COLLECTED PAPERS OF

Michael E. Soulé

EARLY YEARS IN MODERN
CONSERVATION BIOLOGY

INTRODUCTION BY JAMES A. ESTES

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BIOLOGY

by Michael E. Soulé
with Robert L. Peters

CONTENTS

This volume is a collection of previously published seminal papers written by Michael E. Soulé and his coauthors documenting the birth and development of the modern science of conservation biology over the past thirty years. Dr. Soulé, in collaboration with Robert L. Peters, has written a new introduction to each paper that places it in the context of the time and circumstances under which it was written and its importance to the field.

We have chosen to set the papers, which range from journal articles to book chapters, in a consistent format and typeface. We have corrected some typographical and minor errors but have otherwise retained the text, style, documentation, and idiosyncrasies of the originals. We have also removed abstracts and metadata and other associated information provided by the original publishers and have re-created figures based on the originals. Full publishing information for each paper can be found in the Permissions and Original Sources section in the back matter.

Conservation is not a new idea. The first Buddhist king of India, Ashoka, issued the famous Edicts of Ashoka, inscribed on pillars, that established a network of wildlife preserves around 300 BCE. The inscriptions on some of these stone monuments urged tolerance and protection of wildlife, consistent with the moral precepts of Buddhism. The belief that nature (Creation) is inherently good was also enshrined in the slightly older Jewish Pentateuch. The composition of the Pentateuch is thought to have consolidated about 500 BCE.

Notwithstanding the Pentateuch's admonition that Creation is good, Western civilization's commitment to this warning has been dwindling for centuries. Sadly, in recent times science itself has emerged as a potent agent in humanity's global conquest. The biological sciences have turned back on biology, so that the fields of agriculture, medicine, and biotechnology now multiply the effects of the population explosion, probably the major driver of biodiversity loss. And corporations continue to commodify the commons—the water and air—with a perspective symbolized by the anthropocentric term "natural resources."

To be fair, however, blame for nature's diminution is more subtle and dispersed. The roots of the biodiversity crisis go deeper than science and industry, deeper than capitalism and Wall Street. This is because our hypersocial, competitive, primate nature insists that we, the people, struggle for status, stuff, and stunning mates, impelling most of us to compete in virtually all social contexts. As the lyrics from "As Time Goes By" in the classic film *Casablanca* insist: "It's still the same old story / The fight for love and glory / A case of do or die."

My personal fight for glory was subsidized by a Guggenheim Fellowship that enabled my family to live in Australia while I was on sabbatical leave (1973–1974) from the University of California, San Diego. Shortly after settling into my office in the Animal Genetics laboratory of the Commonwealth Scientific and Industrial Research Organization just north of Sydney, I got a phone call from Otto Frankel, a renowned wheat geneticist and transplanted Austrian. Frankel was interested in the protection of traditional crop cultivars. He had read my research publications on the diversification and variability of side-blotched lizards on islands in the Gulf of California and believed that the findings might be relevant to "genetical conservation."

Frankel, who died in 1998 at the age of 98, wanted to discuss my conclusion that the morphological variability in island populations was correlated with the size of the island, a surrogate for population size. By then I was starting to employ starch-gel electrophoresis of proteins to see if the same relationship held at the level of genetics. Indeed, the larger the island the more the genetic variation (heterozygosity) existed in that island's side-blotched lizards. This was the first time such a relationship had been demonstrated in nature.

I believed the "genetic-phenetic" correlation was salient evolutionarily because the amount of genetic variation in a population can limit how fast that population can adapt by natural selection to changing environments. This relationship is now more relevant than ever because rapid climate change and poleward-shifting habitats will severely test the adaptability of many species, particularly in fragmented landscapes. From this century on, the law for survival will be "migrate, evolve, or perish."

What to do? In 1985, some colleagues and I formed the Society for Conservation Biology because we felt compelled to respond to the unprecedented scale and rate of human assaults on nature that had begun to be documented in the 1960s. We thought then, and I still believe, that the reduction of biological diversity of the planet is the most catastrophic issue of our era. Moreover, as scholars, agency biologists, and zoo curators and officials, we believed that

our knowledge might help in the fight to protect nature. Some of us also believed that genetics was being ignored by institutions such as zoos and that "conservation genetics" was one of several new approaches that must be foundational elements in this new discipline.

In the thirty-some years since the Society's founding, conservation biologists have grown in number and influence. Many colleges and universities initiated majors and graduate programs in conservation biology. Membership in the Society for Conservation Biology exploded, reaching a peak of 10,000 before relaxing back to a more humble magnitude. Of course, a large tally of experts in project or field is not a sign of success. As Aldo Leopold wrote in part 3 of *A Sand County Almanac*:

> In 1909, when I first saw the West, there were grizzlies in every major mountain mass, but you could travel for months without meeting a conservation officer. Today there is some kind of conservation officer "behind every bush," yet as wildlife bureaus grow, our most magnificent mammal retreats steadily toward the Canadian border. (*A Sand County Almanac: And Sketches Here and There*, 1966, p. 198.)

Nevertheless, we can mark some important accomplishments. Conservation biologists helped (and still help) to create many new protected areas in the developing world, and we have been instrumental in pulling some species, like the California condor and the black-footed ferret, back from the brink of extinction.

This rather personal book is a kind of history of one biologist's collaborative effort to combine scholarship and activism in the service of nature. It is also a personal history of the origin and development of conservation biology. I hope that it will encourage those at the beginning of their careers and those already established to ask themselves if their lives and works have helped the "others" that cannot speak or write but whose eloquence is projected in their grace, their beauty, and their determination to live and reproduce.

Also, I hope it will inspire younger biologists and citizen scientists to receive and pass on the lamp of compassion for the wild and carry it to the myriad places and communities in need of more light.

Is there a future for the world of creatures, the survivors of the Pleistocene? I say in one of my essays that I believe in "possibilism." By this I mean that I am neither a pessimist nor an optimist, but that I believe that it is still *possible* to save diverse and beautiful creatures and self-willed places and for the dominant species to awaken to the intrinsic value of biological diversity.

Another way to express my feelings is this: Conservation Is Another Way to Love. I believe that conservationists are lovers of the wild, the untrammeled, motorless, self-willed, life-filled places, those remote and even those in the "vacant" lot down the street.

Finally, my tireless, loving wife Joli Soulé provided constant tangible and emotional support throughout this project. Thank you, Joli.

<div align="right">Michael E. Soulé</div>

Introduction

James A. Estes

Until recently, humans perceived wild nature as a vast unknown—something to be feared; something to be conquered; and something that was inexhaustible. There is nothing in our evolutionary history, and thus nothing in our genes, to make us feel and behave otherwise. Despite the popular perception of primitive peoples as wise stewards of natural resources, most early cultures probably exploited natural resources to their maximum abilities. Then as now, the rates of resource exploitation and utilization were linked to survival, power and wealth, and overall quality of life. Although such claims are difficult to demonstrate in the absence of written language, accounts of collapsed civilizations (Diamond 2005) together with a growing weight of evidence for human-caused extinctions of many large vertebrates (Martin 2007, Koch and Barnosky 2006) make me doubt that ancients lived with much in the way of a conservation ethic. The same is true for the period of exploration and discovery by modern societies. Magellan, Columbus, Cook, Bering, Lewis and Clark, and even Darwin—none of the early explorers had reason to think about, much less worry over, conservation. After all, their charge was to

conquer and transform the spoils of their conquests into profits, not to conserve. Thomas Huxley's errant advice to cod fishers in the North Atlantic—continue trawling despite the fishermen's own concern for stock collapse (Kurlansky 1997, Roberts 2007)—captures the prevailing view of nature and natural resources as well as any. The notion of conservation, defined as the measures needed to provide for a sustainable future, was simply not part of our early lexicon.

This all began to change as human numbers marched steadily upward. Recognition of nature's limits in the face of growing populations can be traced back at least to the eighteenth century writings of Thomas Malthus. This principle of population biology—the notion of environmental carrying capacity—was formalized in the logistic growth equation [$dN/dt = rN(1 − N/K)$, where N = population size, r = the intrinsic rate of population increase, and K = environmental carrying capacity]. The logistic growth equation led to the famous Lotka-Volterra competition equations (a simple expansion of the logistic in which two species are limited by a common resource) and subsequently to the first serious efforts to conserve and manage exploited populations of wild plants and animals. Beverton and Holt's (1957) treatise on the biology of exploited populations is a famous example directed primarily at fisheries management. Earth scientists recognized and had become concerned about the finite nature of geological resources even earlier, as evidenced by warnings from such well known people as John Wesley Powell, founding director of the US Geological Survey. Awareness of the need for conservation continued to build into the early twentieth century, no doubt influencing the landmark policies of Teddy Roosevelt's administration.

My point is that a human recognition of the need to conserve natural resources, while thought of by many as something quite recent, in fact has been around for a while. But like most creative human endeavors, the growth of the conservation movement seems to be characterized by long periods of stasis followed by short periods of rapid change. These periods of rapid change are often pushed forward by men and women with two special qualities—the vision to

see what is needed and the charisma and strength of character to draw others along with them. Through the first half of the twentieth century, people like John Muir, Rachel Carson, and Aldo Leopold indelibly influenced the pathway of conservation. History will no doubt add Michael Soulé to this list of influential conservationists.

The impacts of leaders in the conservation movement commonly arise through philosophical transformations that occur during their own lives. Aldo Leopold, arguably the most revered figure in the history of conservation, was a game manager by training who began his career with the US Forest Service during the era of predator control. Early in his professional life, he sought to enhance wildlife by regulating human exploitation while at the same time minimizing losses to predators. Later he came to realize the shortcomings of his early beliefs, embracing a more holistic view of ecology, management, and environmental ethics that was articulated in the poignant prose of his enduring classic, *A Sand County Almanac* (Leopold 1949).

Despite messages for conservation by the movement's early visionaries, natural resource conservation turned in a different direction through the middle decades of the twentieth century—toward the objective of a maximum sustainable yield. A maximum sustainable yield is the ideal of taking as many as possible from an exploited population, while at the same time not so many as to cause that population to collapse. This ideal became the mantra of natural resource management, surfacing as the integrating principle in our efforts to conserve the three main elements of wild living nature—fish, wildlife, and forests. Programs in wildlife biology, fisheries science, and forestry emerged to conduct research and train the next generation of practitioners on how to achieve sustainable yields.

The practices and beliefs that grew out of wildlife, fisheries, and forestry science did not encompass much of what would eventually become conservation biology. Movement in that direction lay largely dormant from the time of Leopold's death in 1948 through the 1960s. Even today, conservation and management conjure up different images, at least in my mind. Management, as I think of it, involves the manipulation of species and habitats for direct and

immediate human benefit, whereas the chief goal of conservation is the maintenance of biodiversity. A tension between these views and philosophies can be seen almost everywhere as modern-day natural resource managers and conservationists struggle to define a way forward. Through the mid decades of the twentieth century, the key disciplinary elements of what would eventually coalesce into what was first called "Conservation Biology" and has more recently been termed "Conservation Science"—ecology, natural resource management, genetics, economics, and environmental ethics—developed mostly in isolation of one another.

As human populations have continued to grow, as technologies have continued to develop, and as the economic imperative of an increasingly democratic global society has ever more strongly pressed natural resources to fuel this imperative, limits to growth and the sustainable use of natural resources inevitably have resurfaced as questions of increasing concern. No rational modern person could deny the fundamental truth in this vision of our planet's future. But the devil is in the details. Just what are the limits to growth, and as we continue to proceed along that path how can we preserve the rest of the natural world for our own future and the generations to come? These are the questions that a small number of biologists, economists, philosophers, and others began asking again in earnest a few decades ago. The result was the birth of modern conservation biology. Michael Soulé had a strong hand in that endeavor and as a result is sometimes referred to as the father of conservation biology.

I was deeply honored when Barbara Dean asked me to write an introduction to the volume. But after agreeing to do this, I faced the question of what to say. I decided to begin with a retrospection—admittedly my own view—of how and why conservation biology came to be. I've done that, briefly and superficially, in the proceeding pages. My focus from here forward will be on Michael Soulé—his history, especially during the period of our acquaintance; his contribution to conservation biology as we know it today; and his sundry influences on the infrastructure of conservation. I'll end with a look to the future, considering in particular the recently emerged

and charged debate over what conservation science is and should become going forward.

Michael grew up in southern California where as a child he fell in love with nature by roaming the area's then undeveloped chaparral canyons. After graduating from high school, he attended San Diego State University as an undergraduate and Stanford University as a graduate student. He studied with Paul Ehrlich at Stanford, whose concerns over human population growth and its resulting environmental effects profoundly influenced Michael's own intellectual development. By this point his career path was established.

Upon completing his doctorate, Michael took a faculty position in the Biology Department at the University of California at San Diego. But his life in San Diego was filled with turmoil as he watched the wild canyons of his childhood succumb to development. Just a few years later he resigned his faculty post at UCSD and moved to a Buddhist commune in Los Angeles where he sought a new peace and understanding. That experience was transformative to his perceptions of self and human behavior. But Michael's love of nature and his desire to help protect it were unfulfilled, and so he left the confines of spiritual study and returned to academia, this time with the Department of Natural Resources at the University of Michigan. Michael emerged as a leader in the developing science of conservation biology during his years at Michigan, helping found the Society for Conservation Biology, serving as the Society's first president, and writing several influential books on the then nascent science of conservation biology. Michael left Michigan in 1989 to revitalize the then foundering Environmental Studies program at the University of California at Santa Cruz. He retired from UCSC in 1996 and moved to southwestern Colorado where he has continued to pursue the fulfillment of his vision for the needs of conservation.

I had first learned of Michael Soulé in the early 1970s during a visit to San Diego, my home town. I was still a graduate student at the time. My mother, who was not a scientist or even an amateur naturalist, was appalled by the unregulated and rampant development of San Diego County. She had heard Michael speak about the

perils of human population increase, was influenced by the force of his logic and personality, and asked me if I knew of him. I didn't at the time, but I later would as interest in conservation biology literally exploded and Michael assumed a leading role in that movement during the late 1970s and 1980s. We met briefly in 1988 in Davis during SCB's first symposium on marine conservation. He struck me then as a man of substance and purpose. We met again when he interviewed for the directorship of Environmental Studies at UCSC. Michael was offered and accepted the job, moved to Santa Cruz later in 1989, and soon thereafter we became professional associates and close personal friends.

I worked with Michael during the first year of the Clinton administration in an unsuccessful attempt to convince the newly created National Biological Survey to locate their California field station at UC Santa Cruz. Michael argued that Santa Cruz would both provide the best intellectual infrastructure for moving the young agency into the arena of conservation biology and serve as a genuine academic collaborator. He tried to convince the powers that were in the Department of the Interior that UCSC and their newly formed agency shared a common ideal and UCSC therefore would provide more than just a place to be. But in the end we lost out to UC Davis, ostensibly because of their higher prestige in ecology and close proximity to Sacramento. The Davis connection eventually collapsed and the California Science Center moved to Sacramento State University, where it presently resides.

Although my endeavor to help Michael build a viable program in conservation biology at UC Santa Cruz never amounted to much, our friendship did. In thinking back over my life as a naturalist, an ecologist, and a conservation biologist, Michael was one of three people who most strongly influenced my own path. The first of these people was my uncle, Frank Springer, a small town physician in western Wisconsin who over the course of my childhood instilled in me a spirit of romance and adventure, and later convinced me to study biology. The second was the eminent ecologist Robert T. Paine, who opened my eyes to the wonders of ecology and taught

me how to learn about these things. And the third was Michael, who helped me define my soul. He did this over the course of our many conversations through his intellect, his openness, his honesty, his charisma, and his depth of understanding of so many things.

The same qualities that drew me to Michael Soulé as a friend and respected colleague also led him to become the single most important force in the development of modern conservation biology. This influence arose further from the interplay of his science and his leadership. There are many strong leaders and there are many excellent scientists. But very few people do both well. Michael is one of those few.

Michael's leadership has come in various ways, some of which are obvious and others less so. He built the very foundations of modern conservation biology by helping to establish the Society for Conservation Biology and then serving as the Society's founding president. He led the development of the Environmental Studies Program at UC Santa Cruz by establishing and then putting in place a vision for research and training in conservation biology, one I might add that emphasized an integration of the natural and social sciences. As Chair of Environmental Studies, he convinced the university to embrace this vision and then cajoled them into providing the human, physical, and financial resources required to move it forward. From the outset Michael recognized the multidimensional and multidisciplinary aspects of what conservation biology needed to be, and with that view in mind he repopulated the Environmental Studies faculty with a cohort of bright new junior faculty from the natural and social sciences. The downside of doing this was living with the often fundamentally different approaches, standards, and philosophies of academics in the natural and social sciences. Then as now, the disagreements were over the needs of people versus the welfare of nature. Michael pressed his agenda forward through all this, not always with a gentle hand. At the same time he mentored a number of graduate students and junior faculty who themselves have gone on to become leaders in the next generation of conservation biologists.

Michael has helped lead the science of conservation biology in two main ways—through his hands-on research, some of which was done in collaboration with students and other colleagues; and through the organization of workshops and symposia designed to address key issues in the emerging science of conservation biology. The papers reprinted in this anthology are a sampling of Michael's essays, reviews, and empirical studies from the peer-reviewed literature and from the various books he organized, wrote or helped write, and published or co-published.

Looking back across Michael's body of scientific work, it is possible to identify three main dimensions that define his view of conservation biology. The first of these is population viability. Biodiversity conservation is and always has been Michael's most deeply rooted objective. In its simplest form, the conservation of biodiversity is akin to preventing extinction. And for species to avoid becoming extinct, they must persist as viable populations. This simple idea underpins much of what Michael has to say in the first four papers. In particular, the fourth, "Conservation Biology and the 'Real World,'" is a classic that asks the question, how many species and how many individuals of each species must we humans prevent from going under through the extinction crisis? A more detailed series of analyses and discussions are available in Michael's edited volume on the subject (Soulé 1987). The appeal of a population viability analysis is almost visceral because it specifies, for any desired range of future scenarios, the probabilities of and/or expected times to extinction. These questions and approaches, pioneered by Michael and his colleagues, resonated with natural resource managers and applied ecologists, as evidenced by the subsequent explosion of methods and analyses. "How to" books have since been written, detailing what are often highly quantitative methods and even providing the code necessary for their specific application. Virtually every new or revised recovery plan for a threatened and endangered species under the US Endangered Species Act includes some sort of population viability analysis. Often these analyses define the most scientifically objective and substantive part of the recovery planning process.

A second dimension in the Soulé science legacy is conservation genetics. Michael's training and basic scientific interests revolved strongly around evolutionary biology. His early work on island-lizards in the Gulf of California focused on isolation, adaptation, and speciation, which among other things led to major contributions in the study of bilateral asymmetry (Soulé 1967, 1982). From the outset of his life as a naturalist, he has understood that populations are not simple collections of similar individuals but instead that those individuals vary to one degree or another in their genetic makeup. Michael understood further that this genetic variation is an essential part of biodiversity because it counters the deleterious effects of inbreeding, allows populations to adapt to diverse and varying environments, and provides the substrate for future evolutionary change in an ever-changing world. Michael's voice on recovery teams (outside experts appointed by the responsible federal agency [usually the US Fish and Wildlife Service] to write recovery plans for species or populations listed as threatened or endangered under the Endangered Species Act) often addressed ways to maintain and promote genetic diversity in critically endangered species. Only the paper "Conservation Genetics and Conservation Biology: A Troubled Marriage" focuses specifically on conservation genetics. But the issue is addressed or surfaces in several other papers and, at least from my perspective, delineates a significant part of Michael's contribution to both science and policy in conservation biology.

A third dimension to Michael's contribution to conservation science and policy is what he refers to as "ecological effectiveness." As noted above, population viability analysis helps promote biodiversity by defining the minimum number of individuals needed to prevent extinction of some particular species or population. Ecologically effective population size is something very different. The notion and the term derive from one of the most important processes in all of ecology—species interactions. All species interact with many other species as predators and prey, competitors, or mutualists. These interactions link together into what Christian Ziegler and Egbert Leigh (2002) aptly called "a magic web." Embedded within this

magic web of species interactions are what R. T. Paine (1969) first referred to as "keystones," species whose influences on the interaction web's structure and function are so wide-ranging and profound that they are essential in holding the web together in any semblance of its natural self. Very often these keystones are the apex predators, which de facto are those species most prone to extinction in human-altered ecosystems and fragmented landscapes.

One of the main ways in which keystone species hold systems together is via trophic cascades, the progressive influence of predators downward through food chains and food webs that ultimately affects the abundance of plants and other more basal species. Most ecologists are now familiar with both the concept of a trophic cascade and the rapidly growing list of examples from diverse natural ecosystems. But for the unfamiliar reader, let me explain them in further detail. Imagine a world in which there were only plants. Those plants would soon increase to an abundance that was limited by resources—space, nutrients, water, sunlight, and so on. Now imagine the addition of herbivores to this world. If the herbivores further limit the plants, as they can and often do, plant abundance will decline. Typically the depressing influence of the added herbivores on the abundance and species composition of plants is staggering. We know this from numerous experimental studies in which herbivores have either been added or removed. Now imagine adding predators to this world. If the predators are capable of limiting the herbivores, and they commonly do just that, the effect is to protect the plant community from overgrazing. This simple conceptualization is the basis for Hairston, Smith, and Slobodkin's famous green world hypothesis (Hairston et al. 1960), a proposal that the great abundance of plants across so many of Earth's ecosystems is fundamentally dependent on the presence of predators. Most other species depend in one way or another on plants, and so the logic underlying an essential role for predators in the maintenance of biodiversity is simple and straightforward. The more difficult question is, how large must populations of these keystone species be for their ecological roles to

become manifest? That number or "population density" defines the ecologically effective population size.

These ideas became imbedded in Michael's view of nature and conservation during his work on chaparral canyons in San Diego County ("Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands"). Michael recognized that the small vertebrate faunas—herps, birds, and small mammals—differed radically among the chaparral habitat fragments that remained from a once much more expansive and unbroken landscape. Some of the canyons supported diverse faunas while others were impoverished. The older and smaller a canyon fragment, the higher the likelihood was of it having an impoverished small vertebrate fauna. But there were exceptions, and subsequent analyses of the data showed that the pattern was most strongly correlated with the presence or absence of coyotes. In addition, the coyote-free habitat fragments had elevated populations of what Michael and his students called "mesopredators," species like foxes, raccoons, and especially domestic cats. A new idea to explain the variation in small vertebrate diversity began to take form, and that idea was just this. Coyotes once ranged widely over the southern California chaparral landscape. With development and the fragmentation of that once expansive and unbroken landscape, coyotes dwindled to extinction in the smaller and older canyon fragments. Fragments with coyotes supported diverse small vertebrate faunas because coyotes held mesopredator populations in check, thereby preventing the mesopredators (including house cats [aka "subsidized recreational hunters"] from the surrounding neighborhoods) from driving many of the species of small vertebrates to local extinction (Crooks and Soulé 1999). Michael earlier referred to this process as "mesopredator release" (Soulé et al. 1988). In the ensuing decades, ecologists have seen these same basic processes play out again and again with many species in a broad range of habitats across our planet.

The implications of these discoveries for conservation and the impact they had on Michael's efforts in conservation biology are

profound. The simple idea that keystone species, which often are apex predators, hold an ecosystem together speaks to both the structure and the scale of biodiversity conservation. Without predators, ecosystems lose biodiversity. And in order to maintain ecologically effective predator populations, the habitats must be large and interconnected. This realization led Michael and his early associates to envision what he called the three C's of conservation—cores, corridors, and carnivores—and shortly thereafter to put that vision into practice. The Wildlands Network (founded in 1991 in San Francisco as The Wildlands Project), which was Michael's conceptual brainchild, is dedicated to promoting biodiversity conservation through the implementation of this vision. Michael's most recent book (Soulé and Terborgh 1999), was written to embrace that theme. The *Spine of the Continent Project*, an effort to maintain biodiversity in the North American Intermountain West by strategically connecting parks, public, and private lands, was built around these ideas and vision. This anthology is a sampling of seminal writings that span the duration of Michael's career. These papers will likely continue to shape our thinking about how to conserve nature for years to come. Read them carefully and you will see signs of the building of this vision of ecological effectiveness and the scale of conservation as Michael's most powerful and enduring contribution to conservation science.

I couldn't possibly write an introduction to this anthology without looking to the future and asking where Michael Soulé's work and his vision may be leading us. Predicting the future is always an uncertain and risky business. And for conservation the uncertainties are amplified by an ever-more-rapidly changing world and even a recent questioning of the core principles of conservation biology as Michael and others have developed them over the past four decades. Given this, what are the most important future challenges to conservation? Three stand out in my mind.

The first of these challenges is human population growth. In 1936, the year in which Michael Soulé was born, the world popula-

tion stood at just over 2 billion people. About a year or two ago it passed 7 billion. Human demographers and economists project that it will top out at about 11 billion by the end of the twenty-first century. Can our planet sustain that many people, much less do so while conserving biodiversity? Given the high current extinction rates, some experts predict that half the species alive today will be extinct by the end of the twenty-first century. One might quibble over the details but the forecast isn't a hopeful one, no matter how one spins it. Human population increase may not be the only reason for this sobering prediction, but it's a big part of the reason. When I was young, some form of conscious control of human populations was on the mind of most serious conservation biologists. Today that idea seems almost taboo. Zero population growth is a thing of the past. None of the major conservation organizations are talking about human population growth, at least in public. Why is that? Has it become too much of a political liability to champion the objective? Have people given up on population control as something that is simply beyond hope? Or has the collective brain trust in conservation science decided that it doesn't matter? The first two of these reasons are understandable, but the last is difficult for me to grasp, even though that is the implied message coming from the conservation community. Human population control is still both our greatest need and our greatest challenge.

The second major challenge to conservation is the global spread of democracy, along with which has come a worldview that is trending rapidly toward increased human rights and an overall increase in standard of living. The question is not whether this is a moral imperative (most peoples in most nations of the world have already decided that it is) but rather whether the per capita increase in demand such change will inevitably place on natural resources is sustainable. I'm not aware of any credible analysis to suggest that it is. The recent downward trend in mean human longevity raises the further question of whether the average standard of living is indeed continuing to improve.

The third challenge is what many conservation biologists see as a recent assault on the principles of conservation from *within* the conservation community. The emerging difference in philosophy has been referred to as "biocentrism" (conservation for nature's sake) vs. "anthropocentrism" (conservation for people's sake) (Hunter et al. in press). I think of the anthropocentrists as "postmodern conservationists" because of their skepticism for many of the principles and core beliefs of traditional conservation. Postmodern conservation seems to be largely motivated by the belief that conservation is not working, or at least is not working as well as it needs to work. But beyond that, the biocentrists and postmodernists see the purpose of conservation very differently. For instance, biocentrists believe that biodiversity is the heart of conservation, whereas postmodernists think that biodiversity has been over-touted; biocentrists think that nature preservation is the central goal of conservation, whereas postmodernists think that conservation must first and foremost serve humans; the conservation priority of biocentrism is to protect wilderness and other undeveloped areas from development, whereas postmodernists see conservation as informing the right kind of development; biocentrists see the corporate world as the enemy of conservation, whereas postmodernists believe the way forward is to engage the corporate world; postmodernists think that nature is resilient to most human-caused disturbances, whereas biocentrists are skeptical of that premise. And so on. The postmodernists and biocentrists clearly maintain different beliefs, but an added problem is defining what those differences really are and even the claim of the postmodernists that they and the biocentrists embrace the same overall goals.

Michael Soulé has helped lead conservation biology to become what it is today. Postmodernists have shaken these foundations on one side of an intellectual tug-of-war. On the other side, core biocentrists like Michael are still speaking out, as are many they have taught or who share their values in other ways. The many published papers, conference presentations, book chapters, emails, and water-cooler type discussions comprise a lively argument. Like so many

other arguments, I suspect that neither side will prevail and that the clash of perspectives and values will never really be resolved. Which is not to say that the debate will have no effect on the future of conservation. But no one can credibly predict where conservation will go in the future. One can only hope that that pathway will lead to a world that can sustain the intimately interlinked quality of human life and the persistence of a natural world that has evolved over the last half billion years.

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Introduction to *Conservation Biology: Its Scope and Its Challenge*

This 1980 essay introduced a multiauthored volume, *Conservation Biology: An Evolutionary-Ecological Perspective*, edited by Bruce Wilcox and me. The essay's purpose was to introduce the new field of conservation biology, a "mission-oriented discipline" comprising both pure and applied science. The field's goal was to develop scientific tools to conserve biological diversity. In my subsequent 1985 article I described conservation biology as a "crisis discipline," but "mission-oriented" and "applied" are also appropriate.

We noted two areas where the field needed strengthening. First, critical biological questions needed answering; for example, how long are small populations likely to survive in nature? Second, until now the academic community had not widely accepted our new discipline, in part because conservation biology was an applied discipline rather than a pure science. So we called for both more scientific rigor and more scientists to join our endeavor to secure the field's credibility. We also noted that there were too few resources to support conservation research and its application, particularly in the

developing world. Even now, in the United States, less than 1 percent of philanthropic giving benefits biodiversity.

The *Conservation Biology* book was a turning point for our field. It inspired students, young academics, and agency employees who yearned to serve by applying science to nature protection; it led indirectly to the creation of the Society for Conservation Biology; and it fueled the field's explosive growth at a time when many parks and other protected areas were being established throughout the world. Unfortunately, however, since then establishment of new protected areas has slowed dramatically, with a few notable exceptions such as in Patagonia.

The book catalyzed an outburst of creative, applied scholarship in population genetics, demography, and ecology that continues to this day. Beneficiaries include landscape ecology, animal health, community ecology, island biogeography, and the design, optimal size, and distribution of protected areas. It also embraced the application of economics, political science, and sociology in conservation. In the years since that book was published, the conservation biology field has been widely accepted, and many colleges and universities now have departments.

The volume was also a call to arms for those wanting to combat the coming extinction crisis. It pointed out that consumerism in wealthier nations drives destruction of biodiversity, not only in those nations themselves but also in the developing countries that provide raw materials and finished products. Recent years have seen dramatic increases in consumption in the developing world, notably China, India, and Brazil.

An associated concern is that some within the field of conservation are advocating for what they call "new conservation," which proposes that, instead of conserving biological diversity because it is the right thing to do, we should use biological diversity to support the economic aspirations of people. In practice this would mean opening protected areas to some form of economic exploitation, with the hope that people would then be more inclined to support conservation of what diversity is left. See paper 14 for a full explanation of why this notion is unwise.

Conservation Biology: Its Scope and Its Challenge

Michael E. Soulé and Bruce A. Wilcox

from *Conservation Biology: An Evolutionary-Ecological Perspective,* 1980

Conservation Biology

Conservation biology is a mission-oriented discipline comprising both pure and applied science. This book is not the first in the field; there are other excellent texts (Dasmann, 1968; Ehrenfeld, 1970). In addition there are symposia with a more traditional approach, or which give specialized treatment to particular habitats, regions or to the status and management of particular taxa (for example, Duffey and Watt, 1971; Duffey et al., 1974; Schoenfeld et al., 1978; Prance and Elias, 1977).

In this book we have attempted to expand the range of topics covered and the depth with which they are usually treated. With regard to breadth, conservation biology is as broad as biology itself. It focuses the knowledge and tools of all biological disciplines, from molecular biology to population biology, on one issue—nature conservation. Among the contributors to this book, for example, are botanists, zoologists, ecologists, geneticists, evolutionists, a statistician, a mathematician-demographer, a cytologist, a biochemist, an

endocrinologist, a sociobiologist and experts in the field of natural resources.

With regard to depth, conservation biology can and should be as profound, intellectually rigorous and challenging as any field, limited only by the capacities of its practitioners. As a science, it is not strictly "pure," but neither is it purely "applied," for most of the chapters in this book contain ideas, data and conclusions that will advance basic science. This is as good a test of originality and rigor as any.

Conservation has a venerable history of scientific (Leopold, 1933; Smith, 1976) and philosophical (Passmore, 1974; Singer, 1975) discourse. Man has sought to protect wildlife at least as far back as Ashoka (around 250 BC). Journalists, poets and scholars of every stripe have written copiously about nature—its values and how to save it from the human menace.

In spite of this scholarly and literary legacy we feel that conservation biology is a new field, or at least a new rallying point for biologists wishing to pool their knowledge and techniques to solve problems. A community of interest and concern is often crystalized by a simple term. Conservation biology is such a term.

Unfortunately, the emergence of conservation biology as a respectable academic discipline has been slowed by prejudice. Until recently, few academically oriented biologists would touch the subject. While wildlife management, forestry and resource biologists (particularly in the industrialized temperate countries) struggled to buffer the most grievous or economically harmful of human impacts (deforestation, soil erosion, overhunting), the large majority of their academic colleagues thought the subject was beneath their dignity. But academic snobbery is no longer a viable strategy, if it ever was. Because many habitats, especially tropical ones, are on the verge of total destruction and many large animals are on the verge of extinction, the luxury of prejudice against applied science is unaffordable. Conservation genetics is an example of such academic disinterest. This field has been one of the weakest in conservation biology. One of the purposes of this book is to begin correcting this handicap.

Given encouragement, a forum, and, one hopes, the funding, biologists will gladly enlist to help save the world's rapidly expiring biota. As the table of contents will verify, "pure" scientists from many disciplines are eager to be conservation biologists. The issue that faces every student of biology today is not whether to be a conservationist, but how. Even if one rationalizes (as do many of our colleagues) that one's esoteric research is far removed from nature in the raw, or from the plight of tigers, gorillas, redwoods and "jungles," it seems to us that the study of life becomes a hollow, rarefied pursuit if the very animals and plants that fired our imaginations as children and triggered our curiosity as students should perish.

A Word on Economics

Conservation biology, strictly speaking, does not include the subject of economics.* For that reason, there are no chapters in this book on the acquisition or maintenance costs of reserves (but, see Chapter 18 and Chapter 11). As shown in Table 1, the industrialized countries have ten times the staff and ten times the money per unit area of national park as do the lesser developed countries. This gap in conservation support is serious enough, but the problem is compounded by the greater needs in many of the tropical countries, particularly in regions where poaching and other forms of encroachment require many skilled and dedicated wardens.

This is just another example of the well-known principle that scientific and technological expertise is worthless in the final analysis, if the money and resources required to implement the expertise is absent. Thus, the issue is not whether scientists should commit some of their time to public education and lobbying, but rather, how much of their time.

Comments on the Design of Nature Reserves

An issue that has been the subject of controversy (see Simberloff and Abele, 1975, 1976; Diamond, 1976; Whitcomb et al., 1976;

TABLE 1. National park budgets and personnel.

Country	U.S. dollars/1000 ha	Staff/1000 ha
Industrialized		
Australia	433	0.042
Canada	48.5	0.135
Japan	975	0.358
United States	4239	0.350
Brazil	3782	3.500
Mean	1895	0.877
Nonindustrialized		
Congo	39	0.026
Ghana	610	0.612
Indonesia	31	0.025
Niger	25	0.013
Senegal	311	0.082
Thailand	48	0.000
Uganda	163	0.017
Zambia	210	0.006
Mean	180	0.098

Data from Anon., 1977.

Terborgh, 1976) and that is mentioned or alluded to by nearly every author in this book is the optimal design of nature reserves—the little fragments of landscape where Man expects to preserve non-human life.** Nature reserves are the most valuable weapon in our conservation arsenal (Chapter 11), so they deserve extra attention in this introductory discussion.

When considering the preservation of a particular biota, a system of nature reserves can be described by reference to three features: number of reserves, size of reserves and density (or proximity) of reserves. With regard to number and size, some biogeographers have argued that reserves should be large and not necessarily numer-

ous; others have argued for many, smaller reserves. Nevertheless, all agree that the best solution from the biogeographical standpoint is many, large reserves. But there are other design considerations and factors besides biogeography that should influence reserve design. Table 2 lists these; it also tabulates our decisions regarding reserve size, number and proximity. This is a simplistic picture, but it has a purpose. It shows that all viewpoints (factors) converge on the same conclusion—reserves should be manifold, large and (for most purposes) dispersed, as is documented in the following comments.

Disease

Can epidemics destroy one or more species in a region the size of a nature reserve (Frankel and Soule, in press)? In recent years disease has eliminated many mammal species from large areas. These diseases include rinderpest, myxomatosis, anthrax, hoof and mouth disease, yellow fever and epidemic hemorrhagic disease. Botulism and avian cholera have devastated bird populations. Plant examples

TABLE 2. The components of nature reserve planning.

| | Design Features | | |
Design Considerations	Number	Size	Dispersed?
Disease	Many	Large	Yes
Genetics	Many	Large	–
Community Ecology	Many	Large	–
Island Biogeography	–	Large	(see text)
Research Potential	Many	–	–
Politics, Economics	Many	–	Yes
Recreation	Many	Large	Yes
Summary	Many	Large	Dispersed

include chestnut blight and Dutch elm disease. The potential for disaster is aggravated by the susceptibility of domestic animals to most of the diseases that can plague wild species. Farms and villages with rabbits, sheep, cattle, swine and fowl will encircle most nature reserves in the near future, and these stocks will be a perennial source of contagion for the wild species.

Another consideration is disease resistance. Small, isolated populations will tend to lose genetic variability, including resistance genes, resulting in a gradual increase in susceptibility to diseases. It is folly, then, to keep all of the individuals of a species in a single reserve regardless of size, unless, of course, several well isolated populations exist within a reserve—an exceptional situation. We do not mean that the prime directive of conservation should be maximizing the number and isolation of reserves. But if the choice is between (1) a single reserve containing the last vestiges of one or more valuable species versus (2) several (perhaps smaller) isolated reserves, each with representative populations of the desirable forms and appropriate habitat, common sense and history give the nod to the latter choice.

Community Ecology

The world is patchy and patches come and go. Even a region as superficially homogeneous as the Amazon Basin will require many reserves to maintain examples of all of its habitats (Chapter 5; Chapter 17). Frequent climatic and geologic disturbances as well as fire can affect entire small reserves (Chapter 5). Reserves must be designed with the largest disturbance type in mind (Chapter 2). Viable populations of high trophic level species, large herbivores and many tropical plants, as well as many butterfly species require large reserves (Chapter 2; Chapter 3). Finally, only large areas will contain a balance of successional stages necessary for the survival of many plants, insects and the animals that depend on them (Chapter 2).

Island Biogeography

Extinction rates in large reserves will be lower than those in small reserves, so it would seem that large reserves are superior. They also hold more species at equilibrium. On the other hand, if extinction rates, particularly for vertebrates, were generally very low (measured in geological rather than historic time), a large number of small, complementary reserves, each harboring a small but unique portion of the biosphere, would suffice. Extinction rates appear to be high (Chapter 6) so it is best to maximize both size and number. Proximity of reserves to one another is also important if it enhances recolonization and gene flow between reserves. But this rule only applies to species that normally traverse wide stretches of inhospitable habitat (those that fly or have efficient wind dispersal mechanisms). Even among flying species, however, only a small minority venture out of their normal habitat (Ehrlich and Raven, 1969; Diamond, 1971; 1976; Terborgh, 1974) and so only a fraction of species would benefit from proximity.

Research

Replication of reserves offers advantages for pure and applied research because it permits management experiments and other kinds of deliberate perturbation such as benign neglect, controlled burning or logging, removal of predators or dominant herbivores and the addition of species. Such treatments would be considered too "dangerous" if there were only one or a few reserves.

Politics and Economics

Destructive political conflicts affecting the. status of reserves can be avoided if opportunities for jealousy are minimized. One political source of jealousy is the hegemony of reserves in regions controlled by powerful interests. The danger is especially great in developing

tropical countries where a game reserve can significantly increase the material well-being of the people living near it. This means that the best policy is the wide deployment of reserves. If there is to be a "conservation pork barrel," everyone should get his share.

A serious and thorough analysis of management costs probably would demonstrate the long-term economic advantages of large reserves. Small reserves are less expensive to establish, but in the long run they are undoubtedly more costly to operate. For example, it is shown in Chapter 6 that the decay of species diversity over time is much more rapid in small reserves than in large ones. This means that costly demographic and genetic rescue operations (especially for large species) will have to be initiated much sooner in small reserves, and that the intensity of such programs will have to be greater. Another factor relating to size is habitat succession and disturbance. In small reserves it will be necessary to undertake heroic and expensive operations just to maintain a viable mix of habitats. Such artificial therapy will rarely be necessary in large reserves (Chapter 5).

Recreation and Education

Reserves scattered liberally throughout a region will be more accessible to the populace, thus providing greater opportunities for education and recreation. Coe (Chapter 16) says this is an essential requirement for the survival of reserves in the poorer, tropical countries.

