of behavior to tools that prevent the loss of biological diversity

Reserve and Landscape Design

Reserve and Landscape Design refers specifically to principles derived from biogeography (species–area curves, equilibrium theory of island biogeography, and relaxation rates), metapopulation dynamics, and the ecological and evolutionary consequences of fragmentation and isolation. Typical principles are: (1) larger blocks of habitat are usually better than smaller ones because they protect more species and result in longer population persistence times; (2) blocks of habitat that are closer together are typically better than blocks that are farther apart because this facilitates dispersal and genetic exchange; (3) some connectedness via corridors is often better than none, for the same reasons stated in (2); (4) buffering existing protected areas with zones of appropriate land use can decrease threats from incompatible land use or direct exploitation; and (5) several reserves often help spread the risk of extinction better than a single reserve. Each principle is stated with a modifier (e.g., 'often' or 'usually'), because each conservation situation is unique and needs to be evaluated in its own context. For example, although corridors may facilitate important exchange of individuals between spatially subdivided populations (Harris & Scheck 1991; Soulé & Gilpin 1991), they can assist the spread of disease, fire, and other catastrophes (Simberloff & Cox 1987; Simberloff *et al.* 1992; Hess 1994). Thus, the potential use of corridors must be evaluated on a situation-by-situation basis, considering as criteria the likely use of corridors by target species and the dangers imposed by linking sites.

Most protected areas have been established or managed for biological or other kinds of diversity based on these sorts of principles, if any at all were used. Many parks were established simply to protect a unique ecosystem or a particular species (Diamond 1986), such as breeding areas of elephants in Africa, penguins in Australia, and Elephant seals (*Mirounga angustirostris*) in the United States, or wintering areas of Monarch butterflies (*Danaus plexippus*) in Mexico. Beyond the significance of where a species was breeding or surviving, knowledge of behavior traditionally has not been a particularly important component of the principles of Reserve and Landscape Design, with the important exception of dispersal behavior, which underlies many of them. Two kinds of dispersal data are critical from the perspective of Reserve and Landscape Design – how far individuals disperse and the willingness of individuals to use corridors if present. A knowledge of dispersal distance, and the effects of different kinds of land uses and barriers on dispersal behavior, is needed to evaluate the current configuration of reserves for many different groups of organisms. In addition, we know little about what species will use corridors for dispersal and what constitutes a minimum or optimal corridor width (Nicholls & Margules 1991; Soulé & Gilpin 1991; Simberloff *et al.* 1992). Thus, behavioral studies that provide correlates of the propensity to disperse across gaps or corridors will be of most value to reserve management design in the future (e.g., Haas 1995) and could help to determine whether it would be useful to make the costly investment in procuring conservation corridors.

Reserves that are specifically created to protect a species are sometimes inadequately designed because the species' life history or behavior was incompletely known. Then, knowledge of behavior can be important in helping to redesign such parks. In many Central and South American countries, for example, most parks and protected areas are found either on the mountain tops or in the lowlands. Yet, nearly one-quarter of the avifauna move annually out of the montane parks partway downslope to search for seasonally fruiting trees or emerging insects in the few small forest fragments which remain mostly on private lands (Guindon 1988; Stiles 1988; Powell & Bork 1995). In this example, a better knowledge of natural history provided by behavioral or ecological studies of the factors likely to be responsible for dispersal behavior would have helped to design the parks properly. Detailed studies of the individual decision rules that triggered dispersal, and variation among individuals in those rules, would probably not be needed.

The immediate need to establish protected areas before ecosystems and species are further destroyed or lost means that delineating park boundaries is usually carried out long before detailed studies have been conducted. Thus, the importance of behavior may only emerge well after protected areas are created. While presently little behavior is explicitly incorporated into the principles of Reserve Design and Landscape Management, in the future a knowledge of behavior may prove to be very useful for redesigning current park boundaries or determining the size of buffer zones around protected areas.

