

What Does It Mean to Successfully Conserve a (Vertebrate) Species?

KENT H. REDFORD, GEORGE AMATO, JONATHAN BAILLIE, PABLO BELDOMENICO, ELIZABETH L. BENNETT, NANCY CLUM, ROBERT COOK, GUSTAVO FONSECA, SIMON HEDGES, FREDERIC LAUNAY, SUSAN LIEBERMAN, GEORGINA M. MACE, AKIRA MURAYAMA, ANDREA PUTNAM, JOHN G. ROBINSON, HOWARD ROSENBAUM, ERIC W. SANDERSON, SIMON N. STUART, PATRICK THOMAS, AND JOHN THORBJARNARSON

The conservation of species is one of the foundations of conservation biology. Successful species conservation has often been defined as simply the avoidance of extinction. We argue that this focus, although important, amounts to practicing conservation at the “emergency room door,” and will never be a sufficient approach to conserving species. Instead, we elaborate a positive definition of species conservation on the basis of six attributes and propose a categorization of different states of species conservation using the extent of human management and the degree to which each of the attributes is conserved. These states can be used to develop a taxonomy of species “recovery” that acknowledges there are multiple stable points defined by ecological and social factors. With this approach, we hope to contribute to a new, optimistic conservation biology that is not based on underambitious goals and that seeks to create the conditions under which Earth’s biological systems can thrive.

Keywords: species conservation, extinction, successful conservation, recovery

Conservation biology was born as a crisis-oriented and crisis-driven discipline (Meine et al. 2006). Conservation was a natural result of the growing global concern about the loss of tropical forests, coral reefs, and endangered species, as well as the increasing realization of the truly global impacts of human activities. To gain the attention of the public, decisionmakers, and students, early pioneers of conservation biology wrote of the sixth extinction, the population bomb, and the end of nature. Their concerns were contagious, and found fertile soil in a younger generation’s worries about pollution and the decline of iconic species such as whales and giant pandas. Extinction was the middle name of conservation biology, and preventing extinctions was seen as the new discipline’s major aim.

The science of modern species conservation came of age with the founding of conservation biology in the 1980s. This foundation was laid in the interplay between genetics and captive breeding (Meine et al. 2006). Among other changes, conservation biology marked a shift in the management of living collections away from displays only and toward population management designed to sustain genetically diverse, demographically stable, and viable captive populations (Hutchins and Smith 2003) that were to serve as assurance colonies should wild populations go extinct (Rabb and Saunders 2005). Combined with the crisis discipline perspective, the three strands of genetics, captive propagation, and crisis were woven into a conservation biology approach to *in situ* and *ex situ* species conservation that defined species conservation as preventing extinction.

Conservation biology as a discipline was not, and is not, the only approach to species conservation. It was grafted to a strong rootstock of species conservation that in some approaches differed from and was overwritten by this emerging discipline. Wildlife management, with its goal of maintaining species in numbers sufficient for significant harvest by humans, has remained largely true to its course and defines successful conservation in terms of harvestable populations. In other approaches, many local and national efforts at species conservation have focused on species with strong human constituencies, irrespective of their conservation status. In this article we focus on the interaction between species conservation and conservation biology while recognizing that this framing does not capture the depth or breadth of all species conservation efforts.

The conservation biology-based definition of extinction avoidance has become codified in science and policy and has directed conservation largely toward rare and threatened species. Extinction avoidance spawned variations of endangered species legislation that focus on what Soulé and colleagues (2003) called “manifest demographic or numerical minimalism.” This perspective is reflected in a statement that attempted to summarize the field of population management: “In conservation, we aim to minimize the chance that a population declines to extinction” (Shea et al. 1998, p. 371).

From its origins in population biology and community ecology, conservation biology focused on minimum viable populations and minimum areas necessary to conserve

species and populations, giving great attention to case studies of individual species and systems (Simberloff 1988). Caughley (1994) observed that conservation biology had settled into an ideological dichotomy: the small-population paradigm, which addressed “smallness” as a predictor of population extinction, and the declining-population paradigm, which deals with the causes of and cures for smallness. Further entraining the discipline’s focus on extinction, Caughley argued that conservation biologists should combine small population theory with the knowledge of declining populations gleaned from case studies. These twin tracks represent two of the ways that the International Union for Conservation of Nature (IUCN) Red List criteria measure extinction risk, codifying this focus (Mace et al. 2008). This trend is still evident in the fact that successful conservation is defined by many conservation biologists with reference to minimum population sizes, minimum areas, and minimally sufficient sets of sites (Redford and Sanjayan 2003, Scott et al. 2005).

Recovery—that is, moving in the opposite direction from extinction—has not been ignored by species conservation. However, when recovery has been discussed, population targets often have been poorly defined or defined using a minimalist approach. Evidence for this is found in an analysis by Tear and colleagues (1995), which showed that more than a quarter of recovery plans for US federally threatened and endangered species set quantitative recovery objectives at or below the species’ existing population size or number of populations.

Here we reexamine the question of what it means to conserve a species, with a focus on vertebrates: What does success look like beyond the avoidance of extinction or a vague notion of recovery? This is a foundational question for conservation biology, but it remains curiously unexamined (but see Scott et al. 2005, IUCN-SSC 2008). Although some conservation biologists believe this is a settled issue, others have raised new questions. We believe it is time to reexamine the commonly accepted notions that successful conservation is defined solely by extinction avoidance or poorly defined notions of recovery, and to move to a proactive definition of positive conservation. From this definition we propose a set of semistable states for recovery that span a continuum; this idea contrasts with the concept of recovery for species used by many in conservation biology, which often is underlain by the implicit concept of a single stable state to which all species should return.