Genetics

The species which are the least dense (large herbivores, trees, large carnivores and scavengers) will probably suffer an attrition of fitness and evolutionary potential if effective population sizes are too low (Chapters 8, 9 and 12). Even the largest existing reserves may be too small for the long-term preservation of carnivores (Chapter 9). A multiplicity of reserves would add another dimension to the con-

servation of genetic diversity. For example, populations of the same species in different reserves would tend to harbor different sets of rare alleles at polymorphic loci.

Conclusion

The conclusion of this brief treatment is not surprising: reserves should be large, manifold and dispersed (except that a few highly vagile species benefit from proximity of reserves). To such questions as "how big?" or "how many?", the answers are "as big as possible" and "as many as possible." By the turn of the century, most options regarding the design, size and organization of nature reserves will be closed, especially in the tropics. It therefore behooves conservation biologists to exert, immediately and forcibly, their influence on these matters.

An Emotional Call to Arms

The green mantle of Earth is now being ravaged and pillaged in a frenzy of exploitation by a mushrooming mass of humans and bull-dozers. Never in the 500 million years of terrestrial evolution has this mantle we call the biosphere been under such a savage attack. Certainly, there have been so-called "crises" of extinction in the past, but the rate of decay of biological diversity during these crises was sluggish compared to the galloping pace of habitat destruction today.

Perhaps the hardest thing to grasp is the geological and historical uniqueness of the next few decades. There simply is no precedent for what is happening to the biological fabric of this planet and there are no words to express the horror of those who love nature. In the lifetimes of many who read this book, the relentless harrying of habitats, particularly in the tropics, will reduce rain forests, reefs and savannas to vulnerable and senescent vestiges of their former grandeur and subtlety. But loss of habitat and loss of species is not the whole disaster. Perhaps even more shocking than the unprecedented

wave of extinction is the cessation of significant evolution of new species of large plants and animals. Death is one thing—an end to birth is something else, and nature reserves are too small (not to mention, impermanent) to gestate new species of vertebrates (Chapter 9). There is no escaping the conclusion that in our lifetimes, this planet will see a suspension, if not an end, to many ecological and evolutionary processes which have been uninterrupted since the beginnings of paleontological time.

We hope it is only a suspension—that the horrible onslaught can be stopped before the regenerative powers of ecosystems are also killed. This book is a statement of that optimism. In one way or another, each of the authors is expressing a determination to protect biotic diversity and to do the enabling research and development. The authors also join in a plea: we can't do it alone, and we can't do it on a shoestring. More scientists must be solicited in the ranks of conservation biology. But this is only a beginning. Wars aren't won on intelligence alone. Money, troops, weapons and strategy are also required (see Chapters 16, 17, 18 and 19). This is the challenge of the millennium. For centuries to come, our descendants will damn us or eulogize us, depending on our integrity and the integrity of the green mantle they inherit.

Notes

*Funding for established scientists who wish to do research in conservation biology is negligible. The National Science Foundation considers grant applications in this field to be "applied" (a pejorative somehow avoided by cancer researchers). Other governmental agencies use most of their funds for in-house research.

**We estimate from the 1975 UN List of National Parks and Equivalent Reserves that the total area of habitat to be preserved in tropical countries amounts to less than 1.5 percent of the original habitat—probably much less than this considering that many reserves are now being destroyed by "legal" and illegal logging operations, while many others are virtually unprotected from poachers, charcoal makers and squatters.

Introduction to *What Is Conservation Biology?*

This paper elaborated basic concepts underlying conservation biology. I described conservation biology as a "crisis discipline," analogous to disciplines like cancer science. In crisis disciplines, workers are motivated in part by apprehension and compassion. In the case of conservation biology, the crisis is raising rates of species and population extinction.

I argued that crisis disciplines are often synthetic and multidisciplinary, drawing on several fields, including social sciences. The paper's following key ideas shaped the development of conservation biology:

1. Given the extent of habitat destruction and other threats (see paper 7), humans must play an active role in managing most species and protected areas. We noted that even the largest nature reserves are too small to maintain viable populations of large carnivores (see papers 3 and 8), and this also may be true for many large herbivores. Because large carnivores and large herbivores such as elephants that determine the patchiness of vegetation are keystone

species, their loss undermines the integrity of the entire ecosystem (see paper 8).

2. I presented what I called "Functional Postulates of Conservation Biology," that is, fundamental rules that govern how ecosystems and species respond to disturbance and that likewise determine which conservation strategies are likely to be successful. These rules include the following: (i) the survival of many species depends on the presence of others, including pollinators dependent on specific plants; (ii) extinctions of keystone species can destablilize and impoverish entire ecosystems; (iii) introduction of invasive or generalist species like brown rats may reduce diversity by predation or competition (see paper 6); (iv) many ecological processes fail in systems that are too small or large, for example, a remnant of southern long-leaf pine forest that is too small to sustain the periodic fires necessary for forest health; (v) very small populations have a high probability of extinction because of genetic or stochastic phenomena; and (vi) natural communities differ significantly from disturbed or synthetic communities.

3. Conservation biologists must often make design and management recommendations before they have all the data and knowledge they need, basing decisions on the best available information. Even though conservation scientists have much better methods, theory, and knowledge than when I wrote this paper, they still often lack the knowledge and resources to make decisions with high degrees of confidence.

4. People value nature primarily in terms of how it can help them. Public land managers, for example, too often manage for production of economic resources benefiting influential people and organizations. One positive development is that some U.S. resource agencies have become more ecologically oriented.

5. Conservation biology must take a long-term view. Species at risk must have populations large enough and genetically diverse enough to persist over years, decades, or longer in order to adapt evolutionarily to changing conditions.

6. This paper gave conservation biology a moral foundation by declaring ethical postulates, which include that (i) diversity of organisms is good, (ii) ecological complexity is good, (iii) evolution is good and should be protected, and (iv) biological diversity has intrinsic value beyond its economic or practical value.

What Is Conservation Biology?

Michael E. Soulé

from the journal *BioScience*, 1985

Conservation biology, a new stage in the application of science to conservation problems, addresses the biology of species, communities, and ecosystems that are perturbed, either directly or indirectly, by human activities or other agents. Its goal is to provide principles and tools for preserving biological diversity. In this article I describe conservation biology, define its fundamental propositions, and note a few of its contributions. I also point out that ethical norms are a genuine part of conservation biology, as they are in all mission- or crisis-oriented disciplines.

Crisis Disciplines

Conservation biology differs from most other biological sciences in one important way: it is often a crisis discipline. Its relation to biology, particularly ecology, is analogous to that of surgery to physiology and war to political science. In crisis disciplines, one must act before knowing all the facts; crisis disciplines are thus a mixture of science and art, and their pursuit requires intuition as well as infor-

mation. A conservation biologist may have to make decisions or recommendations about design and management before he or she is completely comfortable with the theoretical and empirical bases of the analysis (May 1984, Soulé and Wilcox 1980, chap. 1). Tolerating uncertainty is often necessary.

Conservation biologists are being asked for advice by government agencies and private organizations on such problems as the ecological and health consequences of chemical pollution, the introduction of exotic species and artificially produced strains of existing organisms, the sites and sizes of national parks, the definition of minimum conditions for viable populations of particular target species, the frequencies and kinds of management practices in existing refuges and managed wildlands, and the ecological effects of development. For political reasons, such decisions must often be made in haste.

For example, the rapidity and irreversibility of logging and human resettlement in Western New Guinea (Irian Jaya) prompted the Indonesian government to establish a system of national parks. Two of the largest areas recommended had never been visited by biologists, but it appeared likely that these areas harbored endemic biotas.[1] Reconnaissance later confirmed this. The park boundaries were established in 1981, and subsequent development has already precluded all but minor adjustments. Similar crises are now facing managers of endangered habitats and species in the United States— for example, grizzly bears in the Yellowstone region, black-footed ferrets in Wyoming, old-growth Douglas-fir forests in the Pacific Northwest, red-cockaded woodpeckers in the Southeast, and condors in California.

Other Characteristics of Conservation Biology

As illustrated in Figure 1, conservation biology shares certain characteristics with other crisis-oriented disciplines. A comparison with cancer biology illustrates some of these characteristics, including conservation biology's synthetic, eclectic, multidisciplinary struc-

ture. Furthermore, both fields take many of their questions, techniques, and methods from a broad range of fields, not all biological. This illustration is also intended to show the artificiality of the dichotomy between pure and applied disciplines.

Finally, this figure illustrates the dependence of the biological sciences on social science disciplines. Today, for example, any recommendations about the location and size of national parks should consider the impact of the park on indigenous peoples and their cultures, on the local economy, and on opportunity costs such as forfeited logging profits.

There is much overlap between conservation biology and the natural resource fields, especially fisheries biology, forestry, and wildlife management. Nevertheless, two characteristics of these fields often distinguish them from conservation biology. The first is the dominance in the resource fields of utilitarian, economic objectives. Even though individual wildlife biologists honor Aldo Leopold's land ethic and the intrinsic value of nature, most of the financial resources
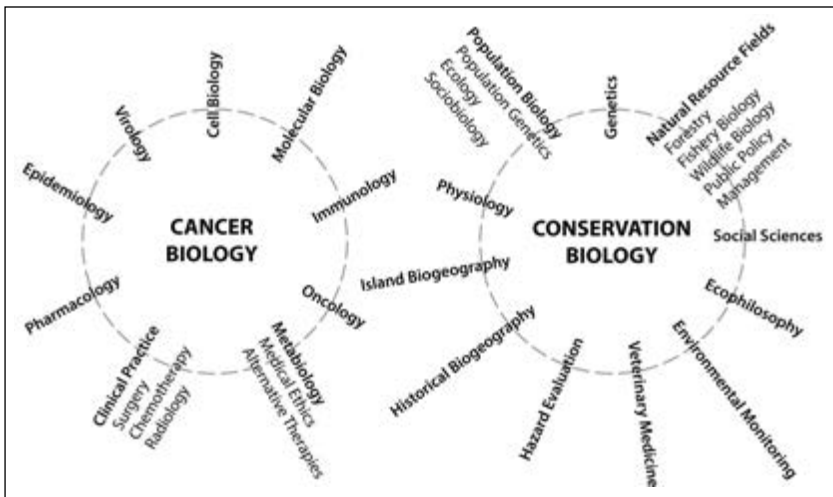
FIGURE 1. Cancer biology and conservation biology are both synthetic, multidisciplinary sciences. The dashed line indicates the artificial nature of the borders between disciplines and between "basic" and "applied" research. See text.

for management must go to enhancing commercial and recreational values for humans. The emphasis is on *our* natural *resources*.

The second distinguishing characteristic is the nature of these resources. For the most part, they are a small number of particularly valuable target species (e.g., trees, fishes, deer, and waterfowl) —a tiny fraction of the total biota. This distinction is beginning to disappear, however, as some natural resource agencies become more "ecological" and because conservation biologists frequently focus on individual endangered, critical, or keystone species.

Conservation biology tends to be holistic, in two senses of the word. First, many conservation biologists, including many wildlife specialists, assume that ecological and evolutionary processes must be studied at their own macroscopic levels and that reductionism alone cannot lead to explanations of community and ecosystem processes such as body-size differences among species in guilds (Cody and Diamond 1975), pollinator-plant coevolution (Gilbert and Raven 1975), succession, speciation, and species-area relationships. Even ecological reductionists, however, agree that the proper objective of conservation is the protection and continuity of entire communities and ecosystems. The holistic assumption of conservation biology should not be confused with romantic notions that one can grasp the functional intricacies of complex systems without conducting scientific and technological studies of individual components (Levins and Lewontin 1985, chap. 6). Holism is not mysticism.

The second implication of the term *holistic* is the assumption that multidisciplinary approaches will ultimately be the most fruitful. Conservation biology is certainly holistic in this sense. Modern biogeographic analysis is now being integrated into the conservation movement (Diamond 1975, Simberloff and Abele 1976, Terborgh 1974, Wilcox 1980). Population genetics, too, is now being applied to the technology of wildlife management (Frankel 1974, Frankel and Soulé 1981, Schonewald-Cox et al. 1983, Soulé and Wilcox 1980). Multidisciplinary research, involving government agencies

and wildlife biologists, is also evident in recent efforts to illuminate the question of viable population size (Salwasser et al. 1984).

Another distinguishing characteristic of conservation biology is its time scale. Generally, its practitioners attach less weight to aesthetics, maximum yields, and profitability, and more to the long-range viability of whole systems and species, including their evolutionary potential. Long-term viability of natural communities usually implies the persistence of diversity, with little or no help from humans. But for the foreseeable future, such a passive role for managers is unrealistic, and virtually all conservation programs will need to be buttressed artificially. For example, even the largest nature reserves and national parks are affected by anthropogenic factors in the surrounding area (Janzen 1983, Kushlan 1979), and such refuges are usually too small to contain viable populations of large carnivores (Frankel and Soulé, 1981, Shaffer and Samson 1985). In addition, poaching, habitat fragmentation, and the influx of feral animals and exotic plants require extraordinary practices such as culling, eradication, wildlife immunization, habitat protection, and artificial transfers. Until benign neglect is again a possibility, conservation biology can complement natural resource fields in providing some of the theoretical and empirical foundations for coping with such management conundrums.

Postulates of Conservation Biology

Conservation biology, like many of its parent sciences, is very young. Therefore, it is not surprising that its assumptions about the structure and function of natural systems, and about the role of humans in nature, have not been systematized. What are these postulates? I propose two sets: a functional, or mechanistic, set and an ethical, or normative, set.

The functional postulates. These are working propositions based partly on evidence, partly on theory, and partly on intuition. In essence, they are a set of fundamental axioms, derived from

ecology, biogeography, and population genetics, about the maintenance of both the form and function of natural biological systems. They suggest the rules for action. A necessary goal of conservation biology is the elaboration and refinement of such principles.

The first, the evolutionary postulate states: *Many of the species that constitute natural communities are the products of coevolutionary processes.* In most communities, species are a significant part of one another's environment. Therefore, their genetically based physiological and behavioral repertoires have been naturally selected to accommodate the existence and reactions of a particular biota. For example, the responses of prey to a predator's appearance or of a phytophagous insect to potential host plants are continually "tuned" by natural selection.

This postulate merely asserts that the structure, function, and stability of coevolved, natural communities differ significantly from those of unnatural or synthetic communities. It does not necessarily rely on deterministic factors like density-dependent population dynamics or the molding by competition of morphological relationships in communities over both ecological and evolutionary time. In addition, this postulate is neutral on the issue of holistic versus reductionistic analysis of community structure. (In practice, a reductionistic methodology, including autecological research, may be the best way to establish the holistic structure of communities.)

There are many "corollaries" of this postulate. Strictly speaking, most of them are empirically based generalizations. The following all assume the existence of community processes as well as a coevolutionary component in community structure.

Species are interdependent. Not only have species in communities evolved unique ways of avoiding predators, locating food, and capturing and handling prey, but mutualistic relationships are frequent (Janzen 1975, Seifert and Seifert 1979). This is not to say that every species is essential for community function, but that there is always uncertainty about the interactions of species and about the biological consequences of an extinction. Partly for this reason, Aldo

Leopold (1953) admonished conservationists to save all of the parts (species) of a community.

Many species are highly specialized. Perhaps the majority of animal species, including phytopagous insects, parasites, and parasitoids, depend on a particular host (Price 1980). This means that the coattails of endangered host species can be very long, taking with them dozens (Raven 1976) or hundreds (Erwin 1983) of small consumer species when they go.

Extinctions of keystone species can have long-range consequences. The extinction of major predators, large herbivores, or plants that are important as breeding or feeding sites for animals may initiate sequences of causally linked events that ultimately lead to further extinctions (Frankel and Soulé 1981, Gilbert 1980, Terborgh and Winter 1980).

Introductions of generalists may reduce diversity. The introduction of exotic plant and animal species may reduce diversity, especially if they are large or generalist species (Diamond 1984, Elton 1958). Apparently, the larger the land mass, the less the impact of exotics (e.g., Simberloff 1980).

The evolutionary postulate and its corollaries formalize the evidence that natural communities comprise species whose genetic makeups have been mutually affected by their coexistence (Futuyma and Slatkin 1983, Gilbert and Raven 1975). An alternative theory, the null hypothesis that communities are randomly assembled, is usually restricted to "horizontal" subcommunities such as guilds, specific taxa, or trophic levels (e.g., James and Boecklen 1984). In general, this latter thesis lacks empirical support, except that competitive structuring within guilds or trophic levels is often absent or difficult to demonstrate (Strong et al. 1984), and that harsh environments or the vagaries of dispersal may often be more important than biological interactions in determining local community composition (e.g., Underwood and Denley 1984).

The second functional postulate concerns the scale of ecological processes: *Many, if not all, ecological processes have thresholds below*

and above which they become discontinuous, chaotic, or suspended. This postulate states that many ecological processes and patterns (including succession, nutrient cycling, and density-dependent phenomena) are interrupted or fail altogether where the system is too small. Smallness and randomness are inseparable.

Nonecological processes may also dominate at the other end of the spatial and temporal scale, in very large or very old systems. In very large systems, such as continents, climatic and physiographic phenomena often determine the major patterns of the landscape, including species distribution. In very old systems, ecological processes give way to geological and historical ones or to infrequent catastrophic events, such as inundation, volcanism, and glaciation. In other words, ecological processes belong to an intermediate scale of physical size and time (MacArthur 1972), and these processes begin to fail or are overwhelmed near the extremities of these ranges.

Two major assumptions, or generalizations, underlie this postulate. First, *the temporal continuity of habitats and successional stages depends on size.* The random disappearance of resources or habitats will occur frequently in small sites but rarely, if ever, in large ones. The reasons include the inherent randomness of such processes as patch dynamics, larval settlement, or catastrophic events. as well as the dynamics of contagious phenomena such as disease, windstorm destruction, and fire. The larger an area, the less likely that all patches of a particular habitat will disappear simultaneously. Species will disappear if their habitats disappear.

Second, *outbursts reduce diversity.* If population densities of ecologically dominant species rise above sustainable levels, they can destroy local prey populations and other species sharing a resource with such species. Outbursts are most probable in small sites that lack a full array of population buffering mechanisms, including habitat sinks for dispersing individuals, sufficient predators, and alternative feeding grounds during inclement weather. The unusually high population densities that often occur in nature reserves can also increase the rate of disease transmission, frequently leading to epidemics that may affect every individual.

Taken together, the corollaries of this postulate lead to the conclusion that survival rates of species in reserves are proportional to reserve size. Even though there is now a consensus that several small sites can contain as many species as one large site (when barriers to dispersal are absent), the species extinction rate is generally higher in small sites (Soulé and Simberloff, in press).

The third functional postulate concerns the scale of population phenomena: *Genetic and demographic processes have thresholds below which nonadaptive, random forces begin to prevail over adaptive, deterministic forces within populations.* The stochastic factors in population extinction have been discussed extensively (Shaffer 1981, Soulé 1983, Terborgh 1974) in the context of the minimum conditions for population viability. The main implication of this postulate for conservation is that the probability of survival of a local population is a positive function of its size. One of the corollaries of this postulate is that below a certain population size (between 10 and 30), the probability of extinction from random demographic events increases steeply (Shaffer 1981).

The next three corollaries are genetic. First, populations of outbreeding organisms will suffer a chronic loss of fitness from inbreeding depression at effective population sizes of less than 50 to 100 (Franklin 1980, Soulé 1980). Second, genetic drift in small populations (less than a few hundred individuals) will cause a progressive loss of genetic variation; in turn, such genetic erosion will reduce immediate fitness because multilocus heterozygosity is generally advantageous in outbreeding species (Beardmore 1983. Soulé 1980, and references cited below). (The genetic bases of these two corollaries may be the same: homozygosity for deleterious, recessive alleles.) Finally, natural selection will be less effective in small populations because of genetic drift and the loss of potentially adaptive genetic variation (Franklin 1980).

The fourth functional postulate is that *nature reserves are inherently disequilibrial for large, rare organisms.* There are two reasons for this. First, extinctions are inevitable in habitat islands the size of nature reserves (MacArthur and Wilson 1967); species

diversity must be artificially maintained for many taxa because natural colonization (reestablishment) from outside sources is highly unlikely. Second, speciation, the only other nonartificial means of replacing species, will not operate for rare or large organisms in nature reserves because reserves are nearly always too small to keep large or rare organisms isolated within them for long periods, and populations isolated in different reserves will have to be maintained by artificial gene flow if they are to persist. Such gene flow would preclude genetic differentiation among the colonies (Soulé 1980).

The normative postulates. The normative postulates are value statements that make up the basis of an ethic of appropriate attitudes toward other forms of life—an ecosophy (Naess 1973). They provide standards by which our actions can be measured. They are shared, I believe, by most conservationists and many biologists, although ideological purity is not my reason for proposing them.

Diversity of organisms is good. Such a statement cannot be tested or proven. The mechanisms by which such value judgments arise in consciousness are unknown. The conceptual mind may accept or reject the idea as somehow valid or appropriate. If accepted, the idea becomes part of an individual's philosophy.

We could speculate about the subconscious roots of the norm, "diversity is good." In general, humans enjoy variety. We can never know with certainty whether this is based on avoiding tedium and boredom or something else, but it may be as close to a universal norm as we can come. This is probably one of the reasons for the great popularity of zoos and national parks, which in recent years have had, respectively, over 100 million and 200 million visitors annually in the United States. Perhaps there is a genetic basis in humans for the appeal of biotic diversity (Orians 1980, Wilson 1984). After all, humans have been hunter-gatherers, depending on a wide array of habitats and resources, for virtually all of the past several million years.

A corollary of this postulate is that the untimely extinction of populations and species is bad. Conservation biology does not abhor

extinction per se. Natural extinction is thought to be either value free or good because it is part of the process of replacing less well-adapted gene pools with better adapted ones. Ultimately, natural extinction, unless it is catastrophic, does not reduce biological diversity, for it is offset by speciation. Natural extinctions, however, are rare events on a human time scale. Of the hundreds of vertebrate extinctions that have occurred during the last few centuries, few, if any, have been natural (Diamond 1984, Frankel and Soulé 1981), whereas the rate of anthropogenic extinctions appears to be growing exponentially.

It may seem logical to extend the aversion of anthropogenic extinction of populations to the suffering and untimely deaths of individuals because populations are composed of individuals. I do not believe this step is necessary or desirable for conservation biology. Although disease and suffering in animals are unpleasant and, perhaps, regrettable, biologists recognize that conservation is engaged in the protection of the integrity and continuity of natural processes, not the welfare of individuals. At the population level, the important processes are ultimately genetic and evolutionary because these maintain the potential for continued existence. Evolution, as it occurs in nature, could not proceed without the suffering inseparable from hunger, disease, and predation.

For this reason, biologists often overcome their emotional identification with individual victims. For example, the biologist sees the abandoned fledgling or the wounded rabbit as part of the process of natural selection and is not deceived that "rescuing" sick, abandoned, or maimed individuals is serving the species or the cause of conservation. (Salvaging a debilitated individual from a very small population would be an exception, assuming it might eventually contribute to the gene pool.) Therefore, the ethical imperative to conserve species diversity is distinct from any societal norms about the value or the welfare of individual animals or plants. This does not in any way detract from ethical systems that provide behavioral guidance for humans on appropriate relationships with individuals from other species, especially when the callous behavior of humans

causes animals to suffer unnecessarily. Conservation and animal welfare, however, are conceptually distinct, and they should remain politically separate.

Returning to the population issue, we might ask if all populations of a given species have equal value. I think not. The value of a population, I believe, depends on its genetic uniqueness, its ecological position, and the number of extant populations. A large, genetically polymorphic population containing unique alleles or genetic combinations has greater due, for example, than a small, genetically depauperate population of the same species. Also, the fewer the populations that remain, the greater the probability of the simultaneous extinction (random or not) of *all* populations, and thus of the species. Hence, how precious a population is is a function of how many such populations exist.

Ecological complexity is good. This postulate parallels the first one, but assumes the value of habitat diversity and complex ecological processes. Arriving at this judgment may require considerable sophistication, training, and thought. Someone familiar with descriptive plant and animal biogeography, trophic levels, nutrient cycling, edaphic heterogeneity, and other aspects of ecological classification is in a better position to fully appreciate the complexity in a tidepool or forest. Like the first one, this postulate expresses a preference for nature over artifice, for wilderness over gardens (cf. Dubos 1980). When pressed, however, ecologists cannot prove that their preference for natural diversity should be the standard for managing habitats. For example, even if it could be shown that a decrease in species diversity led to desertification, eutrophication, or the piling up of organic material, it is still not a logical conclusion that such consequences are bad. For example, such events in the past created fossil fuels (although not everyone would argue that this was good).

Ecological diversity can be enhanced artificially, but the increase in diversity can be more apparent than real (especially if cryptic taxa and associations are considered. such as soil biotas and microbial communities). In addition, humans tend to sacrifice ecological and geographic heterogeneity for an artificially maintained, energy-

intensive, local species diversity. Take, for example, the large numbers of plant taxa maintained in the warm-temperate and subtropical cities of the world. Most of these species are horticultural varieties that do well in landscaped gardens and parks. One sees a great variety of such plants in Sydney, Buenos Aires, Cape Town, Athens, Mexico City, Miami, and San Diego. But the roses, citrus, camellias, bougainvilleas, daffodils, eucalyptus, and begonias are everywhere similar.

This combination of local variety and geographic homogeneity produces several pleasant benefits for humans. Not only are the exotic species more spectacular, but the world traveler can always feel botanically at home. In addition, many cities now have a greater diversity of plant families and tree species than did the original habitat destroyed to make way for the city. But these aesthetic benefits are costly. The price is low geographic diversity and ecological complexity. Botanical gardens, zoos, urban parks, and aquaria satisfy, to a degree, my desire to be with other species, but not my need to see wild and free creatures or my craving for solitude or for a variety of landscapes and vistas.

Evolution is good. Implicit in the third and fourth functional postulates is the assumption that the continuity of evolutionary potential is good. Assuming that life itself is good, how can one maintain an ethical neutrality about evolution? Life itself owes its existence and present diversity to the evolutionary process. Evolution is the machine, and life is its product. One possible corollary of this axiom is an ethical imperative to provide for the continuation of evolutionary processes in as many undisturbed natural habitats as possible.

Biotic diversity has intrinsic value, irrespective of its instrumental or utilitarian value. This normative postulate is the most fundamental. In emphasizing the inherent value of nonhuman life, it distinguishes the dualistic, exploitive world view from a more unitary perspective: Species have value in themselves, a value neither conferred nor revocable, but springing from a species' long evolutionary heritage and potential or even from the mere fact of its existence.[2] A large

literature exists on this subject (Devall and Sessions 1985; Ehrenfeld 1981; Passmore 1974; Rolston 1985, p. 718 this issue; Tobias 1985; and the journal *Environmental Ethics*).

Endless scholarly debate will probably take place about the religious, ethical, and scientific sources of this postulate and about its implications for policy and management. For example, does intrinsic value imply egalitarianism and equal rights among species? A more profitable discussion would be about the rules to be used when two or more species have conflicting interests (Naess 1985).

Contributions of Conservation Biology

Recently, rapid progress has been made by zoos and similar institutions in the technology and theory of captive breeding of endangered species. It is becoming apparent that nearly 2000 species of large mammals and birds will have to be maintained artificially if they are to avoid premature extinction (Myers 1984. Soulé et al. in press). Eventual advances in technology may enable some, if not most, such species to be kept in a suspended, miniaturized state, such as frozen sperm, ova, and embryos. Meanwhile, however, traditional ways to maintain most of the planet's megafauna must be improved.

In recent years, the breeding of endangered species has undergone profound changes as physiologists and geneticists have become involved. Active research is sponsored by many zoos. At the San Diego Zoo, new techniques were developed for the determination of sex in sexually monomorphic bird species (Bercovitz et al. 1978). Other workers (e.g., Benirschke 1983) have found cytogenetic explanations for the poor reproductive performance of several mammal species. Ryder and Wedemeyer (1982) pioneered retrospective genetic analysis of captive stocks with the objective of equalizing founder representation. At the National Zoo in Washington, DC, Ralls and Ballou (1983) have provided incontrovertible evidence for the universality of inbreeding depression in mammals [see November 1984 *BioScience* 34: 606-610, 612].

Many authors have appealed for larger founder sizes in groups of captively bred animals to minimize inbreeding problems and the loss of genetic variability (Senner 1980, Templeton and Read 1983), but specific guidelines have been lacking. Recent analyses have clarified the interrelationships between founder size and several other variables, including generation length, maximum captive group size (carrying capacity), and group growth rate (Figure 2).
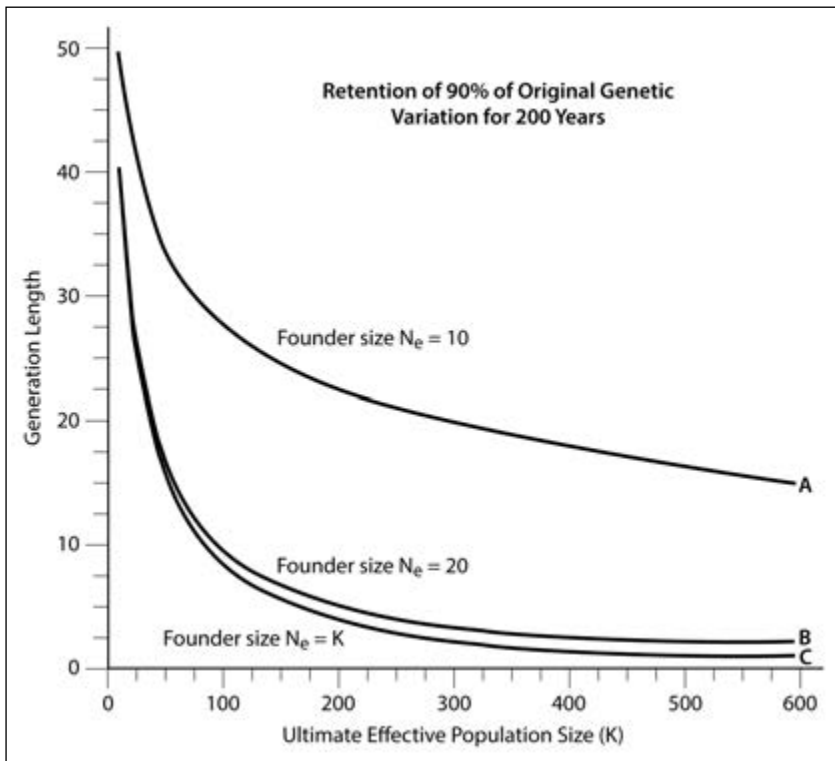
FIGURE 2. Combinations of effective population sizes and generation lengths (in years) in managed populations required to maintain at least 90% of the genetic variation that existed in the source population; the program lasts 200 years. The calculations on which the curves are based assume an intrinsic population growth rate of 1.0% per year. For curve C, the founder size is equal to the ultimate size of the managed population. Minimum founder sizes for most species are in the range of 15 to 30 (from Soulé et al., in press).

Conservation biology has also contributed to the design and management of wildland areas. An example is the new field of population viability analysis, whose goal is to estimate the (effective) number of individuals needed to maintain a species' long-term genetic fitness and ensure against extinction from other, nongenetic causes. Several relatively independent pathways of research in population biology, community ecology, and biogeography are being joined in this effort which I believe will contribute significantly to theoretical population biology. One approach is to integrate demographic stochasticity (random variation in birth and death rates and sex ratio) and environmental variation to predict the probability of survival (Leigh 1981, Shaffer and Samson 1985). This approach is leading to very large estimates for long-term viability.[3]

Genetics is also important in viability analysis. At least in outbreeding species, it appears that relatively heterozygous individuals are frequently more fit than relatively homozygous ones. Many fitness criteria have been studied, including growth rates, overwinter survival, longevity, developmental stability, metabolic efficiency, and scope for growth (for reviews see Beardmore 1983, Frankel and Soulé 1981, and Mitton and Grant 1984). Russell Lande and George Barrowclough[4] are proposing that populations must reach effective sizes of several hundred if they are to retain genetic variation for quantitative traits. Larger numbers will be needed for qualitative traits, including genetic polymorphisms. The US Forest Service is already beginning to integrate viability analysis into its planning protocols (Salwasser et al. 1984).

Field work in conservation biology is supported by several agencies and organizations, including the World Wildlife Fund, NSF, the New York Zoological Society, and the Smithsonian Institution. These studies have contributed a great deal to our understanding of diversity and its maintenance in the Neotropics. Field work by the New York Zoological Society in savanna ecosystems is clarifying the relative importance of environmental and genetic factors in primate behavior and ecology. This organization is also providing

basic information on many of the highly endangered large animals around the world. Such field work is essential for the efficient design of nature reserves.

Conclusions

Conservation biology is a young field, but its roots antedate science itself. Each civilization and each human generation responds differently to the forces that weaken the biological infrastructure on which society depends and from which it derives much of its spiritual, aesthetic, and intellectual life. In the past, the responses to environmental degradation were often literary, as in the Babylonian Talmud (Vol. I, Shabbath 129a, chap. xviii, p. 644), Marsh (1864), Leopold (1966), Carson (1962) and others (see Passmore 1974). More recently, legal and regulatory responses have been noticeable, especially in highly industrialized and democratized societies. Examples include the establishment of national parks and government policies on human population and family planning, pollution, forest management, and trade in endangered species. At this point in history, a major threat to society and nature is technology, so it is appropriate that this generation look to science and technology to complement literary and legislative responses.

Our environmental and ethical problems, however, dwarf those faced by our ancestors. The current frenzy of environmental degradation is unprecedented (Ehrlich and Ehrlich 1981), with deforestation, desertification, and destruction of wetlands and coral reefs occurring at rates rivaling the major catastrophes in the fossil record and threatening to eliminate most tropical forests and millions of species in our lifetimes. The response, therefore, must also be unprecedented. It is fortunate, therefore, that conservation biology, and parallel approaches in the social sciences, provides academics and other professionals with constructive outlets for their concern.

Conservation biology and the conservation movement cannot reverse history and return the biosphere to its prelapsarian majesty.

The momentum of the human population explosion, entrenched political and economic behavior, and withering technologies are propelling humankind in the opposite direction. It is, however, within our capacity to modify significantly the *rate* at which biotic diversity is destroyed, and small changes in rates can produce large effects over long periods of time. Biologists can help increase the efficacy of wildland management; biologists can improve the survival odds of species in jeopardy; biologists can help mitigate technological impacts. The intellectual challenges are fascinating, the opportunities plentiful, and the results can be personally gratifying.

Acknowledgments

Notes

1. Jared M. Diamond, 1985, personal communication. University of California, Los Angeles.

2. Hunters, loggers, and developers often express the same love for nature as do professional conservationists, but for many reasons, including economic ones, honorable people may be unable to behave according to their most cherished values, or they honestly disagree on what constitutes ethical behavior.

3. Gary Belovsky and Daniel Goodman, 1985, personal communications. University of Michigan and Montana State University.

4. Russell Lande and George Barrowclough, 1985, personal communication. University of Chicago and American Museum of Natural History.

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Introduction to *The Millennium Ark:
How Long a Voyage, How Many Staterooms,
How Many Passengers?*

This paper calculated whether the world's large mammal species can be saved in captivity if they become extinct in the wild. We predicted that, without captive breeding, most larger mammals would be lost, including 160 primate species; 100 large carnivores; 15 elephants, rhinos, and other perissodactyls; and 100 antelope, deer, wild sheep, and other artiodactyls. We now know that extinction rates will be much worse than we thought then. Some species or subspecies we were concerned about in 1985 are already extinct, notably the Pyrenean ibex, West African black rhinoceros, Zanzibar leopard, and Yangtze River dolphin.

To survive, captive populations must be large enough to maintain genetic diversity (such as heterozygosity) at many loci in the face of environmental changes and until humans provide sufficient natural habitat. When we wrote the paper, we estimated that captive populations would have to be maintained for 500 to 1,000 years, a period we called the "demographic winter." But given population growth, rampant habitat destruction, and global warming, I now believe this period will be much longer or even permanent.

How large must captive populations be to maintain the needed genetic diversity? We suggested that a reasonable goal would be to maintain captive populations large enough to sustain 90 percent of each species' genetic diversity for 200 years. We calculated that, within limits, the more founding animals taken from the wild to start the captive population, the less genetic diversity will be lost and the smaller the equilibrium captive population can be. Recent refinements of our work by Dick Frankham and others suggest that 100 founders are required to avoid inbreeding depression, and that 1,000 to 5,000 are required to retain sufficient genetic variation for adaptive evolution in rapidly changing and deteriorating environments.

Our paper suggested that, given the challenges and limitations of captive breeding, survival of most large mammals will depend on biotechnology to preserve zygotes and embryonic cells from which adults can eventually be regenerated. Since this prediction, however, there have been important advances in preservation and cloning. Endangered species successfully cloned include the European mouflon sheep and the endangered banteng wild cow. An extinct Pyrenean ibex was cloned in 2009 from ear tissue, but the cloned female lived only seven minutes before dying of a lung defect, underscoring the difficulty of resurrecting extinct species.

The Millennium Ark: How Long a Voyage, How Many Staterooms, How Many Passengers?

MICHAEL SOULÉ, MICHAEL GILPIN,
WILLIAM CONWAY, AND TOM FOOSE

Barring holocausts, demographic forecasts suggest a "demographic winter" lasting 500–1,000 years and eliminating most habitats for wildlife in the tropics. About 2,000 species of large, terrestrial animals may have to be captively bred if they are to be saved from extinction by the mushrooming human population. Improvements in biotechnology may facilitate the task of protecting these species, but it probably will be decades at least before cryotechnology per se is a viable alternative to captive breeding for most species of endangered wildlife. We suggest that a principal goal of captive breeding be the maintenance of 90% of the genetic variation in the source (wild) population over a period of 200 years. Tables are provided that permit the estimation of the ultimate minimum size of the captive group, given knowledge of the exponential growth rate of the group, and the number of founders. In most cases, founder groups will have to be above 20 (effective) individuals.

Introduction

According to the models of the UN [United Nations, 1982] and the World Bank [World Bank, 1984], the world population is likely to level off at around 10 to 12 billion about 100 years from now. The implicit assumptions of these forecasts are (1) that agricultural output continues to increase at current rates, (2) that the climatic and agricultural consequences of CO_2 warming, loss of topsoil, and deforestation are insignificant, and (3) that water supplies on a per capita basis can be sustained. These are all unlikely. Thus, famines and other catastrophes may limit the population, especially in Africa, before it approaches these levels. Nevertheless, we can probably expect a near doubling in population size within 100 years.

Given the rate of habitat destruction today (with only 4.8 billion people), it is likely that the rate will be higher in the year 2100. The reasons are, first, that land and firewood are likely to be in short supply for many decades, especially in the tropical, developing countries. These demands will place additional strains on the remaining 50% of tropical forests. Second, the capacity for regeneration of the renewable resources will be compromised by increased levels of exploitation as it already has been in fisheries owing to overfishing [Nelson and Soulé, in press], in grasslands owing to overgrazing [Eckholm and Brown, 1977], and in forests owing to extraction and erosion [Myers, 1980].

How long will the human population remain at or near the peak level and when will the human usurpation of wildlands end? That is, what is the duration of the "demographic winter?" Ignoring the obligatory disclaimers about extrapolative speculation, our guess is about 500 or 1,000 years. It is obviously impossible to foresee cultural values and public policy in any nation several centuries from now. Nevertheless, we assume that after achieving zero population growth, it will be very difficult to bring down the population to an optimum level. Only in very disciplined, regimented cultures is the goal of one child per family likely to be achieved. On the

other hand, a resolution of the population explosion might occur much sooner as a consequence of famines, epidemics, or a nuclear holocaust.

Even if we assume that the population drops relatively quickly, say in two or three centuries, we cannot be certain that this will result in the abandonment of the lands that, today, are habitat for wildlife, but that tomorrow will be cities, villages and farms. It is unrealistic to assume that peoples will be easily convinced to abandon villages and farms that have become traditional sites of occupation, unless the land is no longer arable. On the other hand, the reconstruction of quasinatural habitats might become a major social goal in the future. People, especially the young, will leave rural areas if there are real or imagined economic incentives, as evidenced by the exodus to cities now occurring in many tropical nations.

There is another problem, as well. Most of the tropical and temperate lands that still support wildlife today, even the forested lands, are hydrologically and agriculturally marginal. Many of these lands will be seriously degraded if they are settled, and their soils eroded, compacted, or turned to brick. So, even if these lands can be relinquished, centuries may pass before they could provide optimum habitat for wildlife.