Ecosystem management

Much biological diversity is found on private lands or multiple-use federal lands, thus falling outside of the protection provided by the coarse filter of parks and reserves. Ecosystem management incorporates aspects of both resource conservation and utilization, or, from another perspective, preservation and development (Slocombe 1993; Grumbine 1994). It is emerging as an approach that combines regional planning methods with ecological risk assessment to find compatible land use at a regional level. The objective of Ecosystem Management is to use holistic approaches to manage land and water to provide products and services to meet the needs of human societies, and to conserve biological diversity. Biological principles of Ecosystem Management appear to come mainly from those presented above in Reserve and Landscape Design, but applied to a larger scale to examine the maintenance and juxtaposition of many types of land use or ecosystems. Employing a multispecies perspective, Ecosystem Management may also take the form of simulations that incorporate habitat suitability models, biophysical models of environmental variation such as hydrological or biogeochemical cycles, and Population Viability Analyses.

Individuals rarely are explicitly considered in large and complex dynamic models of ecosystems and land use at the regional scale, and thus behavior beyond natural history tends to be ignored. For example, one of the largest and most recent ecosystem management exercises in the USA, President Clinton's Forest Ecosystem Management Team (FEMAT 1993), developed different scenarios for every parcel of federal land in the Pacific Northwest based mostly on qualitative assessments of habitat affinities for hundreds of species. It was a combination of natural history and risk assessment using the Reserve and Landscape Design principles discussed above. Behavior was sometimes implicitly incorporated in this assessment, such as the unwillingness of Northern spotted owls (*Strix occidentalis*) to cross clear cuts, but only explicitly used in population models for a couple of well-studied species. An exception is the development and incorporation in Ecosystem Management of individually based models, which will be discussed in more detail below. For example, such models are being developed to examine ecosystem management options in the Florida Everglades for a few species of concern (Fleming *et al.* 1994; Wolff 1994).

Given the complexity of Ecosystem Management and the limits on our ability to develop detailed behavioral models of animal movement for a single species, let alone the tens or hundreds that good Ecosystem Management requires, I believe that for the present the influence of behavioral sciences on Ecosystem Management will remain relatively limited. Nevertheless, behavior could become a much more important component of Ecosystem Management as landscape ecology continues to emerge as a credible science (Turner *et al.* 1995*b*). It places importance on examining the interactions of landscape dynamics, ecosystem processes, and biological diversity through the incorporation of spatially explicit models of the occurrence and movement patterns of individuals. One of the key components of landscape ecology is understanding how landscape features influence the movement patterns of individuals. Patterns of movement are especially crucial, because Ecosystem Management requires an understanding of how current and projected spatial configurations of all ecosystems, not just reserves, will affect both biological diversity and the production of goods and services. What kinds of landscape elements are barriers to movement? Why does the same landscape element enhance movement of some species but retard movement of others? How do species perceive landscapes and how does it affect their patterns of movement? Understanding the demographic implications of and factors affecting habitat choice and settlement patterns are as important as quantifying the patterns and correlates of movements. Mechanistic answers to these and other questions are likely only to come from detailed studies of dispersal and habitat choice behavior across a suite of species and ecosystems. They will have broad implications for Ecosystem Management by clarifying the impacts of the current configuration of ecosystems and predicting the impacts of future spatial configurations.

Population Viability Analyses

Population Viability Analyses (PVA) usually involves the development of species-specific models dependent on detailed demographic and environmental information (Shaffer 1981, 1990; Soulé 1987; Burgman *et al.* 1988; Boyce 1992). Demographic models are used to project populations years into the future and evaluate their risk of extinction in relation to environmental variation and various management options (Fig. 2.1). Spatially explicit population viability models range from simple subdivided populations to patch-based metapopulation models to GIS-based (geographic information system) models that are complete spatial arrays of landscapes (Burgman *et al.* 1993). Genetic models that estimate