In this article we first review what we consider to be the major biological attributes of species conservation, and use that vision of species conservation to propose a categorization of different states of species conservation derived from the extent of human management. Our article lays out an approach to species conservation informed by the research literature but focused on the practice of species conservation, and we provide a conceptual framework for thinking about species conservation. Each of the attributes advanced as part of the framework needs further development. The

framework could serve as the basis for developing a scoring exercise similar to that which has been designed for the IUCN Red List (www.iucnredlist.org), but such an elucidation is not attempted here.

The attributes of species conservation

It is important to provide a more comprehensive answer to what successful species conservation means, beyond the prevention of extinction. In this article we define successful species conservation as maintaining multiple populations across the range of the species in representative ecological settings, with replicate populations in each setting. These populations should be self-sustaining, healthy, and genetically robust—and therefore resilient to climate and other environmental changes.

The scale of species conservation has moved beyond management within protected areas and zoos to solutions that span a species’ entire geographical range (Sanderson et al. 2002). From this framing emerged the development of the population attributes termed “the three Rs”—representation, resiliency, and redundancy (Shaffer and Stein 2000). Using this definition, we make the case that a successfully conserved species will: (a) be self-sustaining demographically and ecologically, (b) be genetically robust, (c) have healthy populations, (d) have representative populations distributed across the historical range in ecologically representative settings, (e) have replicate populations within each ecological setting, and (f) be resilient across the range.

We have chosen to focus on these characteristics because of their importance and the lack of focus they have received in the recent history of species conservation efforts. Though listed independently, these attributes are clearly related, and they cluster as attributes of a population (self-sustaining demographically and ecologically, healthy), attributes of both single and multiple populations (genetically robust), and attributes of sets of populations (representative, replicate, resilient) that define a successfully conserved species.

Demographically and ecologically self-sustaining. In order to have lasting conservation value, individual populations must be self-sustaining in a variety of interconnected ways. For terrestrial animals, the importance of demographic parameters to population sustainability is commonly assessed using population viability analyses (PVAs) (Beissinger and McCullough 2002). However, although PVAs can estimate the efficacy of various recovery plans, they predict only the minimum viable population necessary to avoid extinction in a given time frame.

Less commonly discussed in the conservation literature is the ecological dimension of self-sustaining populations. The goal of self-sustainability requires consideration of population attributes internal to the species (genetic and demographic) as well as those that involve the species’ interactions with other species. Accordingly, a population must be large enough to maintain critical ecological interactions

for its own sake and for those of species with which it strongly interacts. This concept has its roots in early thinking about population targets for wildlife management (Conner 1988) and has been incorporated into conservation thinking (Soulé et al. 2003, Tear et al. 2005).

An ecologically functional population generally will be larger than a demographically functional population (Soulé et al. 2005). In fact, Svancara and colleagues (2005) estimated that such populations may be orders of magnitude larger. This may be particularly relevant when populations need to be recovered from substantially reduced levels (e.g., great whales). Ecological functionality may be an important attribute to allow species to respond to changes in the composition of communities in the face of climate and other environmental changes.

Genetically robust. Protecting genetic diversity in a threatened species has long been a tenet of conservation genetics (Frankel 1974). As once-large populations become small and fragmented, the reduced gene flow between population subunits affects the amount and distribution of genetic variation. Small and fragmented populations suffer increased genetic drift, resulting in the loss of adaptive genetic variation and greater relatedness among individuals. Drift has deleterious consequences for the adaptive response of populations to environmental changes over short and long time periods and for evolutionary and ecological adaptations at both local and rangewide scales (Hedrick 2001).

Genetic robustness within a population is difficult to gauge on the basis of genetic diversity at neutral markers alone. Diversity is affected by factors such as population size, mutation rates, and demography; thus, genetic diversity will vary significantly across taxa and among populations of a species. However, for normally outcrossing organisms, a higher inbreeding coefficient is generally accompanied by inbreeding depression with negative effects on most fitness components. Across species ranges, fragmentation can exacerbate genetic drift and random fluctuations in allele frequencies, causing the genetic variation originally present within a large population to become redistributed among the remaining subpopulations.

Different alleles become fixed in different subpopulations, with some fixed for nonadaptive variants (which are more likely to go extinct), creating an overall reduced level of adaptive variation that in turn leads to a loss of adaptive potential. Both theoretical and experimental studies show that on average, metapopulations have a smaller adaptive response than undivided populations of similar size to several kinds of environmental stressors (Bakker et al. 2010). Therefore, maintaining gene flow among population subunits across landscapes will support continuing adaptive responses (Crandall et al. 2000). We define genetic robustness as the genetic capacity to survive and respond to environmental changes within populations, among populations, and across the range.

Healthy populations. The evidence is clear that population health plays a critical role in the persistence of populations (Daszak et al. 2000). For example, population level immunodynamics influence infection-induced predation and mortality (Lochmiller 1996). Pathogenic parasites also play a key role in wildlife population dynamics: Population size is sometimes determined by the physical condition of the individuals (Beldomenico and Begon 2010).

Environmental stressors (e.g., habitat destruction and climate change) can make a large proportion of a population vulnerable; thus, native pathogens that normally would be tolerated can threaten population health. For example, the virulence of the chytrid fungus implicated in the global decline of amphibians sometimes depends on the condition of the amphibians exposed to the fungus (Garner et al. 2009). Some frog populations decimated by this fungal infection had undergone periods of increasing stress before the outbreaks took place (Alford et al. 2007).

Understanding the dynamic interactions among health, infection, and animal populations is essential for effective conservation. Smith and colleagues (2009) asserted that the most important strategy for promoting healthy species is to maintain species interactions (ecological functions) that promote natural resistance to stressors and the evolutionary potential for it.