This brief futuristic preamble seems to support the pessimistic view that contemporary zoological and botanical gardens must be prepared to be stewards of their charges for many centuries or millennia, barring the development of less spaceintensive ways of maintaining viable populations. But even if technological solutions are found for maintaining many species in miniaturized and suspended states, it may be impossible to recapture a true twentieth century ecosystem, with all its complex biotic and functional diversity. The reason is that the large majority of species are smaller plants and animals. These will have been extinct for a long time unless relatively large and well managed fragments of habitat are maintained during the demographic winter [Soulé and Simberloff, 1986].

How Many Kinds?

How many species will be in the ark? Myers [1984] suggests that we will lose between one-quarter and one-half of all species. Assuming that there are between 10 million and 31 million [Erwin, 1982] species on the planet, we must anticipate losing between 3 million and 16 million species. Of course, the vast majority of these are insects [Raven, 1976; Erwin, 1982].

How many will be vertebrates, especially birds and mammals? A worst case scenario assumes a near total blitzkrieg of national parks and similar reserves in the tropical countries. This is not at all unlikely in the opinion of some [eg, Myers, 1984] with experience in Africa and parts of tropical Asia and Latin America. If this most dreary scenario comes to pass, then we can assume that the larger vertebrates will be the hardest hit. In Table 1 we provide a rough analysis of the number of mammalian species that would be in serious jeopardy. The following groups will all but disappear unless they are captively maintained: primates (160), the large carnivores (ca 100), the perissodactyls (15) and most of the artiodactyls (ca 100). In addition, about 300 species from the other orders will be wiped out. This is about 800 species. We estimate that the same will be true for birds. Locally endemic species in the tropics [Terborgh and Winter, 1983] and migratory birds are especially vulnerable because they are entirely dependent for their survival on habitats (islands, tropical forests) with dismal prospects. There will probably also be several hundred species of reptiles and amphibians in need of special protection. Therefore, we must consider that at least 2,000 species of large, terrestrial vertebrates will be among the missing unless there is room in the ark.

During the past 2 years, about 19% of the world's mammals and about 9% of all the species of birds have been bred by those zoos reporting to the International Zoo Yearbook (IZY) censuses. The mostly North American collections reporting in the International Species Inventory System (ISIS) contain about 60,000 specimens of mammals and birds (reptiles, amphibians, fishes, and invertebrates

TABLE 1. A Preliminary Attempt to Predict the Number of Mammalian Species That Will Require Captive Maintenance in the Next 200 Years*

Order	No. of recognized species	No. of vulnerable species that may require captive breeding
Monotremata	4	
Marsupicarnivora	123	2
Peramelina (bandicoots)	18	
Paucituberculata (shrew-like)	7	
Diprotodonta (herbivores)	101	
Insectivora	409	
Dermoptera (colugos)	2	2
Chiroptera	~900	100
Primates	160	160
Edentata (anteaters, sloths)	25	10
Pholidota (pangolins)	7	5
Mysticeta	10	2
Odontoceta (toothed whales)	65	10
Carnivora		
Canidae	35	35
Ursidae	7	2
Felidae	72	60
Others	193	100
Lagomorpha	53	?
Rodentia	~1,700	100
Tubulidentata	1	1
Probroscidea	2	2
Hyracoidea	11	5
Sirenia	4	4
Perissodactyla	15	15
Artiodactyla	~172	100
Total		815

*The estimates of "Number of vulnerable species that may require captive breeding" assume the virtual destruction of natural habitats in the tropics, with the exception of northern Australia and scattered nature reserves. It is assumed that none of the nature reserves will be sufficiently large to protect the larger mammals [Frankel and Soulé, 1981]

are not yet in this system) in 175 reporting collections. Ninety percent of all mammals and almost 75% of all birds added to these collections last year were bred in captivity, and the numbers of many of the endangered species they hold are steadily increasing.

Between 1973 and 1983, for example, there was a doubling of the numbers of snow leopards (130 to 300). Many other species showed similar increases including Siberian tigers (400 to 1,200), golden lion tamarins (85 to about 400), many endangered ungulates such as barasingha (114 to 291), brow-antlered deer (37 to 101), gaur (32 to 83), scimitar-horned oryx (141 to 511), Arabian oryx (75 to 161), addax (142 to 329), and dama gazelle (58 to 178) and many others.

The ability of zoos to breed most mammals and birds is no longer in doubt, but the ultimate carrying capacity of zoos is far from clear. If zoos are to undertake the long-term maintenance of the increasing numbers of refugee species, organized planning should begin now, and on an international scale. Among the difficult questions that need answers: "Is there enough space in the ark?"

Although there are nearly 540,000 mammals, birds, reptiles, and amphibians in zoos reporting to the American Association of Zoological Parks and Aquaria and the IZY, it is unrealistic to assume that more than half of these spaces can be used for long-term propagation. Analysis of present zoo populations suggests that about 330 mammals could be sustained at a population size of 275; 467 birds, 96 reptiles, and 32 amphibians, each at a population of 300; 925 species in all. These sizes (275 and 300) may be larger than necessary for strictly genetic considerations, and might be reduced eventually. Even the number 925, however, may be optimistic given the present logistical and collaborative disarray [Conway, in press]. Such calculations are quite arbitrary (for reasons elaborated below), but they suggest the magnitude of the problem, and the level of commitment required.

Within two or three decades, it may be necessary to devote most of the space in zoos to the captive breeding of endangered species. Such a statement might alarm many in the zoo community, until

it is realized that most of the species currently held in zoos will be shifted, one by one, from the nonendangered to the endangered category by virtue of habitat destruction. Nevertheless, the message of the preceding paragraphs is that zoos will need help. Current budgets, facilities, and techniques are no match for the gigantic task of conserving the planet's megafauna.

Is help on the way? The ultimate solution, we believe, must come from research in developmental and reproductive biology focused on the preservation and regeneration of viable organisms from zygotes and embryonic cells. Admittedly, cryogenics, like most technological fixes, is no magic solution. Millions of dollars and decades of research have been invested in the development of the techniques for just a single species—cattle—and to a lesser extent for horses. So far, the techniques are not transferable to many other species.

On the other hand, there is continuing progress in this field, especially considering where the science was just 20 years ago. Based on the recent successes in bovids, equids, and primates, we consider it likely that traditional captive breeding programs for many species in these groups will be obsolete in a few decades (given reliable refrigeration), and that the vacated space will become available for other taxa. (Even such technological breakthroughs will not obviate the need to maintain some living representatives of most species to serve educational, cultural, recreational and technical-scientific purposes). In addition, we cannot predict what unforeseen technologies will be developed. We would strongly urge the research community, in and out of zoos, to give high priority to research on cryogenic or other technologies for the long-term preservation of sperm, ova, and embryonic materials, along the lines of the recommendations of the recent FAO/UNEP report on this subject [FAO, 1984].

In the meantime, zoos and similar institutions will have to do their best to maintain relatively large, viable populations of higher vertebrates that are threatened with extinction in their natural habitats. We must therefore determine, as best as we can, the minimum number of individuals in such breeding colonies that will guarantee the maintenance of viability.

How Many of Each Kind?

As has been described elsewhere [Frankel and Soulé, 1981], the number of individuals required for the maintenance of genetic fitness in a population depends on several variables. These are (1) the definition and the criteria for fitness, (2) the intended duration of the program, and (3) the generation time. We must add a fourth variable, one that is only appropriate for breeding programs with a finite lifetime—the maximum tolerable loss of genetic variation. No loss of additive genetic variation should be tolerated in a program of indefinite length. These four variables will be described briefly.

Fitness in the *immediate*, or short-term, sense concerns individuals. It is the current viability and reproductive success of the individuals in the group. Inbreeding can compromise short-term fitness by producing abnormally high levels of homozygosity for deleterious, recessive genes, the genetic load. There is a large body of evidence [Soulé, 1980; Allendorf and Leary, 1986] suggesting that even very modest decreases in heterozygosity can reduce fitness as estimated by physiological efficiency, growth rates, and developmental (morphological) stability. By trial and error, animal breeders have learned that inbreeding problems (depression) can be avoided if the rate of inbreeding per generation, F, remains below 2% [Franklin, 1980; Soulé, 1980]. Employing the approximation

$$F = \frac{1}{2N_e}$$

where N_e is the effective size of the population, the corresponding effective population size is about 25. Franklin [1980], Soulé [1980], and Frankel and Soulé [1981] recommended a slightly more conservative short-term maximum rate of inbreeding (F = 1%), equivalent to an effective size of about 50. A 1% rate of genetic erosion was considered tolerable by these authors because they were assuming that the groups would be released into the wild within a very short time, say 100 years, an interval that now appears optimistic.

Fitness in the long-term or *ultimate* sense means the capacity of the population to maintain itself indefinitely in its environment. Thus, long-term viability or fitness is variously defined as adaptability (genetic) to environmental change, the maintenance of evolutionary fitness, and population homeostasis. Obviously, the retention of long-term fitness or viability requires the preservation of genetic variation.

How do we go about estimating the time-frame of the ex situ conservation effort for vertebrates? In light of the unpleasant demographic scenario painted above, it would not be unreasonable to plan for a voyage of 1,000 years. An optimist, on the other hand, would argue that applications of molecular biology to the fields of development and reproductive physiology are just entering an "exponential growth phase," and that technologies for storage and regeneration of embryonic cells that are unimaginable today will be available in less than a century. As these technologies come on line, more species can be moved from the space- and resource-intensive "living zoo" to the miniaturized, "suspended zoo." If this scencario is correct, our descendents will be able to replace the millennium ark with a "millennium freezer."

We wish to make it clear that none of us is enamored of the "technological fix" as a solution to major social ills. Technology has never permanently "solved" major human problems such as hunger, poverty, injustice, and warfare. But technology, when applied to specific, technical objectives is very successful, as evidenced by word processors, putting humans in space, and refrigeration.

Regarding the security of frozen or suspended zoos, they are as secure as society itself. There would be redundancy in the holdings, with collections dispersed throughout the world. For those who are nervous about the power failing everywhere at once, the consequences of such a planet-wide catastrophe would be just as serious for zoos as for suspended collections—the pillaging of zoos with all their meat on the hoof, would take no longer than the thawing of all the freezers. In this context, it is not as far-fetched as it sounds to begin planning long-term storage facilities on the back side of the moon.

Another obvious caveat is that a suspended zoo cannot protect the vast majority of smaller organisms that are now threatened with extinction, especially in the tropics. The majority of insect species are undescribed taxonomically [Erwin, 1982] as are a large fraction of neotropical plants [Gentry, 1986]. Whether described or not, most organisms, especially those in the tropics, are small, relatively inconspicuous, and unknown ecologically. Their only human constituency is a handful of biologists; their only refuge is in nature reserves.

Returning to the "how long?" issue, the consensus of the authors is that 200 years is a reasonably conservative temporal horizon. Great works of art have been preserved much longer, even if their collectors and repositories were not. A longer time frame ignores the exponential rate of progress in biological technology. Those who think that 200 years is either too short to too long are free to adjust their programs accordingly. Indeed, conservationists of the 21st Century will have the option to modify their time horizons and to make compensatory changes in effective population sizes, if they conclude that such action is necessary. Fortunately, decisions made during the initiation phases about effective size are, to some extent, revocable in the first few decades.

Because ultimate or long-term viability or adaptive potential depends on the store of genetic variability, it is desirable to retain as much genetic variability as possible. Ignoring the input of genetic variability from mutation (which in any case will probably be less than the loss when the effective population size is less than a few hundred), we believe that a 90% criterion is reasonable and realistic. That is, the goal should be to preserve at least 90% of the genetic variability that existed in the source population over the next 200 years. Any such criterion is clearly arbitrary. Nevertheless, it was the consensus that the 90% threshold represents, intuitively, the zone between a potentially damaging and a tolerable loss of heterozygosity.

It is prudent to have as many founder individuals as possible. There are two principal reasons for this. First, the more founders, the more genetic variability. Even though a pair of individuals will contain, on average, 75% of the genetic variation or heterozygos-

ity for quantitative traits in the source population (assuming no dominance and epistasis), rare alleles will not survive such a small bottleneck in the number of founders [Allendorf, 1986; Fuerst et al, 1986]. The ratio of genetic variation in the founders compared to the source population approaches 1.0 asymptotically in the range of 25–30 individuals [Gilpin and Soulé, in preparation].

Second, the more founders, the sooner the group will reach the target population size or N_K. The rate of approach to N_K depends on the population growth rate [Nei et al, 1975]. When the growth rate is low, the loss of genetic variation from genetic drift can be high in the early generations. The optimum situation, therefore, is to have a large number of founders, say more than 20, and to achieve N_K very quickly. Parenthetically, the potential for interaction and gene flow between captive groups and wild populations of a species is important. Where survival of a wild population is possible, the benefits of coordinated management should not be dismissed by purists on either side.

Generation time is critical because reproduction is the only point in the life history when there is loss of alleles or genetic variation. Consequently, the longer the generation time, the fewer opportunities there will be for the loss of genetic variation. For example, there will only be eight such opportunities in 200 years when the generation time is 25 years.

Our principal conclusions are summarized in Tables 2–8. The methodology is presented elsewhere [Gilpin and Soulé, in preparation]. Each of the tables was generated by using a unique value for the intrinsic rate of increase per generation (population growth) for the group, from the time of founding until it reached N_K. These growth rates span the range that is typical of zoo species. The other assumptions used in the calculations include (1) a 200-year program, (2) the retention of 90% of the genetic variation for quantitative traits, and (3) random breeding within the group, as well as (4) non-overlapping generations, (5) an equal sex ratio, and (6) Poisson-distributed family size. The absence of values in the upper parts of some of the tables indicates that more than 10% of the ge-

netic variation is lost even if N_K is infinite. The value 999 indicates that N_K lies between 1,000 and 10,000.

Some remarks about these results are in order. First, note that the founder effective size must always be six or above if the 90% criterion is to be met. With fewer than six founders, the group will lose more than 10% or more of the genetic variation existing in the source population as soon as it reproduces.

Second, N_K is very sensitive to N_F, the number of founders, although above N_Fs of about 25, the effect diminishes very rapidly. A very great decrease in N_K can be achieved by doubling N_F, especially if it is combined with artificially delayed reproduction. As shown in Table 5, for example, a decrease in N_K from 617 to 124 is achieved by an increase in N_F from 12 to 24 while increasing the generation time from 6 to 10 years.

Third, the tables contain regions of biological impossibility. For example, Table 7, which corresponds to the intrinsic rate of increase of small rodents that produce several litters of about five offspring per year, shows generation lengths that are unattainable in such species. It should be noted also that the goal of 90% retention of genetic variance for 200 years is virtually unattainable at generation growth rates of < 0.1, unless both generation length and N_F are $>$ 25. For example, Table 8 tabulates the values for slowly reproducing animals (exponential growth rate per generation $= 0.05$). Very large numbers of founders are required to meet the 90% criterion. Actual growth rates in zoos are often far below those in the wild, for a variety of reasons. Examples of some actual exponential growth rates per year in captive groups might be useful: okapi, 0.1; lion-tailed macaque, 0.05; Siberian tiger, 0.09 (rate is artificially low); Przewalski's horse, 0.10; gaur, 0.11; golden lion tamarin, 0.22.

Figure 1 illustrates a small sample of the tabulated results from Table 5. Curve A was generated with $N_F = 10$; curve B with $N_F = 20$; curve C with $N_F = N_K$. The latter assumption is very unrealistic, but note the small effect on N_K of increasing the founder size above 20.

Our model does not take into account the generation of genetic variation by mutation. Above some theoretical equilibrium size, a

TABLE 2. Carrying Capacities Necessary for the Retention of 90% of the Initial Genetic Variance*

No. of founders	Length of generation (years)										
	1	2	4	6	8	10	15	20	25	30	50
16	—	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—	20
20	—	—	—	—	—	—	—	—	—	—	19
22	—	—	—	—	—	—	—	—	—	—	19
24	—	—	—	—	—	—	—	—	—	—	18
26	—	—	—	—	—	—	—	—	—	31	18
28	—	—	—	—	—	—	—	—	—	29	17
30	—	—	—	—	—	—	—	—	—	29	17
32	—	—	—	—	—	—	—	—	—	29	17
34	—	—	—	—	—	—	—	—	40	28	17
36	—	—	—	—	—	—	—	—	39	28	17
38	—	—	—	—	—	—	—	—	39	28	17
40	—	—	—	—	—	—	—	53	39	28	16

*The exponential growth rate per generation is 0.05.

TABLE 3. Carrying Capacities Necessary for the Retention of 90% of the Initial Genetic Variance*

No. of founders	Length of generation (years)									
	1	2	4	6	8	10	15	20	25	30
6	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	—	—
12	—	—	—	—	—	—	—	—	—	—
14	—	—	—	—	—	—	—	—	—	—
16	—	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—
22	—	—	—	—	—	—	—	—	—	—
24	—	—	—	—	—	—	—	—	—	32
26	—	—	—	—	—	—	—	—	—	30
28	—	—	—	—	—	—	—	—	—	29
30	—	—	—	—	—	—	—	—	43	29

*The exponential growth rate per generation is .1.

TABLE 4. Carrying Capacities Necessary for the Retention of 90% of the Initial Genetic Variance*

No. of founders	Length of generation (years)									
	1	2	4	6	8	10	15	20	25	30
6	–	–	–	–	–	–	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	–	–
16	–	–	–	–	–	–	–	–	–	–
18	–	–	–	–	–	–	–	–	–	39
20	–	–	–	–	–	–	–	112	60	34
22	–	999	999	999	642	384	137	77	50	32
24	999	999	999	582	362	243	106	66	45	30
26	999	999	768	424	274	192	92	60	43	30
28	999	999	617	348	234	164	84	56	42	29
30	999	999	538	309	208	148	79	54	40	29

*The exponential growth rate per generation is .3.

TABLE 5. Carrying Capacities Necessary for the Retention of 90% of the Initial Genetic Variance*

No. of founders	Length of generation (years)									
	1	2	4	6	8	10	15	20	25	30
6	–	–	–	–	–	–	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–
10	–	–	–	–	–	–	–	–	–	–
12	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	157	55
16	999	999	999	936	617	424	188	110	70	39
18	999	999	882	517	348	253	124	80	55	35
20	999	999	655	384	269	196	102	69	49	32
22	999	999	538	321	225	167	90	62	45	31
24	999	999	468	285	200	148	84	59	43	30
26	999	936	432	258	184	137	79	55	42	30
28	999	865	399	243	174	129	76	54	41	29
30	999	815	376	229	164	124	73	52	40	29

*The exponential growth rate per generation is .5.

TABLE 6. Carrying Capacities Necessary for the Retention of 90% of the Initial Genetic Variance*

No. of founders	Length of generation (years)									
	1	2	4	6	8	10	15	20	25	30
6	–	–	–	–	–	–	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–
10	–	–	999	999	999	999	682	392	225	102
12	999	999	999	617	432	321	174	117	80	49
14	999	999	655	399	285	216	122	85	61	40
16	999	999	517	321	229	174	102	71	53	35
18	999	955	450	280	200	154	90	65	48	33
20	999	848	399	253	184	140	84	60	45	32
22	999	783	376	234	170	132	79	57	43	31
24	999	738	355	220	161	124	76	55	42	30
26	999	709	334	212	154	119	73	53	42	30
28	999	682	321	204	151	117	71	52	41	29
30	999	655	315	200	145	115	70	52	40	29

*The exponential growth rate per generation is 1.

TABLE 7. Carrying Capacities Necessary for the Retention of 90% of the Initial Genetic Variance*

	Length of generation (years)									
No. of founders	*1*	*2*	*4*	*6*	*8*	*10*	*15*	*20*	*25*	*30*
6	–	–	–	–	–	–	–	–	–	–
8	999	999	999	723	527	407	239	167	122	80
10	999	999	617	392	291	225	134	98	73	49
12	999	993	477	303	225	174	106	77	59	40
14	999	848	407	264	192	151	92	67	52	37
16	999	768	369	239	177	140	85	62	48	34
18	999	709	348	225	167	129	79	60	46	33
20	999	682	328	212	157	124	76	57	44	32
22	999	655	315	204	151	119	74	55	43	31
24	999	630	309	200	148	115	73	54	42	30
26	999	617	297	192	143	112	71	53	42	30
28	999	605	291	188	140	110	70	52	41	29
30	999	593	285	184	137	108	69	52	40	29

*The exponential growth rate per generation is 3.

TABLE 8. Carrying Capacities Necessary for the Retention of 90% of the Initial Genetic Variance*

No. of founders	Length of generation (years)									
	1	2	4	6	8	10	15	20	25	30
6	—	—	—	999	999	999	999	999	999	738
8	999	999	831	527	392	303	184	134	100	67
10	999	999	538	341	253	200	122	89	67	47
12	999	899	432	280	208	164	100	73	56	40
14	999	783	384	248	184	145	89	66	52	37
16	999	723	355	229	170	134	82	62	48	34
18	999	682	334	216	161	127	79	60	46	33
20	999	655	321	208	154	119	76	57	44	32
22	999	630	309	200	148	117	74	55	43	31
24	999	617	303	196	143	115	73	54	42	30
26	999	593	291	188	143	112	71	53	42	30
28	999	582	285	184	140	110	70	52	41	29
30	999	582	285	184	137	108	69	52	40	29

*The exponential growth rate per generation is 5.
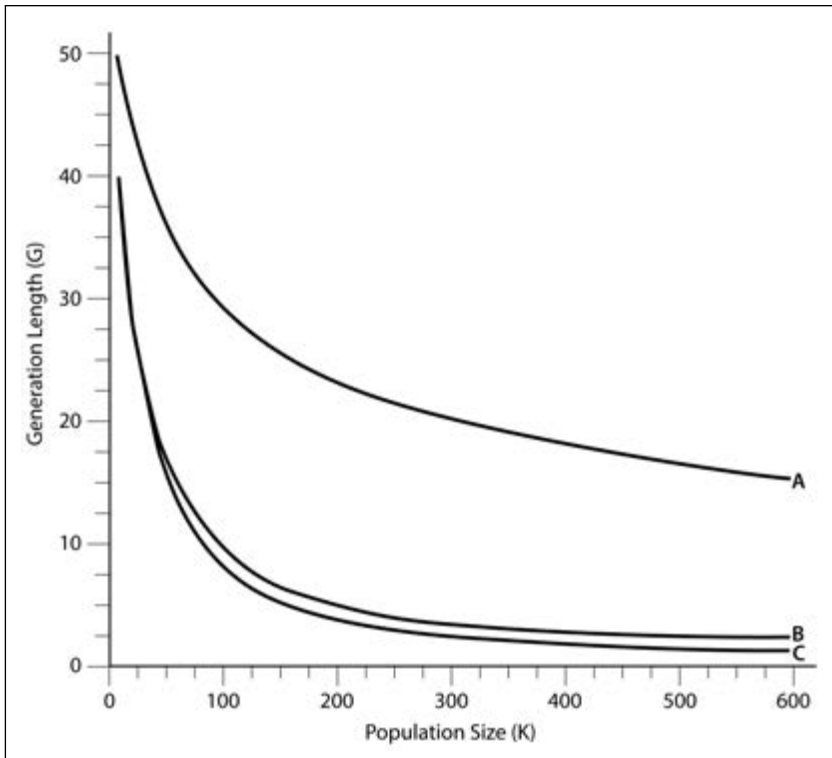
FIGURE 1. Combinations of ultimate effective population sizes and generation lengths in years required to maintain 90% of the genetic variation in the source population. Curve A, founder size of 10; curve B, founder size of 20; curve C, founder size equals ultimate size.

population will gain genetic variance by mutation faster than it loses it by genetic drift [Franklin, 1980]. Existing data do not permit an estimate of such an equilibrium. (Actually, there are as many equilibria as there are categories of phenotypic traits for which mutation rates can be measured.) Nevertheless, we are in agreement that the marginal genetic advantage of an effective size of 500 versus 250 is probably insignificant. Because space and facilities will continue to be limiting resources for zoos in the foreseeable future, we believe that the maintenance of more than 200 to 300 effective individuals of a given species is a profligate use of precious resources. For example, one popular species (such as tigers) could monopolize

much of the space available for large cats. Parenthetically, it is often pointed out that the census number can be significantly reduced by any manipulations that tend to equalize the reproductive output of families.

A certain amount of subdivision will often be desirable, as discussed by Foose et a1 [1986]. For large animals, the unit of subdivision may often be all the zoos on a continent. Therefore, the values in the tables could represent the target sizes for either the European or the North American subpopulation, though a strict application of this principle would reduce by half the number of species that could be maintained.

Conclusions

We have considered the questions "how long, how many staterooms, and how many passengers?" as a cryptic way of asking

1. How long will it be before habitat for wildlife begins to increase rather than decrease?
2. How many species of terrestrial vertebrates will require captive maintenance and propagation?
3. What population sizes are necessary to prevent the decay of fitness and genetic variation in captively bred species?

To the first question, our answer is a millennium, plus or minus 500 years, barring human catastrophes. With regard to captive breeding, however, we qualify this: Assuming that our institutions, and, with them biological technology, survive, a planning horizon of 200 years appears sufficient. By this time, in all likelihood, entirely new technologies for maintaining and regenerating species in miniaturized and suspended states will have been developed.

To the second question, our answer is about 2,000 species of vertebrates (excluding fish), probably plus or minus 500. The captive breeding of so many species will saturate the available space and resources, but, hopefully, advances in cryogenics and similar technologies will obviate the need to maintain all of these at one time as living organisms.

To the third question, the answer is more complex. Our approach is to assume that a reasonable goal is to retain at least 90% of the genetic variance in the founder group for the interval of two centuries. (Considering such a finite period of time permits much more concrete and tailored answers to the question.) The actual target number is found to depend on the effective size of the founder group, the rate of growth of the population in captivity, and the generation time. The results are tabulated for a range of parameter values.

Even with the highest rates of population growth, the effective size of the founder group must be six or more, assuming that 90% of the genetic variation in the source populations is to be conserved. Larger founder sizes allow substantial decreases in N_K. This should not be construed, however, to mean that hope should be abandoned if such founder sizes are impractical. The goal of 90% retention is arbitrary, but it was the consensus that it intuitively represented the zone between a potentially damaging and a tolerable loss of heterozygosity. With careful management, the viability of a captive group should be sustainable, even with fewer founders, and even if the 90% goal is not attainable.

Animals with very long generation times can be maintained with relatively few individuals. For example, an effective size of only about 40 need be kept if the generation time is 25 years. On the other hand, such small populations may be vulnerable to the misfortunes and vagaries of disease, accidents, and occasional breakdowns in curatorial vigilance. Though zoos, to a large extent, are able to buffer the random variation in their environments and in the demographics of their captive groups, formal captive breeding management plans should estimate the frequencies, probabilities, and genetic consequences of such stochastic perturbations.

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Introduction to *Conservation Biology and the "Real World"*

The 1960s and '70s saw an explosion of knowledge about community ecology and island biogeography that scientists began testing in conservation programs. The yearning to use this abstract knowledge to save ecosystems and their species resulted in the formation of the Society for Conservation Biology in 1985, the fastest-growing scientific body of its time. To quote Victor Hugo, "There is one thing stronger than all the armies in the world: and that is an idea whose time has come."

The paper you are about to read introduced *Conservation Biology: The Science of Scarcity and Diversity*, my 1986 update of the 1980 book *Conservation Biology*, edited by Soulé and Wilcox (see paper 1). The 1986 book was a compendium of thought by pioneers in the new field and a testament to how fast the new discipline had evolved.

My introduction laid out the moral and philosophical context for this new discipline, whose ultimate success will be measured by how well it preserves biological diversity "in the real world." I reminded practitioners that conservation biology is much more than

the formulaic application of scientific theory. Successful conservation also depends on understanding people's cultural and personal philosophies, religions, and economic aspirations. I asserted that no contributing discipline is superior to another; theoreticians and practitioners, biologists, psychologists, and political scientists must work together as equals to save biodiversity. Happily, mutual appreciation has flourished since I wrote this, as evidenced by the fact that the social sciences are solidly at home in conservation biology journals and conferences.

I emphasized in this essay two issues that remain challenging today. The first is what I called the Nero Dilemma, referring to fiddling while Rome burns. This is the idea that conservation biologists do not have the luxury of endlessly refining their science while species go extinct (see paper 2). They must advocate for measures that are timely, even if based on less than conclusive evidence.

The second idea, adjunct to the first, I called the Bottom Line Dilemma. Many impatient conservationists, land managers, and politicians want to know, "Will this particular conservation intervention save the species?" But such "bottom-line" questions do not recognize that ecosystem and species interactions are so complex that it is difficult to be sure ahead of time whether a particular conservation intervention will be successful. As I wrote in 1986, "Just as in social issues, there is rarely an answer in conservation biology that is both simple and politically appealing." Nonetheless, now we do know enough about conservation science to frequently make the right choices, as exemplified by the 1987 decision to capture all remaining California Condors for captive breeding. Since then numbers have risen from 22 to more than 400, with reintroduced wild populations in Arizona and California. The challenge to conservation biologists is to help the public, particularly decision makers, understand that just because we cannot always predict the future with certainty does not mean that we cannot make informed decisions that will be right in most instances.

4

Conservation Biology and the "Real World"

Michael E. Soulé

from *Conservation Biology: The Science of Scarcity and Diversity,* 1986

A good field biologist is often more concerned with what is missing in a situation than with what is present. Similarly, the perspicacious reader will ask what was left out of this book. It is a healthy sign that the answer is "a lot." Entire disciplines and many topics could not be included, simply because the boundaries and activities of the science keep expanding. Ideally, we would also have preferred to include many more contributions written from the perspectives of people who work with nature reserves and zoological and botanic gardens. In addition, there could have been much more about captive breeding, about introductions, about genetic engineering, about restoration and rehabilitation of degraded habitats, and about management conundrums and insights. In fact, most of these areas and topics have had recent conferences of their own, and there are several excellent books and publications either recently published or in press (Mooney, 1985; Regal, 1985; Ralls and Ballou, in press; Jordan and Gilpin, in press). One daring exception is the interface between theory and practice, especially from the viewpoint of the

manager of parks and forest reserves. This deserves its own project, although many of the authors (especially [in] Sections V and VI) have been involved at various levels with management agencies and managers.

Another area that was regretfully omitted is integrated agro-ecosystems—the study of the traditional knowledge and methods in rural life that are gentler on the landscape than is high subsidy, highly mechanized agriculture. We could not have done justice to this field [in] the space available. It also deserves a book of its own.

The line had to be drawn somewhere, and with the exception of the last two sections, it was drawn around the "core" areas, including biogeography, ecology, systematics, genetics, and behavior (Sections I through IV).

Section V takes us from the realm of theory and experiment (in more or less natural communities) to the realm of human impact. This section is by no means an attempt to provide a comprehensive overview of the status of all of the planet's sensitive or threatened habitats; it is merely a sampling of some of the most obvious (tropical forests, the Sahel) and some of the most neglected (cave faunas, tropical marine and freshwater habitats). The status of some other habitats is referred to in Chapters 7 (Mediterranean climates), 8 (tropical montane regions), and 14 (islands).

Section VI examines several of the interfaces between conservation biology and society (Chapters 23 and 24), and between conservation biology and ethics (Chapter 25). Thus, this volume steps gingerly into the "real world." Many of the authors also appear to be suggesting that the perennial reluctance of scientists to discuss matters of ethics may imperil the very organisms and processes they hold most dear. The omission of any subject, regardless of how arbitrary it may appear, is certainly not meant to imply any limits to the content of conservation biology. This discipline should attract and penetrate every field that could possibly benefit and protect the diversity of life.

What Is the "Real World"?

The term "real world" appears in the title of this chapter, and it is always part of the banter during conferences and workshops when the subject matter is conservation. This is because the ultimate test of conservation biology is the application of its theories in actual management situations. Like many colloquialisms, however, the term is somewhat problematic. To most of us, I think, the term "real world" means the part of our lives that involves face-to-face interactions with others and with their desires, priorities, and prejudices; it is the world "out there," the world of politics and economics, and all the vagaries of human nature that we associate with these areas.

But the term "real world" implies that other worlds are less than real. It begs the question, for example, of the "internal world" of subjective experience, and the "middle world" of cognition, experiment, and discourse. Such distinctions are oversimplified, but this one is so ingrained that attack is futile. However, it is important to bear in mind that there is traffic bridging these so-called worlds. Events and prevailing philosophies in the real world influence and determine our private intellectual lives. Therefore the activity of these private worlds, including models and theories, are in part the products of learning and conditioning in the social-cultural milieu. Just as the idea of a "star wars" defense shield had to await the development of nuclear missiles, so the idea of conservation biology had to await a serious threat to biological diversity.

Mission-oriented crisis disciplines such as conservation biology straddle the frontier between these worlds. Perhaps a better metaphor is that they are like a shuttle bus going back and forth, with a cargo of ideas, guidelines, and empirical results in one direction, and a cargo of issues, problems, criticism, constraints, and changed conditions in the other.

As I will suggest, however, none of these worlds is at bottom any more real or important in a social or physical sense than any other. Each is part of a larger whole. When this fact is ignored, we

generate disciplinary hierarchies that inhibit progress in solving conservation problems. Conservation biology will succeed to the degree that its theoreticians, practitioners, and users acknowledge the larger context in which they exist, and to the degree that they respect one another's roles, contributions, and problems. Anyone wishing to cultivate such an attitude of respect, or wishing to counter a narrow, chauvinistic definition of the discipline need only consider the history and diverse intellectual tributaries of conservation biology. This is the subject of the following section.

The Origins of Conservation Biology

There used to be a popular saying in taxonomic circles that a species was "good" (real) when enough systematists agreed that it was good. Consensus is an important part of any human enterprise.

Consensus can also define a discipline. Disciplines are not logical constructs; they are social crystallizations which occur when a group of people agree that association and discourse serve their interests. Conservation biology began when a critical mass of people agreed that they were conservation biologists. There is something very social and very human about this realization.

When and why did conservation biology become a discipline? The preliminary groundwork occurred in the early decades of this century with the emergence of such disciplines as forestry, fisheries, and wildlife management. The history of the current crystallization has been documented by Brussard (1985). It seems to have happened in the early years of this decade. "Why" is a little harder to explain, but I think it is possible to identify a few of the important tributaries that fed this social and scientific confluence.

One of these was intellectual. The 60s and 70s saw an explosion of theories and data in community ecology and island biogeography. By the end of this period, there were many people who were testing these ideas in conservation programs.

At the same time, there was a perception of a widening gulf separating modern population biology (including the above fields)

from the more traditional disciplines in the natural resources. Biology departments were fragmenting into modern versus traditional, botany versus zoology. Departments and schools of conservation, forestry, fisheries, wildlife management, and similar "applied" fields had become institutionally isolated from each other and from the "mother" scientific disciplines. This inhibited the natural diffusion and application of new ideas and information from one discipline to another and into agency and management circles. Isolation leads to alienation, alienation to hostility. Maybe some reconciliation was overdue.

Social trends may also have contributed to the origins of conservation biology. In the late 70s, many academics in the "pure" sciences wanted very much to contribute to conservation—to be "relevant." Altruism was part of it. The environmental movement had begun. Care for the planet, appropriate and harmonious lifestyles, and a healthy environment were the lenses that focused the energies of a generation. Even today, many university students wish to find a career that promises idealism along with security. But another part of it was a defensive reaction; many of us were finding that development projects were obliterating our research sites, whether they were tropical forests in Costa Rica or vacant fields and canyons next to the campus.

Still another factor has been the extinction crisis. The probable disappearance of the majority of species during the next 50 to 100 years is—or certainly should be—a matter of great concern. This concern will grow as the fruits of poor planning and greed, particularly in the tropics, begin to foul the lives of more and more hungry and deprived people, and to destroy the environments in which they live. As first hundreds, then thousands, and finally millions of species are threatened with extinction over the next century, there will be a crescendo of protest from those to whom "right to life" is more than just a chauvinistic movement by and for Homo sapiens.

Finally, the current interest in conservation biology owes much to the intellectual leadership and vision of individuals in the zoo and herbarium world, in some government agencies, and in some pri-

vate foundations. Some of these people have been posing challenging questions (such as "how big must a population be to minimize the risk of extinction?"). Others have generously supported research, conferences, and publications. From all of these sources, conservation biology was born. Its current polymorphism reflects this.

The idea of conservation biology seems to convey several things at once, including scholarship, a common purpose, and the potential for making a significant personal contribution to the world. For students and established scientists alike, conservation biology seems to represent a community of commitment, and something of value to identify with. The famous quotation of Victor Hugo is relevant: "There is one thing stronger than all the armies in the world: and that is an idea whose time has come."

I referred above to the tendency for suspicion and hostility to grow out of disciplinary fission and isolation. A related tendency is the inevitable tension generated by anything new. To the extent that conservation biology is perceived as a new field, and as enthusiasm for it grows, it will become threatening to some people. It need not, and it can minimize conflict if it can avoid repeating the errors of the past. These errors are elitism and isolation.

Elitism lurks whenever a field has a strong academic foothold. Whether the root of elitism is arrogance from within the ivory tower or fear from without, it is always a danger. There is no hiding the fact that much of the current interest in conservation biology is occurring within academic circles, because it is. But it would be a mistake to lose sight of the fact that the origins of the current movement can be traced back to Thoreau, Pinchot, and Leopold, to Darwin and Elton, to Marsh and Carson, to Teddy Roosevelt and Ashoka, and to Lao Tzu and Saint Francis. More recently its predecessors and contemporaries include many practitioners of ecology, biogeography, systematics, genetics, evolution, epidemiology, sociobiology, forestry, fisheries, wildlife biology, and of the auxiliary sciences of agronomy, veterinary science, resource economics and policy, ethnobiology, and environmental ethics.

Another, related, danger is isolation—elitism's child. If conservation biology becomes isolated in the mental world of academia, it will be of little use. Its prescriptions will not be informed by the real-world problems of the managers, by the actual circumstances of the people who are most involved and affected, and by the knowledge and experience of other consultants (agency employees, extension workers, social scientists, etc.). On the other hand, it is just as important that managers make an effort to be informed about the real world of science as it is that the scientist make an effort to be informed about the real world of management. The only thing that is really real is the whole thing.

The Dilemmas of Going Public

Avoiding the social and psychological pitfalls just described will be the greatest social challenge faced by conservation biologists. Simply, most of us received little or no training in the skills needed for functioning in the real worlds of institutions, government, and management. Many academic scientists, in particular, have had no training or preparation for "going public." Speaking out takes courage. Here I will explore two dilemmas associated with speaking out. In different ways, both are concerned with the problem of insufficient data, or, "when is it time to go public?"

The Nero Dilemma

In many situations conservation biology is a crisis discipline (Soulé, 1985). In crisis disciplines, in contrast to "normal" science, it is sometimes imperative to make an important tactical decision before one is confident in the sufficiency of the data. In other words, the risks of non-action may be greater than the risks of inappropriate action. Warfare is the epitome of a crisis discipline. On a battlefield, if you observe a group of armed men stealthily approaching your lines, you are justified in taking precautions, which may include firing on the

men. To a remote and objective observer, however, the behavior of the men does not prove that they are enemy troops. Alternative possibilities include (1) they are "your" troops returning from a mission; (2) they are forces belonging to a third, neutral, or friendly, force; (3) they are illusory manifestations of hysteria. Of course, this objective observer, like most pure scientists, is free to entertain such alternative hypotheses, because being wrong is not a matter of life and death for him or her. Except in a few highly competitive fields (which, indeed, are war-like), there are no severe penalties for "fiddling" with such ideas for as long as one likes—or until Rome is in ashes.

Here we are dealing with the problem of provisional validity. In pure science, the idea of provisional validity is often enveloped by the term "working hypothesis." In the world of management, however, the situation rarely permits the time-consuming testing of all the relevant working hypotheses. Rather, the "best" hypothesis must be chosen and implemented. As an example, the evidence presented in Chapters 4 and 5 supports, in my opinion, the inference that any significant loss of genetic variation is likely to reduce fitness significantly. Therefore, such genetic erosion should be avoided in managed species or populations, especially in small ones where the loss of genetic variation is chronic and irreversible. Strictly speaking, such a statement is a working hypothesis because it probably lacks sufficient empirical backing to satisfy many experts, and because there are several categorical exceptions (as there are with all biological "laws"). The possible risks of choosing a bad hypothesis, however, must be weighed against doing nothing.

In general, the provisional nature of a hypothesis is no impediment to its operational validity, as long as there are no contradictory, equally supported, guidelines. To ignore such a hypothesis may endanger a species that is being managed, and it exposes the manager to the criticism of reviewers and peers. This is because the manager exists in the real-time world of risks and benefits, not in the null-time world of pure science. In conservation, dithering and endangering are often linked.