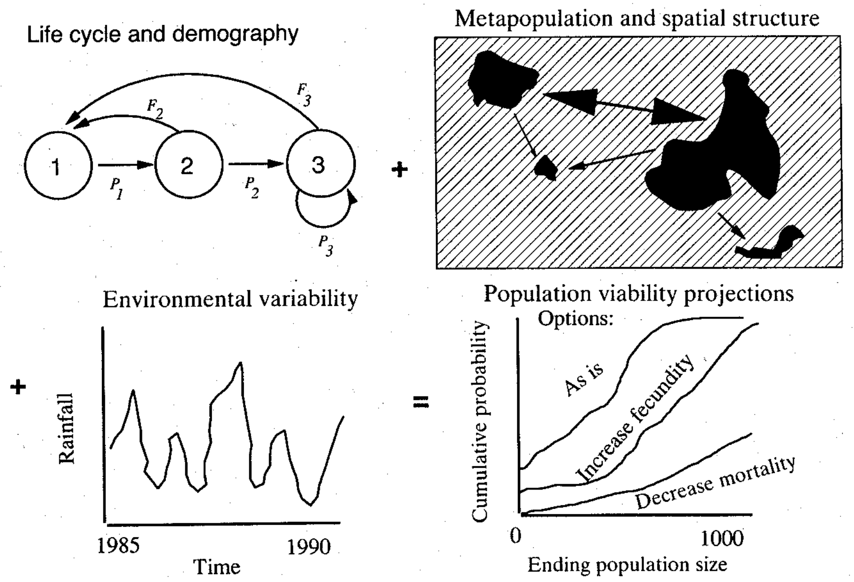

Fig. 2.1. Population viability analysis (PVA) incorporates the life cycle, demography, and spatial structure of the organism under consideration, and the relationship of these factors to environmental variability, to project populations into the future to yield predictions of population size and viability at different time spans under various management options.

effective population size can rarely be directly linked to extinction probabilities (Lande 1988; Reed *et al.* 1988), and are employed less frequently in management and policy decisions. Some approaches try to establish direct links between extinction probabilities and ecosystem management options. Population viability of the Snail kite (*Rostrhamus sociabilis*), for example, was shown to be strongly impacted by Everglades hydroperiod characteristics, especially the interval in years between low or drought water conditions which has been greatly influenced by water management regimens (Beissinger 1995).

Most applications to date use population-based demographic models rather than individual-based models (Menges 1992; Burgman *et al.* 1993). Measurements of demographic rates, of course, implicitly rely upon studies of individuals, but behavioral components may be no more explicit than survivorship, reproductive success, and age. Many PVA applications are based on glorified life table analyses. Thus, behavior is only rarely explicitly treated in these models, with two exceptions. First, behavior can assist in structuring the underlying life cycle diagram (Fig.

2.1) used for demographic modeling (McDonald & Caswell 1993), which may improve model accuracy. Instead of basing the life cycle diagram simply on age classes, behavioral studies led to the formulation of demographic models that incorporated social systems (e.g., breeders, helpers, non-breeders) into the model structure in PVA analyses of threatened woodpeckers (Heppell *et al.* 1994) and gorillas (Harcourt 1995). Behavior was used with demography to partition Everglades water levels into different environmental states in the Snail kite PVA (Beissinger 1995). Incorporation of behavior into PVA analyses should result in substantially improved model prediction, but this needs further investigation given the increased financial investments often required to construct such detailed models. Second, dispersal dynamics are very important to spatial models. Usually detailed data on dispersal rates, mean dispersal distance and the nature of the distribution of dispersal distances (e.g., negative exponential, step function, uniform, etc.) are absent. Thus, mathematical distributions of dispersal distances and rates are often simply assumed based on little information (e.g., Gibbs 1993; Lindenmayer & Lacy 1995), neither is there much information on the role of landscape elements and barriers on dispersal dynamics, as discussed above. The effects of these assumptions on model outcomes are rarely examined. Yet, they probably have an important effect on viability estimates and the conservation conclusions drawn from spatial models. Behavioral studies that supply spatially explicit details of demography and movement patterns would be helpful to PVA models.