Representative populations. From a biological perspective, there are many ways to prioritize populations for conservation (Wikramanayake et al. 1998, McDonald-Madden et al. 2008). Of chief concern is the protection of populations distributed across the full ecological gradient of species' historical ranges, which protects local adaptations in extant populations, and consequently, the evolutionary potential of the species (Crandall et al. 2000), as well as the full range of ecological interactions within the full range of ecological settings. Rangewide conservation programs to protect American crocodiles (*Crocodylus acutus*), tigers (*Panthera tigris*), bison (*Bison bison*), and other species have used a systematic, spatially explicit approach to prioritize conservation areas that capture the range of ecological settings for a species (Wikramanayake et al. 1998, Sanderson et al. 2002, 2008, Thorbjarnarson et al. 2006). Two major questions must be answered to proceed within this framework.

First, what time frame in a species' history should we consider when developing criteria for conservation success? The geographic range limits of species can be formed in the presence or absence of hard boundaries, environmental gradients, or biotic interactions, and for many species, historic range information is lacking. The IUCN's Species Survival Commission suggests using a geographic range from a time when anthropogenic threats were not a major constraint on a species' range (IUCN-SSC 2008). For example, a planning team for tigers selected the year 1850 because of significant hunting in the latter half of the 19th century (Dinerstein et al. 2007). In practice, determining range limits before anthropogenic threats emerged is often problematic

because of a lack of good-quality population data. Moreover, as Gaston (2009) notes, species' ranges neither are nor were at equilibrium, but rather expand or contract as a result of natural and anthropogenic changes.

Second, for rangewide species conservation, extant suitable or potentially suitable habitat must be defined. Combining historical presence and absence data with probabilistic niche modeling for suitable habitat (Elith and Leathwick 2009) may help in establishing what part of a historical range is feasible for conservation efforts. The importance of knowing a species' historical range is again underscored by research showing that many threatened species currently exist in what might be suboptimal portions of their ranges (Channell and Lomolino 2000). Despite the challenges of achieving representation over the full ecological gradient of a species' current and historical range, we believe it is essential for effective conservation.

Replicate populations. Securing replicates of prioritized population types helps maximize the fitness of the species as a whole. If the units of conservation are representative populations across a species' range, it follows that multiple populations of each type should be protected (Shaffer et al. 2002). This redundancy guards against irreplaceable losses of representation caused by disease or physical disasters that could eliminate single populations within an ecological setting (Shaffer and Stein 2000, Tear et al. 2005).

Resilience across a range. Until recently, species conservation has been viewed in terms of present or past conditions and threats. But the world is constantly in a state of flux. Successful conservation must manage populations in ways that will best allow them to adapt to the changing environment and related challenges. Resilience can best be understood as the ability to maintain population integrity in the face of disturbance (Holling 1973), an essential characteristic for successful conservation. Long-term survival of high-priority populations requires that they be resilient to climate change and other environmental stresses (Parmesan 2006) and therefore able to contribute to species resilience. This means that abundant and broadly distributed species may experience changes in distribution, but their potential to express the key attributes—demographic, genetic, behavioral, and ecological—will remain much the same. Resilience may be achievable through large dynamic metapopulations in a landscape that allows for shifts in distribution (perhaps supplemented by translocation and assisted migration).

A range of states of species conservation

In an ideal world, in which all natural systems return to a state of equilibrium after human interference is eliminated, there would be a single answer to the question of what it means to conserve a species. An unrealistic understanding of the natural world prevailed during the early years of the development of ecology, and it exerted a powerful hold on conservation biology and conservation practice (Botkin 1990).

We have since come to understand that we live in a world of multiple stable states, irreversibility, strange attractors (Walker and Salt 2006), and a pervasive human influence that has penetrated all of nature. Conserving a species is no longer as conceptually straightforward as removing human influences to allow the species to sustain itself (or not) according to natural processes. Although it is vital to continue to establish and maintain protected areas where human influence is limited and minimal, we also must recognize the extent to which many species have become reliant on the direct and indirect ways humans manage the world. In some cases species rely on the land-use changes, physical structures, and altered energy flows humans have created; in others, species have avoided almost certain extinction thanks to active, directed human management to conserve them. The human-dominated nature of the world demands that we embrace the plurality of means by which conservation can be achieved while recognizing the different histories, ecologies, and trajectories of species.

In the previous section we proposed six attributes that, when fully realized, collectively contribute to successful species conservation. But the full realization of each attribute may not currently be achievable for many species. The reasons for this vary among species but can largely be explained by the human dominance of space and ecosystem processes and the ways that this dominance interacts with species' biology and history.

In this section we propose a way of examining the conservation condition of species on the basis of the type and extent of ways that species are reliant on human interventions, both directed and nondirected, to ensure their ongoing survival. We propose five general states to illustrate this continuum; these states do not represent a jointly exhaustive classification system but are heuristic signposts along a continuous distribution of states. For each state we summarize the condition of the six attributes (table 1), provide an example of one species that typifies the state, and discuss the extent to which each of the attributes would be conserved. The states range from "captive managed," in which a species no longer occurs in the wild and humans provide all of the support for the survival of individuals, to "fully conserved," in which species are not at all reliant on direct human intervention for their survival. This taxonomy is similar to one proposed by Scott and colleagues (2005), which focused on US species and their treatment under the US Endangered Species Act (ESA), but our approach was developed independently and addresses the conservation status of all vertebrate species.

Captive managed species. Captive managed species are found almost exclusively in captivity and within management interventions that provide food, care, and breeding for individual animals. Species in this state are entirely reliant on humans and will remain so until they go extinct or move to another state. This category encompasses a range of species, from those that are still extant but extinct in the wild

Table 1. Relationship between states of conservation and attributes of fully conserved species.