The "Bottom Line" Dilemma

Another dimension to the problem of "speaking out" has to do with the issue of complexity. Facing this problem also requires courage. Biologists, including managers of wildlands, are painfully aware of this complexity in organisms and ecosystems, but many people are not, and nonscientists are often unprepared to deal with the conditional, qualified, diffuse, and nonlinear nature of Nature. Stuart Pimm (Chapter 14) points out, for instance, that engineers and politicians, who are always looking for "the bottom line," will not be pleased with community ecologists, in part because the latter are unable to provide a straightforward, one-line statement about community structure and stability.

One solution is to simplify to the point of meaninglessness. A better one is to educate nonbiologists at every opportunity about the nature of complex systems. Simply put, the "bottom line" for complex, nonlinear systems is usually "it depends."

One reason why "it depends" is diversity. Communities and ecosystems are like individuals—no two are alike. Therefore, the quest for a simple bottom line on such issues as stability, extinction thresholds, effects of atmospheric pollution, effects of overharvesting or species introductions, effects of eutrophication, etcetera, is a quest for a phantom by an untrained mind. Qualification of generalizations is inherent in the subject matter of biology, just as it is in the social sciences. It benefits no one to be defensive about the "bottom line" issue. Just as in social issues, there is rarely an answer in conservation biology that is both simple and politically appealing.

One perennial solution to this dilemma is the call for more research. This slogan is often abused when it is used as an excuse to delay action. But it can usually be justified; we can always use more research. But this brings us back to the Nero dilemma—"more research" is sometimes a dangerous luxury when the world is coming down around our heads.

Courage in Education and Communication

Dealing with emotionally and ethically complex material often requires courage. It is natural to back away from "nonscientific" or "messy" matters, leaving such issues to journalists, ethics committees, popularists, and "nature lovers." For example, there are probably conservation biologists who would be reluctant to lecture their students on how to love nature. In their defense, one could argue that loving nature is not a scientific subject, that ardor reveals subjectivity, and, above all, that a biologist is not an expert on loving nature.

This is rubbish. Everyone knows that ardor and enthusiasm are inspiring, and that love of subject matter is infectious. Regarding the issue of expertise, no one has more expertise on loving nature than the professional naturalist or manager who has spent his or her career (or lifetime) studying and admiring plants and animals.

Arne Naess (Chapter 25) points out that it is very important that experts be heard to espouse the intrinsic value of species and nature, and that they try to communicate their spontaneous, inner experience of their unique insights. Admittedly, most of us find it hard, at first, to overcome our lifelong conditioning and inhibitions. But we don't have to go around kissing flowers and beetles. We should, however, let our students and audiences know that nature is more than just a collection of useful research tools or genetic resources for industry and agriculture.

Not that there is anything bad about utilitarian or instrumentalist arguments for nature protection, especially when talking to economists and some politicians. But these arguments are dry, and besides, they have no shortage of effective spokespersons. More to the point, I agree with Naess that most people respond better to appeals that come directly and spontaneously from one's private experience of nature, including our anguish as we witness its slow death. Who is more capable than biologists to spread the word that it is wrong to terminate evolutionary lines, and that it is wrong to wipe out entire communities?

It is often tempting to leave speeches to the politicians, to leave morality to the priests, and to leave ethics to philosophers; however, few of them can speak with authority and familiarity about the exquisite detail and amazing diversity of life.

Students and other people respond well to honesty and emotion. Emotions are as real as cognition, and emotional appeals are often effective in the real world. (Just look at television commercials.) I don't mean that appeals to emotions and intuition should always replace rational and materialistic arguments, or that one true ethical structure exists that can provide answers to all complex problems and conflicts. It is simply that it is approaching "high noon," and we should use every (ethical) tool at our disposal to minimize the damage to this planet.

In this context, it is important to note that many of the authors in this volume touch on ethical issues. Several of them imply or suggest that the "right" of humans to produce as many babies as they like, or as God wills, is arrogant, callous, and selfish. Other conflicts about values are pointed out. These include the rights of wolves versus those of sheep in Scandinavia, the benefits for wildlife (and ultimately for humans) of the tsetse fly versus the rights of cattle and contemporary African pastoralists, and the rights of rivers and traditional human cultures in Amazonia versus those of dams and developers. Here again, biologists should ask for the help of professionals in other disciplines, including philosophers, anthropologists, sociologists, and community development workers. Otherwise, we risk espousing solutions that are theoretically robust, but socially and politically naive.

Progress and the Future

Conservation biology has made significant strides recently. Much of value has been learned about the utility and limitations of island biogeography, about area effects, edge effects, genetic management, disease, the results of removals and introductions, endemicity, rarity, etcetera. Much of this information is already being applied in the

design and management of natural areas, in captive breeding programs, and in other conservation projects. These are encouraging tidings. But they are not enough.

One major impediment is the virtual absence of any formal training in this field. There are no degree programs, and resources for training and research, in relative terms, are negligible. The rate of technology transfer is too slow, and the communications between our colleagues "on the ground" and colleagues in the academy is often poor at best. And last, but certainly not least, there is pitifully little funding for research. Our principal social challenges in the years to come will be:

1. To strengthen the financial and institutional supports for conservation biology, in both its research and educational roles.
2. To strengthen the contacts with related, natural resource disciplines.
3. To strengthen contacts with the management community itself.

The Necessary Research

What research problems need addressing next? I suppose that the number is infinite, but certain ones stand out to me as especially important and challenging. Before mentioning these, however, it might be helpful to note that just as the genetics of nature conservation is the genetics of scarcity (Frankel and Soulé, 1981), so conservation biology is the biology of scarcity. The conservation biologist is called in when an ecosystem, habitat, species, or population is subject to some kind of artificial limitation—usually a reduction of space and numbers.

Scarcity is an obvious issue when there is gross habitat destruction or when a species suffers a great reduction in population size from poaching or overexploitation. These are examples of quantitative scarcity. But there is also qualitative scarcity—as when air pollutants or hazardous chemicals degrade a habitat without necessarily reducing its area.

Problems of scarcity can be examined at various levels, from that of the local population, through the metapopulation, the en-

tire species, to the community and the ecosystem. But three levels of complexity and problems are clearly identifiable. The first level is the population; the principle issue is population viability (or extinction), often referred to as the minimum viable population (MVP) problem (Chapter 2).

I propose that the MVP problem is one of the most seminal issues in population biology, let alone in conservation biology. Not only does the problem of viability require the simultaneous consideration of demography, genetics, behavior, and ecology, but it forces us, as biologists, to come face to face with the ultimate inquisitor. Shaking his finger in our faces, he demands, "If you say that you are a population biologist, and if you say that population biology is a genuine science, then tell me how I can predict the length of time that a population will persist?" Until we can answer such questions (at least within an order of magnitude), the maturity of conservation biology (and population biology) and its status as a predictive science will be in serious doubt.

Challenging problems also exist at higher levels of biological organization. One of the obvious problems at the community level is the question of community structure, and the relative weights of stochastic versus deterministic forces affecting such structure. The specific questions include:

1. What is community equilibrium?
2. Is it ever achieved?
3. Is it more or less likely to exist in the humid tropics than elsewhere?
4. Are there multiple stable states or equilibria?

The skeptic might ask how such arcane questions could ever be germane to the day-to-day management of wildlands and preserves. In answer we might appeal to such nebulous rationalizations as "we cannot manage what we don't understand." A better answer would be to point to real issues where a more mature theory would help us prescribe better guidelines. For example, if communities are often saturated or supersaturated with species, it is harder to justify try-

ing to prevent the extinction of rare species; there could be ecological and economic arguments for allowing the community to "settle" into a lower, but more stable, level of diversity. On the other hand, if it is common for there to be a relatively large random element in community composition, and if species are not packed very tightly, then there might be less concern about the impacts of reintroductions and the introductions of "analog species" to replace lost elements; furthermore there would be less justification for permitting any extinctions.

Pressing multidisciplinary research problems also abound at the level of the ecosystem and biosphere. An incomplete list of these problems includes the greenhouse effect, acid rain and symptomatically similar forms of atmospheric pollution, the biological and climatic consequences of nuclear war, and the climatic, economic, and ecological effects of deforestation and desertization. In addition, we would like to predict the effects that damming most of the world's large rivers will have on climate, commerce, the oceans, and biological communities.

Finally, we cannot ignore people. For example, the implementation of "biosphere reserves" as sites for the harmonious coexistence for humans and nature (UNESCO-UNEP, 1984) depends on both a good grasp of the local biology and on the enthusiastic support of the indigenous peoples. In fact, the survival of many natural biological communities is going to require the creative cooperation of biologists, social scientists, and politicians, especially in the tropics. It won't be long before many conservation biologists are spending more time at community meetings than in the field or laboratory.

Clearly, there is no scarcity of issues—only a scarcity of time and the resources to address them.

Coda

The planetary tragedy is also a personal tragedy to those scientists who feel compelled to devote themselves to the rescue effort. It is painful to witness so much termination. The other side of the coin is

that most humans want to contribute something of social value, and want to be recognized for that contribution.

It is the fortunate scientist who can do this without compromising standards and without taking time off from his or her career. Conservation biologists are such people. Not many scientists, during the few decades of their careers, are able to commit their minds and labors to an epochal task like saving the planet.

It will be a long struggle; many generations of conservation biologists have been and will be conscripted. In the process there will be as much pettiness and jealousy as always, but this will not be a serious impediment if we keep in mind that no one individual or subgroup can ultimately accomplish much on its own. Complementarity is inherent in conservation biology, not only because it is multidisciplinary, but also because it is just one of several fields that are essential for the protection of natural systems in places where humans are part of the landscape.

This book is dedicated to the students who will come after, who will witness the worst and accomplish the most.

Introduction to *Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands*

While teaching at the University of California, San Diego, I realized that each canyon in western San Diego County was an "island" of California sagebrush, black sage, and wild buckwheat chaparral surrounded by a sea of homes. I set out to test MacArthur and Wilson's recently published *Theory of Island Biogeography*, which predicted that extinction rates are higher on smaller, more isolated islands.

My students and I counted chaparral-dependent bird species in 30 of these island-like canyons, including roadrunners, California quail, California thrashers, cactus wrens, and rufous-sided towhees. We found that when one of these species is extirpated from an isolated canyon, rarely will birds from neighboring canyons cross suburban landscapes to recolonize it. Taken together, our research in these 30 canyons gave results predicted by island biogeography:

- Large canyons had more species than small ones.
- Isolated canyons had fewer than those close to others.

We also discovered something shocking—some canyons had lost all their chaparral-dependent bird species, which were replaced by generalists like house sparrows, scrub-jays, and mockingbirds. At first we were puzzled because those canyons without chaparral bird species were not necessarily the smallest or most isolated. Then we realized they had something in common—they were too far from large undeveloped areas to be visited by coyotes. We had discovered a pattern that has since become a major tenet of conservation science—"mesopredator release." When top predators like coyotes, wolves, jaguars, or eagles disappear, populations of midsized predators (mesopredators) like foxes, raccoons, and house cats can explode.

In our case the dynamic worked like this: people around the canyons kept many domestic cats as pets. Where coyotes were present, they killed cats or chased them away. Where coyotes were lacking, the cats were free to commit avian mayhem. Because pet owners provided limitless food, the cats did not starve when their bird prey dwindled, and cat populations remained unnaturally high. Absent coyotes, the cats became "subsidized recreational predators," hunting for fun, not for food.

Globally, there are now many known cases where the removal of a top predator has contributed to "mesopredator release." For example, without wolves, coyotes have prospered in the West. The same process works at lower trophic levels—if coyotes are in turn removed, cats and foxes rule.

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Michael E. Soulé, Douglas T. Bolger, Allison C. Alberts, Raymond Sauvajot, John Wright, Marina Sorice, Scott Hill

Introduction

In many places the increasing attrition of habitat is accompanied by fragmentation of the remaining patches. The analysis of fragmentation and its consequences has been facilitated by the study of species-area patterns in groups of oceanic and continental islands (MacArthur & Wilson 1967) and by the documentation of "relaxation" of species-area curves for archipelagoes of continental islands (land-bridge) and in groups of habitat islands (Soulé & Sloan 1966, Diamond 1972, Terborgh 1974, Brown 1978, Wilcox 1978, Diamond 1984, Patterson 1984, Lawlor 1986, Heaney 1986, Newmark 1987; also see *Biological Journal of the Linnaean Society* 1986; 28 [1 & 2]). Faunal collapse in isolated habitat fragments has been extensively documented, especially on continental shelf islands (Diamond 1972, Terborgh 1975, Case 1975, Soulé et al. 1979) and in recently isolated forest fragments in rural areas (Burgess & Sharpe 1981, Whitcomb et al. 1981, Lynch & Whigham 1984, Wilcove

et al. 1986). This is the first in a series of reports on the biogeographical consequences of recent habitat fragmentation in a Mediterranean scrub landscape in coastal, southern California.

Relatively few studies have been conducted in Mediterranean scrub habitats, especially in urban contexts. Many Mediterranean scrub habitats are characterized by high species diversity (α-diversity) and by high rates of geographic replacement of species within a habitat type (γ-diversity) (Cody 1983). The latter feature, and the likelihood of low vagility of the endemic species in these habitats, may predispose Mediterranean scrub habitats, when fragmented, to higher rates of local extinction than many other temperate zone communities (e.g., see Fig. 10 in Cody 1986, Jones et al. 1985).

The mesas and hills of the coastal region of southern San Diego County are penetrated by valleys extending into the mountainous backcountry. These valleys and their flood plains contain seasonal rivers and streams, and some have well-developed riparian habitat dominated by sycamore (*Platanus racemosa*) and willows (*Salix* ssp.). On a smaller scale, the coastal plain is dissected by systems of dendritic, steep-sided canyons. Canyons in undeveloped areas rarely have surface water or riparian habitat, but in urban areas runoff and irrigation frequently permit the establishment of willows and other mesic species.

The term *chaparral* is sometimes used generically for the Mediterranean type scrub in this region that extends from sea level to over 2000 meters in places. A major component of this vegetation is "coastal sage-scrub," dominated by California sagebrush (*Artemisia californica*),wild buckwheat (*Eriogonum fasciculatum*), and black sage (*Salvia mellifera*). Depending partly on slope and orientation, the coastal canyons may also have stands of chamise (*Adenostoma fasciculatum*), scrub oak (*Quercus dumosa*), and many other genera (*Rhus, Coeanothus, Baccharis*, etc.). Here, the term *chaparral* is used in the broadest sense to refer to all the native scrub habitats.

During the settlement and urbanization of this region, the steepness of the canyons has impeded development. As a result, canyons became the natural boundaries for many neighborhoods, and, until recently, these canyons provided an extensive, interconnecting system of natural open space hosting a rich biota of native wildlife. In recent years, however, both the availability of modern earth-moving equipment and the escalating land values in Southern California have led to the filling, terracing, and fragmentation of these canyons. Also, many of the larger canyons and valleys have been used for the construction of major roads and interstate highways. A significant fraction of the riparian and canyon habitats in the city of San Diego has disappeared altogether, and much of the remaining canyon habitat within the city exists only as isolated remnants, many of which are highly disturbed. In this paper we document some of the effects of fragmentation of canyons on the native chaparral birds inhabiting them.

Methods

The Birds

For biogeographic purposes, the local birds can be placed in three ecological categories: 1) those that require chaparral habitat for breeding in this region—the chaparral-requiring species (Table 1); 2) those locally breeding species that are year-round residents but do not have an absolute requirement for chaparral—such as the Common Flicker (*Colaptes auratus*), the House Finch (*Carpodacus mexicanus*), and Scrub Jay (*Apbelocoma coerulescens*); 3) migratory species that rarely if ever breed locally—for example, the White-crowned Sparrow (*Zonotricbia leucocepballus*). We refer to categories two and three as facultative chaparral species. Many facultative chaparral species frequently feed and breed in exotic, ornamental vegetation in nonnative habitats such as yards and parks. In addition, most facultative chaparral species prefer to nest in trees and

TABLE 1. Common and scientific names of chaparral-requiring bird species in the canyons.

California Quail *(Callipepla californica)*

Greater Roadrunner *(Geococcyx californianus)*

Wrentit *(Chamaea fasciata)*

Bewick's Wren *(Thryomanes bewickii)*

Cactus Wren *(Camplyorhynchus brunneicapillus)*

Black-tailed Gnatcatcher *(Polioptila melanura)*

California Thrasher *(Toxostoma redivivum)*

Rufous-sided Towhee *(Pipilo erythrophthalmus)*

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other nonnative habitats and are capable of relatively long flights. This study is restricted to chaparral-requiring bird species (scientitic names listed in Table 1) because our primary objective was to describe the consequences of fragmentation in this habitat. Facultative chaparral birds would respond little if at all to fragmentation, and our preliminary results collected during the course of this study (unpublished data) seem to confiim this.

Chaparral-requiring species rarely fly far. When flying, they usually ascend no higher than a meter or so above the vegetation. Their feeding behavior also reflects this lack of vagility. The California Thrasher, Rufous-sided Towhee, California Quail, and Roadrunner feed on or near the ground. Bewick's Wren and the Wrentit feed almost exclusively within the bushes. Black-tailed Gnatcatchers feed on insects on the edges and near the tops of bushes and sometimes hawk for insects immediately above the bushes. Although chaparral-requiring species are found mostly in scrub habitats, two of the eight chaparral-requiring species, the Roadrunner and the California Quail, will feed in open or grassy areas adjacent to chaparral habitat, where they return for cover. Some of the chaparral-requiring species, including the Rufous-sided Towhee and Bewick's Wren, will occasionally be found in dense, ornamental vegetation in yards or

parks. The distribution of chaparral-requiring birds in the study sites (canyons) is in Table 2.

Biogeographic Variables

Most of the study locales are canyons, though a few are parks or other sites that contain slopes and mesa top, natural habitat. For simplicity, we refer to all sites as "canyons," defined operationally as fragments of undeveloped land that retain some native chaparral vegetation. Most of our canyons have some slopes greater than 25 percent. As shown in Figure 1, all are surrounded by development. In selecting the 37 study locales (Table 3), we attempted to include sites that are representative of the range of both the sizes of canyons in the San Diego area and the amount of elapsed time since the canyons were isolated by development.

The age of a particular canyon (Table 3) is the number of years since it was isolated by development from a patch of habitat of equal or larger size. In most cases this is equivalent to the canyon's isolation from the main canyon-mesa system, or a large section of it. Ages were determined from aerial photographs, which clearly show the removal of vegetation, and from the subdivision records of the City of San Diego Building Department. In some cases we depended on the latter method because of the long intervals (ca 20 years) between photographic surveys in the early part of this century. When both procedures could be used, they usually gave ages within two or three years of each other.

Areas of the canyons (Table 3) were determined from contour maps produced from aerial photographs, obtained from the planning departments of the city of San Diego and San Diego County. For this purpose, canyon borders were considered to be either backyard fence lines or the edges of streets where there were no houses. Area measurements were made with an Apple computer digitizing tablet. We also estimated the percentage of each site that still retains natural cover ("% Chaparral" in Table 3) from the maps and by

TABLE 2. The distribution of chaparral-requiring species and predators*

No.	Canyon	Wrentit	Bewick's Wren	Rufous-sided Towhee	Thrasher	Quail	Roadrunner	Black-tailed Gnatcatcher	Cactus Wren	Coyote	Gray Fox
										Predators	
1	Florida	1	1	1	1	1		1		1	1
2	Sandmark	1	1	1	1	1				1	1
3	34th St.	1	1	1	1	1				1	1
4	Balboa T.	1	1	1	1	1	1			1	1
5	Alta L.J,	1	1	1	1	1				1	1
6	Kate Ses.	1	1	1	1	1	1			1	1
7	Pottery	1		1	1	1	1			1	1
8	Laurel				1						1
9	Cam. Cor.	1	1	1	1					1	1
10	Canon										1
11	Zena	1	1			1				1	1
12	Baja	1	1	1						1	1
13	Auburn	1	1								1
14	Washington	1							1		1
15	Solana Dr.	1	1	1	1	1	1	1		1	
16	Syracuse	1	1	1	1	1	1			1	1
17	32nd St. S.	1									1

#	Location								
18	47th St.	1							1
19	Mil Cumbres	1	1	1	1	1	1	1	1
20	Chollas	1						1	1
21	60th St.	1	1					1	1
22	Juan St.	1	1					1	1
23	Acuna	1	1				1		1
24	Edison	1	1	1			1	1	1
25	Raffee	1	1				1	1	1
26	Spruce							1	1
27	Oak Crest	1	1	1	1	1	1	1	
28	54th St.	1	1				1		1
29	Titus	1	1				1		1
30	Chateau	1	1				1		
31	Newport	1							
32	Aber	1	1	1					1
33	Talbot								1
34	Montanosa	1	1	1	1	1	1	1	
35	Poinsettia								
36	El Mac								1
37	32nd St. N.	1							1

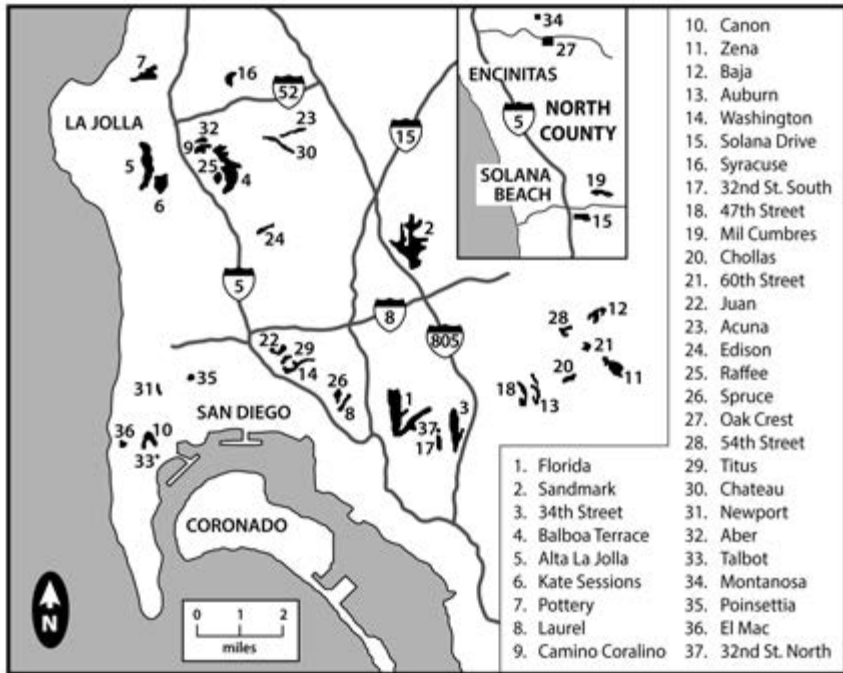*The scientific names of the birds are listed in Table 5-1.

FIGURE 1. Map showing the location of the study sites (canyons) in the vicinity of San Diego, California.

visual inspection from the ground. To obtain an estimate of the area of natural chaparral habitat in each canyon ("Chaparral" in Table 3), we multiplied the area of the canyon by % Chaparral.

We estimated isolation of the canyons from each other and from unfragmented chaparral-like habitat using two kinds of distance measurements (Table 3). Distance X is the distance in meters to the nearest "source" canyon that contains the common chaparral-requiring species (Roadrunners, California Quail, California Thrasher, Rufous-sided Towhee, Bewick's Wren, and Wrentit). Distance Y is the distance to the closest canyon that is equal or larger in size than the canyon being considered.

The variable Fox/Coyote is designed to assess the impact of mammalian predators on chaparral-requiring birds. Canyons were

assigned values for the Fox/Coyote variable according to the following scheme: 1 = gray foxes (*Urocyon cinereoargenteus*) present, coyotes (*Cunis Zatruns*) present or absent; 2 = foxes absent, coyotes absent; 3 = coyotes present, foxes absent. We hypothesize that the presence of coyotes is beneficial because they control the number of gray foxes, domestic cats, and other avian predators, while rarely preying on birds themselves. A Fox/Coyote value 3 is, therefore, "best" for chaparral-requiring birds.

The Census Technique

Our objective was to sample the chaparral-requiring species exhaustively. The censuses were conducted from November 1985 to June 1986, and from September 1986 to February 1987. Some of the species were easier to detect in the spring, but there were no cases of species being detected in a canyon in the fall or winter that were absent from that canyon in the spring. Teams of two or more persons visited each site at least three times for two hours or more each time. The teams walked slowly through the area, recording the presence of each species seen or heard. Several observers visited each site in order to minimize individual differences between observers. If after three visits there was still any doubt about the presence of a particular species, additional visits were made to the site until we were satisfied that we had recorded each chaparral-requiring species present. There were no cases of disappearances of chaparral-requiring species from canyons during the course of this study. The occurrence of Roadrunners was based on the questionnaire (see below) and on interviews with residents living on canyon edges. The absence of Rufous-sided Towhees, a cryptic species that rarely sings in the fall, was verified by follow-up censuses in the winter and spring. The only chaparral-requiring species whose distribution appears to be determined by postfire succession is the Rufous-crowned Sparrow (*Aimophila ruficeps*); it was never observed by us.

In addition to the censuses, we distributed questionnaires to residents living on the edges of the canyons to obtain information

TABLE 3. Biogeographic data used in the multiple regressions analysis (variables defined in text)

No.	Canyon	No. Chaparral-Requiring Species	Area (ha)	Chaparral (ha)	% Chaparral	Dist. X (m)	Dist. Y (m)	Age (yrs)	Fox/Coyote
1	Florida	6	102.77	67.83	66	2100	2100	50	1
2	Sandmark	6	84.05	75.65	90	914	914	20	1
3	34th St.	6	53.76	40.32	75	1676	853	34	1
4	Balboa T.	5	51.77	38.82	75	243	121	34	1
5	Alta L.J.	6	33.14	16.57	50	121	121	14	1
6	Kate Ses.	6	25.56	15.33	60	822	121	16	1
7	Pottery	5	17.92	10.75	60	700	45	14	1
8	Laurel	0	9.72	0.49	5	1554	1554	79	1
9	Cam. Cor.	4	9.08	8.62	95	331	61	20	3
10	Canon	0	8.66	1.73	20	1219	1219	58	1
11	Zena	3	8.51	2.55	30	2865	2865	36	1
12	Baja	3	8.40	4.37	52	670	670	31	1
13	Auburn	2	8.37	2.51	30	1737	1737	32	1
14	Washington	2	8.07	1.31	15	365	365	74	1
15	SoIana Dr.	7	7.64	6.87	90	550	550	11	3
16	Syracuse	5	7.51	6.38	85	40	40	18	1
17	32nd St. S.	1	6.36	.95	15	304	304	56	1

18	47th St.	1	6.31	2.52	40	1981	213	32	1
19	Mil Cumbres	6	6.23	5.61	90	550	550	11	3
20	Chollas	1	6.22	1.56	25	1005	1005	36	1
21	60th St.	2	6.11	2.14	35	2386	335	37	1
22	Juan St.	2	5.97	2.99	50	228	228	23	1
23	Acuna	3	5.08	1.52	30	662	110	22	2
24	Edison	5	4.75	4.28	90	61	61	8	1
25	Raffee	3	4.74	2.37	50	61	61	19	1
26	Spruce	0	4.28	0.43	10	1767	1767	86	1
27	Oak Crest	6	3.88	1.94	50	1000	400	6	3
28	54th St.	2	3.61	1.81	50	609	609	20	1
29	Titus	0	3.50	0.25	7	335	280	77	1
30	Chateau	3	3.27	1.80	55	304	110	20	2
31	Newport	1	2.14	1.60	75	2895	2895	60	2
32	Aber	2	1.60	1.04	65	331	91	15	1
33	Talbot	0	1.41	1.27	90	1219	1219	55	1
34	Montanosa	5	1.32	1.25	95	91	91	2	3
35	Poinsettia	0	1.20	0.30	25	350	350	50	2
36	El Mac	0	1.10	0.66	60	883	883	32	1
37	32nd St. N.	1	0.40	0.10	23	487	45	77	1

about the distribution of vertebrate species that were not easily observed in the time period over which we sampled. These species included Roadrunners, coyotes, gray foxes, jackrabbits (*Lepus californicus*), brush rabbits (*Sylvilagus bachmani*), raccoons (*Procyon lotor*), opossums (*Didelphus virginiana*), skunks (*Mephitis mephitus*), and bobcats (*Felis rufus*). Suspicious or unexpected occurrences were checked by following up with telephone interviews or with further field work.

The smallest of our 37 sites is 32nd St. North. It is a "satellite" canyon of 32nd St. South, from which it is separated by a gap of only 25 to 45 m. Statistical analyses showed 32nd St. North to be an outlier and an exceptionally influential observation. The Cook's distance and studentized deleted residual, calculated during a general linear model analysis of the variables shown in Table 4, were several times the magnitude of any other canyon.

For this as well as for other reasons explained below, it was excluded from the following analyses. When included, the general form of the results does not change, but the level of significance of the regressions is reduced.

Statistical analyses were performed with Statview (BrainPower, Inc., Calabasas, California) and SAS (SAS Institute, Inc., Carey, North Carolina) software.

Results

Species-Area Relationships

The species-area relationships for chaparral-requiring birds are shown in Figures 2*a* and 2*b*. The apparent sigmoidal pattern of these curves is expected when the range of canyon size includes both habitat islands where the number of species (*S*) is much less than the number of potential (or pool) species (*P*) and habitat islands on which *S/P* approaches 1.0 (Cain 1938, Diamond & Mayr 1976, Gilpin & Diamond 1976, Connor & McCoy 1979). *S* correlates more strongly with Chaparral (Fig. 2*b*) than with area (Fig. 2*a*). This suggests that

TABLE 4. Product-moment correlation coefficients between variables in the multiple regression analysis (see Table 3 and text for definitions of these variables).

	S	ln Area	ln Chaparral	ln % Chaparral	ln Dist. X	ln Dist. Y	ln Age	Fox/Coyote
S	1							
ln Area	0.584	1						
ln Chaparral	0.803	0.851	1					
% Chaparral	0.645	0.114	0.584	1				
ln Dist. X	-0.27	0.14	-0.018	-0.294	1			
ln Dist. Y	-0.413	0.045	-0.148	-0.345	0.767	1		
ln Age	-0.673	0.079	-0.276	-0.616	0.489	0.585	1	
Fox/Coyote	0.352	-0.281	-0.048	0.4	-0.107	-0.234	-0.538	1

$p \leq 0.01$ for coefficients ≥ 0.418; $p \leq 0.05$ for coefficients ≥ 0.325.
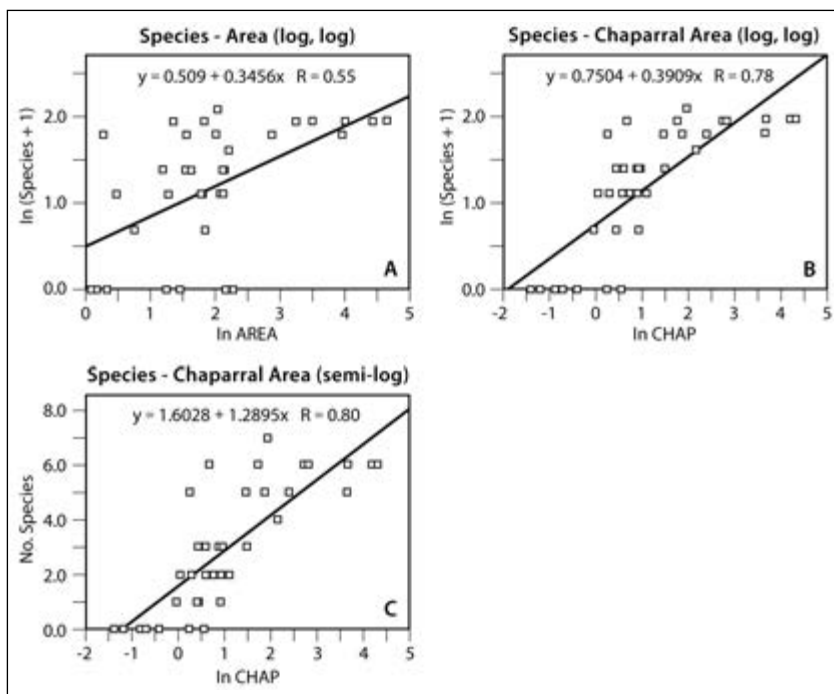
FIGURE 2. (A) Species-area (ha) relationship for chaparral-requiring bird species in 36 isolated canyons in western San Diego Couny, California. The value "1.0" is added to the number of chaparral-requiring species for computational purposes. (B) Same as A except that the abscissa is the hectarage of actual chaparral (natural habitat) in the canyons. (C) Same as B except that the number of species is not transformed to natural logs.

the amount of chaparral habitat in a canyon is more important than total area in determining the number of chaparral-requiring species present. The semi-log plot, Figure 2*c*, is shown for comparison. In addition to these area effects, a strong effect of age on the number of chaparral-requiring species is apparent in Figure 3. "Older" canyons clearly have fewer species of chaparral-requiring birds. Bolger et al. (1988) provides further analysis of the species-age relationship.

Nevertheless the covariation among Area, Chaparral, Age, and some of the other variables (Table 4) necessitates further analysis and explanation. Chaparral, for example, depends on two, independent
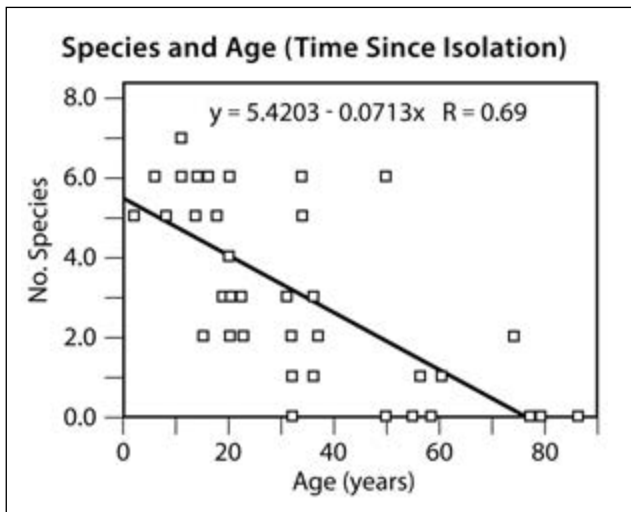
FIGURE 3. The relationship between number of chaparral-requiring species and the number of years since canyon isolation (age).

factors: 1) the original area of the canyon, and 2) the cumulative loss of habitat since isolation or since the onset of disturbance. Figures 4*a* and 4*b* illustrate the association of absolute and relative loss of habitat, respectively. Based on inspection of Figure 4*b*, it appears that most canyons in this region will lose 90 percent or more of their natural cover within 90 years. Because variables such as Chaparral can confound habitat and time effects on species number, a more complex statistical methodology is needed to understand the interplay of potential causative factors.

Stepwise Multiple Regression — Chaparral-Requiring Species

Stepwise multiple regression (MR) was used to assess the possible contributions of the independent variables to S while controlling for their covariation. In addition to the primary variables shown in Table 3, we tested many "secondary variables," including combinations of transformed variables and interaction variables (the pairwise products of Age, the distance variables, and Chaparral).
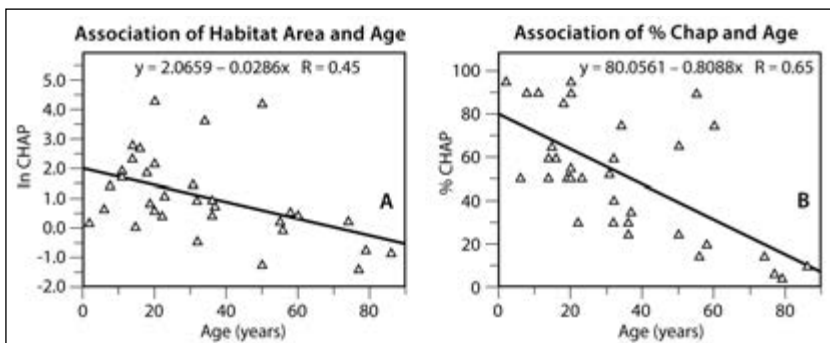
FIGURE 4. (A) The association between habitat area (ha) and time since isolation (age) for the canyons. (B) The association between the percent cover of natural habitat and the age for the canyons.

The combination of independent variables that gave the highest R-squared values was ln Age, ln Chaparral, ln Area, and Fox/Coyote ("ln" indicates that the values shown in Table 3 were transformed to natural logs). This set of predictors accounts for 90 percent of the variation in S as shown in Table 5, and $p < 0.01$ for all steps in this regression analysis. The other variables in Table 3 do not add significantly to the adjusted R-squared when they are included in the same MR analysis with the above four. Residuals were normally distributed. Because a stopping rule (F-to-enter $= 4$) was used to select the independent variables, and the total number of candidate variables was greater than the number (4) in the selected subset, the ordinary F tables cannot be used; instead we used the tables provided by Wilkinson and Dallal (1981).

Discussion

The Evidence for Extinction

Before discussing the results in detail, it is necessary to determine if the supposed extinctions of chaparral-requiring birds are real. Our results do not establish unequivocally that the chaparral-requiring

TABLE 5. Stepwise multiple regression analysis. All adjusted R^2 values have associated p values <0.01 according to tables in Wilkinson and Dallal (1981).

| | | Independent Variables | | | | | | | | | Adjusted Regression | |
| | | In Chaparral | | In Age | | Fox/Coyote | | In Area | | | | |
Step	Intercept	b	F	b	F	b	F	b	F			R^2	F
1	1.6	1.23	61.7									0.63	61.66
2	6.42	1.07	100.7	-1.4	53.9							0.86	105.69
3	4.55	2.23	122.7	-1.1	25.3	0.57	6.2					0.88	83.61
4	4.58	0.56	6.7	-1.42	40.1	0.67	10.3	0.79	8.7			0.90	80.1

species missing in a given canyon have become extinct. It is possible that the missing species were not present in a canyon at the moment of its separation. Indeed, it is quite likely that some of the smaller canyons may not have contained some of the rarer species, such as Black-tailed Gnatcatchers, Cactus Wrens, and Roadrunners, because the preferred habitats may have been lacking for some of these species, or they were absent, simply by chance, at the moment the canyons were isolated.

On the other hand, we have evidence that many of the chaparral-requiring species missing in canyons were present at the time of isolation. First, our youngest canyons, even the smallest ones, contain most of the chaparral-requiring species. The Montanosa (1.1 ha) and Oak Crest (3.9 ha) sites, for example, have five and six species, respectively, out of an observed maximum of seven chaparral-requiring species (Table 3). Second, species-area data from census plots in unfragmented habitat in nearby areas (Bolger et al. 1988) have low slopes ($z = 0.13$) when compared with those in this study; (z [ln Area] = 0.35; z [ln Chaparral] = 0.39). Even the smallest census plots sampled (0.1 ha) had two or three chaparral-requiring species. This indicates that many of our canyons are indeed impoverished for bird species, and that most of the missing species, with the probable exceptions in some canyons of the Roadrunner, Cactus Wren, and Black-tailed Gnatcatcher, were once present in even the smallest canyons. Third, canyon age is a highly significant variable in the MR analysis, even after removing the correlated effect of reduction in habitat area with time (ln Chaparral). Therefore, the most parsimonious interpretation is that species diversity in isolated canyons has decayed over time due to local extinctions.

Causes of Extinction: The Roles of Area and Time Since Isolation

Species diversity decreases with canyon age (Figure 3 and Table 4), and it appears that virtually all the chaparral-requiring species will disappear in a century, even in the largest canyons. A major factor contributing to these local extirpations appears to be the loss of hab-

itat, some of which (such as fire) is catastrophic. Habitat attrition has many causes, including fires, removal for fire breaks, removal by residents (for gardens, orchards, kennels, etc.) and casual attrition due to recreational activities. The most disturbed canyons retain as little as 5 percent to 15 percent of their natural cover, the chaparral having been replaced by exotic Mediterranean grasses, forbs, and trees (palms and species of *Eucalyptus*, *Acacia*, etc.), by gardens, or by fire-retardant ground covers. Two of the variables in the MR analysis reflect the importance of space or habitat area. Chaparral estimates the amount of natural habitat in the canyons, while area measures the total amount of undeveloped open space. Some of the chaparral-requiring species may make use of open habitats, particularly the Roadrunner and the California quail. It is therefore possible that ln Area contributes signrfcantly because it accounts for some residual habitat area not estimated by Chaparral.

It was our impression that many extinctions occur before there has been much loss of habitat. This is consistent with the MR analysis, which shows Age to be important, independent of the effects of Chaparral and Area. Several mechanisms could account for early disappearances of chaparral-requiring species. These include 1) stochastic environmental variation in such variables as rainfall and temperature, 2) deterministic pressures such as predation, and 3) demographic stochasticity (Shaffer 1981, Gilpin & Soulé 1986, Goodman 1987), especially in the smaller canyons. In addition, 4) when small populations persist for longer than a few generations, their uncertain fortunes are exacerbated by loss of heterozygosity and inbreeding (Frankel & Soulé 1981, Gilpin & Soulé 1986, Lande & Barrowclough 1987). In theory, mechanisms 3) and 4) could play a major role in small canyons, assuming the mean number of individuals per species is quite low.