There is hope for more incorporation of behavior into PVA models through the use of individual-based spatially explicit models (Dunning *et al.* 1995; Turner *et al.* 1995*a*). For example, Bart (1995) developed such models for the Northern spotted owl: individuals are followed through time and disperse or settle among territories depending upon simple rules based on mating status and territory quality. Thus, behavior is included but it is a far step from a model that incorporates ethology or behavioral ecology – such as the effects of mating system, sexual selection, energetics, psychological influences, or optimality on the pattern of individual movements. Rarely will we have that kind of detailed information for conservation applications! In fact, the demography of most threatened species is not known well enough to construct population-based PVA models, and it is very unusual when there is enough information to construct even simple individual-based models for species of concern. Thus, our ability to develop individual-based models will be severely constrained. Nevertheless, for behavior to become better incorporated into PVA models, it must be able to be translated directly into spatial or demographic consequences that can be used to estimate the probability of extinction in individual- and population-based models.

Contribution of behavior to tools that compromise conservation and development

Sustainable Development

Sustainable Development, like Ecosystem Management, is a buzzword without a single meaning. It has been referred to as the 'use it or lose it' approach to conservation. Sustainable Development can be applied in two contexts: (1) to single-species sustainable harvesting programs such as those with parrots (Beissinger & Bucher 1992; Stoleson & Beissinger, Chapter 7) or Vicuña (Cattan 1989); or (2) to ecosystem-level approaches for sustainable development schemes which identify regional land uses (e.g., certain kinds of agriculture or agroforestry practices) or economic activities (e.g., ecotourism or extractive reserves) that might be compatible with the retention of biological diversity (Reid 1989; Simon 1989; Vincent 1992). For example, development in areas of tropical montane forest might maintain a greater proportion of insects and insectivorous birds (i.e., be sustainable) if farmers planted agroforestry crops, such as shade tree coffee, instead of yucca or banana monocultures (Vannini 1994; Thiollay 1995). Likewise, macaws may be worth more to local people if their populations are protected for ecotourists to view rather than harvested for the pet trade (Munn 1992).

Animal behavior studies seem to have played a small part in examining the impact of land use changes proposed by sustainable development schemes. Like Ecosystem Management, there are just too many species impacted by sustainable development schemes to be considered by behaviorists one at a time. In the ideal case, the response of dozens of species to changes in land use is determined. Thus, it is frequently difficult to gather field data that are more detailed than changes in species occurrence, density, or resource utilization, except in the case of studies of specific target species. Detailed studies of the behavioral ecology of target species, however, could be used to validate the assumptions of coarser approaches. Also, animal behaviorists may be able to provide enlightened estimates of the impacts of development schemes on biological diversity by making comparisons of behavior with species that have been relatively well studied. Just as congeneric species can show unexpectedly different life history patterns or responses to environmental change, so behavioral responses to management can sometimes be surprising. Conservation problems are often site- or situation-dependent, and very different factors can be at work in the field than appear to be acting when viewed from the armchair (Snyder & Snyder 1989).

Behavioral studies could play a significant role in determining the impact of 'sustainable' economic activities on individual target species. Activities like ecotourism can make important contributions to local economies, promote development and provide impetus for habitat protection (Groom *et al.* 1991; Munn 1992; Maille & Mendelsohn 1993; Kangas *et al.* 1995). Ecotourism operations can also impact animal populations or damage ecosystems (Boo 1990; Blane & Jaakson 1994; Jacobson & Lopez 1994; Rinkevich 1995). The ecological impacts of ecotourism operations have received little study, although past experience suggests that wild animals rarely benefit from direct interactions with humans. Behaviorists should conduct more studies of the impacts of ecotourism on particular species.

Demographic models of sustainable harvesting typically have been based on population-level characteristics and, with few exceptions, do not explicitly integrate behavior. Such models have been important for estimating sustainable harvest levels of game populations (i.e., game hunting or fishing) in developed countries, but have been used less frequently in developing countries (Robinson & Redford 1991). Of course, such models have not necessarily prevented overharvesting because of two factors (Ludwig *et al.* 1993). First, the models are often not actually used to manage populations. Market and political forces can cause governments to set harvest quotas without true regard for model results. Second, the models have only been partially successful in predicting population trends. This has occurred in part because many modeling efforts have not incorporated detailed information on mating systems, sex ratio variation, and behavioral characteristics, and environmental variation has made it difficult to distinguish true trend signals. Continued integration of behavior with demographic models may help improve their accuracy, but not necessarily their use by policy makers.