States	Attributes					
	Representative	Replicated	Self-sustaining	Healthy	Genetically robust	Resilient across range
Self-sustaining	Fully conserved	Fully conserved	Fully conserved	Fully conserved	Fully conserved	Fully conserved
Conservation dependent	Fully conserved	Fully conserved	Partially conserved	Fully conserved	Partially conserved	Partially conserved
Lightly managed	Partially conserved	Partially conserved	Partially conserved	Partially conserved	Partially conserved	Minimally or not conserved
Intensively managed	Partially conserved	Partially conserved	Minimally or not conserved	Minimally or not conserved	Minimally or not conserved	Minimally or not conserved
Captive managed	Minimally or not conserved	Minimally or not conserved	Minimally or not conserved	Minimally or not conserved	Minimally or not conserved	Minimally or not conserved

Note: These are modal values that will vary on a species-by-species basis.

to those that are in the process of reestablishment but that are still wholly dependent on captive management for their continued existence.

Species that are completely managed in captivity do not fully manifest many or any of the six attributes except to the extent for which these are managed in collections. They have low to nonexistent representation and functional redundancy in the wild—attributes that could be addressed artificially during reintroduction. For species held only in captivity, genetic robustness is predetermined by the number of founders in the captive population, and in fact, survival in captivity may result in a loss of variability (Frankham et al. 1986). Some analysis may be possible to determine the degree of heterogeneity, inbreeding, introgression, and so on, but the genetic structure of the population may be unknown, making genetic robustness difficult to evaluate. Species held in captivity can be assessed for individual or population health, but these assessments may not be indicative of physiological health if the species is reintroduced. Both the health and ecological function of species held in captivity might be recoverable, but this would most likely depend on the degree to which the biological community to which they were reintroduced had changed.

One notable example of a captive managed species is the Kihansi spray toad (*Nectophrynoides asperginis*), discovered in 1996. In 1999 this species had a global population of 17,000 and a global range of two hectares around Kihansi Falls in Tanzania (Channing et al. 2009). The species was brought into captivity in 2000 before the construction of a dam that reduced the river's flow by 90%, thus reducing the spray upon which the toad depended. The wild population was further compromised by the fungal disease chytridiomycosis, and by 2004 only three individuals were seen in the Kihansi Gorge. There have been no reports of wild individuals since 2005 (Channing et al. 2009). The founding captive population of 499 animals has increased several-fold as a result of breeding. Attempts have been made to create appropriate habitat in the river gorge using an artificial misting system, but for the time being the species exists only in captivity.

Intensively managed species. The second state belongs to intensively managed species, which are found in the wild but are reliant on direct human intervention at the individual and population levels through augmentation from captive populations or very extensive, directed habitat manipulation. What sets this group apart from captive managed species is the existence of habitat containing small numbers of wild individuals (relative to the captive population) and the possibility of reintroduction of captive-reared individuals. Most intensively managed species exist primarily as captive populations with incipient reintroduction programs; they share many of the characteristics of captive managed populations, although some have had a longer history of successful programs linking captive and wild populations, and may have higher degrees of representation, redundancy, and resilience. The genetic health of a species is frequently a function of the genetic variability of the captive population, but with possible significant components of genetic variation in wild groups.

The Chinese alligator (*Alligator sinensis*), for example, was historically widespread in the middle and lower Yangtze River basin, but today exists only as a small and highly fragmented population of about 150 individuals in southeastern Anhui Province, in China. Breeding is occurring at approximately five sites within the National Chinese Alligator Reserve, established by the Chinese State Forestry Administration in the 1980s, but the habitat is composed almost entirely of highly modified natural wetlands around farming villages or small reservoirs. Captive breeding programs established in 1979 in Anhui and Zhejiang provinces have resulted in fewer than 10,000 animals in these two breeding centers. Although the number of animals in captivity is large, their genetic variability is relatively low. Analysis of mitochondrial and nuclear DNA indicates very limited variability (Wang et al. 2006). Though there have been no attempts to evaluate the genetic variability of the wild population, it is assumed to be similar to or less variable than that of the captive population as a result of its smaller number of individuals and the fact that the breeding groups were established in the 1980s by collecting as many individuals as possible from the wild population.

Small-scale trial efforts to reinforce existing wild groups of alligators or establish new breeding populations are now under way (Thorbjarnarson and Wang 2010), but their ultimate success will require a greater commitment to the protection of existing wetland sites and restoration of new areas for alligators and other wetland fauna in eastern China, as well as the development of a coordinated program to manage the captive and wild populations together as a metapopulation.

Lightly managed species. The third state is lightly managed species: species that rely on a relatively limited set of human interventions directed at both population enhancement and influencing extrinsic factors, such as habitat management. Species in this state are largely capable of sustaining themselves. Generally speaking, they will have a lower population size and a more restricted distribution compared with historic levels, but will still sustain redundant, healthy, genetically robust populations across ecologically representative settings unless some ecological settings have been extirpated. The key attribute of these species is their inability to maintain self-sustaining populations without long-term human management to sustain the resources on which they depend.

Lightly managed species are typified by the corncrake (*Crex crex*), a species of rail historically distributed across northern and central Eurasia and probably initially associated with riparian meadows. The species has maintained a patchy presence across much of its range—probably because of a strong association with agricultural areas managed for hay and silage—but habitat conversion and more intensive agricultural practices have led to reduced and even more fragmented populations (Schäffer and Green 2001). Because of a positive association with certain human-manipulated habitats, management of the species may be possible largely through policy directed at agricultural practices. Efforts are being made to protect suitable habitat, the European Union's Common Agricultural Policy mechanism has been used to provide premium payments for cattle grazing at reduced intensity, and both voluntary and compensation programs have been used to promote delayed, strip, and center-out mowing, activities that reduce chick mortality (Crockford et al. 1996). Theoretically, at least, this species is capable of maintaining populations as a result of long-term policies designed to promote crane-friendly agricultural practices, without actual management of the animals themselves.