Based on the densities of each of the chaparral-requiring species in chaparral habitat, we have calculated the average population sizes of the chaparral-requiring species in hypothetical canyons of 2 ha and 20 ha (Table 6). These population sizes range from <1.0 to 10 individuals in 2 ha canyons, and from <1.0 to 100 individuals for

TABLE 6. Correlates of occurrence or vulnerability and estimated mean population sizes of the chaparral-requiring species in canyons of 2 ha and 20 ha in area at their moment of isolation.

Species	Density (pairs ha⁻¹)*	Body Weight (g)	Occurrence (no. canyons)	Estimated N in 2 ha	Estimated N in 20 ha
Wrentit	2.5	14.1	32	10	100
Bewick's Wren	1.75	9.4	25	7	70
Rufous-sided Towhee	1.29	37.0	16	5.2	51.6
California Thrasher	1.10	93.5	15	4.4	44
Valley Quail	0.96	184.2	15	3.84	38.4
Roadrunner	0.02	304.0	11	0.1	0.8
Black-tailed Gnatcatcher**	0.25	ca 8.0	2	1	10

*Data from Cody (1983 and personal communication, 1986).
**Population density estimate from Harold Wier (personal communication, 1986).

hypothetical 100 ha canyons. Based on these low population sizes, we believe that rapid extinction of most chaparral-requiring species is inevitable in small canyons, given 1) the low vagility of these species, 2) random fluctuations in birth and death rates (Leigh 1981, Goodman 1987, Belovsky 1987), 3) normal stochastic variation in weather and brush fires, and 4) deterministic environmental factors such as predation that are discussed below. Isolated populations of this size will lose genetic variation at rates of up to 20 percent per generation. For example, a population with an effective size of 10 will lose additive genetic variation at an average rate of about 5 percent per generation, much too high for an outbreeding species to sustain for more than a few years (Franklin 1980, Soulé 1980, Allendorf & Leary 1986).

When Area, Chaparral, and Age are log transformed, they explain more of the variation in species number than when untransformed. This is probably because of the nonlinear relationships between species number and both area and age. Species-area curves are typically curvilinear, even sigmoidal (Cain 1938, MacArthur & Wilson 1967), and a log transformation is commonly used to linearize the relationship. Inspection of Table 3 will show that the number of chaparral-requiring species increases rather quickly as canyon size increases to about 20 ha, but levels out at that size (for canyons no older than 30 to 50 years). Therefore, canyons of 20 ha or larger probably have sufficiently large populations of most chaparral-requiring species to buffer them, at least in the short run, against the random events that quickly eliminate the same species in smaller canyons. Regarding the relative efficacy of Age vs. ln Age, it has been recognized for some time (Diamond 1972, Terborgh 1974, Wilcox 1978, Gilpin & Diamond, 1976, Soulé et al. 1979) that the relaxation rate in isolated patches is curvilinear, being high at first, and slowing later.

Mesopredator Release

In the absence of large, dominant predators, smaller omnivores and predators undergo population explosions, sometimes becoming

four to 10 times more abundant than normal (Eisenberg et al. 1979, Terborgh & Winter 1980, Glanz 1982, Emmons 1984). Similar explosions occur in spider populations in the absence of lizards on tropical islands (Pacala & Roughgarden 1984, Schoener & Spiller 1987). This phenomenon appears to be quite general; we refer to it as "mesopredator release." The term *mesopredator* in this context was suggested by Larry Harris (personal communication, 1987). Mesopredator release has been implicated in some of the bird extinctions on Barro Colorado island and other localities (Willis & Eisenmann 1979, Matthiae & Stearns 1981, Whitcomb et al. 1981; see Wilcove et al. 1986 for discussion).

In our analysis, the Fox/Coyote variable is designed to represent the interactions between coyotes, foxes, and domestic cats, and to estimate the impact of those animals on chaparral-requiring birds. The results are consistent with the hypothesized roles and interactions of these predators (methods). Fox/Coyote is a minor but significant predictor of S in the MR analysis (Table 4). There is also circumstantial and anecdotal evidence that gray foxes and domestic cats are a major factor in the disappearance of wildlife from canyons. Gray foxes frequently prey on birds, especially those that nest on or close to the ground (Ewer 1973), and they tend to be more arboreal than other canids. Cats are usually "subsidized" predators—most of their food is provided by human benefactors, and bird predation is a leisure time activity for many of them. Consequently, there is virtually no limit to the number of cats that can occur in an urban canyon. Domestic cats can continue to take wildlife in a canyon long after the density of prey is too low to sustain a native predator that must rely on wildlife for most of its food. At present we cannot say how much damage cats are doing, but other studies have shown that birds constitute as much as 19 percent (Eberhard 1954) or 25 percent (Hubbs 1951) of the stomach contents (by volume) of feral cats. One pet cat in Michigan ate 62 birds during a period of 18 months (Bradt 1949).This would be enough predation to wipe out several of the rarer species from a small canyon. There is abundant evidence

for the disappearance in urban areas of bird species that nest on or near the ground, and cats are usually implicated (Tomialojc 1982, Emlen 1974, Weber 1975).

The significance of Fox/Coyote (Table 4) suggests to us that coyotes are helping to control the smaller predators (including cats) in the canyons, possibly contributing to the maintenance of the native, chaparral avifauna. At first, this may sound contradictory because coyotes are predators and will eat birds on occasions but coyotes rarely prey heavily on birds, even relatively sedentary species like quail (Leach & Frazier 1953). Instead they feed mostly on rabbits, rodents, and opportunistically on smaller predators and omnivores such as foxes and cats (Korschgen 1957).

Coyotes apparently are common and ubiquitous in recently isolated canyons, whereas foxes are rare or absent (Tables 2 and 3). Other bird predators, such as raccoons, skunks, and opossums, all of which are preyed on by coyotes (Young & Jackson 1951, Korschgen 1957, Beckoff 1978), are much more frequently reported in older, highly disturbed canyons than in large or young canyons (unpublished data). Therefore, both statistical and circumstantial evidence point to mesopredator release as a significant factor in the disappearance of chaparral-requiring bird species from isolated canyons.

Based on the considerations in this and the preceding sections, the avifaunal collapse in the canyons is likely the product of three interacting phenomena or processes. First, there is a primary wave of extinctions initiated by random demographic and genetic events, compounded by environmental variability. Second, these stochasticities are exacerbated by predation, especially cat and fox predation, which tends to press larger populations to the domain of the random processes. Third, chronic habitat loss eventually exposes all of the chaparral-requiring birds, even those in the largest canyons, to the stochasticities that constitute the first group of phenomena. This illustrates the operation of the interacting extinction vortices described by Gilpin and Soulé (1986).

Species Vulnerability

Certain chaparral-requiring species appear to be more vulnerable to local extinction than others. Diamond (1975*a*) has used incidence functions to illustrate the relationship between occupation (the proportion of patches occupied) and a biogeographic variable such as patch size. In Figure 5*a* we have plotted incidence as a function of Chaparral area. It is evident that some species achieve 100 percent occupancy before others. Wrentits and Bewick's Wrens, for example, occupy virtually 100 percent of canyons that have 7 ha or more of habitat, whereas California thrashers require areas of about 20 ha to achieve full occupancy. Taken together, these results are consistent with the hypothesis that species disappear from isolated canyons in a predictable order, namely Black-tailed Gnatcatcher, Roadrunner,
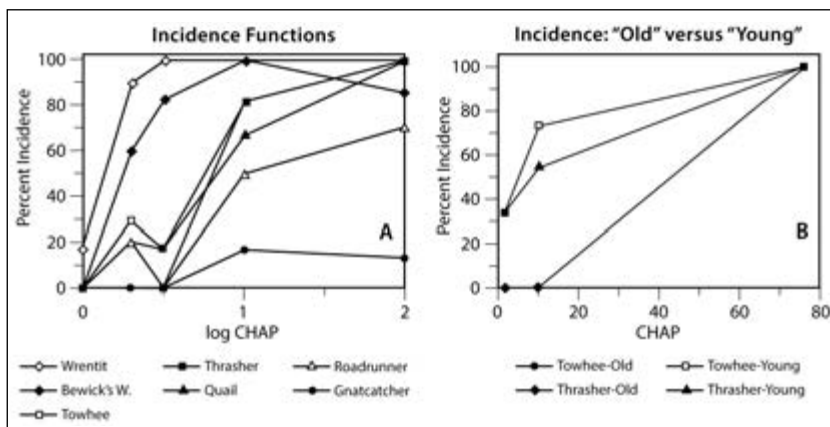
FIGURE 5. (A) Incidence functions of seven species of chaparral-requiring birds in isolated canyons in San Diego. The canyons were divided into five groups based on habitat "CHAP" of six to 10 canyons each. The ranges of areas of the five groups are 1) < 1.0 ha, 2) 1.0 to 1.99 ha, 3) 2.0 to 3.99 ha, 4) 4.0 to 9.99 ha, 5) 10 to 100 ha The abscissa is graduated in $\log_{10}$ units. (B) Incidence functions for two moderately abundant species of chaparral-requiring birds. "Yng" refers to incidence functions based on canyons with "ages" less than 32 years. "Old" refers to incidence functions based on canyons that are "older" than 32 years.

California Quail, [California Thrasher and Rufous-sided Towhee], Bewick's Wren, and Wrentit.

In theory, incidence functions in these canyons should have shifted to the right with time, as species gradually drop out of canyons. In other words, incidence at the moment of isolation should have been higher for most size categories of canyons, especially the smaller ones, than it is now. To test this hypothesis, we analyzed the data for Rufous-sided Towhees and California Thrasher. These species were chosen because they have intermediate levels of vulnerability, though the data for the other chaparral-requiring species follow the same pattern. The incidence functions compare recently isolated (< 32 years since isolation) with the older (32 to 88 years) canyons. Each of these two groups was divided into three size categories for this analysis, a number that allowed at least three canyons in each size category. Evidence for the predicted incidence shift with canyon "age" is shown in Figure 5*b*. The only "old" canyons that retain these two species are those that are larger than 50 ha.

What factor or factors explain the difference in relative vulnerability of these species? Terborgh and Winter (1980) and Diamond (1984) surveyed a number of factors that might account for the differences in extinction vulnerability. Both surveys concluded that rarity or naturally low population density was most important, though other factors, such as body size (Belovsky 1987), trophic level, dependence on patchy or seasonal resources (Karr 1982*a*) and temporal variation in population size (Karr 1982*b*, Newmark 1987, chapters in Soulé 1987) might be significant or even paramount in some circumstances. Body size is thought to be important because larger animals are better buffered against short-term changes in resource availability and weather (Pimm et al. 1988).

Here we examine two hypotheses that might account for the order of chaparral-requiring species disappearance in canyons: 1) the body size hypothesis, and 2) the abundance (or rarity) hypothesis. The average body weights and estimates of population densities of these species are tabulated in Table 6. The correlation between body

size and the number of canyons in which a species occurs is nonsign-rficant ($r = -0.3$; $p = 0.51$).

The best single predictor that we have found for the occurrence of particular species in canyons is the estimated average population density of the species in undisturbed habitat. The highly significant relationship ($r = 0.93$; $p = 0.0025$) between abundance and persistence is shown in Figure 6a. Further support of the abundance hypothesis is provided by the incidence analysis. The order in which species disappear from canyons (Fig. 5a) is virtually the same as the ranking of the species abundance in Table 6. This also suggests a cause-effect relationship between abundance and vulnerability. Our results add yet another example to the substantial number of cases where population size or density is an important general predictor of vulnerability to extinction (see also Diamond et al. 1987).

Might some of the variation in occupancy that is unexplained by abundance ($1 - R^2 = 0.14$) be attributed to an effect of body size? MR analyses (Table 7) show that most of the residual variation in canyon occupancy is indeed removed by the addition of body
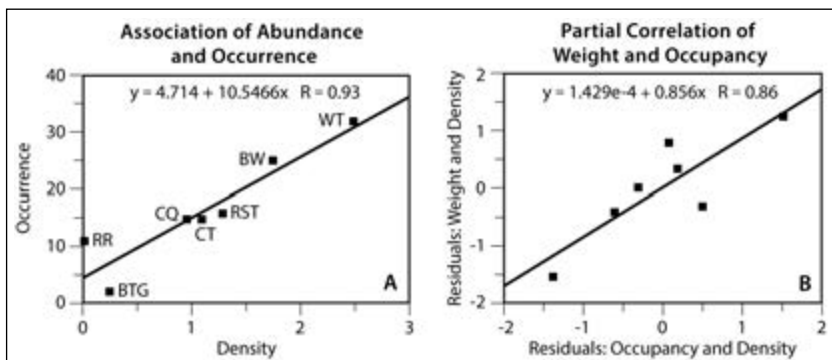

FIGURE 6. (A) The association of density (in pairs per ha) in relatively undisturbed habitat and the number of canyons in which a species of chaparral-requiring bird occurs. RR = Roadrunner; BTG = Black-tailed Gnatcatcher; CQ = California Quail; CT = California Thrasher: RST = Rufous-sided Towhee; BW = Bewick's Wren; WT = Wrentit. (B) Regression of the residuals of density on weight and occupancy demonstrating the significant association of weight and occupancy after statistically removing the effect of density; $p < 0.02$

TABLE 7. Stepwise multiple regression analyses of factors contributing to the number of canyons occupied by the particular chaparral-requiring species (all p values are <0.01).

| | | Independent Variable | | | | | | |
| | | Density | | Weight | | | | |
Step	Intercept	b	F	b	F	Adjusted R^2	Regression F
Dependent variable = number of canyons occupied:							
1	4.71	10.55	31.28			0.84	31.28
2	−1.44	13.23	92.38	0.034	10.62	0.94	51.02
Dependent variable = arcsin of square root of % of canyons occupied:							
1	0.362	0.322	22.60			0.78	22.60
2	0.127	0.424	114.41	0.0013	18.67	0.95	60.57

size to the regression. As shown in Figure 6*b*, the partial correlation between occupancy and body weight, holding density constant, is 0.86, $p < 0.02$. Together, abundance and body size explain about 95 percent of the variation in canyon occupancy. The results are slightly more significant when the independent variable is the arcsin of the square root of the proportion of occupied canyons. It will be worthwhile to continue surveying the younger, more saturated, canyons, in order to test whether the order of disappearance of their chaparral-requiring species is predictable from this two-factor causation hypothesis.

Predicting the Future

Multiple regression is often used to obtain an equation that is used for predictive purposes. Urban planners and conservationists wishing to anticipate the fate of chaparral-requiring birds in habitat fragments could use an equation derived from the MR analysis. The equation (from Table 4) is

$$S = 4.58 - 1.42 \ln \text{Age} + 0.56 \ln \text{Chaparral} + 0.79 \ln \text{Area} + 0.67 \text{ Fox/Coyote}$$

Such an equation can be used to predict the number of species of chaparral-requiring birds in a canyon at some time in the future, assuming conditions stay the same. Say, for example, that a 4 ha canyon was to be isolated by a pending subdivision. One might want to estimate the number of species of chaparral-requiring birds that would remain in the canyon in five years, 25 years, and 75 years. Assuming for the sake of simplicity that the Fox/Coyote value is 3 (coyotes present, foxes absent), and using the above equation, the corresponding numbers of chaparral-requiring species are 5.41, 3.12, and 1.56, respectively. (The 95 percent prediction intervals around these values are approximately plus or minus 1.9 species.)

Because nearly all canyons lose natural habitat with time, let us assume that 25 percent of the chaparral has been replaced by non-

native vegetation in 25 years, and that 50 percent is replaced in 75 years. Recalculating the number of surviving chaparral-requiring species with these reductions in habitat gives 2.95 in 50 years and 1.17 in 75 years, respectively.

We caution that predictions such as these are rough approximations, both for statistical and biogeographic reasons. Nevertheless, this statistical tool can provide planners with a qualitative estimate of the impact of fragmentation. Because our sample of canyons lacks cases of very small "satellite" canyons (like the deleted outlier 32 St. North), the above equation should not be used to predict extinctions in such canyons.

Is Chaparral More Vulnerable to Faunal Collapse than Forest?

Relaxation might occur more quickly in fragmented Mediterranean scrub habitats than in temperate forest fragments, patch sizes being equal. One reason is that these scrub habitats are more brittle, so habitat loss will occur at higher rates. This relative fragility of chaparral habitat is accounted for by several factors, including lower levels of precipitation, and the vulnerability of the vegetation to irreversible destruction by frequent burning, trampling, and, in parts of the world, overbrowsing by domesticated animals. Whereas the destruction of a forest usually requires considerable energy, the effects of traffic alone in chaparral habitat can cause the replacement of a patch of scrub with grassland or other exotic, xeric-adapted species.

Another reason for the relatively high rates of faunal collapse of some chaparral biotas, in this case the chaparral-requiring birds, is their low vagility (Johnson 1972, Power 1972, Jones & Diamond 1976). The complete absence of some of these species from the California Islands is suggestive. For example, the very common Wrentit and the California Thrasher do not occur on any of the California Islands (Johnson 1972) in spite of large areas of suitable habitat. The Roadrunner is also absent (Jones & Diamond 1976). Low vagility alone will lead to rapid relaxation because remnant populations cannot be "rescued" (Brown and Kodric-Brown 1977) by occasional

dispersing individuals, and because recolonization (replacement of extirpated species) of canyons will rarely occur. In contrast, facultative chaparral birds often migrate or disperse through nonnative habitats such as suburbs or farmland.

These two reasons, then, habitat fragility and low vagility, appear to account for the rapid collapse of chaparral-requiring bird communities in the fragments of canyon habitat. (The two rarest species in our canyons, Black-tailed Gnatcatcher and Cactus Wren, are relatively strong flyers, but they are also extremely rare throughout the entire urbanized coastal region.)

The canyon fragments, therefore, may represent true islands to the chaparral-requiring birds. Why, then, did none of the isolation variables enter any of the MR analyses? Jones et al. (1985) remarked on the absence of an isolation effect for refugal populations of reptiles, suggesting an inability to recolonize across inhospitable habitat following local extinction. Our results are similar and consistent with the hypothesis that immigration is virtually negligible if the development barrier is wider than 50 to 100 m, at least in the time scale of a century or so. The presence of the Wrentit in the small outlier satellite canyon, 32nd St. North, does not contradict this hypothesis. The distance between this canyon and the larger 32nd St. South is only 30 to 45 m, and because the larger canyon also has Wrentits, we suggest that the narrowness of the habitat gap permits occasional exchange. Our sample of 37 canyons did not include other such satellite canyons, precluding the statistical resolution of such a truncated distance effect. (The MR equation predicts that 32nd St. North should have –2 species. We attribute this to the dominance of chaparral and age.)

Z Values: Vagility and Relaxation

Preston (1962), MacArthur and Wilson (1967) and May (1975) predicted that most z values would fall within the range 0.15–0.35 for the power (log-log) form of the species-area curve. Other factors, however, can account for values within this range. Connor and

McCoy (1979) point out that z values in the range 0.2–0.4 are "characteristic of any regression system with a high r value and a small range in the dependent variable [S] relative to that in the independent variable [area]." It may not be legitimate, therefore, to speculate about the z values in this study, but we note that the slopes of our species-areas curves (0.35 and 0.39 for area and chaparral, respectively) approach the upper limit of the "null" range. Many examples of even higher z values are in the literature (e.g., Culver et al. 1973, Case 1983, Jones et al. 1985, Martin 1981a, Connor & McCoy 1979, Rusterholz & Howe 1979).

Some of the reported values of z above 0.4 are associated with archipelagoes that comprise small islands or island-like isolates. Several studies have described such high z values for vagile birds. Rusterholz and Howe (1979), Martin (198la), and Howe (1984) obtained z values of 0.44, 0.40, and 0.39 to 0.62 for birds on small islands in a Minnesota lake, for forest (shelterbelt) islands in South Dakota, and for isolated forest patches in New South Wales, respectively. Rusterholz and Howe (1979) and Martin (1981a) interpreted their results according to a model developed by Schoener (1976). Schoener's model predicts that a combination of competition, high vagility, and $S < < P$ would produce steep slopes (approaching 0.5), conditions that apparently apply in the Rusterholz and Howe (1979) and Martin (1981a) studies.

The paradox is that we observe an even higher z value for very small habitat islands, even though our situation is virtually the opposite of that predicted by Schoener: competition among our chaparral-requiring species is problematic, vagility is very low, and S/P is high. We obtain a z value of 0.64 for the relationship of ln Chaparral and ln S for the set of canyons with Chaparral < 7 ha, the same upper bound for island size used by Howe (1984), who obtained z values of 0.39 and 0.62 for total species and resident birds, respectively.

Is there a reasonable explanation for the high slopes of the species-area curves in systems that differ so greatly in the variables considered important by Schoener? Jones et al. (1985) state that "A steep slope probably reflects a low or nonexistent rate of coloniza-

tion [Case 1983] and limits on species occurrence imposed by small island size [Martin 1981*b*].” These conditions apparently apply to the canyon–chaparral-requiring bird system. First, in our system the y-intercept is very low because many of the smaller patches lack any chaparral-requiring species. (Note that these vacant patches are large enough to support one or more pairs of many of the chaparral-requiring species [Table 6] assuming the birds were capable of finding the empty patches.) Second, on inspection of Figure 3 it is apparent that the vacant or near-vacant canyons are among the “oldest” in the survey. Such canyons appear to be too small to sustain many chaparral-requiring species for more than a few decades. If the dispersal and colonizing abilities of these species were greater, then the slope of the species-area curve would obviously be lower. A third factor accounting for the steep slope is the near saturation of small “young” canyons that still retain most of their chaparral-requiring species. Taken together, these three factors describe a system in the process of relaxation.

Hence, an alternative explanation for high z values is the relaxation process itself. Briefly, an archipelago, such as the small subset (< 7 ha) of canyons, comprising a mixture of old and young islands, or relaxed and unrelaxed biotas, will necessarily produce a high slope, but only during the process of relaxation (Brown 1971, Diamond 1972). Before relaxation begins, the z is low and the intercept is high (Bolger et al. 1988). When, several decades later, the canyons have lost most of their chaparral-requiring species, the slope will again be low. In the meantime, however, the larger and younger canyons still retain many of their chaparral-requiring species, while the smaller and older ones have already lost most of theirs; this size-related but transient asymmetry accounts for the high slopes.

Clearly, quite different sets of conditions can lead to high slopes for species-area curves, especially for small islands. We have discussed two such sets (Schoener's model: high vagility and low S/P; our nonequilibrium model: low vagility, and high S/P). There are likely to be several others. For example, Blake and Karr (1984) reported a z value of 0.57 for migratory, forest-interior birds in isolated forest

tracts in Illinois. One of the reasons for this pattern is apparently a pronounced threshold effect: habitat islands smaller than about 25 ha appear to be unsatisfactory for breeding; those patches larger than 100 ha are acceptable to about five or more species. On a log scale this produces a very high z, especially when $S < < P$.

Potential Migration Measures

Is there any way to abate the rapid and dramatic decline in chaparral-requiring bird species in isolated canyons? Other students of fragmentation (e.g., Goldstein et al. 1981, Beissinger & Osborne 1982, Vizyová 1986) have suggested some principles (mostly referring to maximizing patch size and complexity) for mitigating the effects of fragmentation in urban areas, but these proposals concern mostly forest species, so their relevance is probably greater for non-chaparral-requiring birds than for chaparral-requiring species.

For relatively sedentary species, connectivity of patches is probably the most important landscape feature for maintaining species diversity of native biota. In the long run, habitat corridors linking two or more patches are likely to be the cheapest and most effective treatments. Corridors, even relatively narrow ones, counteract the effects of fragmentation, and should eliminate or minimize the attrition of species over time by facilitating dispersal and recolonization (Willis 1974, Diamond 1975, Brown & Kodric-Brown 1977, Frankel & Soulé 1981, Harris 1984, Soulé & Simberloff 1986, Noss & Harris 1986, Forman & Godron 1986, Diamond et al. 1987, Noss 1987).

A question that naturally arises concerns the minimum width of corridors. To our knowledge, there have been no studies of this issue, but our own observations suggest that most, if not all, of the chaparral-requiring species can use relatively narrow strips of vegetation. We have observed Wrentits and Rufous-sided Towhees taking advantage of strips as narrow as 1 m. California Quail, California Thrashers, and Bewick's Wren have been observed in strips less than 10 m in width, and we believe that corridors half this width

probably would be effective, as long as the chaparral was dense and formed a nearly continuous cover. Further studies would be necessary to determine if taxa such as reptiles and mammals require a different geometry of corridors and patches.

With proper planning and execution, existing or planned linear stretches of open area or amenities, such as highway and freeway verges and roadcuts, power line rights of way, sections of parks, and, possibly, hiking and bicycle paths, could serve as wildlife corridors. Where feasible, vegetated underpasses should be constructed to link natural habitat that is being fragmented by road and highway construction. Such underpasses would also reduce the number of animals killed on highways; could help prevent the local extirpation of large or rare species such as mule deer (*Odocoileus hemionus*), bobcat, and mountain lion (*Felis concolor*); and could serve hikers and bicyclists. Corridors permitting the movement of coyotes will probably minimize mesopredator release.

Many authors have commented on the possible disadvantages of corridors (Frankel & Soulé 1981, Soulé & Simberloff 1986, Simberloff & Cox 1987, Noss 1987). These include poaching, exposure, and transmission of disease and parasites, the spread of fire, and some possible genetic and ecological drawbacks. Most of these potential biological problems, however, apply to remnant populations of large animals that are rare or endangered. When dealing with common species of wildlife in urban or suburban settings, these problems pale in significance when compared to the advantages of corridors.

Finally, we raise the possibility of the reintroduction of native birds into depauperate canyons. Such projects would be feasible under certain circumstances, and could be managed by state, county, or city agencies, or by neighborhood, school, or conservation groups. There are many technical issues that should be considered before such projects are instituted, but we feel that the "reanimation" of defaunated habitat fragments is a socially and biologically desirable objective for planners and conservationists.

Summary

1. Chaparral-requiring species of birds have very high rates of extinction in isolated canyons in the San Diego area. Most species disappear within a few decades following the isolation (by development) of habitat patches.

2. Habitat area and time since isolation are sigtllficantly correlated with the current number of surviving species. These factors probably reflect the roles of space and population size in determining the viability of isolated groups. The prompt disappearance of many populations in small canyons is expected, given the combination of 1) very small populations in recently isolated canyons, 2) low vagility of the chaparral-requiring species, and 3) the unavoidability of random demographic, genetic, and environmental events. Those populations that survive for a few decades will eventually succumb as habitat attrition and predation press their populations below the thresholds where stochastic events overpower their genetic fitness and reproductive capacities.

3. Our data are consistent with the growing body of evidence suggesting that the elimination of large predators from a system can be destabilizing. In the absence of large predators, smaller predators can become more abundant (mesopredator release) and, in turn, may cause the local extinction of vulnerable prey species. It appears that coyotes may lower the rate of extinction of chaparral-requiring birds by reducing the abundance of smaller predators, including gray foxes and the ubiquitous domestic cat.

4. The vulnerability of particular species appears to be highly predictable in these canyons. Persistence probability is highly correlated with population density in relatively undisturbed habitat. Large-bodied birds, however, seem to persist longer than smaller birds of equal abundance.

5. Chaparral birds may be more vulnerable to local extinction than forest birds, in part because of the poor dispersal abilities of the former, especially in a fragmented landscape.

6. Slopes (z values) of species-area curves for the chaparral-requiring species are high, especially for canyons with less than 7 ha of chaparral. Such high slopes can occur under several sets of conditions, including, as in this study, when the set of islands includes both relaxed and relatively unrelaxed biotas.

7. The most effective tool for the prevention of extinction of chaparral-requiring species in an urban landscape is the prevention of fragmentation in the first place by proper planning of urban and suburban development. Corridors of natural habitat, even quite narrow ones, are probably very effective in permitting dispersal between patches, thereby preventing or minimizing faunal collapse.

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Introduction to *The Onslaught of Alien Species, and Other Challenges in the Coming Decades*

As president of the Society for Conservation Biology, I delivered this address on the destabilizing effects of invading species to the 1989 annual meeting. Most invasions happen when people transport species, either on purpose or by accident. Disastrous purposeful introductions include the Australian broadleaved paperbark tree (*Melaleuca)* in the Everglades, Asian "jumping" silver carp in the Mississippi River Basin, and rabbits, foxes, and domestic cats in Australia. Accidents include zebra mussels in US waterways, the voracious brown tree snake in Guam, and avian malaria in Hawaii, which killed most native birds below an altitude of 4,000 feet.

Generalist species like the common raven and sunflower invade new areas when people disturb native ecosystems, for example, by clearing forests for agriculture and cattle ranching. Because ravens find food around human communities, their numbers in the Mojave Desert have exploded by 1,500 percent over the past 25 years, killing 100 percent of young desert tortoises where raven populations are high.

Our tactical response to these aliens will depend on how we view biological communities. The traditional view was that the species making up a community "belong" together and that a disturbed community eventually "heals" itself by returning to the same species composition. Now, in part due to advances in paleobiogeography, we know that when past climates changed, communities broke apart as species shifted their ranges at different rates. This realization that communities are not static entities, coupled with the impossibility of preventing the flood of exotics, is forcing conservationists to adopt a tacit triage in which serious control efforts are directed only at the more harmful and destabilizing exotics.

Recognizing that present communities are likely to be shuffled as climate changes, habitat is degraded, and aliens arrive, I posited the birth of a new field, *recombinant ecology*, in which biologists study ways in which these "new" communities differ from the "normal" communities present before the industrial age. We are already seeing significant work in this field as researchers study such things as ecosystem-process dynamics, variation in fluctuations of population size, and dynamics of predator-prey interactions, including release of alien mesopredators following extirpation of top carnivores (See paper 5).

A few years ago I was hoping that this appreciation of fluctuating community membership would lower the psychological barrier to the reintroduction to North America of cheetahs, elephants, rhinos, camels, and yaks that were part of the landscape until they disappeared, likely extirpated by the first peoples in North American at the end of the Pleistocene. Although this prediction has not largely come true, there are positive signs, such as the 19,000 Indian blackbuck now found on Texas game farms and the giant Bolson tortoise successfully reintroduced by the Turner Endangered Species Fund to three localities in the southwestern United States. As people drain western aquifers like the Ogalalla that extends from South Dakota and Wyoming to New Mexico and Texas, farmland will be abandoned, which may be an opportunity for the rewilding of the missing Pleistocene genera.

6

The Onslaught of Alien Species, and Other Challenges in the Coming Decades*

MICHAEL E. SOULÉ

from the journal *Conservation Biology,* 1990

Social and Ecological Impacts of Biological Invasions

Where will the field of conservation biology go in the coming decade? Some of the many areas of probable significance will be (1) climate and ecosystem processes, (2) habitat fragmentation, (3) community truncation, (4) restoration, and (5) biological invasions. I want to very briefly look at these general issues in turn. Global warming, drying, ozone depletion, and toxification will produce many unpredictable ecosystem-level effects that will have dramatic impacts on biodiversity. Fragmentation will continue to harry habitats; its bitter fruits will provide many opportunities to discover and treat new kinds and degrees of area and edge effects and related maladies. The truncation of biological communities by the removal of top carnivores, important herbivores, plants that provide critical resources, and habitat-reforming taxa (beavers, elephants, pocket gophers, termites, etc.) will yield valuable information about the roles of keystone species. Restoration ecology and conservation biology will tend to merge because most so-called wild places on the

planet will be relatively denatured[1] and will need intensive rehabilitation and management.

In this address, however, I wish to emphasize the inexorable invasion of all biotas by alien species from other regions, biomes, and continents (recent reviews include Groves & Burdon 1986; Macdonald et al. 1986; Mooney & Drake 1986; Drake et al. 1989; Hengeveld 1989), and I will point out some of the challenges and opportunities they represent. The consequences of these invasions may be surprising, and all will demand ingenious countermeasures and creative accommodation.

The Concept of "Natural"

A major controversy in conservation biology in the early twenty-first century will concern the relative virtues of natural versus artificial assemblages for the maintenance of biodiversity. The concept of *natural*, however, is already anachronistic due to the pervasive influence of humans. Even ignoring the effects of hunting and fire wrought by aboriginals in Australia, Oceania, and the New World, and the extinction of about one-quarter of all bird species prior to or soon after European contact (Diamond 1989; Olson 1989), no part of the biosphere is untouched by modern technology and the recent growth in human populations. We are all familiar with the deficits of ozone in the upper atmosphere, with the global distribution of DDT, with the fallout of radionuclides produced by bomb testing, with the effects of ecosystem acidification and of greenhouse gases, and with the impacts of humans on populations of large vertebrates in forests, lakes, and oceans, even in the most remote regions.

The concept of "natural" is subverted further by the universal flood of exotics (alien species). In Kruger National Park in the northern Transvaal, for example, the number of alien plant species listed in 1937 was six. A detailed survey in the 1950s recorded 43. Today, the number is over 160 (Macdonald & Gerbenbach 1988). The Hawaiian Islands have 4,600 species of exotic plants; this is three times the number of indigenous species (St. John 1973).

The intercontinental traffic of exotic organisms, including their associated pathogens, will grow with the increasing mobility of people and commodities. At the same time the distributions of many human-associated species will continue to expand *within* their native continents, as we are seeing already in North America with coyotes (*Canis latrans*), red foxes (*Vulpes fulva*), opossums (*Didelphus virginiana*), gulls (*Laridae*), cow birds (*Mololthrus ater*), prickly pear (*Opuntia* spp.), common sunflower (*Helianthus annuus*), and cattail (*Typha* spp).

The flood of exotic species will tend to homogenize ecological communities, especially those subject to anthropogenic disturbance. As the number of exotics in most regions produces a cosmopolitanization of remnant wildlands, there will be an agonizing period of transition, especially for ecologists.

With some exceptions invasions will be random, unplanned events. Among these exceptions will be biological control agents— organisms purposely imported to attack more harmful aliens. Another set of exceptions will be large and rare vertebrates, particularly tropical and subtropical forms. Many such species will be unable to persist in their homelands because of the human usurpation of their habitats and will find their only semiwild salvation in places like the American Southwest and Great Basin.

In addition to the irresistible force of alien invasion, shifts in scientific fashion will facilitate the transition between the traditional view of biogeographic integrity and the postmodern acceptance of cosmopolitanization. The first shift is the decline in status of the "niche paradigm" and its accompanying view of biological communities as highly integrated by competitive interactions. The other trend, one that overlaps with and reinforces the first one, is the acceptance of the "individualistic" paradigm of community composition (Gleason 1917; Hengeveld 1989), which posits that the collection of species that exist in a particular place is a matter of historical accident and species-specific, autecological requirements.

The latter view is reinforced by analyses of Holocene distributions of contemporary species. These studies are undermining

typological concepts of community composition, structure, dynamics, and organization by showing that existing species once constituted quite different groupings or "communities" (Raven & Axelrod 1978; Davis et al. 1986; Webb 1988; Thompson 1988). Graham and Lundelius (1984), for example, point out that small mammal species that now coexist only in the southern Appalachians or that are completely allopatric occurred together not long ago in the grasslands of southern New Mexico and Texas. In addition, many of the genera of animals that most conservationists would consider alien in North America were actually part of that continent's biota only moments ago in evolutionary time. Thirty-seven genera (57 species) of large mammals (with adult weights > ca 40 kg) went extinct just a few thousand years ago in North America (Kurtén & Anderson 1980; Martin 1984), whereas most of their plant prey survived. Some of these animal genera still persist in the Old World, and many species in these genera could probably adapt to current North American conditions if they were allowed to "return."

For many North American ecologists, the psychological adjustment to biogeographically recombined communities will be painful, but it might be facilitated by the realization that lions, cheetahlike cats, camels, elephants, horses, saiga antelope, yaks, and spectacled bears are native taxa to North America that disappeared very recently. The reintroduction of these large animals will be controversial, but I would not be surprised to read someday that cheetahs are helping to control deer and that mesquite is being "overbrowsed" by rhinoceroses. A cheerful way of viewing such faunal mixing is that it represents the restoration to the Nearctic of the great paleomammalian megafauna.

Even if such megafaunal restorations are prohibited, it will become more and more difficult, in both management and philosophical senses, to defend and protect the ecological *status quo ante* (Westman 1990). I am not suggesting that we abandon the control of aggressive exotics that threaten the persistence of native species and entire communities. The control and extirpation of damaging aliens, especially species like fire-conducting grasses, will remain among the

most urgent of all management activities. But a policy of blanket opposition to exotics will become more expensive, more irrational, and finally counterproductive as the trickle becomes a flood. Only the most offensive exotics will be eliminated in the future, using such criteria as degree of potential hazard to humans and to indigenous species and the probable cost of extirpation (Westman 1990).

A new ecological discipline will develop to deal with the interactions within these new, biogeographically complex assemblages. This field might be called "recombinant ecology" or "mixoecology," and it will offer manifold opportunities for research (Dobson 1988) and controversy. Among the theoretically interesting questions that this new field will address are whether recombinant communities differ from "normal" communities in (1) variance in fluctuations of population size, (2) resiliency, (3) dynamics of predator-prey interactions, (4) frequency and pathogenicity of disease and parasite outbreaks, (5) degree of species packing, and (6) ecosystem process dynamics and rates.

Conflicts with Animal Rights Enthusiasts

In their efforts to control both expanding native species and destructive exotics, conservationists will come into conflict with well-meaning animal welfare enthusiasts.

In the Southwest, for example, native ravens, whose recruitment is enhanced by human-generated garbage and also by the proliferation of power lines from which the ravens can more economically view wide areas of desert habitat, are preying more effectively on hatchling desert tortoises. But attempts to control the numbers of these subsidized mesopredators (Soulé et al. 1988), and other species of this genre such as opossums, skunks, raccoons, and cowbirds will meet resistance from some elements of the animal rights community.

Another case involving a native species is that of the red fox, which is expanding its range rapidly into wetlands in California. The effect of foxes on ground-nesting birds, such as the endangered

Light-footed Clapper Rail and the Least Tern has been devastating, but animal rights groups such as the Animal Lover's Volunteer Association have sued the California Department of Fish and Game and the U.S. Department of Fish and Wildlife to prevent fox control, and have succeeded to the extent of preventing the shooting and poisoning of foxes (Kent A. Smith, personal communication). Many similar stories could be told.

Fortunately, such conflicts are not universal. In Hawaii it has been possible to virtually exterminate goats in Hawaii Volcanoes National Park without public outcry using the "Judas goat method" (Charles P. Stone, personal communication). Radio-collared female goats were released. These lonely females quickly attract remnant feral goats. Following the elimination of the feral animals, the collared female was released again. Unfortunately, the method doesn't work on less gregarious species such as feral pigs.

Conflicts between animal rights groups and management agencies are increasing in frequency and cost—the cost being borne by endangered species and ecosystems as well as by the public that pays for expensive rescue operations and time-consuming court battles. The minimization of such conflicts will require both public education and courageous leadership. Journalists can have a major role in this important public policy issue by helping to inform the public about the complex biological and ethical issues involved in these conflicts.

Sociological and Public Health Implications of Biological Invasions

The invasion of the temperate zones by alien species has sociological implications. The enjoyment of field, forest, and stream will diminish in stepwise fashion as pests, vectors, and diseases are added. One of the greatest pleasures of being outside has already been foreclosed in most of North America. This is the simple act of drinking from a cool stream. The spread of the intestinal parasite *Giardia lamblia* to wild hosts such as beaver and elk now requires the unaesthetic intrusion of filter pumps or iodine pills into the wilderness experience.

The public health and economic challenges implied by biological invasions are also formidable (May 1988). For example, mosquitoes such as *Aedes albopictus* and *A. aegypti*, the former already established in the Southeast, will spread as the climate warms. These mosquitoes can vector dengue fever, yellow fever, equine encephalitis, filiariasis, and also the viruses that cause hemorrhagic fevers.

The interaction of climate warming, human immigration, and biological invasions may also lead to higher risks of hookworm (*Anclyostoma* and *Necator*) infection, an increase in distribution and number of species of chiggers, including some tropical ones such as *Trombicula batatus*, and the introduction of many tick- and mite-borne diseases. Malaria, carried by *Anopheles*, is also likely to become a problem again in North America.