Nevertheless, as the world population is expected to double from 5.7 billion to 11 billion in the next 40 years (UNFPA 1991; Tuckwell & Koziol 1992), humanity is likely to exploit natural ecosystem products at an ever increasing rate and governments will try to find easy ways to apply science to assist in setting animal harvesting quotas. One of the simplest ways to develop harvesting schemes that might truly be sustainable could be to use behavioral and demographic studies to determine what factors limit the population growth of target species, determine if productivity can be increased through simple management options, and then harvest only the extra productivity created by management (Beissinger & Bucher 1992; Stoleson & Beissinger, Chapter 7). This very conservative approach to sustainable harvesting is particularly useful for situations where information needed for quantitative models of harvest rate are lacking or difficult to obtain. As discussed above, such situations seem to be extremely common.

Contribution of behavior to tools that recover threatened populations, species, and ecosystems

Field Recovery of Endangered Species

Field Recovery of Endangered Species depends upon determining what factors limit population growth *in situ* and then reversing those factors. Determining what factors limit population growth is best accomplished by a combination of individual and population level approaches (Caughley 1994). Limiting factors are like specific hypotheses that can be tested only by examining the behavior of individuals in the field – foraging behavior, reproduction, disease infection levels, etc. – and linking behavior to demographic consequences.

Behavioral science has been integrated into recovering endangered species in the wild. Behavioral studies can provide not only the evidence needed to indicate what limits population growth, but can lead to suggestions for creative management practices to reverse those trends. Many chapters in this volume demonstrate this point clearly, so my treatment will be brief. Good behavioral ecology becomes an essential ingredient for the successful recovery of threatened or endangered species, and behavioral ecologists are often quite skilled in hypothesis testing approaches needed to discriminate among potential limiting factors.

Field Recovery of Endangered Species is a tool designed primarily to result in single-species conservation. It has been applied mostly to a handful of lucky terrestrial vertebrates in temperate countries. Nevertheless, recovering endangered species often involves protecting their habitats, and in this way the 'coattails' of these species can be extended to protect whole ecosystems. Endangered species have also acted as 'flagship' species in campaigns to preserve whole ecosystems, and sometimes

the success of such programs has been very impressive (Butler 1992; Dietz *et al.* 1994). This requires mounting intensive educational and promotional campaigns that are very time consuming and far removed from the expertise and interests of most behavioral biologists. Such campaigns have sometimes been conducted independent of field recovery efforts and on species that are not the subject of field research (e.g., Butler 1992). Unfortunately, overusing flagship species for conservation gains can unintentionally result in a political backlash that can decrease the effectiveness of conservation programs, as in the use of the Spotted Owl to promote the conservation of old growth forests. To date, the impact of Field Recovery of Endangered Species on conserving whole ecosystems has been smaller than many of the multispecies tools previously discussed which are oriented toward preventing the loss of biological diversity.

Captive Breeding and Reintroduction

Captive breeding of endangered species for conservation has increased tremendously over the past two decades. Techniques for breeding species in captivity have improved, as have techniques for reintroducing captive-bred animals into the wild (Gipps 1991; Wiley *et al.* 1992). Captive breeding has been the difference between survival and extinction in the short term for species like the California condor (*Gymnogyps californianus*), the Guam rail (*Rallus owstoni*), and the Black-footed ferret (*Mustela nigripes*) (Snyder & Snyder 1989; Derrickson & Snyder 1992; Miller *et al.* 1996).