Conservation-dependent species. The fourth state is conservation-dependent species, those that will almost always need significant conservation action directed not at management of intraspecific aspects such as feeding, breeding, or habitat management, but at extrinsic factors, necessitating changes in human behavior. This category is typified by species that have significant commercial value and will remain threatened by overexploitation for the foreseeable future.

Conservation-dependent species typically will be self-sustaining demographically and ecologically, at least across most of their range. They are likely to be genetically robust and meet the definition of healthy, at least in most places. Such species will usually satisfy the representation and replication attributes. Finally, in terms of resilience, conservation-dependent species may lose large parts of their current range as a result of climate change, human population growth, and expansion of agriculture and infrastructural development, but these species' tolerance of a wide range of habitat types suggests that they will be able to withstand such changes.

African forest elephants (*Loxodonta cyclotis*; here considered a separate species ranging from West Africa into the forests of the Congo basin and parts of East Africa; Roca et al. 2001) are an example of a conservation-dependent species. The distribution and status of forest elephants in West and central Africa is very different from other parts of their range. These populations are in trouble because of their small size, isolation, habitat loss, human–elephant conflicts, ineffective management, and poaching.

At first glance, the conservation status of forest elephants in central Africa would seem to benefit from very extensive areas of acceptable elephant habitat. However, despite occurring in relatively high numbers in some areas, central Africa's elephants have been, and continue to be, affected by large-scale poaching and declines in the extent and quality of their habitat as the region is opened to logging, mining, and concomitant increases in human populations. Thus, although African forest elephants are faring better than some species, reversing the declines and maintaining the attributes discussed in this article will require continual, intense human investment in elephant conservation. Forest elephants will also require management outside of protected areas, most of which are too small to contain them.

Self-sustaining species. Finally, the fifth state is self-sustaining, in which species express full levels of all the conservation attributes and can be expected to survive with little to no human subsidy directed intraspecifically or extrinsically. The status of these species is expected to remain stable unless conditions change; for example, if the species were suddenly demanded in trade or were faced with a new health threat. Self-sustaining species have redundant populations across a representative range of ecological settings, and their populations are healthy, genetically robust, and resilient; however, if populations have been recovered, as in the example below, then they may differ genetically from the original stock.

One example of a currently self-sustaining species is the peregrine falcon (*Falco peregrinus*). This species has a broad geographic distribution and occupies a fairly wide range of habitats, but because of its high trophic position it was vulnerable to the effects of bioaccumulation of organic contaminants in certain parts of its range. In North America, three subspecies were affected to differing degrees: *Falco peregrinus anatum* was extirpated east of the Mississippi River, depleted by up to 90% in the western United States,

and was listed as endangered under the ESA; *Falco peregrinus tundrius* populations declined up to 50% in the Arctic and the subspecies was listed as endangered; and populations of *Falco peregrinus pealei* in the Pacific Northwest remained largely unchanged (Cade 1982). Arctic populations began to increase by 1980 without management following the ban of DDT (dichlorodiphenyltrichloroethane) in 1972, and *F. peregrinus tundrius* was delisted in 1994. In the lower 48 states, *F. peregrinus anatum* populations grew following an intensive recovery effort and the subspecies was delisted in 1999 (White et al. 2002). Populations have remained stable or grown following cessation of recovery efforts and, in the absence of a new threat, are expected to remain viable and self-sustaining.

Conclusions

Modern species conservation efforts have been informed by a variety of approaches, sciences, and disciplines. In this article we address the role conservation biology has played in shaping the theory and practice of species conservation. Conservation biology has provided a scientific framework for species conservation that quantifies the risks of extinction and how many individuals must be conserved to avoid it. Within this framework, the avoidance of extinction has in certain quarters become synonymous with successful species conservation (Shaffer 1981). Meanwhile, the explosion in quantitative thinking and portfolio development that characterizes systematic conservation planning has concentrated almost exclusively on place-based conservation, leaving the question of rangewide species conservation largely untouched (Groves 2003).

The literature on species conservation remains largely focused on viability targets (e.g., Traill et al. 2009), continuing a long-standing debate over the appropriate way to assess minimum viable population sizes. A number of biologists have argued for a broader view of what should be considered necessary for conservation of populations (Soulé et al. 2003, Tear et al. 2005). Scott and colleagues (2005) looked at the US ESA and suggested the need to create a taxonomy of recovery based on the conclusion that most forms of species recovery will continue to involve some form of active management. After Scott and colleagues (2005) coined the term “conservation reliant” species, they demonstrated in a subsequent analysis (2010) that 84% of the species listed under the US ESA could be classified as “conservation reliant” and will require continuing, species-specific interventions.

Much of the conservation biology literature on species conservation is focused on the conservation of only a population or set of populations. We built on this literature to make the case for redefining species-level conservation, laying out a framework for defining successful species conservation using a set of continuously distributed attributes, most of which are well defined and have been written about extensively (with the exception of the health attribute, which is a relative newcomer to conservation biology). We chose

these attributes because we believe they comprise the essential characteristics of a successfully conserved species.

On the basis of these six attributes we define successful species conservation as maintaining multiple populations across the range of the species in representative ecological settings, with replicate populations in each setting. These populations should be self-sustaining demographically and ecologically, healthy, and genetically robust—and therefore resilient to climate and other environmental changes.