Other diptera also have the potential to inflict new dimensions of hardship. Tropical biting midges of the genus *Culicoides* are already on our southern doorstep. Sandflies of the genus *Phlebotomus*, which serve as vectors of sandfly fever, kala-azar, other forms of leishmaniasis, and serious diseases such as bartonellosis, might invade the southern United States from southern Europe or Mexico as tropical conditions push northward.

Another parasite, *Borrelia burgdorferi*, a sprirochaete related to the organism that causes syphilis, may have recently arrived (possibly from Europe), and has infected ticks such *Ixodes dammini*. The result is Lyme disease. The public is alarmed. According to Paul Etkind of the Massachusetts Department of Public Health, "Lyme disease is second only to AIDS in public interest and concern." This is merely the thin edge of the wedge, however. Increased mobility of humans, their pets, and smuggled wildlife may bring about an epidemiological onslaught of staggering proportions. It would not be surprising if dogs, cats, and other pets fall into disrepute because they harbor increasing numbers of human pathogens.

The traffic of species between continents is two-way. In Africa, an infestation of the Western Hemisphere screw worm, *Callitroga hominivorax*, a serious pest of cattle and other mammals, was just discovered in Libya. It is by no means certain that it can be

contained, given the political and administrative barriers to international cooperation in North Africa. If this infestation crosses the Sahara, which is not unlikely, the consequences for wildlife could be serious. In South Africa, 12 percent of the fish species are introduced, and many of these, including rainbow trout (*Salmo gairdneri*) and smallmouth bass (*Micropterus dolomieu*), are serious threats to many native species, particularly minnows (Bruton & van As 1986).

Conservation Implications of Biological Invasions

What are the implications of these real and potential problems for the wilderness and conservation movements? When outdoor enthusiasts perceive that they can't drink the water because of parasites, they can't risk exposure to the sun because of ozone depletion, and they can't wear shorts for fear of disease-bearing ticks, not to mention fire ants and killer bees, they will run gibbering to their indoor exercise machines.

I worry that this might trigger a bandwagon of biophobia—that it might undermine the current interest in conservation and biodiversity. How will it affect experiential outdoor education? How will it affect the emerging biocentric credos of bioregionalism and deep ecology? It can't help.

The outdoors will lose its appeal to hunters as well. Hunting is a cultural tradition most typical of rural areas. Often it is passed on patrilineally. Aside from the environmental dangers mentioned above, hunting will gradually decrease in popularity because of increasing urbanization, the increasing power and influence of animal rights activists, and possibly because of the lessened status of males and their role in child-rearing. Many will hail the passing of hunters from the woods and fields, but how will wildlife managers control pest species such as deer and feral pigs without their aid? Perhaps coyotes will continue to become larger and more brazen, because the reintroduction of wolves surely will not be tolerated except in remote wilderness areas.

The control of exotics is a growth industry. More grant funds will flow to those who study the epidemiology, genetics, and the ecological relations of exotic organisms. The bad news is that there will once again be calls for the widespread application of herbicides, insecticides, and rodenticides. On ecological grounds it is to be hoped that such shotgun approaches can be avoided, but this will depend on the existence of integrated management programs, which in turn will depend on basic research (Soulé & Kohm 1989).

Some Challenges to the Society for Conservation Biology

Diversity and Dissension

Biological invasion is just one of many issues that the Society for Conservation Biology and our discipline will face. The scientific challenges are immense, and we must overcome many obstacles, internal and external, to make a dent in them. Like physicists using the arguments of economic competitiveness to strengthen their demands for billions of dollars for massive accelerators, like astronomers rallying public support for orbiting telescopes and missions to planets, and like molecular biologists using the specter of cancer to promote the human genome project, conservation biologists must band together to support the level of funding that will have a real impact on global biodiversity and on environmental problems. We must reject our tendency, with its false assumptions of scarcity and a zero-sum world, to circle the wagons and shoot inward. We must question whether feathering our own institutional and disciplinary nests is part of the solution. We must reject the divide-and-conquer strategy and the dualistic mind set that for the past 20 years has kept us preoccupied with internecine squabbles such as those between ecosystem ecologists and community/population ecologists, between determinists and nullists in community ecology, between gradists and pheneticists, and between populationists and ecosystemists in conservation biology.

Our "enemy" is not other biologists, it is this disciplinary provincialism, this chauvinism. As Arne Naess has said, "The ecopolitical frontier is immensely long but we can only work effectively at one place at a time" (Naess 1989). We should be grateful that there are others to defend distant barricades and to push forward other campaigns.

Our objectives make us unique among professional organizations, and because of our multidisciplinary makeup, we are inherently unstable. Why? Diversity itself. I offer the following metaphor of a group house as a model of this Society. Students and young professionals share a large house providing facilities that none alone could afford. Periodically, the cohabitants advertise for housemates with similar values. The common value may be a particular political agenda, a smoke-free environment, vegetarianism, or an interest in conservation. To keep the metaphor remote, let us say that the common value is vegetarianism.

Now, there are many varieties of vegetarian. *Spiritual vegetarians* may deny themselves meat because of their belief in the oneness of life or in reincarnation, or merely for the benefits of renunciation itself as a spiritual practice. The *ethical vegetarian* does not want to cause unnecessary suffering in animals. The *skinhead vegetarian* believes that eating meat diminishes his virility and pollutes his racial purity. The *environrnentalist vegetarian* actually likes meat but foregoes it because of the ecological damage and human suffering wrought by cattle grazing, by feed lots, and by lengthening the human food chain.

Herein, in this normative diversity on a common theme, lies the problem. Each member of the group house feels strongly about his or her own values and finds those of the others ill-conceived or even repugnant. Such a house could be torn apart by dissention.

The Society for Conservation Biology is like this house of vegetarians. Indeed, we all share the goal of protecting biodiversity and wish to apply our professional expertise to this historic task. But our means differ, and conflicts are often engendered by a careless, either-or dichotomy: for example, to let burn "naturally" *or* to con-

trol wildfires, to eliminate wild horses *or* let them become renaturalized, to focus on endangered species *or* on ecosystems, to champion single large nature reserves *or* several small ones, to emphasize inbreeding *or* environmental stochasticity in population viability analysis, and to promote biosystematic surveys *or* shorter-term programs in other fields of conservation biology. (Even the most casual student of biology knows that truth and success usually lie somewhere in between the extremes.) The point is that many of us discover that our disagreements with our allies are more bitter than our confrontations with our "enemies."

Indeed, what hope is there for an organization that comprises social scientists, natural scientists, managers, agency administrators, educators, and lawyers? This is why I say that the Society is inherently unstable. We may be unique, we may be important, we may even be precious. But preciousness will not help us survive. What will? Tolerance—resisting the temptation to polemicize every disagreement.

Dispersal

It is time for our young society to disperse—to go overseas. In the process of internationalization, however, we must not ignore North America with its potential for securing and protecting vast areas of wild lands and waters, with its majestic mountains and immaculate deserts, its huge inland seas and dramatic coasts, its remnants of virgin redwood, Douglas-fir, and Sitka spruce, its species-rich chaparral, its vast plains and deciduous forests, its tundra and taiga, and the multitudes of plants and animals contained in them.

Nevertheless, perhaps only 10 percent of this planet's species diversity lies in North America. In part of this reason the Society has just become a member of IUCN; we must look outward and provide encouragement and support to conservation biologists everywhere. Fortunately, the dispersal phase is inevitable. Many of our more honored members are tropical biologists, and our new president had the foresight 20 years ago to initiate one of the world's most important of tropical research projects in Brazil.

Advocacy and Quality

We are not an advocacy organization, although most of us are members of many such organizations. In criticizing the American preference for action over thought, Ralph Waldo Emerson said, "Why should we be cowed by the name of Action? 'Tis a trick of the senses, —no more. We know that the ancestor of every action is a thought. … To think is to act." (Spiritual Laws).

Such a plea for deliberation sounds heretical—a betrayal of our fundamental assertion that conservation biology is a crisis discipline, often calling for decisions and actions in the absence of sufficient information (Soulé 1985). The contradiction is not real. It rarely takes long to gather the experts and to reach an informed consensus. This is *not* a call for endless research while the atmosphere is charged with our gaseous wastes, the land is shaven of its living skin, the seas are coated with fossil hydrocarbons, and the right to life comes to mean a new totalitarianism—*lebensraum* for the technological ape. It is only a reminder that if the Society becomes nothing more than another special interest group, its opinions should receive nothing more than passing notice.

Above all, the pursuit of scientific excellence in conservation research, publication, and application must be our herald. We should be the supreme court, the ultimate arbiter of what is the best in conservation science. And if other organizations provide more considered counsel to society, then we have no raison dêtre.

Coda

Each year our members come together to celebrate the birth of a new kind of professional, a professional whose commitment goes beyond technical competence, recognition, financial security, and other victories in which normal professionals find solace and identity. Your commitment to nurture the evolutionary process and the spectacle of life on this planet makes me optimistic about the future.

I am optimistic also because of your willingness to bridge disciplinary barriers. I am optimistic because you have focused so much heat and light on the tropics and on the international development banks. I am also optimistic because we have real heroes in this movement, those recognized by awards and many who are heroes all the more because they are unsung. Among these unsung heroes are our field workers who face primitive conditions, life- and health-threatening diseases, and even death at the hands of terrorists. We have graduate students and assistant professors who ignore warnings about the professional dangers of doing so-called applied science. We have managers who venture into the no man's land between theory and practice. We have natural resource professionals who tolerate the smug elitism of Washington, Canberra, New Delhi, and Rio in order to carry on the political and funding battles.

What don't we have? We don't have a membership that is sufficiently large to make us financially independent. Our financial break-even point is about 4,000 members. We could accomplish this virtually overnight if each member, before our next meeting, recruited one additional person. I ask each of you to please make this a personal goal.

What else do we lack? Fortitude, perhaps. There are moments when the destruction of a favorite place, of entire biotas and ecosystems, seems unbearable and the future looks bleak indeed, and when the temptation to turn and walk away is almost overpowering. If you've ever despaired at the sheer magnitude of the problems facing our planet, consider the words of Nobel Prize winner Murray Gell-Mann in a recent *Orion*:

> History shows clearly that humanity is moved forward not by people who stop at every moment in an attempt to gauge the ultimate success of their venture, but by those who think deeply about what is right and put all their energy into it.

I would add that such people walk a high and lonely path. Those less committed and those with other agendas will say that the path is

elitist and they will cajole and ridicule the high walkers. But is there a choice? As Yogi Berra is supposed to have said, "If you come to a fork in the road, take it."

Acknowledgments

Notes

*Presidential address at the third annual meeting of the Society for Conservation Biology in Toronto on August 11, 1989. Paper submitted November 14, 1989; revised manuscript accepted March 2, 1990.

1. The term "development" often evokes positive associations because of its potential social and economic benefits (the creation of jobs, food/fiber; wealth, etc.). The term should be avoided, however, in the context of landscape alteration per se or when emphasizing habitat disturbance or destruction. For the latter, I prefer the more accurate term "denaturation."

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Introduction to *Conservation: Tactics for a Constant Crisis*

This paper systematized threats to biodiversity and the tactics for countering them. I observed that six types of "interference" diminish biodiversity, namely loss of habitat, fragmentation of remaining habitat, overexploitation, alien species, pollution, and climate change. These operate throughout the world, but magnitude differs with geography. For example, habitat loss wipes out more species in the tropics where they have small ranges and are densely packed, while climate change is more severe in the temperate and polar regions, places already experiencing massive die-offs of trees and changes in distributions of birds.

The fundamental driver underlying these types of interference is population growth. The arithmetic is simple—more people gobble up more land and resources. Conservative projections by the United Nations in 2013 estimate that by 2100 there will be an additional 3.7 billion people, mostly added to the developing world, home of most biodiversity.

Ehrlich and Wilson showed early on how to calculate the environmental impact of humans by multiplying the number of people

by their individual impact, namely the amount of resources required by each. My 1991 paper predicted that "It is probable that the price of raising human economic welfare [in the developing world] to a standard similar to that in the wealthier countries will be biotic devastation in the tropics on a scale inconsistent with the persistence of wildlands." And indeed we are seeing a huge surge in per capita consumption in the developing world as nations like China and India modernize. Global coal use, a major contributor to greenhouse warming, reached an all-time high in 2012 at 3.7 billion tons of oil equivalent, massively influenced by China, whose appetite quadrupled from 1990 to more than 1.8 billion tons.

The effects of population growth are modulated or potentiated by other fundamental processes that include the anthropocentric belief that humans are more important than other beings, the global reach of a world economy that deforests Indonesia to make coffee tables for Poughkeepsie, the inability of governments to accept short-term sacrifices for the long-term benefits of a healthy environment, and unequal wealth distribution that makes it hard for individuals and poor societies to take the long view.

Finally, I divided conservation measures into eight paths to biotic survival, which can be divided into in situ and ex situ conservation approaches; that is, saving species in wild habitat versus using artificial methods such as zoos and cryogenic "frozen zoos." To be successful, both in situ and ex situ methods require adequate financial and human resources and political stability, but these are rare in much of the developing world. The preferred alternative is always conservation in situ, but if this is impossible because of war, corruption, or lack of political will, then ex situ conservation may be the best solution until reintroduction is possible in a hypothetical future when the human population is stabilized and reduced.

Conservation: Tactics for a Constant Crisis

Michael E. Soulé

from the journal *Science*, 1991

Is wildlife conservation failing? In the United States, species diversity appears to be declining at an accelerating rate (1). Even the Endangered Species Act of 1973 (ESA) has not significantly slowed the deterioration of the nation's biological estate, although this is largely the result of lack of support from the federal administration. Currently there are over 4000 species and subspecies recognized as candidates for endangered species status, but the listing process administered by the U.S. Fish and Wildlife Service is bogged down because of lack of funding. There are no recovery plans for nearly half of the 600 or so species in the United States that have been officially listed as threatened or endangered, and the score or so of recovering species is balanced by an equal number that may be extinct (2).

The situation is generally much worse in other nations. Biologists with extensive experience in developing countries are saying that by almost any quantitative standard conservation is failing, and that current approaches to conservation, such as traditional parks and reserves, are unlikely to succeed (3,4). Worldwide, only about 3% of the land is set aside in 5000 nature reserves or protected areas

(5), but many of these reserves are deteriorating (6). Because the moist tropics are far richer in species diversity than other biogeographic regions, and because deforestation will probably eliminate almost all of the tropical forests outside of protected areas by 2100 (7), biogeographers estimate that from 25 to 50% or more of tropical species will vanish in the next century or sooner (Fig. 1) (8). Even if humanity were to depart the earth, recovery of biotic diversity by evolutionary mechanisms would require millions of years, depending on how deep, taxonomically, the extinction crisis cuts (9).

Such dire predictions are now leading to a reappraisal of conservation's goals and tactics. In this article, I conclude that this reappraisal would be more fruitful if there were a deeper appreciation of the biological and social contexts of conservation actions, particu-
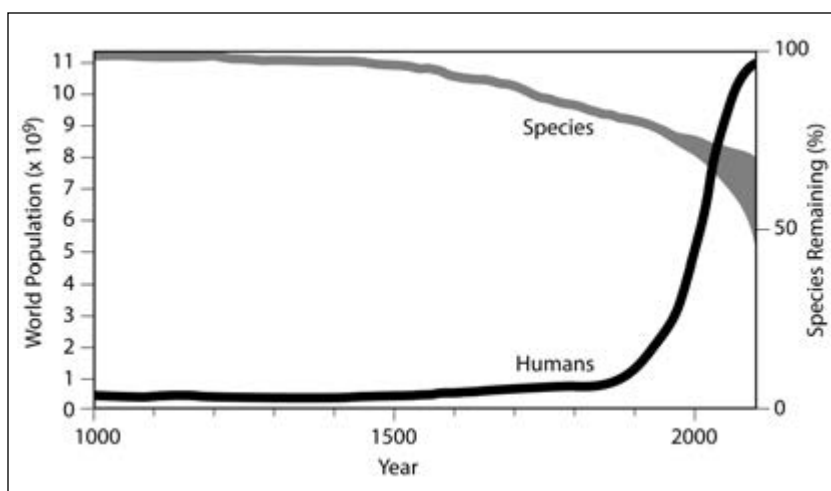

FIGURE 1. The expected inverse correlation between human population size and the survival of species worldwide. Extinction rates depend on the size of the habitat fragment and occur at a decreasing rate as habitat fragments age. Anthropogenic extinctions before A.D. 1000 are ignored. The shape and width of the extinction curve reflect the uncertainty of the predictions; the curve is based in part on the assumption that most of the extinct species will be small organisms with geographically limited distributions.

larly how both biogeography and political geography dictate differ-ent conservation tactics in different situations. I also argue for an actuarial approach to the viability of protected areas—one that con-siders the social factors determining the half-life of nature reserves.

The Biospatial Hierarchy

Effective conservation is impossible without some knowledge of biotic (biological) diversity (biodiversity). For most scientific pur-poses, "life" is classified taxonomically, based on similarity and presumed evolutionary relationship. For purposes of protection, however, the living components of nature are usually classified in a "biospatial" hierarchy of nested sets. In practice, there are about five levels to this hierarchy: (i) whole systems at the landscape or eco-systems levels, (ii) assemblages (associations and communities), (iii) species, (iv) populations, and (v) genes (10). Place, not evolutionary relationship, is the basis for the biospatial hierarchy, because most conservation strategies are geographically anchored (11, 12).

The targets at the top of the biospatial hierarchy are ecosystems (or landscapes and seascapes making up interacting ecosystems), in-cluding such topographic features as entire drainages. A frequently cited example is the Yellowstone National Park region, including the adjacent Grand Teton National Park and other federally man-aged lands. Ideally, ecosystem conservation protects the contained biotic communities: habitats, species, populations, and genes, not to mention all ecological interactions, processes, and some of the traditional, human cultural practices that have been historically as-sociated with the ecosystem.

At the second level, an arbitrary number of biotic assemblages can be defined within ecosystems, although the species themselves show little correlation in their distributions when climate changes (13). Nevertheless, state federal, and international conservation pro-grams often base their conservation strategies on the completion of the network of biotic community types—the so-called coarse-filter

approach. The discovery of "gaps" in the network of assemblages is most often based on systems of biogeographic classification (12, 14).

The third biospatial level, species, is defined as groups of populations that routinely exchange genes or are phenotypically similar (15). The selection of protected areas is frequently based on the presence of one or more endangered species, often large-bodied or attractive ones. In addition, regions with high species diversity, such as tropical forests, coral reefs, or regions with large proportions of local endemic species, such as isolated mountain ranges or oceanic islands, are frequently identified as targets of conservation. Another reason for focusing on species is that the management of protected areas is often facilitated by attending to a relatively small number of so-called keystone or indicator species; these species may not be endangered themselves but they are used to monitor the status of a much larger assemblage of species (16–18).

Next is populations. Populations, whether mobile or sedentary, are dynamic assemblages of individuals which maintain genetic and sometimes social information in lineages that may ramify and merge as individuals are born, reproduce, and die. Endangered populations, and those of species that mediate important ecological processes, are often targets of conservation, so that their viability is a major concern (18, 19). Theoretical treatments of population viability are influencing public policy, such as the debate over the spotted owl in the Pacific Northwest (20).

At the small end of the biospatial hierarchy of conservation targets are genes. Genes are sometimes conserved ex situ (21, 22) as seed collections, in tissue culture or germplasm collections, or as cryopreserved semen, ova, embryos, and tissues. The extraction of genes from nature annually produces multibillion dollar benefits for agriculture, biotechnology, and public health (23). In nature, genetic variation maintains the fitness and evolutionary flexibility of natural populations (16). Reserves in seminatural areas have been set aside to preserve the wild relatives of commercially important plants, especially to protect genes and gene combinations providing resistance to pests, drought, and other climatic factors (24).

The Six Classes of Interference and the North-South Distinction

The five levels of the biospatial hierarchy—are being undermined by six major classes of human interference (25), as shown in Fig.2. These six factors are (i) the loss of habitat; (ii) the fragmentation of habitat—producing deleterious area, edge, demographic, and genetic effects; (iii) overexploitation; (iv) the spread of exotic (introduced and alien) species and diseases; (v) air, soil, and water pollution; and (vi) climate change. These factors have all been discussed in great detail (16, 19, 22, 26, 27). The intensities of shading in the two parts of Fig. 2 are subjective, but suggest that the present and future hazards posed by the six factors are not equal in strength or concordant in rank across the range of conservation targets, or from economically poorer to economically richer nations.

Clearly the impact of a given factor depends on the time, the place, and the circumstances. As indicated in Fig. 2, economics, culture, as well as the temperate-tropical disparity in species diversity and other biogeographic patterns, explain the differences in biotic vulnerability between tropical, poor countries, and temperate, wealthier ones. The vastly greater number of species in the tropical nations, the much smaller geographic ranges of tropical species on average (28), in addition to the high rates of habitat destruction in most of these countries, means that species in the tropics are particularly vulnerable to habitat loss and fragmentation. Similarly, not all parts of the planet will be equally susceptible to the impacts of acid rain, ozone thinning, or greenhouse warming; for example, the effects of greenhouse warming will be much greater at high than low latitudes, except, perhaps for marine systems (29). Other aspects of biogeography are relevant to geographic heterogeneity in biotic vulnerability; on oceanic islands, for example, introduced predators are typically more damaging than on continents (16, 25, 30), and introduced animals (goats, pigs, rats, mongooses, snakes, and predatory snails for instance) and plants may have catastrophic effects (31).
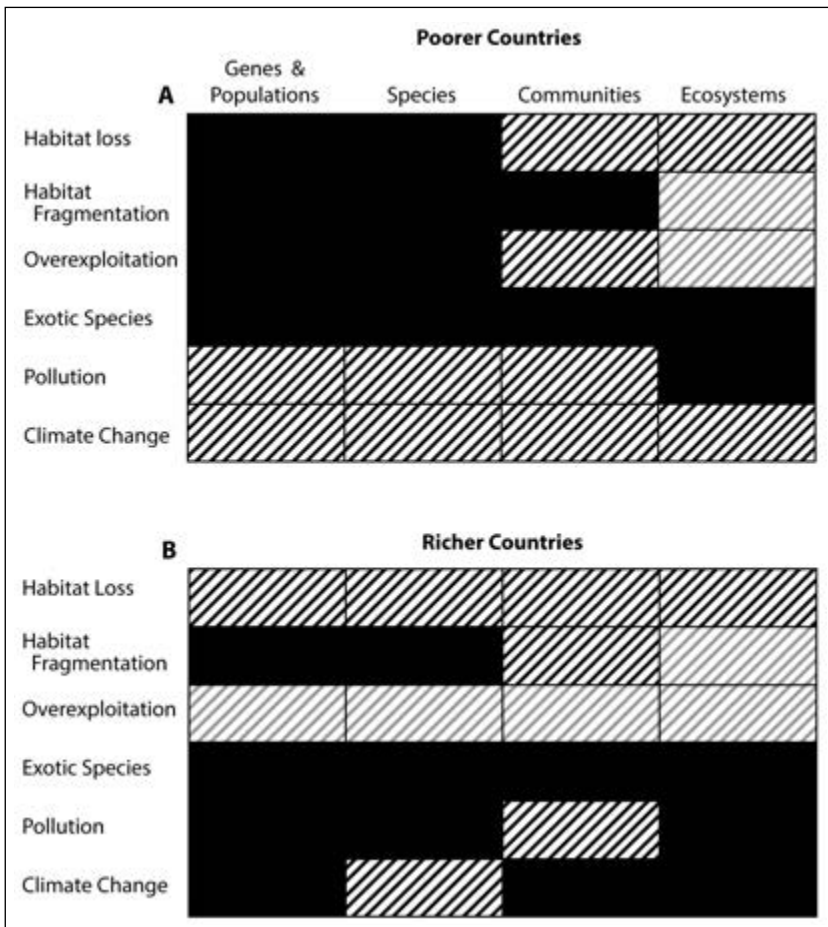
FIGURE 2. Relative impacts of factors affecting terrestrial biotic diversity in (A) poor and (B) rich countries. Shading indicates intensity of impact: solid = highest; thick lines = intermediate; thin lines = lowest. Ecosystems refers to landscape level formations including, for example, mangrove habitats, coral reefs, riverine/riparian systems, forests, and savannas. The distribution of impacts on aquatic and marine systems differs somewhat from those shown here.

Although it is difficult to generalize, one can point to some rough principles about the global vulnerability of terrestrial biodiversity (32). Habitat loss, fragmentation, and the direct and indirect effects of exotic species are problems everywhere (Fig. 2A), but overhar-

vesting of economically important species is now of greater concern in poorer countries. Pollution and climate pose major threats in the temperate zone nations (Fig. 2B). As discussed below, north-south differences in socioeconomic variables and biogeography mean that conservation tactics must be tailored to the location.

The Seven Sources of Biotic Degradation

The six classes of interference may constitute the most obvious proximal causes of biotic attrition, but the more fundamental causes are rooted in the contemporary human condition, especially as they are amplified by the explosive growth in human numbers in the last three centuries (Fig. 1). These more fundamental causes are listed in Table 1. The following brief descriptions of these factors are neither systematic nor exhaustive, but even this superficial treatment demonstrates why simple approaches (such as a network of protected areas alone) will fail.

TABLE 1. Categories of fundamental human factors that contribute to the erosion of biological diversity.

Factor	Example of impact on conservation
Population growth	Population pressures
Poverty	Hunger, deforestation, trade in rare and endangered species, failure of grass roots support
Misperception	Desire for quick results and denial of long-term failures
Anthropocentrism	Lack of support for nonutilitarian causes
Cultural transitions	Unsustainable resource management during colonization and rapid social change
Economics	Failure of planning because of internationalization of markets and erratic pricing of commodities
Policy implementation	Civil disruption, wars, corruption, failure of law enforcement

Population growth. The continuous increase in human numbers exacerbates nearly every other environmental problem (33, 34). The population reached 1 billion about 1800, and appears to be headed toward 10 billion by 2046 and 12 billion by 2100, according to recent World Bank and United Nations projections. Ecologists argue that such numbers are incompatible with many ecological and evolutionary processes, including the persistence of large predators, the continuation of annual migrations of birds (35), speciation in large organisms (36), and the protection and maintenance of native biotas in the face of increasing pressure from human beings and introduced species. For nonhuman species, this "demographic winter" will last until human beings decide to reduce their numbers to levels compatible with the restoration of pre-explosion biotic processes (37). Human populations are already declining in many industrialized countries.
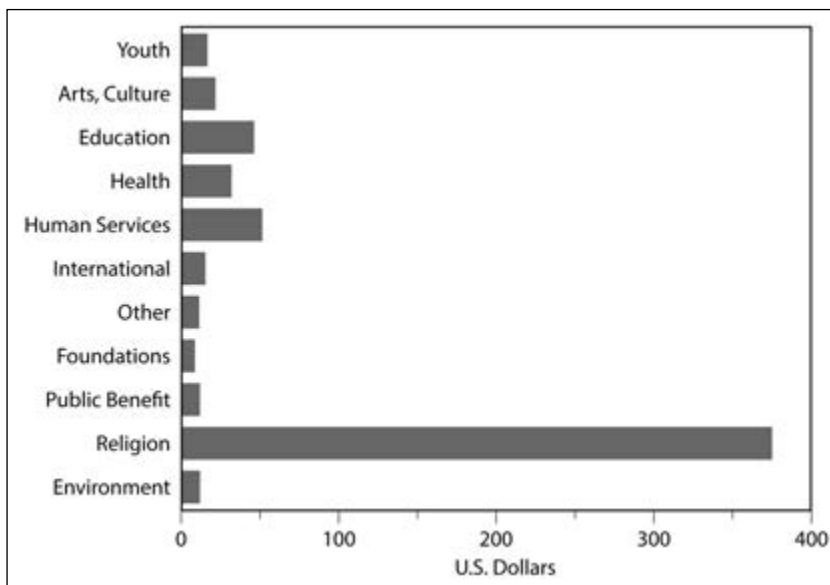

Figure 3. Average charitable contributions per household in the United States [Adapted from (67)].

Poverty. The problem is not merely the shear magnitude of human numbers, however; it is compounded by poverty, the aspirations of people the world over for a better quality of life, and by social and political forces that impede the smooth transition to minimum (let alone "optimal") levels of prosperity, health, and justice (38). Disparities in income produce disparities of impacts. The per capita contribution to atmospheric pollution (and, hence, global climate change) is often orders of magnitude higher for citizens of the industrialized countries than for those in poorer nations (34), and economic pressures from the former contribute to unsustainable land use practices in the latter. Habitat destruction and extinction, however, will occur most rapidly in the tropics (Fig. 2A), where lack of economic opportunity, demographic momentum, and restrictions on reproductive choice are the engines that power the destruction of life.

It is probable that the price of raising human economic welfare to a standard similar to that in the wealthier countries will be biotic devastation in the tropics on a scale inconsistent with the persistence of wildlands except, perhaps in remote nonarable regions (39). Ehrlich and Wilson (40) point out that the magnitude of human aspirations, including demands on natural resources, if multiplied by the expected increases in human numbers, would require the human co-option of most remaining wildlands for grazing, farming, energy production, mining, transportation, and other uses. Therefore, the loss of most tropical wildlands in the next 50 years or so, an epochal catastrophe for earthly life, appears a virtual inevitability.

Misperception and time scale. Gradual environmental degradation goes almost unnoticed (41), whereas governments often overreact to sudden events of lesser overall impact. This short-term mentality is also reflected in current social mores and public policies favoring quick profits and results. The problem is that the benefits of conservation projects can only be measured on a scale of centuries. This difference in time scales between economic development projects and some conservation projects leads to conflicts because the

business of conservation is keeping options open, whereas business as usual (economic development) often forecloses them.

Anthropocentrism. Many conservationists argue that current cultural values are antithetical to effective conservation policies, and that a new ethic or a revolutionary change in human consciousness in necessary before significant progress is possible (42). There are many calls for less human-centered, more biocentric economic policies. The anthropocentric orientation of most societies (43) however, augurs poorly for behavioral revolutions. If charitable donations reflect how Americans rank society's needs, it is evident that humanitarian concerns are dominant; money flows primarily to religious organizations and to medical, cultural, and social welfare causes. Figure 3 shows that only 1.5% of donated monies go to support environmental (nonhuman) groups and causes. This percentage is likely to increase, though, as donors learn about the environmental foundations of physical and social welfare.

Mindful of biases favoring our own species, nearly every book, report, or "strategy" written to promote or guide the conservation of biodiversity presents a list of utilitarian justifications, including the free services and amenities provided by nature (for example, water purification and storage, habitat for fish and livestock, vistas), and the promise of life-extending pharmaceuticals and agro-industrial products that are yet undiscovered in the tissues of organisms (23). Unfortunately, the political effectiveness of narrowly utilitarian arguments for large protected areas in the tropics and elsewhere is weak, in part because the promise of long-term economic and health benefits to society as a whole appears abstract to individuals and corporations more concerned with survival and short-term economic gains.

Cultural transitions. The most destructive cultures, environmentally, appear to be those that are colonizing uninhabited territory and those that are in a stage of rapid cultural (often technological) transition (44). The cultural groups that appear to be the least destructive to natural systems are those that have been occupying the same place for centuries or more (45). Overharvesting of wild

animals, of aquatic and marine organisms, and of forests, is predictable, therefore, when human groups (i) have little or no experience in their current geographic setting or (ii) are undergoing integration in the world economy. Wealthy, well-educated, industrialized cultures may have the potential for minimizing environmental damage, but show little promise of this at present. Because most of the world's people are not only poor, but in a transitional phase between traditional agrarian self-sufficiency and a modern, high-input agricultural or industrial-urban society, relatively little value is placed on the protection of nature, and even where nature is highly valued, such valuation is often left out of the economic calculus.

Economics. Environmental destruction and the erosion of biological diversity in the tropics and elsewhere is exacerbated by systems of commerce that create demands from the industrialized north for products, the production of which causes massive habitat destruction (46). The "cool chain" industry, for example, produces fresh produce such as fruit, vegetables, cut flowers, and mariculture produce (such as, shrimp) in the poorer countries and ships them in refrigerated carriers to the richer countries (47). This new industry contributes to the destruction of many habitats including lowland forests, mangrove, estuarine, and reef habitats. Better known are the coffee, sugar cane, banana, cacao, forest products, and cattle industries that account for the loss of a large proportion of tropical forests in developing countries (23, 48). In addition, a major contributor to forest and woodland destruction is the cutting of trees for the production of fuel wood and charcoal for domestic cooking and heating uses. Before the international price-fixing agreements among petroleum producers, most people in developing countries could afford to cook with kerosene. Now they must rely on wood, charcoal, and dung, contributing to the deterioration of forests and soils (49).

Notwithstanding the grave moral, social, and geopolitical implications of current economic disparities, the redress of such imbalances is unlikely to occur in time to save most seminatural biological systems from massive attrition. Few would question the goals of economic and social justice or their fashionable surrogate,

sustainable development, but the premise that a new economic order would, alone, solve the biodiversity crisis (50) is suspect. The North American, let alone the Costan Rican experience (4), suggests that social justice and other progressive changes cannot protect biological diversity in the face of rapidly changing economic conditions including the internationalization of markets, increasing human numbers, the loss of cultural and ecological traditions, not to mention ethnic and religious conflicts. Even wealthy countries such as the United States and Canada justify the removal of the last remnants of ancient forests on the grounds of economic necessity; attempts to save the remaining 15% of original forests in the Pacific Northwest have yet to prove successful (18). In addition, corruption and bureaucratic inefficiency appear to be virtually indelible.

Policy implementation. There are many reasons for inability of modern states to enforce laws and implement conservation policies, especially policies that require short-term sacrifices for the sake of long-term benefits. For example, the setting aside and long-term protection of land from the national estate is improbable in societies with many poor or landless people, powerful oligarchies, or corruptible judges and bureaucrats.

In countries where adequate resources are lacking for the protection and management of protected areas, even relatively secure reserves are subject to the removal of trees and to the poaching of game. Most poor nations simply lack the resources to preserve biotic diversity in situ (51). Such attrition is frequent during "normal" times (52), but during periods of social unrest, the loss of biodiversity can be catastrophic (53).

Many conservation and development projects are destined to fail in a statistical sense, given their unstable social or political contexts. Wars and the breakdown of civil administration can undermine decades of successful policy implementation. In Africa, recent wars in Ethiopia, Sudan, Liberia, Libya, Morocco, Somalia, South Africa, Zimbabwe, Uganda, Chad, Angola, Mozambique, Rwanda, Burundi, and other countries have led to the partial or complete collapse of nature reserves, the destruction of habitat, and the local extinc-

tion of endangered species (53). The frequency of events such as wars should be built into the planning processes of responsible agencies and organizations. This is not to say that we should abandon reserves in regions where civil chaos is frequent. Rather, expectations and policies must be tuned to appropriate distributional parameters—for example, to the mean and variance of persistence times of protected areas in similar situations and to the kinds of damage that protected areas are likely to suffer, including the killing of most large animals. The lower the mean and the higher the variance, the greater the emphasis there must be on redundancy, on alternative approaches, and on backup, ex situ projects. It would be prudent, in other words, to think of nature reserves as ephemeral islands, and to plan accordingly.

The human condition is dynamic and unpredictable and will remain so for at least a century, if for no other reasons than the momentum of the population explosion and the unsatisfactory economic and social status for billions of people during the 21st century. The "biotic condition," therefore, will also be tenuous during this interval. Fortunately, conservationists have an increasing number of tools with which to deal with the crisis.

Tactics and Conflicts

The eight paths to biotic survival. What tools are available to protect living nature from humanity? Table 2 presents a brief survey of eight conservation tactics or systems (5). The tactics are defined roughly in order of least to most artificial or intrusive.

1) *In situ* refers to those conservation systems based on bounded wild areas with relatively little human disturbance; it includes most protected areas, from wilderness parks to the core areas of biosphere reserves (54). Persistence may depend to some extent on the economic benefits, as generated, for example, by tourism, but protected areas tend to degrade, even in the best of circumstances, and few, if any are large enough to maintain viable populations of large predators and omnivores without ex situ supplementation (16, 19, 26, 55).

TABLE 2. The relative potential significance of eight different conservation systems for the protection and maintenance of natural biological diversity. The "0" indicates little or no role; "X, XX, and XXX" indicate low, moderate, and high significance, respectively. The order of the systems does not imply a ranking of value.

						Conservation system		
Targets of conservation	In situ	Inter situ	Extractive reserves	Restoration projects	Zooparks	Agroecosystems & agroforestry	Living ex situ	Suspended ex situ
Entire systems (ecosystems)								
Processes or functions	XXX	XX	XX	XX	XX	X	0	0
Biosocial (traditional human uses)	X	XX	XXX	XX	X	X	0	0
Biogeographic assemblages	XXX	XX	XX	X	XX	0	0	0
Indigenous and endemic species	XXX	XX	XX	X	XX	X	XX	X
Local populations of species	XXX	XX	XX	X	XX	X	X	X
Genetic variation within species								
Wild relatives of domesticates	XXX	XX	XX	X	X	X	XXX	XX
Traditional domesticated varieties	X	X	X	0	X	XX	X	XXX
Noneconomic genetic variation	XXX	XX	XX	X	X	0	X	X
Ownership	Public & private	Private & public	Public & private	Private & public	Private	Private	Private & public	Private & public

2) *Inter situ* refers to conservation systems or activities in regions where native species still persist, but which are outside the boundaries of established protected areas. Most of the lands belonging to this category are nonarable; typically they are relatively infertile, cold, steep, rocky, or arid. In the United States, most such regions are administered by the Bureau of Land Management and the U.S. Forest Service.

3) *Extractive reserves* permit certain kinds of resource harvesting on a (theoretically) sustainable basis. Examples include rubber tapping, the collection of edible fruits and nuts, thatch grasses, and perhaps, even limited logging and hunting. Sustainability of such practices, however, depends on a low population density, a stable economy, and careful management (56). In practice there may be little difference between extractive reserves and inter situ projects, except that the latter are more circumscribed.

4) *Ecological restoration projects* refers to intensive management activities intended to increase species richness or productivity in degraded habitats. Among the necessary conditions for such activities are political and institutional stability.

5) *Zooparks* refers to facilities in secure locations where a mix of local and exogenous species can be maintained under seminatural conditions—in other words, sanctuaries for sensitive species of diverse provenance (57). The assumptions underlying the establishment of such reserves are that protected areas, in many places, are not viable for social or political reasons and the inevitability of highly recombined biotic communities in the future given current rates of species introductions (58). This category differs from in situ reserves because of the conscious intoductions of target species.

6) *Agroecosystems and agroforestry projects* are highly managed, production-oriented systems with a wide range of dependence on artificial chemical and energy inputs (59). The number of native species that can survive in such systems is highly variable, depending mostly on the proximity of garden, farm, and plantation to wildlands, the use of artificial chemical inputs, and the tolerance of farmers to wildlife (60).

In addition to zooparks, there are two kinds of ex situ tactics or backup systems (14). These are essential where particular reserves are likely to fail or lose significant numbers of their species.

7) *Living ex situ* programs refers to botanical gardens, zoos, aquaria, and similar institutions that maintain and propagate living organisms for noncommercial (education, research, conservation) purposes in a highly controlled, usually urban, context.

8) *Suspended ex situ* programs are completely artificial; living material is metabolically slowed or arrested. Among these projects are germplasm storage facilities such as seed banks, tissue culture collections, and cryopreserved collections of gametes, zygotes, and embryos.

As shown in Table 2, this typology of tactics manifests a current trend—the privatization of conservation. For many reasons, non-profit groups and individuals increasingly are complementing if not supplanting government agencies in protecting biodiversity. Private zoos, botanical gardens, and others are taking responsibility for the captive propagation of endangered species. Responsibility for the restoration of degraded forest, pastures, and farmlands on both public and private lands is being assumed by private groups. Organizations like The Nature Conservancy and Conservation Internatinal are acquiring new sites for protected areas (61), though governments are usually the ultimate owners.

Social Context and the Debate Over Tactics

Current discussions have tended to oversimplify the diversity in conservation approaches by exaggerating the differences between the so-called species approaches and the ecosystem approaches. The former emphasizes the protection, both in situ and ex situ, of endangered, often charismatic vertebrates, whereas the objective of the latter is to set aside and manage natural areas based on systems of landscape classification that will capture as much species and ecological diversity as possible (62). Critics of species-level approaches have emphasized the shortcomings of the Edangered Species Act and point out that most of the federal dollars are directed at a few birds and mammals (62). Some of these critics argue that success in captive breeding and cryopreservation will lead to complacency about the need

for more and better protected areas. Supporters of endangered species might counter that if it were not for the charismatic species, the public appeal of conservation would be much less, that endangered species justify many of the larger protected areas in the United States and elsewhere, and that endangered species legislation is providing the economic leverage to bring developers and government agencies into negotiations about the preservation of large areas of habitat for general biodiversity conservation in the United States (63).