Behavioral considerations are an extremely important component of breeding endangered species in captivity and reintroducing them into the wild for conservation (Lyles & May 1987; Kleiman 1989; Snyder *et al.* 1994). While maintaining genetic diversity has often been emphasized as critical to the success of captive breeding programs (e.g., Foose & Ballou 1988; Allendorf 1993), the real barriers to successful captive breeding are usually behavioral, such as mate choice, social structure, domestication, and disease prevention (Snyder *et al.* 1996). Predator avoidance, habitat choice, and even flocking behaviors are often learned (Kleiman 1989; Miller *et al.* 1990; Snyder *et al.* 1994), and are critical for survival of reintroduced individuals into most wild environments.

Unfortunately few species will be conserved by employing captive breeding and reintroduction. Captive Breeding and Reintroduction for conserving endangered species in the wild is a last-ditch approach that should rarely be invoked because of severe limitations (Snyder *et al.* 1996). (1) Achieving self-sustaining captive populations can be difficult. While some species breed too well in captivity (Lacy 1991; Lindburg 1991), only a handful of taxa have bred in captivity (Conway 1986; Rahbeck 1993) and many species breed poorly in captivity despite extensive efforts (Snyder *et al.* 1996). Predicting which species will breed well in captivity is often difficult, as the breeding success of *Amazona* parrot species has shown (Derrickson & Snyder 1992). (2) Successful reintroduction is rarely achieved. Recent surveys of reintroduction programs of captive-bred animals have shown that few have successfully established wild populations (Griffith *et al.* 1989; Beck *et al.* 1994). Causes of failure ranged from behavioral deficiencies in released animals (e.g., Lyles & May 1987; Kleiman 1989; Fleming & Gross 1993; Snyder *et al.* 1994), especially for species that learn a large portion of their behavioral repertoires, to failure to correct the factors originally causing extirpation. (3) Domestication in captivity is inevitable (Allendorf 1993; Snyder *et al.* 1996), can be quite strong (Belyaev 1979), can proceed rapidly (Moyle 1969; Swain & Ridell 1990), and is difficult to reverse (Knoder 1959; Lyles & May 1987; Derrickson & Snyder 1992). Captive environments differ greatly from wild environments, and species become progressively more adapted to captivity despite comprehensive genetic management. (4) Reintroduction of captive animals risks introducing diseases to wild populations. Disease risks are high for endangered species in captivity owing to enhanced exposure to exotic pathogens (Snyder *et al.* 1996) and perhaps owing to susceptibility from reduced genetic diversity in small populations (O'Brien & Evermann 1988; Thorne & Williams 1988). (5) Financial and space limitations greatly limit how many species can be conserved in captivity and reintroduced to the wild. Costs of captive breeding programs for endangered species run from \$250 000 to \$500 000 per year (Derrickson & Snyder 1992; Balmford *et al.* 1995), and zoological institutions do not have enough space to accommodate viable populations of threatened species (Conway 1986; Sheppard 1995). (6) Captive breeding can divert attention from the problem causing a species' decline (Frazer 1992; Meffe 1992) and preempt investments in better techniques for *in situ* conservation (Snyder *et al.* 1996). Finally, (7) it is difficult to ensure the administrative continuity needed to carry out long-term captive breeding programs (Clark *et al.* 1994).

Nevertheless, Captive Breeding and Reintroduction to the wild truly will be needed for a small percentage of endangered species recovery programs. Behavioral studies have much to contribute to present and future hopes for the successful use of this tool. Behavioral studies may be able to assist in addressing the first three limitations discussed above for specific situations. Behavioral studies have reduced barriers to reproduction in captivity and to survival upon reintroduction to the wild for some species (Kleiman 1989; Beck *et al.* 1994). There is also a real need to understand the process of domestication that inevitably occurs in captivity, and if it can be reversed to make a captive-bred animal into a wild one again, especially if the animal is to be reintroduced into an ecosystem that still has healthy populations of predators. Here studies of animal psychology and ethology may have an especially important role to play.