Many species, particularly those of conservation concern, do not exhibit the full range of these attributes. However, keeping in mind what “success” would look like, even if it is not currently possible, is a critical component of our framework that should inform the course of recovery work. The predominant thinking in conservation today advocates simply reducing threats to species in hopes they will gradually return to prelapsarian states of full conservation. Recognizing that this baseline species concept does not, and perhaps never did, exist, we have laid out a continuum of conservation states, most of which are well below the condition of fully conserved. The continuum is based on two sets of management actions that operate in opposite directions. At the “captive managed” end of the continuum, most management is directed at intraspecific actions having to do with ensuring food supplies, successful breeding, and maintenance of genetic diversity. The other set of management actions, most fully expressed at the “conservation dependent” point on the continuum, is directed at managing human behavior to allow species to fully manifest their attributes independent of direct intervention. Fully conserved species, by definition, are largely free of direct human management of any sort.

This illustrative set of states can reorient the discussion on species recovery, a concept that has been much discussed but little defined. Recovery should not be considered as a single state but as multiple states. As environmental changes increase in speed and extent, recognizing multiple states is not only important for conservation planning but it also more closely reflects the reality of the practice of species conservation. Although conservation action can move species from one state to another, not all species can be moved to a fully conserved state. We must view captive management as only a stop-gap measure in efforts to move species up the continuum.

A commitment to long-term conservation success requires that conservationists maintain species attributes that have enabled species to persist into the present era and the potential to express these attributes in the future. Thus, researchers must try to understand species’ recent historic distribution, abundance, genetic diversity, and ecological roles and ensure that these attributes are maintained over time. Humans need to encourage and allow species to exhibit variation, speciation, dispersal, evolution, and therefore adaptation in a changing world.

Our framework erases the binary classification of “captive” and “wild” species, as there is a gradation in management action between the two at both the population and

species level. In recent decades, there has been an increase in the number of species conservation efforts that link captive breeding or rearing programs with the restoration or bolstering of wild populations. As habitat losses and global climate shifts proceed, it is expected that greater numbers of species will require intensive demographic, health, and genetic management.

The shift beyond a focus on threatened, vulnerable, and endangered species helps move the conservation community toward addressing Gaston's (2010) concerns about the lack of attention to the population trajectories of common species and the ecological importance of abundance. Gaston pointed out that waving attention away from common species of no conservation concern may cause us to miss very important ecological impacts of decreases in species numbers. Questions are beginning to emerge about the important role played by common or abundant species, for example through physical movement (e.g., jellyfish and their brethren; Dewar 2009) or ecosystem functions (e.g., water filtering from oyster reefs [Schulte et al. 2009], carbon sequestration by wildebeest herds [Holdo et al. 2009], and seed dispersal by birds [O'Brien et al. 2005] and bats [McConkey and Drake 2006]). A focus only on species near extinction will cause conservationists to overlook a wide array of important conservation issues—just as health care practiced only at the door of the hospital emergency room will never slow the tide of patients in need of critical care. Conservationists need the equivalent of preventative health care, derived from a positive vision of a fully conserved species.

The focus of this article has been on a set of larger-bodied vertebrate species with broad geographic distributions. We recognize that most species have very limited geographic distributions but see no reasons that the arguments we have advanced here could not be scaled to all species. This article does not address the species that will increase in numbers as a result of these same changes—those that thrive in settings modified for human use. Instead, our focus is on those species whose existence has seemed too often at odds with human uses and desires.

Conservation biologists must have a framework for thinking that includes targets for species recovery, as well as extinction avoidance. With this in mind, we stress that the categories and criteria used in the IUCN Red List of Threatened Species serve to assess the relative extinction risk of species (IUCN-SSC 2001, Mace et al. 2008). The 2010 biodiversity target, the objective of which by 2010 is a “significant reduction of the current rate of biodiversity loss” (www.twentyten.net/about/2010biodiversitytarget), is an example of a target with insufficient ambition, focusing on slowing down bad things rather than achieving good things. We believe that future conservation targets should be based on desirable conservation outcomes, not merely on extinction avoidance.

Conservationists have often taken defensive stands in their positions, objecting to the actions of others rather than proposing what they think should be done. Some of

the early enthusiasm has turned to pessimism and even catastrophism that we believe inhibits the creative search for new solutions. We need a new, optimistic conservation biology, one that recognizes the rising dangers to the natural world while abjuring extinction and seeking to ward off the latest threat and create the conditions through which the planet's biological systems, of which species are a key part, can be sustained and helped to thrive long into the future. Working to achieve positive goals would build on a vision for conservation success for each species that incorporates our proposed attributes. Our experience from working on a variety of species conservation projects tells us that developing such a positive vision with a broad range of stakeholders produces a positive atmosphere, facilitates cooperation, and allows for development of essential partnerships and political support. Recent advances in psychology (e.g., Kaplan and Kaplan 2009) and the rise of conservation psychology (Clayton and Myers 2009) reinforce the importance of hope in bringing about change and the existence of tools for helping humanity do so.

We fully recognize that conservation cannot be achieved by biologists alone, or with only the use of conservation biology tools. A vital element of successful species conservation that we have not included in our examination is unending vigilance. In a world marked by pervasive human impacts, constant attention must be paid to changes in economic drivers, land-use change, and the effects of a changing climate. Moving beyond biological values is essential for increasing the importance and effectiveness of species conservation, and incorporating sustainability of both extractive and nonconsumptive use (Robinson 1993).

Conservation biology is a self-acknowledged “value-laden” discipline with strong ethical roots, including a conviction of the rights of all forms of life (Meine et al. 2006). The question of what it means to conserve a species does not have a single empirical answer. The answer depends on the values of those asking the question (e.g., Sanderson 2006), which are all too often elided or poorly understood. The values underlying our definition of successful species conservation are unabashedly biocentric—a belief that extinction is a bad thing; a belief in the intrinsic value of life on Earth as well as the importance of this richness in realizing the fullness of human existence. We work toward a world in which species will be conserved not at minimum population sizes, but in ecologically and evolutionarily significant numbers—a rich world for human and nonhuman species.