Such adversarial discussions, however, often ignore social context. As shown in Fig. 4, conservation tactics can be ranked according to the degree each is integrated into the local human community and the degree that each is dependent on artificial (technological)
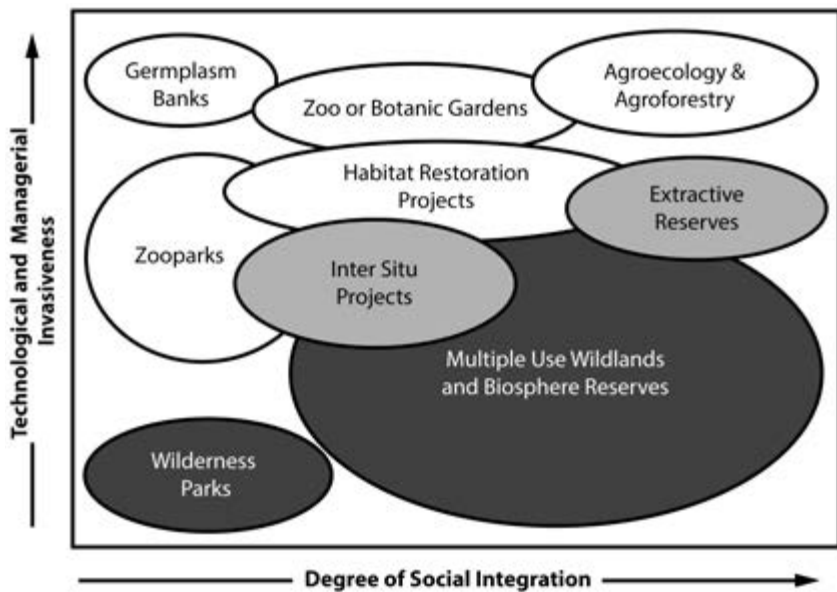
FIGURE 4. Descriptive distribution of conservation tactics according to the degree of social integration at the local level, and the degree of technological input or management intensity. Shading indicates relative degree of human interference with natural processes; darker shades indicate less interference. The positions shown for each tactic are meant to suggest the center of the probable zone of action for the tactic. The term "Biosphere Reserves" refers to multiple use, production-oriented projects, with a relatively sacrosanct core protected area.

means and invasive management practices. Implicit is [the] idea that different tactics require different degrees of social and technical sophistication.

A more prescriptive classification is shown in Fig. 5. It distributes the tactics in a plane of human population pressure and political stability. It is based on the untested assertion that the persistence of conservation projects, particularly protected areas, is related to the frequency and degree of political unrest and the rate of population growth. The combination of the two figures suggests that the choice of tactics should be influenced by the probable impact of demographic, economic, and social conditions as discussed above. For example, ex situ tactics are prescribed where political instability is frequent and where population pressure is building.
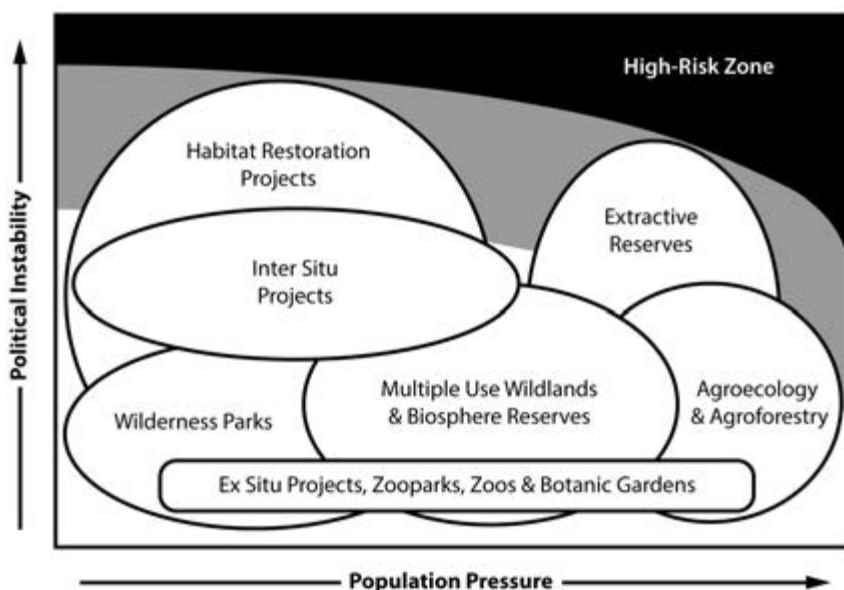

FIGURE 5. Prescriptive distribution of conservation tactics based on the probability of increasing population pressure and the likelihood of political instability or violent conflicts. Backup, ex situ facilities are placed in relatively secure, politically stable locations.

Much of the debate in the United States over approach and tactics stems from uncertainty and bias about landscape and geography, the importance of socioeconomic conditions and the stability of political structures, confidence in new legislative and legal remedies, and the identity of target organisms. For example, conservationists with experience in the species-rich tropics—where infrastructure is fragile at best, episodes of social chaos are inevitable, human populations are doubling every few decades, laws are ignored, and hunting of rare animals and deforestation are a way of subsisting—should support a pluralistic approach that includes ex situ backup for protected areas. On the other hand, those with experience in wealthy, stable, temperate zone regions—where most species have wide geographic ranges and where there exists extensive areas of low productivity, government-owned lands—are more likely to promote systems of protected areas linked by corridors in multiple use zones that can be managed for conservation and sustainable forms of exploitation (64). They will also have more faith in legislative remedies and law enforcement. Figure 5 illustrates this tactical pluralism.

Conclusions

Today, the conservation of biodiversity is virtually equivalent to the ex situ protection of wildlands. In the future, however, such reserves will come to be seen actuarially, their life times dependent on many biogeographic, social, and poltical factors. Unless a much denser and more secure network of protected areas is established soon, the importance of less appealing alternatives will be greater than conservationists would wish.

This awareness has led some observers to call for a greater emphasis on adjunctive approaches, including inter situ projects—the management of wildlife in nonarable lands outside of traditional reserves (65). Though appropriate in certain places, these lands are not immune to overexploitation, desertification, and to other forms of abuse, as the recent history of Tibet, the Sahel of Africa, and the

American Southwest have shown. The inter situ tactic is an important backup, however, especially in socially and demographically stable nations and regions. The point is that every tactic has its limitations; sole reliance, for instance, on ecological restoration or on cryopreservation technologies would be premature, if not immoral, because these technologies could protect only a tiny fraction of species diversity for the foreseeable future, especially in tropical seas and forests.

Progress in conservation is hampered by the lack of a clearly articulated public policy on biodiversity. The United States and many other countries lack a coherent conservation strategy. In part, this may stem from confusion about tactics, as discussed above. The United States should join the nations that have developed a national conservation or biodiversity strategy. There is also a need for new institutions such as a National Institutes of the Environment (similar to the National Institutes of Health) to provide intellectual leadership and sustainable funding for planning and research in biodiversity. In addition, a high level review of federal agencies is necessary so that either the authority for the protection of biodiversity is vested in a new agency with clear directives, or the organic acts (if any) of the agencies should be restructured, making conservation a prime directive of the U.S. Forest Service, the Bureau of Land Management, and the National Wildlife Reserve System.

Everywhere, nature reserves must be defended and bolstered by social experimentation in "sustainability." But there is too much at risk to gamble on any one social ideology, theory, or approach. All human institutions are transient expedients, and the conservation systems that are fashionable today will certainly undergo many changes in the next century. Opportunism and tolerance must be the watchwords of the science, the politics, and the art of nature protection (66). The issue, therefore, is not the "failure" of conservation; it is whether it can stay the course. During the construction of cathedrals in the Middle Ages, planners and artisans were not dismayed that "success" might require centuries. Like those workers, conservation scientists and practitioners must accommodate their objectives to the social complexity and temporal scale of their enterprise (67).

References and Notes

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Introduction to *Conservation Genetics and Conservation Biology: A Troubled Marriage*

Beginning with the prophetic observations of Otto Frankel in the early 1970s, conservation geneticists recognized that, at or below a certain population size, loss of genetic variation causes a loss in reproductive success called inbreeding depression. Our "Troubled Marriage" paper used mathematical modeling to demonstrate that inbreeding could by itself cause small populations of slowly reproducing species like large mammals to crash. We predicted that even rapid reproducers like rodents would see the growth of small populations slowed by inbreeding depression in both captivity and the wild.

Most zoo curators at the time had little understanding of inbreeding and discounted it, with the result that their tiny captive populations frequently became extinct and had to be replenished from the wild—not a sustainable model for rare or endangered species. Fortunately, in the early 1980s two far-seeing curators, Bill Conway of the Bronx Zoo and George Rabb of the Brookfield Zoo, teamed up with conservation biologists like Katherine Ralls, John Ballou, Christine Schonewald-Cox, and me to spark a revolutionary shift in

attitude. Today, instead of keeping three or four undocumented individuals of each species, the best zoos cooperate by exchanging animals and manage the captive animals as a unit by exchanging them between zoos so that a species is effectively a single, managed genetic population. All reputable zoos keep studbooks with accurate genetic records so that mating between relatives can be avoided.

When Scott Mills and I wrote this paper in 1992, we were concerned about a trend to discount the importance of inbreeding depression. Some ecologists and zoo curators asserted that inbreeding depression was inconsequential compared to both demographic and environmental effects, as when by chance an entire generation contains only males or when populations crash because of disease or war (during World War II the Berlin Zoo was destroyed and only 91 of 3,715 animals survived). Nevertheless, we argued that inbreeding depression is universally relevant. In the subsequent two decades, conservation biologists have recognized that all three of these factors combine to threaten small populations. Conservation plans for small populations now contain strategies for countering inbreeding depression as well as sex imbalances. The best programs also plan for environmental disasters, for example, by maintaining redundant populations in case one is hit by disease, as occurred in 1985 when most of the last wild population of the black-footed ferret in Meeteetse, Wyoming, was wiped out by canine distemper.

Our paper also noted the tension between those conservationists who focused on conserving entire ecosystems but ignored keystone species and those who focused on species like rhinos and eagles that are large and charismatic. We argued that these two approaches are complementary—individual species may not survive if their ecosystems are degraded or lost, but likewise ecosystems will lose integrity if keystone species such as large carnivores, elephants, and beavers disappear.

Conservation Genetics and Conservation Biology: A Troubled Marriage

Michael E. Soulé and L. Scott Mills

from *Conservation of Biodiversity for Sustainable Development*, 1992

A Glance Backward

The chapters in this section constitute an authoritative status report on conservation genetics. Instead of presenting a summary of these summaries, we first tip our hats, as it were, to the people and events that helped shape the present, and second, peer ahead at some looming controversies. Some of these controversies could jeopardize our mission to protect genetic and biological diversity.

Until the middle 1970s, most of the people in charge of conservation ignored genetics, and most of the people in charge of genetics ignored conservation. But beginning around 1970, plant geneticists started to become alarmed about the disappearance of primitive or traditional crop varieties and their replacement by modern, genetically uniform, cultivars. Geneticists suspected then as they do today that the seeds of the green revolution contained the agents of their own ultimate collapse, namely, genetic uniformity. They began to question the wisdom of discarding, in a single human generation, the products of thousands of years of artificial selection for

adaptation to microhabitat diversity, and for resistance to stress and drought, disease, and attacks by pests.

Several publications appeared in the early seventies that called for or contained protocols for the sampling and maintenance of germplasm collections (Bennett 1965; Frankel and Bennett 1970; Marshall and Brown 1975; Frankel and Hawkes 1975; see Frankel and Soulé 1981 for further citations). An international system of gene banks was endorsed by the United Nations Conference on the Human Environment in Stockholm, 1972. The International Board of Plant Genetic Resources (IBPGR) was established within the Food and Agriculture Organization of the United Nations in the same year in order to further the collection, conservation, documentation, and use of germplasm for crop species (Williams 1988). Plant geneticists, we can now see with hindsight, knew that sustainable agroecosystems were impossible without genetic, as well as species diversity. Today, a fairly sophisticated, global system of economic plant germplasm collections is assembled.

In 1970 and 1974, Otto Frankel, the prophet of conservation genetics, published two landmark papers (Frankel 1970, 1974). In the second paper entitled "Genetic conservation: our evolutionary responsibility" he issued a challenge to the field of genetics, a rather unusual one too, in that it was basically ethical. To quote him (1974), ". . . genetics has social responsibilities in two directions: first to collaborate in planning the biological system of conservation so as to establish the highest possible evolutionary potential; second, to help in establishing an evolutionary ethic, as part of our social ethics, which will make it acceptable and indeed inevitable for civilized man to regard the continuing existence of other species as an integral part of his own existence. This demands continuing evolution." Frankel (1974) also foresaw the need for pervasive management of nature, noting that "[wild] species almost everywhere in the world will depend on organized protection for their survival" and such protection is predicated on management that facilitated "continuing evolution."

Frankel (1974) asked the important questions, including what were the conditions for continuing evolution. "The prime parameters," he said, "are the level and distribution of variation, the size of the **minimum viable population** (emphasis ours), and the optimal and minimal sizes of reserves. We need to know the minimum population size which is likely to yield a required level of variation." Harlan (1975) made a similar statement soon thereafter, and *in situ* conservation of traditional crop germplasm has been promoted more recently (e.g. Wilkes 1983; Nabhan 1985; Altieri and Merrick 1988). Soon thereafter, zoologists (Flesness 1977; Denniston 1978; Seal 1978) were to sound the alarm about the impact of genetic drift and bottlenecks on the amount of genetic variation in small, isolated, natural populations, although at that time there was little published data confirming these theoretical expectations.

As evidence for effects of genetic drift, Frankel cited our own work on island lizards (Gorman et al. 1975; Soulé 1980) that demonstrated the "small island effect." Lizard populations on islands smaller than five or ten hectares have lower than normal levels of heterozygosity. Based on these data, Frankel (1974) quotes Soulé (personal communication) as concluding that minimum population sizes assuring long-term survival (thousands of years) should be of the order of 10^4 or more, a number derived from the estimated population size of island lizard populations having levels of genetic variation typical of those of related mainland populations.

Frankel anticipated a controversy known later as the SLOSS debate among biogeographers and ecologists—the relative benefits of **Single Large Or Several Small** conservation units. He noted that "It has been argued that population subdivision maximizes the potential rate of evolution . . . . But it will be rash to conclude that many small reserves are more effective than fewer larger ones." Indeed, the subsequent discovery that persisting species in isolates are distributed as nested subsets (i.e. the species that persist in small patches are virtually always a sub-set of those persisting in larger patches, and those that disappear in small patches are virtually the same set

from patch to patch), argues for larger reserves. This predictability in patterns of extinction has confirmed the advantages of large protected areas for some taxa (Patterson and Atmar 1986; Blake 1991; Bolger et al. 1991).

Frankel did not eschew philosophy either. Elaborating on the need for an ethical stance in genetics, Frankel came close to embracing a version of the intrinsic value argument for conservation. He asks if it is not our responsibility to keep evolutionary options open, so far as we can, for the sake of future humans? He went further in the direction of extending the ethical community to non-humans, hoping that this idea of evolutionary responsibility would deepen into an ethic "if and when men come to regard other species as an essential part of their own existence." This latter view expresses a concept of "self" that includes identifications with non-human species, and is not far from the deep ecology philosophy as enunciated by Arne Naess (1989, this volume).

The first international meeting concerning the application of conservation genetics to wild species occurred at a conference in La Jolla, California in 1978. The results of that conference (Soulé and Wilcox 1980) produced the first specific recommendations about genetical MVPs for animals, including the 50/500 numbers (effective population sizes) for short-term and long-term programs, respectively (Franklin 1980; Soulé 1980; Frankel and Soulé 1981; Hedrick and Miller this volume). An effective size of 50 was thought to provide some protection against short-term loss of fitness due to inbreeding; an effective size of 500 was thought to prevent loss of genetic variation, *per se*. These rules of thumb have fallen into disrepute for several reasons. First, they are based solely on genetical argumentation and data; since their publication in 1980, other fields, including demography and population ecology have started to advance their own recipes for the estimation of MVPs (Shaffer 1981; Soulé 1987). Nowadays, MVPs usually are based on assumptions or objectives about the probability of persistence (say 0.95) and time intervals (say 200 years). Some recent MVPs incorporate popula-

tion, environmental, as well as genetical considerations (e.g. Gilpin 1989; Doak 1989).

Second, these numbers have been misused more often than they have been applied correctly. As pointed out by Harris and Allendorf (1989), many practitioners have ignored the difference between census size and effective size, thus grossly underestimating the actual MVP, especially for long-term conservation purposes.

Third, and related to the first point, it is currently fashionable to denigrate the significance of genetics in the estimation of MVPs, on the grounds that the effects of environmental variability on population persistence (Goodman 1987a; Belovsky 1987) will swamp any impact that inbreeding and loss of genetic fitness might have (Schwartz et al. 1986; Dawson et al. 1987; Lande 1988; see also Pimm et al. 1988, 1989). This conclusion, in our opinion, is premature (see below).

Just as it does in most other cultural phenomena, the pendulum in science swings back and forth. Thus, the current unpopularity of genetics is neither unprecedented nor unexpected. In the past, many conservationists have been extremely reluctant to accept the role of genetics in conservation. The reasons are not difficult to discern, and they had nothing to do with science, *per se*. Genetics is an arcane field, in part because of its difficult jargon, and in part because it is quantitative. It kindles fear in many biologists and laypersons alike, and fear creates hostility. Second, genetics is associated with theories of racial differences, human instincts, and similar deterministic ideas that were anathema to many left-leaning intellectuals during the middle decades of this century. Only recently has the role of genetics in human psychology, physiology, and disease been tolerated once more (e.g. Bouchard et al. 1990).

Another reason for the reluctance of some to accept the role of genetics in conservation is that acceptance would have meant the abandonment of cherished practices. In the zoo world, for example, many curators wished to maximize the number of species in their respective collections. A result was competition for species diversity;

group sizes for many species were commonly in the range of two to six individuals; rarely were there interchanges between zoos. To acknowledge that inbreeding might be a factor in the frequent loss of these small groups would have necessitated the abandonment of many species in favor of larger population sizes for those retained. It took the encouragement of a few leaders (Benirschke et al. 1980; Conway 1986) and the inspired work of Katherine Ralls, Jon Ballou and their colleagues (Ralls and Ballou 1983; Ralls et al. 1988), not to mention the growing governmental red tape and economic costs of replacing lost groups, to convince many zoo curators that inbreeding was a leading cause of group morbidity and extinction.

The role of genetics in nature conservation was consolidated by the publication of two books (Frankel and Soulé 1981; Schonewald-Cox et al. 1983). In the latter volume, Frankel (1983) reiterated that a central concept of conservation genetics is fitness. These days when we ask such questions as (1) why do we census for heterozygosity?, (2) why do we calculate effective population size (N_e)?, (3) why do we do pedigree analysis?, (4) why do we do molecular genetic studies?, the answers are usually framed in terms of (1) either minimizing the loss of genetic variance which is thought to be associated with fitness, (2) minimizing the costs of inbreeding, or (3) avoiding trans-specific crosses between morphologically similar species. Conservation genetics exists for one reason only—to promote the fitness of targeted populations (e.g. Ralls and Ballou 1986). This is our commandment.

Conceptually, though, fitness is not as straightforward as it might seem. The concept of fitness is often dichotomized—always a danger sign in biology. The first category is immediate or short-term fitness, such as the average viability or fecundity of individuals living now. This kind of fitness is easy to define operationally and is relatively easy to measure. The second category is "potential" fitness. It represents the idea that genetic variation in a lineage is required to adapt, through natural selection, to changing conditions. It is based on the premises that (1) genetic variation can be limiting, and (2) any loss of genetic variation can compromise the future capacity of

a population to adapt and survive. Long-term fitness, as represented by genetic variation, is like wealth, as represented by gold coins buried in the garden. It is a hedge against future disasters.

Potential **anything** is problematic, and potential or long-term fitness is no exception. First, it is a different kind of concept altogether from short-term fitness, because, unlike gold, there may not be a straightforward relationship between genetic variation and wealth. Whereas it may be assumed that two pieces of gold will buy twice as many pigs as a single piece, there is no guarantee that a population with 8 % heterozygosity has twice the probability of surviving 1,000 years as one with 4 % heterozygosity. Nevertheless, a proportionality between genetic variation and persistence time (long-term fitness) is assumed; this idea could be expressed as follows:

$$E_t \approx A[V_A]$$

where E_t is the expected time of persistence of a population, A is a species-specific constant representing general "adaptiveness," and V_A is the current level of additive genetic variation. The evidence for such a relationship is remarkably thin, being limited to a few short-term studies (Frankel and Soulé 1981). Nevertheless, much of what we call conservation genetics is based on this premise.

Is Genetics Relevant to Population Persistence?

As already mentioned, genetics has lost its short-lived hegemony in the MVP arena for natural populations. Will the pendulum ever swing back, or is conservation genetics banished to the computers of those managing gene banks, captive groups in zoos, and botanical gardens? This leads us to the subject of persistence, *per se*, and our ability to predict it.

The issue of population persistence or viability is intellectually fascinating, in part because it requires a multidisciplinary, systems approach (Gilpin and Soulé 1986). Consider a population restricted to a patch of habitat; assume there is negligible immigration. Given

that one knew enough about this population's demography, its environment, and the relationships between the two, one could, at least in theory, estimate the mean and variance of its persistence time (Goodman 1987a; Belovsky 1987). In spite of the complexity and elegance of such an analysis, however, the result could be very misleading.

At least two factors would have been left out. One of these is the possibility of a catastrophe (Ewens et al. 1987); we won't elaborate on this subject here. The other factor is the interplay between population dynamics and the loss of fitness due to inbreeding or genetic drift (Soulé 1987). Returning to the population mentioned above, could it persist at a small size (say, $N \leq 50$) long enough to lose about 10 % of its genetic variation? If it could, would this amount of genetic attrition produce detectable and ecologically significant impacts on the fecundity and viability of its members? For example, Frankel and Soulé (1981: p. 68) predicted on the basis of laboratory results with domesticated animals and plants that a 10 % increase in the inbreeding coefficient is often likely to produce a 10 to 25 % lowering of total reproductive performance. It has been suggested that reproductive depression of this magnitude could significantly compromise r, the intrinsic rate of increase, thus compromising a small population's ability to persist in a fluctuating environment (Soulé 1987).

Simulating the Effects of Inbreeding

One of us (LSM) is exploring this question by simulating the impact of inbreeding on population growth. Only a brief overview of preliminary results are presented here. Consider two small, recently isolated populations with three age classes and no density dependence. One has an r near zero, but positive (approximately 0.06), a reasonable rate for many natural mammal populations; the other has an r of approximately 0.75, near the high end observed for mammals in the wild (Pianka 1970; Robinson and Redford 1986). The demographic costs of inbreeding on survivorship and fecundity may be

obtained from the literature (e.g. Ralls et al. 1988). These costs may then be incorporated into a Leslie matrix growth model by weighting survivorship and fecundity by the fitness reduction due to inbreeding. For example, p_x (survivorship during age x) values are replaced by $p_x(F,t)$, where F is the average inbreeding coefficient for individuals born during time period t, and m_x (fecundity at year x) values are replaced by $m_x(F,t)$, age-specific reductions in these parameters due to inbreeding. In essence then, age-specific demographic values are reduced according to empirically measured inbreeding costs at each age. Based on the modified values of survivorship and fecundity, the constant Leslie matrix L is replaced by a variable matrix $L(F,t)$, which can be projected to estimate population sizes in the future.

The results of two such population projections are shown in Figures 1 and 2. Both are initiated with a population of 30; four pro-
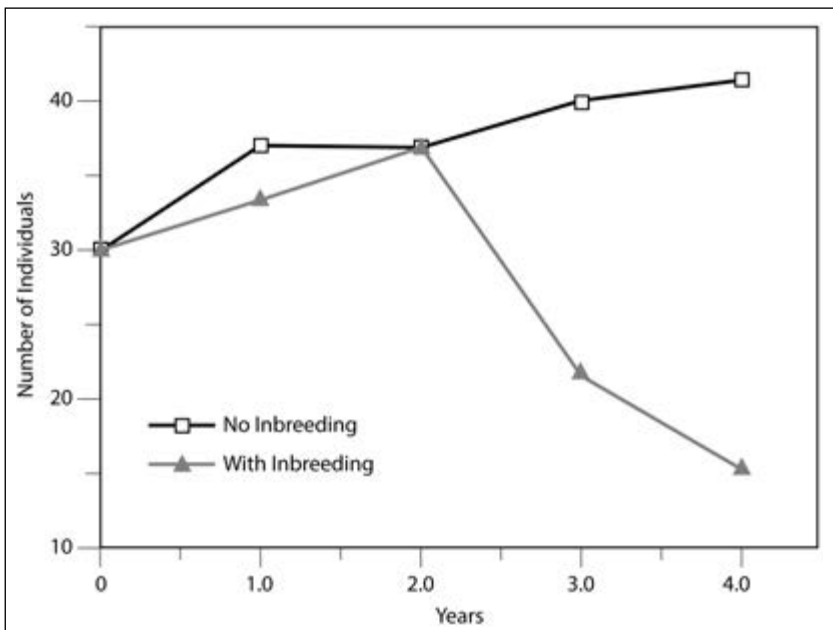
FIGURE 1. The effect of imposing an inbreeding depression cost on a population with a low but positive intrinsic growth rate (r_m = 0.06) typical of mammalian species in nature. The model is a deterministic Leslie Matrix based on a population with two age classes. See text.
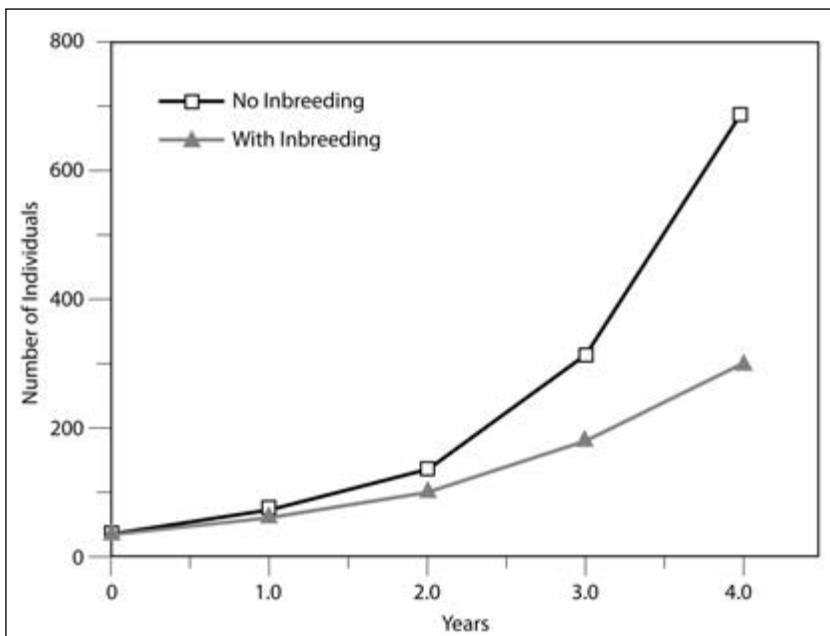
FIGURE 2. The effect of imposing an inbreeding depression cost on a population with a very high intrinsic growth rate (r_m = 0.75J. The model is a deterministic Leslie Matrix based on a population with two age classes. See text.

jection intervals (years) are shown. The population with r = 0.06 (Figure 1) grows to over 40 in four years with no inbreeding effects. With inbreeding, however, the population declines to 15. For the population with a very high intrinsic rate of increase, the size reached in four years is large, even with inbreeding costs, but it is less than half that of the same population without inbreeding costs (Figure 2).

As mentioned, it is currently fashionable to dismiss the role of inbreeding depression when projecting the viability of small populations. Some experts (Schwartz et al. 1986; Dawson et al. 1987; Lande 1988; see also Pimm et al. 1988, 1989) argue that when a population is so small that its fitness may be compromised by inbreeding, that it is in much greater danger of crashing from demographic and environmental stochasticity. And such a population,

they argue, is unlikely to persist long enough to experience enough inbreeding to do it significant damage. We believe, to the contrary, that theoretical and empirical studies such as the one just summarized will demonstrate that inbreeding can affect population size, and therefore persistence, in the face of random demographic events and environmental fluctuations.

Current simulation studies in collaboration with Peter Smouse at Rutgers University are incorporating age-specific costs of inbreeding as variables in a stochastic population growth model (L. S. Mills and P. Smouse, in preparation). In addition, LSM is testing the implications of the model using natural populations of the California red-backed vole (*Clethrionomys californicus*) in forest remnants.

MVP Hyperinflation

The second problem we would like to mention derives from the success of conservation biology as reflected in the startling changes in the last 25 years. Recall that in the sixties, MVPs (demographic) were in the range of 25 to 50 (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972). A population larger than this is not much threatened by demographic stoehasticity (Leigh 1981; Goodman 1987a). The next stage in MVP studies, the genetic era, could be characterized by the 50/500 criteria. The 500 number refers to a genetically effective size of 500, which often translates to a census size of 2,000 to 5,000 or more (Nei and Graur 1984; Harris and Allendorf 1989; Michael Smith, personal communication; R. Frankham, personal communication). Then came the era of MVP hyperinflation, with values in the range of 10^4 to 10^6 based on analyses of persistence based, in turn, on the effects of random environmental fluctuations on the dynamics for single populations (Goodman 1987a; Belovsky 1987). (Note that the numerical criteria used for germplasm collections is not covered in this discussion.) These large numbers, however, are problematic for both pragmatic and scientific reasons. The pragmatic problem is that administrators and managers are confronted with unreachable population targets; to follow expert advice

in many cases would not be economically or politically expedient. Consider, for example, the home range of a mountain lion (*Felis concolor*) in North America may be 100 km² or more (Hempker et al. 1984; Hopkins et al. 1986). If the MVP is 10^5, a viable population in the USA would require more than all the land in the contiguous 48 states.

In the United States, let alone in nations where wildlife is competing for space with many landless or poor, only a very single-minded conservationist would stand up in public to argue that an area of these dimensions be given back to nature. But neither should we disguise the truth as we see it. How do we escape from this dilemma? The only answer, we believe, is to accompany the arguments for such huge numbers with practical management alternatives. Among these would be (1) the establishment or enhancement of multiple populations, (2) a combination of *in situ* and *ex situ* approaches, including the storage of germplasm (e.g. seed banks, tissue culture, cryopreservation of sperm, embryos, and larvae), and even, at some risk to the species, (3) accepting proposals that buy time instead of achieving an ideal solution in one step.

Finally, an MVP in the range of 10^5 to 10^6 may not be defensible on purely biological grounds (Soulé 1987; Goodman 1987b) for the simple reason that a single, very large population is neither the prudent strategy nor the natural solution. The total number needed may be much less if the individuals are living in two or more places, the environments of which are not perfectly correlated. In nature, many species are distributed as metapopulations—a patchwork of interacting populations over a wide and heterogeneous geographic region; at any given time some of the patches are extinct and some are newly colonized. Partly as a consequence of the environmental differences that these manifold, dispersed population units encounter, the persistence of a metapopulation of a given N or N_e is expected to be superior to that of a single population of the same numerical order (Soulé 1987; Goodman 1987b; Gilpin and Hanski 1991). It seems probable, therefore, that the incorporation of both spatial and temporal heterogeneity along with metapopulation dynamics into MVP

analysis will reduce the number of individuals required to ensure long-term viability. Metapopulation dynamics could either increase or decrease the rate of loss of genetic variation, however, depending on the extinction and recolonization rates (Gilpin 1987), as well as the population growth rates.

The "Failure" of Species Conservation

Another potential cloud on the horizon is the growing reaction against species-based conservation. More and more these days, we hear voices raised against the emphasis on species rather than on habitat, ecosystem, or landscape approaches (e.g. Harris 1984; Scott et al. 1987; Simberloff 1987; Kohm 1991). Because conservation genetics is inherently a species or population-based discipline, conservation genetics is guilty by association with so-called species chauvinists.

The anti-species movement could produce a backlash against endangered species and the scientists and managers who work to protect them. The tendency among some conservation biologists to dichotomize nature into species and ecosystems almost guarantees that many innocent species and dedicated scientists and professionals will be characterized as "bad guys." The new heroes are the plant geographers, the ecosystem ecologists, restoration ecologists, and landscape ecologists who favor a more holistic, comprehensive and proactive conservation strategy.

The Growing Backlog of Endangered Species

It is easy to see why many people are becoming frustrated, indeed infuriated with species-based conservation. Consider the statistics on endangered species in the US. There are about 570 officially listed threatened and endangered species, but only about half of these have recovery plans. Recovery plans establish the criteria for recovery and recommend the management interventions that should be implemented. But these plans have no teeth. No funds accompany the

approval of recovery plans, and rarely do the plans identify critical habitat, let alone protect it. In fact, most plans are nothing more than a promise cloaked in a prayer. Granted, the provisions of the Endangered Species Act prohibit the so-called "taking" of individuals or the destruction of its habitat, but a determined developer can often find a way to circumvent the recommendations in a recovery plan.

These problems of implementation and enforcement, however, are not the only reasons for the growing hostility to species-based approaches. Even if recovery plans were efficient and well funded, this strategy would still be unpopular. One excuse for attacking the species approach is that many of the species that receive special attention are large and attractive, ignoring many species-rich groups such as plants and insects (Wilson 1988). Another reason for the growing concern is that species are listed more slowly than they are nominated, and the backlog increases yearly. In the US, there are now more than 4,000 candidate species. Recovery and delisting of species are rare, and recovery plans are produced and implemented at a much slower rate than species are nominated and listed. Many people are now saying that the system has broken down (Scott et al. 1991).

Endangered Species Are Symptoms, Not Causes

There are other problems. A question asked by growing numbers of conservationists throughout the world is "what is the point of adding a name to a list of moribund species if little or nothing is being done to counteract the causes that produce so many species crises?" These causes are all too familiar: (1) the loss and disturbance of habitat, (2) the fragmentation of habitat, (3) air and water pollution, (4) the spread of exotic species and diseases, (5) climate change, and (6) overexploitation of populations.

Simply put, the **species approach to conservation is a crisis management approach** (Salwasser 1991). Even those activists who are successful in obtaining funding for their favorite endangered

species may perceive the futility of trying to rescue a particular taxon where nothing is being done to prevent many more species from becoming endangered. Of course, endangered species are very popular, and organizations can raise a lot of money for them, but the supporters of less popular species or of whole systems are frustrated when millions of dollars are spent on a few flagship species, leaving little or nothing for less charismatic creatures, nor preventing further environmental deterioration.

In Defense of Pluralism

We are concerned, though, that the conservation crisis could evolve into a very destructive conflict. On the one side are the species enthusiasts who generally defend large, charismatic vertebrates and keystone species; on the other side are the ecosystem enthusiasts who favor a habitat approach based on (1) the identification, classification, and protection of representative samples of all biotic communities (e.g. Jenkins 1988; Huntley 1988; Crumpacker et al. 1989) and (2) the management of these protected areas at the appropriate physical and temporal scales (Clark and Harvey 1988). In theory, there should be no conflict. Just as assessment of impacts at the ecosystem level must depend on the monitoring of individual species (Van Horn 1983), so the conservation of species requires attention to ecosystem processes and disturbance dynamics.

In practice, though, supporters of a species approach are not convinced that a habitat approach can be implemented and maintained for many decades or centuries, particularly in the many parts of the tropics; the list of protected areas that are being overrun, overexploited or destroyed by mining, agriculture, forestry and water projects is growing at an alarming rate, according to the Threatened Parks Register of the International Union for Conservation of Nature and Natural Resources' Commission on National Parks and Protected Areas. Thus, while supporters of systems approaches see money being "wasted" on a few charismatic vertebrates, the supporters of endangered species and captive propagation point to the

increasing rate of park failure and the need for a backup system that is more secure, even if less natural.

A naive expression of the ecosystem approach is one that holds the extremist assumption that design and management of protected areas can ignore species altogether, focusing instead on ecosystem processes and patch dynamics. Clearly, though, ecosystem management must attend to the viability of certain, critical species, even if they are not yet endangered. Any protected area will undergo biotic collapse unless designers and managers understand the natural history and viability of certain species. A corollary of this premise is that the failure to manage or maintain these species will lead to the collapse of the system, or at least to a significant reduction in species richness (Frankel and Soulé 1981; Botkin 1990).

Table 1 presents three sets of questions that may clarify this point. The first question is the amount of area needed to prevent the loss of biological diversity in the system. Strictly speaking, ecosystem approaches do not explicitly identify this question, nor can they approximate a general answer or identify the criteria that should be considered. A biologically defensible solution must be based in part on the minimum genetical and spatial requirements of certain, strongly interacting, species (L. S. Mills and M. E. Soulé, in preparation). For example, if trees of the genus *Ficus*, invertebrates such as starfish or termites, fishes such as groupers, or vertebrates such as beavers, tapirs, alligators or elephants are important in the long-term maintenance of habitat diversity in the system, special attention must be devoted to the needs and viability of their populations within the protected area or the system of protected areas. The point is that in most places, **system viability cannot be disassociated from species viability.**

A related point is that the fragmentation of wildlands will usually threaten elements of biodiversity that depend on long-range dispersal movements, migratory movements, or foraging movements. Some of these species may be important mutualists (e.g. pollinators, mycorrhizal fungi). For example, if bats are important pollinators of many tree species, it will be necessary to insure that their roost-

TABLE 1. Some questions for the designers and managers of protected areas that demonstrate the roles of species and process management in an integrated, "ecological" approach to conservation.

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1. How much area is needed to prevent the loss of biological diversity in the system?
    – What constitutes a substantial loss of biodiversity for the system?
    – What criteria can be used to predict whether such losses will occur?
      - Does the system contain viable populations of all the strongly interacting ("keystone") species? How large an area is needed for these viable populations?
      - Is the system sufficient in size and topographic heterogeneity to generate an appropriate level of disturbance to maintain the necessary diversity of habitats under foreseeable changes in climate and other conditions?

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2. What sensitive species or processes are threatened by loss of connectivity?
    – Would the loss of any species (e.g. mutualist or migratory species) lead to extinction cascades and compromise biodiversity?
      - What interventions or new design features would mitigate such threats?

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3. What management interventions will be needed to prevent the spread of deleterious exotic species?
    – What plants, animals, pathogens are contributing to habitat changes, to decreases in the diversity of native species and assemblages, and to deleterious edge effects?
      - How will these species and changes compromise the viability of critical species or processes?
      - How can these deleterious species and changes be managed/controlled?

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ing and breeding sites are protected within the system of protected areas, and that human activities around and in the reserves do not compromise their long-term viability. If deep forest birds or sphingid moths must migrate between wet-season and dry-season sites (Karr 1982; Janzen 1986), conservation corridors may have to be established.

The third question in Table 1 points to another category of species—those that are harmful to system stability and species richness. Many of these deleterious species will be exotics, often but not always originating in other continents (e.g. Soulé 1990). Exotic or

expanding species of plants, predators, herbivores, or nest parasites (such as cowbirds in the US) often create the conditions for wildfire, for the invasion of weeds, for the mortality of critical pollinators or seed dispersers, for the spread of disease, and the inviability of sensitive species. Management protocols tailored to specific species are a necessity for most such situations.

In conclusion, the design and management of conservation areas will rarely succeed without attending to the needs and control of critical or problem species. The species vs. ecosystem dichotomy, like almost every other dichotomy in biology, is fatally flawed conceptually and operationally. A pure ecosystem approach is just as contradictory as a pure species approach. As we write, the popularity of genetical and species approaches to conservation is waning. So-called holistic approaches are in the ascendency. To the extent that these trends bring about a biologically realistic synthesis, they are welcomed. A purely genetic approach to population viability is absurd (Frankel and Soulé 1981). A conservation strategy blind to anything except species on the brink of annihilation is absurd. The danger is that the pendulum could swing too far in the other direction. The deep-seated antagonism against genetics, and the hostility that sometimes exists between ecosystem ecologists and species-oriented biologists could undermine the emergence of new, synthetic approaches and technologies.

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Introduction to *The Social and Public Health Implications of Global Warming and the Onslaught of Alien Species*

This paper was published in the same year as the landmark proceedings of the first conference on Global Warming and Biological Diversity organized by Robert Peters at World Wildlife Fund. That conference brought together biologists who were challenged to start thinking about how natural communities would be affected by warming. I contributed a paper.