Ecosystem Restoration

Ecosystem Restoration can be considered the ecosystem analogue to recovering endangered species. It requires an understanding of the flow of energy and materials, and how organisms interact with each other and their abiotic environments in order to restore functions and biological diversity to degraded and damaged ecosystems (Cairns 1986; Jordan *et al.* 1988). Restoration can help decrease the rate of conversion of natural ecosystems (e.g., deforestation) by repairing land damaged by natural phenomena or human activities to a state that can again productively sustain economic development or biological diversity (Brown & Lugo 1994).

Ecosystem Restoration efforts often concentrate on reducing or removing the factors that limit plant establishment and succession by changing the frequency or intensity of abiotic stressors. For example, altering ecosystem hydrology by increasing flooding frequency can restore functions to wetland ecosystems. The addition or deletion of plant species is often used to create conditions that increase ecosystem retention of nutrients, or provide shade, soil moisture, or soil organic matter necessary for the establishment of desired communities.

While animal behavior has not been a cornerstone of Ecosystem Restoration, it can be incorporated into restoration approaches (e.g., Janzen 1988). Of particular interest is the use of animals to enhance vegetation recovery (e.g., seed dispersers and pollinators) and the role of species that retard vegetation recovery (e.g., seed predators). The regeneration of tropical forests from pastures or abandoned agricultural lands, for example, can be impeded not only by improper abiotic conditions but by a lack of propagules (Nepstad *et al.* 1991; Aide *et al.* 1995). Seedlings, sprouts, and seed banks of forest species are often eliminated after a few years of continuous grazing or cultivation (Uhl *et al.* 1990). Seed predators, such as ants and small rodents, can impede the establishment of trees and shrub by removing seeds that have reached abandoned pastures (Nepstad *et al.* 1991). Seed dispersers, such as birds, bats, and other mammals, play an important role in moving seeds away from the seed shadow of parent trees to new sites. Behavioral studies are investigating how movements of seed dispersers are affected by landscape elements like isolated dead trees, corridors, and living fences (Harris & Scheck 1991). Research is beginning to test ways to attract seed dispersers to visit restoration sites by adding desirable food sources or perches (Robinson & Handel 1992; McClanahan & Wolfe 1993).

Present and future spheres of influence of behavior in conservation biology

Consider for a moment the relative magnitude of the challenge facing modern conservation biologists. Threatened with local or global extinction are one-fourth of the 40 000 known invertebrates in the western half of Germany, one-third of the freshwater fish species in North America, about half of Australia's surviving mammals, 11% of the 9000+ species of the birds in the world, and more than two-thirds of the world's 150 species of primates (Ryan 1992; WCMC 1992). Obviously, a species-by-species approach to conservation problems of this magnitude will not be sufficient.

While there are potentially important ethological contributions to be made to nearly every tool being employed by modern conservation biologists, to date behavioral studies have made their most important contributions to those tools that recover threatened populations or species, rather than to tools that prevent the loss of biological diversity or that promote conservation compromises. Yet, by the very nature of scale and because of their multispecies approaches, most biological diversity will initially be conserved by the 'coarse filter' approach to conservation embodied in the tools that prevent the loss of biological diversity (Table 2.1), rather than the 'fine filter' approach which acts as a safety net to catch those species whose ranges fall between the protected and managed areas embodied in the coarse filter. This may be partly why behavior has presently taken a back seat to the domains of ecosystem, community, and population biology in the efforts to conserve biological diversity and the

development of conservation biology theory. The exception to this trend has been the role of behavior in endangered species conservation problems, many of which are among the most critical and controversial conservation problems of our day! Behavioral studies have made important contributions to detecting and reversing factors that limit endangered populations and to successful captive breeding and reintroduction to the wild. This is the scale where behavior's present contributions to conservation dominate.