Acknowledgments

We would like to dedicate this article to John Thorbjarnarson, a world-class herpetologist and conservationist valued by people from China to Brazil and a treasured colleague at the Wildlife Conservation Society, who died suddenly in February 2010. He will be sorely missed by many. We would like to thank the White Oak Conservation Center and its director, John Lukas, for their

continued support of the Wildlife Conservation Society and its conservation partners. We would also like to thank Eva Fearn and particularly Catherine Grippo for support in preparing this article.

References cited

- Alford RA, Bradfield KS, Richards SJ. 2007. Ecology: Global warming and amphibian losses. *Nature* 447: E3–E4.
- Bakker J, van Rijswijk M, Weissing F, Bijlsma R. 2010. Consequences of fragmentation for the ability to adapt to novel environments in experimental *Drosophila* metapopulations. *Conservation Genetics* 11: 435–448.
- Beissinger SR, McCullough DR. 2002. *Population Viability Analysis*. University of Chicago Press.
- Beldomenico PM, Begon M. 2010. Disease spread, susceptibility and infection intensity: Vicious circles? *Trends in Ecology and Evolution* 25: 21–27.
- Botkin DB. 1990. *Discordant Harmonies: A New Ecology for the 21st Century*. Oxford University Press.
- Cade TJ. 1982. *The Falcons of the World*. Cornell University Press.
- Caughley G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63: 215–244.
- Channell R, Lomolino MV. 2000. Trajectories to extinction: Spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography* 27: 169–179.
- Channing A, Howell K, Loader S, Menegon M, Poynton J. 2009. *Nectophrynoides asperginis*. International Union for Conservation of Nature Red List of Threatened Species. Version 2009.2. IUCN.
- Clayton S, Myers G. 2009. *Conservation Psychology: Understanding and Promoting Human Care for Nature*. Wiley.
- Conner RN. 1988. Wildlife populations: Minimally viable or ecologically functional? *Wildlife Society Bulletin* 16: 80–84.
- Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK. 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution* 15: 290–295.
- Crockford N, Green R, Rocamora G, Shäffer N, Stowe T, Williams G. 1996. Action Plan for the Corncrake (*Crex crex*) in Europe. BirdLife International.
- Daszak P, Cunningham AA, Hyatt AD. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287: 443–449.
- Dewar WK. 2009. Oceanography: A fishy mix. *Nature* 460: 581–582.
- Dinerstein E, et al. 2007. The fate of wild tigers. *BioScience* 57: 508–515.
- Elith J, Leathwick JR. 2009. Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.
- Frankel OH. 1974. Genetic conservation: Our evolutionary responsibility. *Genetics* 78: 53–65.
- Frankham R, Hemmer H, Ryder OA, Cothran EG, Soulé ME, Murray ND, Snyder M. 1986. Selection in captive populations. *Zoo Biology* 5: 127–138.
- Garner TWJ, Walker S, Bosch J, Leech S, Rowcliffe JM, Cunningham AA, Fisher MC. 2009. Life history tradeoffs influence mortality associated with the amphibian pathogen *Batrachochytrium dendrobatidis*. *Oikos* 118: 783–791.
- Gaston KJ. 2009. Geographic range limits: Achieving synthesis. *Proceedings of the Royal Society B* 276: 1395–1406.
- . 2010. Valuing common species. *Science* 327: 154–155.
- Groves CR. 2003. *Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity*. Island Press.
- Hedrick PW. 2001. Conservation genetics: Where are we now? *Trends in Ecology and Evolution* 16: 629–636.
- Holdo RM, Sinclair ARE, Dobson AP, Metzger KL, Bolker BM, Ritchie ME, Holt RD. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem conservation. *PLoS Biology* 7: 1–12.
- Holling CS. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1–23.
- Hutchins M, Smith B. 2003. Characteristics of a world-class zoo or aquarium in the 21st century. *International Zoo Yearbook* 38: 130–141.
- [IUCN-SSC] International Union for Conservation of Nature Species Survival Commission. 2001. *IUCN Red List Categories*. Version 3.1. IUCN.
- . 2008. *Strategic Planning for Species Conservation: A Handbook*. Version 1.0. IUCN.
- Kaplan S, Kaplan R. 2009. Creating a larger role for environmental psychology: The reasonable person model as an integrative framework. *Journal of Environmental Psychology* 29: 329–339.
- Lochmiller RL. 1996. Immunocompetence and animal population regulation. *Oikos* 76: 594–602.
- Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland EJ, Stuart SN. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology* 22: 1424–1442.
- McConkey KR, Drake DRR. 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* 87: 271–276.
- McDonald-Madden E, Baxter PWJ, Possingham HP. 2008. Subpopulation triage: How to allocate conservation effort among populations. *Conservation Biology* 22: 656–665.
- Meine C, Soulé M, Noss RF. 2006. “A mission-driven discipline”: The growth of conservation biology. *Conservation Biology* 20: 631–651.
- O'Brien TG, Kinnaird M, Groom MJ, Coppolillo P. 2005. Ecologically functional populations. Pages 435–438 in Groom MJ, Meffe GK, Carroll R, eds. *Principles of Conservation Biology*. 3rd ed. Sinauer.
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–639.
- Rabb GB, Saunders CD. 2005. The future of zoos and aquariums: Conservation and caring. *International Zoo Yearbook* 39: 1–26.
- Redford K, Sanjayan MA. 2003. Retiring Cassandra. *Conservation Biology* 17: 1473–1474.
- Robinson JG. 1993. The limits to caring: Sustainable living and the loss of biodiversity. *Conservation Biology* 7: 20–28.
- Roca AL, Georgiadis N, Pecon-Slattery J, O'Brien SJ. 2001. Genetic evidence for two species of elephant in Africa. *Science* 293: 1473–1477.
- Sanderson EW. 2006. How many animals do we want to save? The many ways of setting population target levels for conservation. *BioScience* 57: 911–922.
- Sanderson EW, Redford KH, Chetkiewicz C-LB, Medellin RA, Rabinowitz RA, Robinson JG, Taber AB. 2002. Planning to save a species: The jaguar as a model. *Conservation Biology* 16: 1–15.
- Sanderson EW, et al. 2008. The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conservation Biology* 22: 252–266.
- Schäffer N, Green RE. 2001. The global status of the corncrake. *Royal Society for the Protection of Birds Conservation Review* 13: 18–24.
- Schulte DM, Burke RP, Lipcius RN. 2009. Unprecedented restoration of a native oyster metapopulation. *Science* 325: 1124–1128.
- Scott JM, Goble DD, Wiens JA, Wilcove DS, Bean M, Male T. 2005. Recovery of imperiled species under the Endangered Species Act: The need for a new approach. *Frontiers in Ecology and the Environment* 3: 383–389.
- Scott JM, Goble DD, Haines AM, Wiens JA, Neel MC. 2010. Conservation-reliant species and the future of conservation. *Conservation Letters* 3: 91–97.
- Shaffer ML. 1981. Minimum population sizes for species conservation. *BioScience* 31: 131–134.
- Shaffer ML, Stein BA. 2000. Safeguarding our precious heritage. Pages 301–322 in Stein BA, Kutner LS, Adams JS, eds. *Precious Heritage: The Status of Biodiversity in the United States*. Oxford University Press.
- Shaffer ML, Watchman LH, Snape WJ, Latchis IK. 2002. Population viability analysis and conservation policy. Pages 123–142 in Beissinger SR, McCullough DR, eds. *Population Viability Analysis*. University of Chicago Press.
- Shea K, NCEAS Working Group. 1998. Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution* 13: 371–375.