This is not to say that the implications of advances in behavioral sciences will not affect the business of conserving biological diversity, or that behavior cannot play a larger role in conservation biology in the future. From the above review, I see three very important areas that strategic research in the behavioral sciences could contribute directly to conservation biology. First, there is a need to integrate behavior into spatial and demographic models, whose applications in conservation are burgeoning. Individual-based models of population and landscape dynamics appear to be the wave of the future. They may affect how we practice Landscape and Reserve Design, Ecosystem Management, Population Viability Analysis, and sustainable harvesting programs. If these models are to achieve a high level of accuracy and precision, they will require a good understanding of the behavioral and ecological factors that influence animal dispersal, movements, and habitat choice. It is a golden opportunity to meld experimental and theoretical behavioral ecology and ethology into conservation biology, assuming these data-intensive models actually are an improvement over less demanding population- and community-level approaches. Just as important is the application of behavior to target species in models for PVA, Ecosystem Management, and sustainable harvesting programs. *To succeed, behavior must be directly translated into either demographic or spatial consequences.* This is one manner in which behavior can be translated across scales from individuals to populations to ecosystems, and become more accessible for making conservation policy decisions.

Second, the rate of establishment of national parks and reserves has been decreasing or is beginning to slow down in most countries around the world (WCMC 1992). I believe that the 'coarse filter' for conserving biological diversity will mostly be in place within the next two decades. What is not protected by 2040, when the total world population is projected to have doubled in size from 1990 levels to 11 billion people (UNFPA 1991; Tuckwell & Koziol 1992), is likely to be converted into urban, agricultural, or other managed ecosystems. Expect behavioral science to make greater contributions to conserving biological diversity as the rate of land preservation continues to slow. Species management issues are likely to grow within and around reserve areas, and in the matrix of agricultural and managed ecosystems. Species do not necessarily remain in protected areas. Wolves currently being reintroduced into Yellowstone National Park, for example, have been found on private lands, and bison have spread brucellosis to cattle on ranches adjacent to national parks (Aguirreo & Starkey 1994; Meagher & Meyer 1994). As top or keystone predators disappear from ecosystems, prey populations have grown out of control and in some cases threaten other species (Goodrich & Buskirk 1995). Behavioral ecology can play an important role in the management of species in human-dominated landscapes.

Third, successful long-term conservation of biological diversity will require multidisciplinary approaches based on the best possible biology, but developed with people in mind. In other words, we need a better understanding of economic, social, and political behavior of individuals and societies. Here, studies of behavior, especially human behavior, may have much to contribute (Heinen & Low 1992; Low & Heinen 1993).

Finally, behavioral scientists that want to contribute more directly to the effort to conserve what remains of the world's biological diversity need to consider two departures from the usual research program that we employ if we are to make our research relevant. First, incorporate human beings into the research questions that we ask. Humans are implicit in nearly every environmental problem that we face, and even the most remote field sites where we conduct our studies of animal behavior have been affected by modern or historical human factors. Whereas we usually strive in our basic research paradigms to purge all effects of people on our study systems, conservation requires incorporating anthropogenic and natural factors. Second, pick systems, animal models, or questions to study that have conservation or economic significance, and invest at least 20% of your effort in conservation issues. Often it is not hard to find interesting basic behavioral questions while studying threatened or endangered species to determine the factors that limit population growth (e.g., Beissinger 1986, 1987, 1995; Berger *et al.* 1993; Berger & Cunningham 1994, 1995). Even studies of common species or species with economic value can have immediate implications for conservation if they are conceived and executed as tests of conservation strategies or models (Beissinger & Bucher 1992). It does require making an extra commitment of time and energy to gather additional data, and to translate that work into products that are useful for conservation.

In conclusion, perhaps the greatest challenge for the biological sciences as we begin the 21st century is to understand the factors promoting the diversity of life and to find ways to conserve biological diversity before it disappears (Wilson 1992). Efforts from all areas of biology will be needed, both because the problem is so great and because there are contributions that can be made by every discipline. Behavioral ecologists and ethologists played an important early role in stimulating public interest in conserving biological diversity, long before conservation biology emerged, through studies of rare and endangered birds and mammals beginning in the early 1960s. Behaviorists can expand upon their present contributions to conservation biology and catalyze future conservation innovations by broadening their research to include the kinds of data needed to translate behavior into currencies relevant to conservation at large spatial scales and by conducting strategic studies that have direct relevance to conservation tools or policy.

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