- Simberloff D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* 19: 473–511.
- Smith KF, Acevedo-Whitehouse K, Petersen AB. 2009. The role of infectious diseases in biological conservation. *Animal Conservation* 12: 1–12.
- Soulé ME, Estes JA, Berger J, Del Rio CM. 2003. Ecological effectiveness: Conservation goals for interactive species. *Conservation Biology* 17: 1238–1250.
- Soulé ME, Estes JA, Miller B, Honnold DL. 2005. Strongly interacting species: Conservation policy, management and ethics. *BioScience* 55: 168–176.
- Svancara LK, Brannon R, Scott JM, Groves CR, Noss RF, Pressey RL. 2005. Policy-driven versus evidence-based conservation: A review of political targets and biological needs. *BioScience* 55: 989–995.
- Tear TH, Scott JM, Hayward PH, Griffith B. 1995. Recovery plans and the Endangered Species Act: Are criticisms supported by data? *Conservation Biology* 9: 182–195.
- Tear TH, et al. 2005. How much is enough? The recurrent problem of setting measurable objectives in conservation. *BioScience* 55: 835–849.
- Thorbjarnarson J, Wang X. 2010. *The Chinese Alligator: Ecology, Behavior, Conservation and Culture*. Johns Hopkins University Press.
- Thorbjarnarson J, et al. 2006. Regional habitat conservation priorities for the American crocodile. *Biological Conservation* 128: 25–36.
- Traill LW, Brook BW, Frankham RR, Bradshaw CJA. 2009. Pragmatic population viability targets in a rapidly changing world. *Biological Conservation* 143: 28–34.
- Walker B, Salt D. 2006. *Resilience Thinking: Sustaining Ecosystems and People in a Changing World*. Island Press.
- Wang Y, Zhu W, Huang H, Zhou K, Wang R. 2006. Genetic diversity of Chinese alligator (*Alligator sinensis*) revealed by AFLP analysis: An implication on the management of captive conservation. *Biodiversity and Conservation* 15: 2945–2955.
- White CM, Clum NJ, Cade TJ, Hunt WG. 2002. Peregrine falcon (*Falco peregrinus*). In Poole A, ed. *The Birds of North America Online*. Cornell Lab of Ornithology. (25 October 2010; <http://bna.birds.cornell.edu/bna/>)
- Wikramanayake ED, et al. 1998. An ecology-based method for defining priorities for large mammal conservation: The tiger as case study. *Conservation Biology* 12: 865–878.

Kent H. Redford (kredford@wcs.org), Elizabeth L. Bennett, Nancy Clum, Robert Cook, Simon Hedges, John G. Robinson, Howard Rosenbaum, Eric W. Sanderson, and Patrick Thomas are with the Wildlife Conservation Society. George Amato is director of the Sackler Institute for Comparative Genomics at the American Museum of Natural History. Jonathan Baillie is director of conservation programs at the Zoological Society of London. Gustavo Fonseca is the natural resources team leader at the Global Environment Facility. Frederic Launay is chief executive officer at Al Ain Wildlife Park and Resort, United Arab Emirates. Susan Lieberman is deputy director of the Pew Environment Group. Georgina M. Mace is a professor, and Akira Murayama is a PhD candidate, at the Centre for Population Biology at Imperial College London. Andrea Putnam is a postdoctoral researcher at Princeton University. Simon N. Stuart is chair of the International Union for Conservation of Nature Species Survival Commission. At the time of this article's preparation, John Thorbjarnarson was with the Wildlife Conservation Society.