Global warming exacerbates the effects of habitat destruction and other threats to wildlands enumerated in paper 7. The paleontological record shows that warming causes habitats to shift toward the poles and to higher elevations. This is a grave issue for rare species when they are restricted to isolated reserves and cannot track their shifting climate envelope because cities, farms, and interstates block their paths. The Spine of the Continent project is meant to mitigate such blockages and ensure that continental-scale connectivity persists.

But the main thrust of this paper was to warn that people in a disturbed and warming world will experience more disease. As discussed in paper 6, civilization has dramatically increased the rate at

which species are transported to new locations. Recent new immigrants to North America from the tropics include human West Nile virus and HIV.

New infectious diseases are emerging, often because more people are settling in or near natural ecosystems where wild species are reservoirs or vectors of diseases like HIV, Lyme disease, yellow fever, dengue, simian immunodeficiency virus, Ebola, Nipah virus, leishmaniasis, and malaria. The World Health Organization estimates 207 million malaria cases with 627,000 fatalities worldwide in 2012, down from a peak in 2004, but still higher than 30 years ago.

As people disturb natural ecosystems, they often create conditions that facilitate disease transmission. For example, in the eastern United States people created a patchwork of forest and clearings that increased populations of deer and white-footed deer mice, alternate hosts of Lyme disease.

What about global warming? A 2006 *Nature* review by Wolfe, Dunavan, and Diamond concluded that 80 percent of human diseases in the tropics are transmitted by insects (versus 13 percent in the temperate regions). The distributions of tropical insects are typically limited by temperature, and warming will facilitate spread to higher latitudes and elevations. For example, malaria and dengue are projected to spread further into temperate regions. Temperate diseases may also change their ranges: A 2005 study by Brownstein et al. in *Ecohealth* projected that by 2080 global warming would cause an overall 213 percent increase in suitable habitat for the ticks that spread Lyme disease.

Disturbingly, the warming that will drive these disease expansions may be greater than current climate models predict. In 2012 a United Nations Environment Programme report identified positive feedback loops, not included in current climate models, that would significantly speed up warming. The most serious is probably melting of Arctic permafrost, which liberates carbon dioxide and methane, potent greenhouse gases. Melting will liberate more gases, which will speed up warming, which will liberate even more gas.

The Social and Public Health Implications of Global Warming and the Onslaught of Alien Species*

M. E. Soulé, PhD

from *Journal of Wilderness Medicine*, 1992

Humans are engaged in an uncontrolled experiment in planetary heating. Each decade, the concentration of CO_2, methane and other greenhouse gases in the atmosphere is increasing by about 4%. All signs point toward unprecedented rates of warming and climate change. Many plant and animal species living in natural ecosystems will perish because they will be unable to keep up with shifting climatic zones. Warming exacerbates another biomedical problem—the influx of alien animals, plants and pathogens. These introduced species, many from the tropics, will not only increase the variety and incidence of tropical diseases, but will also affect the quality of the wilderness experience and hence, the popularity of outdoor recreation. Some personal actions and political prophylaxis are recommended.

Global Warming

The planet appears to be heating up, and for the first time in evolutionary history the source of the heat is a single species—man [1]. Human activities, such as the burning of fossil fuels and forests,

cultivation of methane-producing rice paddies and husbandry of methane-belching livestock, are injecting more greenhouse gases into the atmosphere than can be removed by photosynthesis and other natural phenomena. These byproducts of human agriculture and commerce are analogous to a thickening atmospheric blanket which allows sunlight in, but traps the heat that is radiated back from the planet's surface.

Given the youth of the atmospheric sciences, it is almost impossible to prove that the recent warming trend is linked to the greenhouse effect, but most climate modelers are convinced by the available evidence. They predict an increase in average surface temperature of 1–3° C by the year 2030, although predictions span a much broader range [2–4]. These estimates are based on the current rates of production of greenhouse gases such as CO_2, methane (CH_4), nitrous oxide (N_2O), and chlorofluorocarbons (CFCs). Studies of gas bubbles trapped in glacial and polar ice show large increases in CO_2 following the inventions of agriculture and industrial technologies, including the burning of fossil fuels. Pre-modern levels were about 275 ppmv, compared with 1987 levels of 375 ppmv [5].

Global Warming and Disease

Carbon dioxide is now increasing at about 1.5 ppmv per year, or about 4% per decade [5]. Reversal of the warming trend would require an environmental negative feedback mechanism dependent on complex oceanic/atmospheric processes. There is no evidence for such a mechanism. Failing a last minute rescue, the signs point toward climatic change on a scale that humans haven't witnessed since the end of the last ice age, about 10000 years ago.

The planet will not warm uniformly; temperatures will increase least in the tropics and most in the arctic. In addition, it is expected that warming will continue for many decades, in part due to the thermal inertia of the ocean, and in part because of the continuing releases of greenhouse gases. One should not ignore the uncertainty

in these predictions; there are still many questions, especially about positive and negative feedbacks. Nevertheless, public policy ought to be based on the best information and judgment available. At this time, the consensus is that we can expect rapid warming.

Precipitation patterns are expected to change as well, but resolution in the models is too coarse and confidence limits too broad to justify local predictions. Globally, however, mean precipitation may increase by 3–11%; the tropics will probably be wetter, but all we can say about the mid-latitudes is that the distribution of rainfall and snowfall will be different. Tropical storms are likely to increase in intensity, perhaps by 30–60%, and shift poleward by 200–400 km. Sea levels will also rise from about 0.25 to 1.0 m in the next century [3].

The ripple effects of global changes of this magnitude would cause major changes in the distributions of organisms. As climatic regimes shift at historically unprecedented rates, some species will not be able to track them, and will be extinguished. Other species, including undesirable tropical disease vectors, will become established in places that were previously too cold for them. Not only will these alien species add to the load of insect- and tick-borne diseases, but they may also constitute new challenges for the hiker, rafter, and climber.

Impacts of Global Warming

The Distributions of Species

Historical shifts in average temperature have been very slow, about 1° C per 2–3000 years [6]. This rate is about 100 times less than the rate of greenhouse warming predicted for the current anthropogenic episode. How did biological communities respond to more sedate heating events in the past? From the work of palynologists and vertebrate paleontologists, we know that in the past species have shifted their geographic ranges hundreds or thousands of kilometers [7–9]. But there are limits to how fast organisms, especially sedentary ones,

can migrate. Those unable to move will have to adapt genetically to heating and drying climates, or perish. The vast majority of plant and animal species are adapted to quite narrow ranges of climate. Except for microorganisms and some invertebrates (such as insects) with short generation time and large population sizes, evolutionary adjustment to these rapid changes will be difficult or impossible.

Consider the case of trees. The ranges of temperature and precipitation in which trees and other plants reproduce effectively (in contrast to just surviving) are usually quite narrow. Even if climate change does not kill plants outright, they will often be unable to produce viable seedlings. According to Roberts, forest fronts can move as much as 2 km per year [10].

How fast will they need to move in the near future? An increase of 1° C is equivalent to a latitudinal shift poleward of 150 km or an elevational climb of 250 m [11]. A 1°C increase over 20 years in North America would require a northward shift of about 7.5 km per year, or about one meter per hour. During a week-long conference in Utah, therefore, a tree in Salt Lake City would have to move about 150 m closer to the arctic to maintain its biogeographic position *vis-a-vis* climate; a tree in Snowbird, Utah, would need to climb 5 m up the mountain. In reality, vegetation often lags behind climate by hundreds of years, even when the rate of climate change is one-hundredth of that anticipated during the next century [7,12]. Within the next few decades, we should begin to see evidence of forest dieoffs from heat and dessication effects at the lower elevational limits of the ranges of many tree species.

The implications for wildlife communities are grave [13–15]. Not only is the climate shifting out from under many organisms, but even if they could track these rapid changes, the non-flying organisms are blocked by man-made barriers such as highways, reservoirs, farms, cities and other landscape 'improvements.' Nature reserves were set aside to protect unique and threatened species and phenomena, but massive climate change was the last thing in the minds of the designers of these parks. In light of the impending warming,

such reserves could become hospices for moribund species, instead of hotels for healthy ones. The exceptions will include those reserves that are situated in mountainous regions; mountains provide organisms with a variety of climatic regimes that are accessible over relatively short distances.

Human Transport of Species

I don't wish to over-emphasize the importance of warming. It is only one of many current factors causing the erosion of biological diversity. Other factors include (1) the loss and fragmentation of habitats, particularly forests, (2) pollution, including toxic compounds in rivers and lakes, acid precipitation, and ozone-thinning CFCs causing higher fluxes of ultraviolet radiation, (3) poaching of rare and endangered species, and (4) the introduction of non-native species. This section emphasizes the latter problem for two reasons. First, an invasion of vectors, parasites, and pathogens carried by tourists, refugees, and commerce is of inherent interest to physicians. Second, an influx of exotic species interacts with and is exacerbated by warming. In other words, greenhouse warming and the transport of species act synergistically, not only on nature, but also on human health and welfare.

Even without warming, we would be witnessing the biggest biological diaspora in the history of life. This diaspora is mostly passive (but see below), occurring in suitcases and backpacks. People are moving plants and animals around the world at an unprecedented rate. In their travels, people and their commodities are accompanied by domesticated plants and animals, weed seeds, commensal vermin (e.g., fleas, cockroaches, rats), and pets, (fish, reptiles, birds, etc.), not to mention the pathogens and parasites harbored by all of these organisms. The result, whether conscious or unconscious, is a universal flood of non-native species, (the terms 'introduced,' 'exotic,' and 'alien' are used almost interchangeably by biologists for non-natives.) For example, in Kruger National Park in the northern

Transvaal, the number of alien plant species listed in 1937 was six. A detailed survey in the fifties recorded 43; today, the number is over 160 [16].

The Hawaiian Islands offer another example. They have 4600 species of exotic plants; this is three times the number of indigenous species [17]. It is the rare tourist that suspects that the native Hawaiian plants and animals have been extirpated from the lowlands, and that virtually all the plants and birds that the tourist sees (except in the highlands of some islands) were introduced. Incidentally, one of the reasons that there are almost no native birds below 1500 m is the occurrence of introduced pathogens, avian malaria and avian pox [18]. The vectors of these diseases are introduced mosquitoes; the reservoirs of the plasmodium are mostly introduced birds [19].

While most introduced species never adapt well to local conditions, a minority are successful, often overwhelming the native flora and fauna and leading to many kinds of unpredictable, deleterious consequences. Prominent among these invasive exotics are weedy annual grasses. In North America, Hawaii, Australia and elsewhere, these grasses are outcompeting native bunch grasses. Because the exotic grasses reproduce faster, burn hotter, and conduct fire better than the native species, the aliens are causing vast changes in plant communities. Fires caused by humans and natural events sweep through savannas and woodlands, extirpating fire-sensitive plants and animals. Among the hundreds of other examples of invasive exotics are paperbark trees (*Melaleuca* spp) in the Everglades, pampas grass in coastal habitats, ice plant on sand dunes in coastal Calfornia, Nile perch in Lake Victoria, and starlings in North America. Invaders, by the way, are never endangered species.

The intercontinental traffic of exotic organisms, including their associated pathogens, will grow with the increasing mobility of people and commodities. At the same time, the distributions of many human-associated species will continue to expand within their native continents, as we are seeing already in North America with

coyotes, red foxes, opossums, gulls (Laridae), giardia (*Giardia lamblia*), prickly pear (*Opuntia* spp) and cattail (*Typha* spp).

Most of these biological invasions will be random, unplanned events. Among the exceptions are conscious introductions of biological control agents. Entomologists sometimes introduce ichneumonid and other parasitoid wasps for control of native or exotic insect pests—a kind of agricultural homeopathy. Public health officials also introduce control agents, including *Gambusia* (mosquito fish), to control disease vectors.

Another group of species that are actively introduced is the large and rare vertebrates, particularly tropical and subtropical forms. Many such species will be unable to persist in their homelands, especially Africa, because of human usurpation of their habitats. Such sensitive species may find their only semi-wild salvation in places like the American Southwest and Great Basin. In a decade or two, naturalists in Texas or Utah may record mountain lions feeding on introduced endangered species, such as oryx and adax.

Public Health and Epidemiological Implications of Biological Invasions

What are some of the medical, particularly epidemiological, implications of species invasions, and how are these affected by global warming? This question was reviewed recently by Dobson and Carper [20]. Here, I have used a few of their examples and embellished where appropriate.

Anyone who thumbs through a parasitology text is struck by the diversity of parasites in the warm, tropical parts of the world. The photographs of diseased humans in such books testify to the suffering caused by these agents. Implicit, but usually unstated, are the social and economic burdens imposed by these parasites and pathogens upon tropical societies. Could this happen further north? It is quite apparent that climate is the major barrier to the invasion of the northern regions by these agents of misery. If the climate becomes

more favorable for the vectors of these diseases, we may expect colonization of new regions and new hosts, including ourselves.

Domesticated animals provide some useful examples. Interactions between temperature and humidity are often important factors in limiting the distribution of pathogens that infect livestock. These interactions can be expressed graphically by plotting the ranges of temperatures and precipitation over which a pathogen or parasite is (1) able to persist without becoming epidemic and (2) able to undergo epidemic outbreaks. Such graphs are called 'bioclimatographs.'

Figure 1 is a bioclimatograph for a nematode parasite, *Haemonchus contortus* (the barber's pole worm), of sheep at two localities in Australia [21]. The bioclimatograph is constructed by plotting the
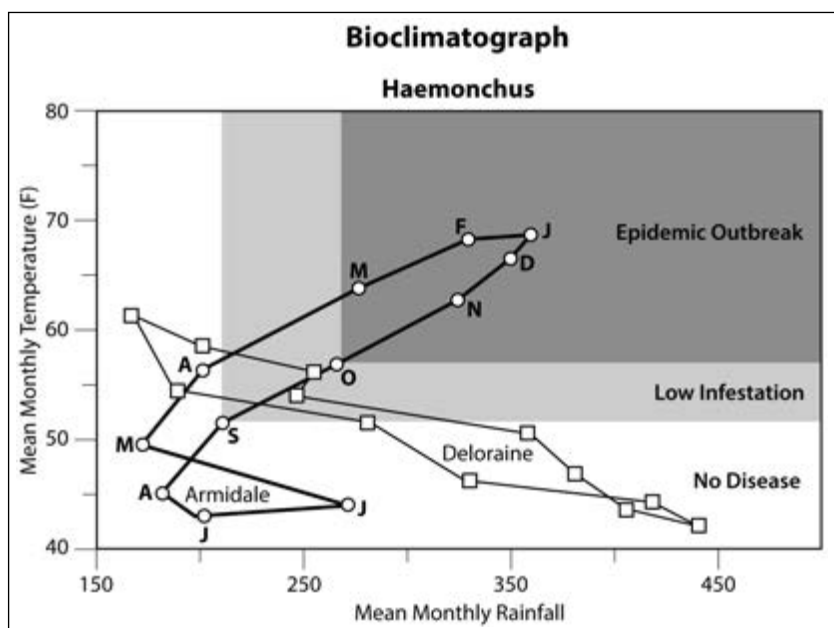
FIGURE 1. Bioclimatograph for *Haemonchus contortus* for two regions in Australia (after Gordon 1948 and Dobson & Carper in press). See text. The letters J, F, M, etc. indicate the mean monthly temperature and rainfall for January, February, March, etc. in Armidale in Northern New South Wales. At the other locality, Deloraine (Tasmania), the necessary combination of simultaneous high temperature and rainfall rarely occur, and outbreaks of *H. contortus* are rare.

mean monthly temperature and rainfall for each locality. *H. contortus* can just persist at 51° F (11° C) and 210 pts rainfall. Epidemic outbreaks are probable above 57° F (14° C) and 260 pts. of rainfall. In other words, a small increase in temperature and rainfall can precipitate a change from a persistent, low level disease to an epidemic. Threshold phenomena like this are not uncommon in host-parasite and environment-parasite interactions.

Figure 2 provides another example of a threshold, or non-linear ecological interaction, with possible epidemiological implications. The mosquito *Aedes aegypti*, a vector of malaria, cannot initiate egg development until it has a blood meal. At 27° C, egg development in the ovary of a recently fed female is relatively slow, requiring about 48 h or more. By then it is too late to deposit her eggs, and oviposition cannot occur until the following evening. At 29° C or above, egg development is faster, and oviposition occurs during the second activity period following a meal. As pointed out by Gillett [22] and Dobson and Carper [20], this difference in egg laying interval can be critical ecologically. *Aedes* populations will be larger and much more resilient at slightly higher temperatures. The point is that long term increases in temperature are likely to cause the expansion of geographic ranges and higher rates of population growth for many tropical and sub-tropical arthropod vectors.

Another factor contributing to the spread of pathogens and parasites is the population density of the hosts. Most parasitic diseases become epidemic when the density of hosts reaches a certain threshold [23–25]. Humans in many parts of the planet are at record high densities [26].

Drug or vaccine resistance is another concern [20]. Troubling levels of resistance are now developing to many antihelminthic and anti-malarial drugs. It is not at all certain that molecular approaches such as recombinant DNA will be any more successful than are traditional ones. We can anticipate some of the same problems with these modern approaches that medical science has experienced with antibiotics and that agriculture has discovered with pesticides. Darwinian natural selection can mount effective counterattacks against
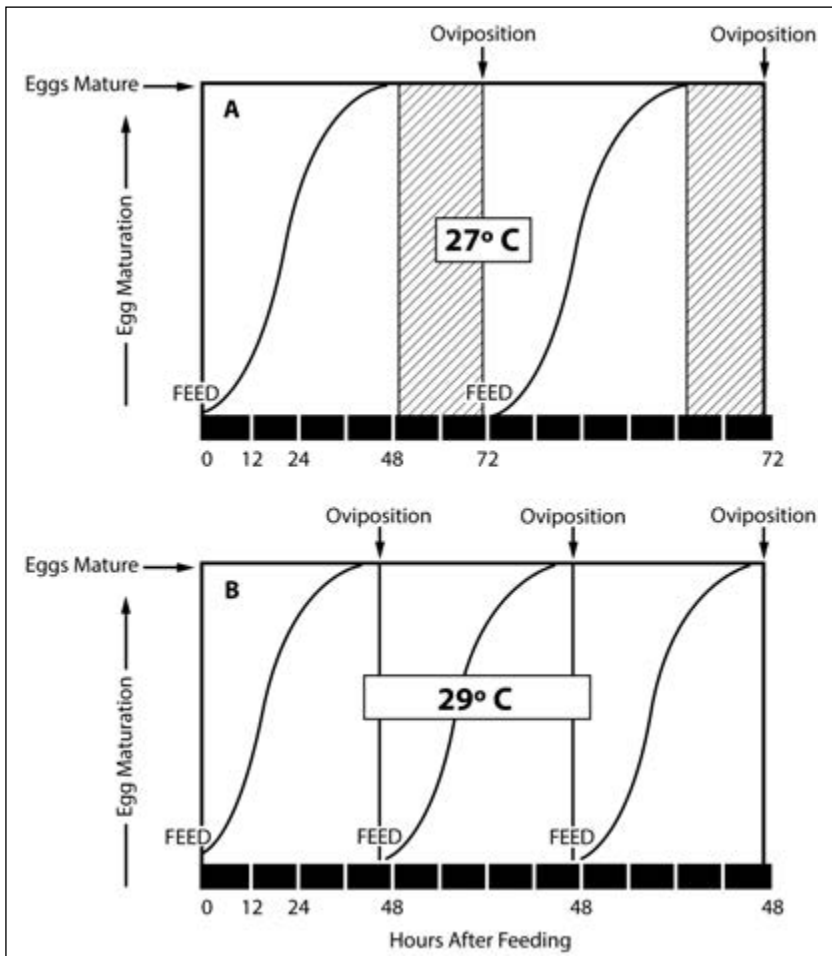
FIGURE 2. Egg (oocyte) development and oviposition intervals for the mosquito *Aedes aegypti*. A. At 27°C eggs are not fully developed in time (before 48 h) to be oviposited by the second activity period, so oviposition is delayed (cross-hatching) until the subsequent activity period, about 70 h after the blood meal. B. At 29°C eggs are fully developed at 48 h, just in time for oviposition during the second activity period after a blood meal (after Gillett 1975).

almost any technological blow that humans may deliver to their biological enemies.

The public health and economic challenges implied by biological invasions are formidable [27]. For example, mosquitoes, such as *Aedes albopictus* and *A. aegypti*, will spread as the climate warms. These mosquitoes can vector dengue fever, yellow fever, equine encephalitis, filariasis, and the viruses that cause hemorrhagic fevers.

The interaction of climate warming, rapidly increasing flows of humans from the tropics, and biological invasions may also lead to higher risks of hookworm (*Anclyostoma* and *Necator*) infection, an increase in distribution and number of species of chiggers, including some tropical ones such as *Trombicula batatus*, and the introduction of some additional tick- and mite-borne diseases. Malaria, carried by *Anopheles*, is also likely to become a problem again.

Other diptera also have the potential to inflict new dimensions of hardship. Tropical biting midges of the genus *Culicoides* are already on the southern US doorstep. Sandflies of the genus *Phlebotomus*, which serve as vectors of sandfly fever, kala-azar, other forms of leishmaniasis, and serious diseases such as bartonellosis, might invade the southern US from southern Europe or Mexico as tropical conditions push northward.

An example of what could happen is the case of the parasite *Borrelia burgdorferi*, a spirochaete that in recent years has become epidemic in the tick *Ixodes dammini* and its relatives, which in turn are external parasites of deer and rodents, such as deer mice. When the infected tick bites humans, the result is Lyme disease. According to Paul Etkind of the Massachusetts Department of Public Health, 'Lyme disease is second only to AIDS in public interest and concern.' Could HIV (from tropical Africa) and Lyme disease be the thin edge of the wedge? Increased mobility of humans, their pets, and smuggled wildlife, in combination with climate change, may bring about a costly epidemiological onslaught. Another possible effect of global warming is that dogs, cats, and pet birds may fall into disrepute because they or their external parasites might be found to be intermediate hosts of increasing numbers of human parasites and pathogens.

The international traffic of species occurs in all directions. In Africa, an infestation of the Western Hemisphere screw worm *Callitroga hominivorax*, a serious pest of cattle and other mammals, was recently discovered in Libya. If this infestation were to cross the Sahara, the consequences for wildlife in sub-Saharan Africa could be serious. Massive releases of sterile males appear to have controlled this outbreak.

Recreational Implications

What are the implications of these real and potential problems for the seeker of physical, aesthetic and spiritual renewal in the wilderness? The enjoyment of mountain, forest, and gorge will diminish in stepwise fashion as pests, vectors, and diseases are added. One of the greatest pleasures of being outside has already been foreclosed in most of North America. This is the simple act of drinking from a mountain stream. The trans-species spread of *Giardia lamblia* from humans to wild hosts such as beaver and elk imposes the cumbersome filter pumps or iodine pills on hikers, rafters and climbers. Children born today will never know the joy of spontaneously drinking from mountain streams.

Soon, other kinds of armament may be required before venturing out of doors. Back-country enthusiasts will be less keen to be in the wilderness when they can't drink the water because of parasites, can't risk exposure to the sun because of increased fluxes of ultraviolet radiation, and can't wear shorts for fear of disease-bearing ticks and diptera, not to mention fire ants and killer bees. At least it will be quieter in the backcountry.

Public Policy Conflicts

How will government agencies react to the onslaught of noxious species and disease vectors? If recent history is a guide, there will be calls for the widespread application of herbicides, insecticides and rodenticides, as we have witnessed recently in California in an attempt to control the Mediterranean fruit fly. Whether such shotgun

approaches can be avoided depends on the existence of integrated management programs, which in turn will depend on continuing research. In the meantime, anxious public health officials and farmers will demand the chemical eradication of pests. They will be opposed by outraged citizens protesting the use of pesticides.

Another area of conflict is that between the animal rights community and conservationists. In their efforts to control both expanding native species and destructive aliens, public health officials, ecologists and conservationists will be thwarted by animal rightists and welfarists. For example, we can expect animal protectionists to protest the poisoning of rodents, although these animals may be reservoirs of plague.

Conservationists have already been in the ring with animal protectionists. One case involves the red fox. Its geographic range has expanded into wetlands in California, following its escape from a breeding farm. The effects of foxes on ground-nesting birds, such as the endangered light-footed Clapper Rail and the Least Tern, have been devastating, but animal rightists have successfully sued the California Department of Fish and Game to prevent fox control. Many similar stories could be told. Better communication is essential between conservationists and the animals rights movement.

Fortunately, such conflicts are not universal. In Hawaii, it has been possible to virtually exterminate goats (which destroy the native vegetation) in Hawaii Volcanoes National Park using the 'Judas goat method' (Charles P. Stone, pers. comm.). Radio-collared female goats are released. These lonely females quickly attract feral goats. The feral goats are shot and the collared female is released again. Unfortunately, the method doesn't work on less gregarious species, such as feral pigs.

Conclusions and Recommendations

Is there some good news? Maybe not, but the control of exotics and the prevention and cure of tropical diseases certainly will be a growth industry. More grant funds may flow to those who study the epidemiology, genetics, and ecology of exotic organisms.

What can concerned people do to help? The two-thirds of American households which donate to charities give about 2.5% (about $800) of their gross income. More than 98% of this amount is given to churches and to organizations that benefit people (the poor, health related charities, cultural institutions). Only about 1.5% is given to environmental groups. Those with different priorities or with a longer view of public welfare might consider giving 2.5% of our gross income to environmental causes, especially to those organizations that support energy conservation, voluntary family planning, and research in conservation biology.

America adds more carbon to the atmosphere, on both gross and per capita bases, than does any other nation [1]. Most environmentalists believe that the current energy policy of the United States administration is flawed, and that humanity and nature would be better served by establishing targets for the releases of greenhouse gases, giving support for an international climate treaty, and returning to policies that favor energy efficiency over intensive oil drilling in Alaska and elsewhere. We could also consider becoming examples to our international peers by adopting life styles that are less wasteful and consumptive of energy.

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Introduction to *Rewilding and Biodiversity: Complementary Goals for Continental Conservation*

In this 1998 paper, Reed Noss and I described the conservation strategy of "rewilding," the restoration of self-sustaining populations of top predators like wolves, bears, and jaguars, keystone species in most environments. Keystone species are "those whose influence on ecosystem function and diversity are disproportionate to their numerical abundance." Thus, the removal of top predators profoundly destabilizes ecosystems, causing loss of habitats and extirpation of some species. Top predators may also be considered "umbrella" species, meaning that if we protect enough habitat for them, we automatically protect a host of other species.

One key role of top predators is to control herbivores. For example, John Terborgh and his colleagues found that South American islands lacking jaguars, harpy eagles, and other top predators rapidly lost plant species because they were eaten by exploding populations of tapirs, monkeys, and rodents. Likewise without wolves and pumas, populations of white-tailed deer in the United States have reached pest levels and prevented recruitment of eastern hemlock and northern white cedar trees, depressed populations of understory

plants like lily-of-the-valley and white-flowered trillium, and extirpated as much as 81 percent of herb and shrub species in old-growth forests.

Top predators like wolves also limit the abundance of smaller "mesopredators," such as foxes, skunks, and domestic cats, often by killing them or preventing them from obtaining food. Typically, when dominant predators are absent, populations of the mesopredators increase—what is called "ecological release" (see paper 5)—whereupon they drive down populations of birds and other prey.

Because large carnivores have low population densities, viable populations require areas that are often greater than any national park or protected reserve. A solution is to connect multiple reserves by secure corridors. The ambitious Spine of the Content project would link secure areas stretching from the Rocky Mountains to Mexico's Sierra Madre.

Rewilding will be difficult if many people are unwilling to accept large predators. The federal Red Wolf Recovery Program's efforts to augment the 90 wolves surviving in the wild are obstructed by frequent shootings, which killed nine in 2012. Every year in Colorado dozens of "nuisance" black bears are killed because they frequent areas, such as apple orchards, near people; this despite the fact that only seven people were killed by all species of bears in the 2010s. Compare this to the 22,000 Americans killed by prescription drugs or the 33,000 killed in traffic accidents every year.

The "Complementary Goals" in our paper refers to the tension between two conservation strategies, namely conservation based on protecting habitat for predators and other species that require large ranges, and conservation based on protecting representatives of plant communities. We explain that protection schemes based only on protecting predator habitat would miss some biodiversity, while schemes based only on plant communities would not provide the large areas needed by large predators, leading to ecosystem degradation. Both strategies must be used intelligently when setting land protection priorities.

10

*Rewilding and Biodiversity:
Complementary Goals
for Continental Conservation*

Michael Soulé and Reed Noss

Disputes about goals and methodology are nothing new in the nature conservation movement. Gifford Pinchot's insistence on responsible use and Juhn Muir's emphasis on strict preservation have survived as distinct ideologies for nearly a century. Currently, conservationists are discussing and implementing two versions of science-based or science-informed methodologies for conservation. We refer to the older and more conventional of these as *biodiversity conservation*; it stresses the representation of vegetation or physical features diversity and the protection of special biotic elements. The other we refer to as *rewilding*; it emphasizes the restoration and protection of big wilderness and wide-ranging, large animals—particularly carnivores. Differences between these two approaches have led to some tension about goals within wildlands conservation circles, in part because of the human tendency to dichotomize and to perceive different emphases as competitive rather than complementary. In this paper we define rewilding, placing it in the context of older conservation currents in North America.

Nature Protection in North America

The roots of current conflicts about how best to conserve nature in North America reach back into the Pleistocene when huge mammals dominated the continent's ecosystems. Starting between 11,000 and 12,000 years ago, the megafauna virtually disappeared. The die-off was brief, lasting only about 2,000 years. Human beings are implicated in this catastrophic extirpation—sometirnes referred to as the Pleistocene Overkill—of more than 50 species of large mammals in North America including mammoths, mastodons, horses, giant ground sloths, American camels, lions, and the saber-tooth cats. Paleoecologists generally agree that two of the major factors in this short but profound event were, first, the arrival from Asia of efficient big-game hunters—now called the Clovis people—who came armed with a new and effective spear technology (Ward 1997) and, second, the lack of evolutionary experience of the prey species with strategic, cooperative, two-legged hunters.

It is not widely appreciated, however, that North American ecosystems remain profoundly altered by that extinction episode. For example, a dozen large mammalian herbivores once coexisted in the eastern US; now only one or two remain (Terbotgh et al. 1999). The truncated nature of contemporary ecosystems is relevant to debates about the design and management of protected areas. The link is the ecological role of large predators; now, only a handful of large carnivore species persist, including the cougar, the black bear, the grizzly bear, and the wolf.

The Clovis technology, and later Stone Age successors, have been replaced by even more efficient tools—steel traps and firearms—facilitating a second wave of carnivore extirpation. Guns helped eliminate nearly all grizzly bean and wolves from the lower 48 states. Cougars and black bears have been extirpated from more than half of their original geographic range in the United States. Predator "control" (killing), even on public lands, is still the default policy in many areas of North America, and the unsustainable hunting of

grizzly bears is still permitted in Canada (Hummel and Pettigrew 1991).

Other modern technologies have helped convert highly productive wildlands to farmlands, clearcuts, tree plantations, and overgrazed rangelands. Human population growth also contributes to habitat destruction, not just in Mexico and Central America, but throughout North America. Population pressures are aggravated by corporate-driven consumerism, new technologies such as refrigerated transport, and political innovations such as the North American Free Trade Agreement that encourage habitat conversion in tropical nations. The rapid growth in the importation of perishable produce and seafood from the South is directly linked to loss of tropical forests, mangroves, and estuaries. As we import flowers, fruits, coffee, vegetables, shrimp, and forest products, we export habitat destruction to Latin America, Asia, and Africa (Thrupp 1995).

Monumentalism

Conservationists in North America have responded to the loss of wild nature by employing several major arguments—or currents—to sway public opinion and private behavior.[1] The first argument, sometimes called *monumentalism* (Runte 1987), was articulated by the founding preservationists almost a century ago. Among these early pioneers, John Muir was the most famous. Muir and allies wished to save places of extraordinary natural beauty—the grand spectacles of nature, places that today are the crown jewels of National Park systems. Muir, Bob Marshall, and the other preservationists appealed to patriotism, deism (respect for God's creation), spiritual inspiration, and aesthetics in their advocacy for wild places.

Over time, monumentalism evolved into the wilderness movement. The Wilderness Society was founded in the 1930s; among its founders were two early opponents of predator control, the biologists Olaus Murie and Aldo Leopold. The emphasis of this movement gradually shifted from preserving spectacular natural scenery

to providing recreation opportunities in primitive areas, and to a belief in the intrinsic value of self-willed nature (Nash 1989, p. 149). Another branch in this lineage was the creation of National Parks dedicated to protecting particular charismatic species; these parks include Wood Buffalo and Antelope National Parks in Canada.

Biological Conservation, Including Representation of Ecosystems

The next important current—*biological conservation*—can be traced to the second and third decades of the 20th century, when ecologists and naturalists began to realize that nature didn't always achieve its apex of biological productivity and richness in aesthetically notable places like Yosemite and Banff, and that many kinds of ecosystems were unrepresented in National Parks. They observed that the diversity of species and habitats was often greatest in less grandiose ecosystems, particularly the warmer lowlands, wetlands, streams, humid forests, and in coastal areas.[2] Unfortunately, many of these habitats and attendant resources are also favored by real estate developers, industrial loggers, and agriculturalists.

Two committees of the Ecological Society of America, chaired in the early years by Victor Shelford and involving such well-known scientists as Aldo Leopold, E. T. Seton, and Charles Kendeigh, were instrumental in calling for an end to the persecution of carnivores and for the protection of large, unmanaged wilderness landscapes to represent all of North Amcrica's major ecosystems (Shelford 1926, 1933a, 1933b, and unpublished documents; Kendeigh et al. 1950-51). One of these committees, the Committee on the Preservation of Natural Conditions, left the Ecological Society after arguments over the role of advocacy in the Society, and became the Ecologists' Union. This group was later renamed The Nature Conservancy (which, ironically, now avoids direct advocacy).

By the late 1970s and early 1980s, biological conservationists were beginning to employ sophisticated classifications of landscapes and vegetation, plus lists of vulnerable species, to assist in seques-

tering representative samples of all ecosystem types and "special elements" in a system of nature reserves. The state natural heritage programs established by Bob Jenkins of The Nature Conservancy led this effort. Later, the Endangered Spaces Campaign of World Wildlife Fund Canada assessed representation of landscape features throughout Canada. Contemporary scientific conservationists call for the protection of representative ecosystems, "hot spots of biodiversity," centers of endemism (locales relatively rich in species with limited geographic distributions), and the habitats of rare or vulnerable species.

A significant elaboration of biological conservation grew out of the recognition that landscapes are dynamic and that natural disturbance regimes must also be maintained. More recently, there has been a focus on the scale and intensity of natural disturbances such as fires, floods, and catastrophic weather events (Pickett and Thompson 1978, White 1979, Pickett and White 1985, Foster 1980). Fire, for example, can have profound effects on ecosystem structure, diversity, and function, and might be referred to as a keystone process (Noss 1991).

By the early 1980s biologists recognized that large carnivores —such as grizzly bears, wolves, and cougars—require extensive, connected, relatively unaltered, heterogeneous habitat to maintain population viability (e.g., Frankel and Soulé 1981). These became the animals used to justify large nature reserves, earning them the title "umbrella species." The assumption in this approach is that large, wide-ranging carnivores offer a wide umbrella of land protection under which many species that are more abundant but smaller and less charismatic find safety and resources. We note, however, that large carnivores also figured prominently in arguments advanced earlier by Shelford, Kendeigh, and others. These ecologists sought to preserve complete, self-regulating ecosystems with all native species.

For example, Kendeigh et al. (1950–51) observed that "it is in the absence of the large predators that many sanctuaries are not entirely natural and have unbalanced populations of the various species."

Island Biogeography

A third major current in conservation advocacy arose with *island biogeography*, which emerged as a field of scientific inquiry in the late 1960s. Arguably, the most salient generalization from island biogeography is the species-area relationship (MacArthur and Wilson 1967), which was actually recognized decades earlier (Arrhenius 1921) but became the basis, much later, for quantitative prediction of extinctions in isolated habitat remnants and natural reserves (e.g., Diamond 1975, Soulé et al. 1979, Newmark 1995). The principles of island biogeography were soon incorporated into the emerging synthesis called conservation biology (Terborgh 1974, Diamond 1975, Wilson and Willis 1975, Simberloff and Abele 1976, Frankel and Soulé 1981, Noss 1983, Harris 1984, Soulé and Simberloff 1986; see review in Noss and Cooperrider 1994).

Conservation biologists had identified weaknesses with the existing conservation approaches, based on their understanding of the scale on which ecological processes operate, and noted the empirical correlation of area with both species diversity (positive) and extinction rates (negative). Small habitat remnants were recognized as being relatively vulnerable to many other dissipative phenomena—edge effects, and invasions of exotic plants, animals, and pathogens (Soulé and Wilcox 1980)—hastening the local extirpation of species and ecosystem disintegration.

A detining moment in the acceptance of island biogeography in conservation circles was the publication of William Newmark's paper (1985) demonstrating the loss of mammal species in all but the largest North American park complexes. Newmark discovered that the rate of local extinction in parks wars inversely related to their size. By then it was understood that small, isolated populations of animals were vulnerable to accidents of demography and genetics and to environmental fluctuations and catastrophe, underlining the need for bigness and connectivity (Franklin 1980, Frankel and Soulé 1981). Inter-regional connectivity was seen as necessary for providing genetic and demographic rescue and for viability of wide-

ranging species (Soulé 1981, Noss 1983, Harris 1984, Noss and Harris 1986, Soulé 1987); even regions as large as the Greater Yellowstone Ecosystem could not provide sufficient demographic resilience and genetic-evolutionary fitness for animals such as wolverines and grizzly bears (Shaffer 1981). It became clear that island biogeography needed to be integrated into conservation planning and practice.

Rewilding

The fourth current in the modern conservation movement is the idea of *rewilding*—the scientific argument for restoring big wilderness based on the regulatory roles of large predators. Until the mid-1980s, the justification for big wilderness was mostly aesthetic and moral (see, e.g., *Earth First! Journal* 1981–1988, Foreman and Wolke 1989, Fox 1981, Nash 1982). The scientific foundation for wilderness protection was yet to be established.

We recognize three independent features that characterize contemporary rewilding:

- Large, strictly protected, core reserves (the wild)
- Connectivity
- Keystone species

In simplified shorthand, these have been referred to as the three C's: Cores, Corridors, and Carnivores (Soulé, in prep.). A large scientific literature supports the need for big, interconnected reserves (Frankel and Soulé 1981, Soulé 1986, Noss and Cooperrider 1994, Noss and Csuti 1997). Keystone species are those whose influence on ecosystem function and diversity is disproportionate to their numerical abundance (Paine 1980, Gilbert 1986, Terborgh 1988, Mills et al. 1993, Power et al. 1996). (By definition, species that are typically abundant or dominant, such as fig trees, salmon, coral, and social insects including termites and ants, though often critical interactors, are not classified as keystone species, even though the effects are

similar when they are greatly diminished in abundance.) The critical role of keystone species is gaining acceptance (Terborgh et al. 1999). Conservatively, though, the role of keystones might still be categorized as a hypothesis, its validity depending on the ecological context and the degree to which large carnivores and herbivores persist in the particular ecosystem. In any case, the keystone species hypothesis is central to the rewilding argument.

Keystone species enrich ecosystem function in unique and significant ways. Although all species interact, the interactions of some species are more profound and far-reaching than others, such that their elimination from an ecosystem often triggers cascades of direct and indirect changes on more than a single trophic level, leading eventually to losses of habitats and extirpation of other species in the food web. "Keystone species" is an inelegant but convenient way to refer to these strong interactors (Mills et al. 1993). Top carnivores are often keystones, but so are species that provide critical resources or that transform landscapes or waterscapes, such as sea otters, beavers, prairie dogs, elephants, gopher tortoises, and cavity-excavating birds. In North America it is most often the large carnivores that are missing or severely depleted.

Three major scientific arguments constitute the rewilding argument and justify the emphasis on large predators. First, the structure, resilience, and diversity of ecosystems is often maintained by "top-down" ecological (trophic) interactions that are initiated by top predators (Terborgh 1988, Terborgh et al. 1999). Second, wide-ranging predators usually require large cores of protected landscape for secure foraging, seasonal movement, and other needs; they justify bigness. Third, connectivity is also required because core reserves are typically not large enough in most regions; they must be linked to insure long-term viability of wide-ranging species. (Note, however, that "frontier" regions like Canada, north of the 50th parallel, are exceptions because of very low human population density.) In addition to large predators, migratory species such as caribou and anadromous fishes also justify connectivity in a system of nature reserves. In short, the rewilding argument posits that large predators

are often instrumental in maintaining the integrity of ecosystems; in turn, the large predators require extensive space and connectivity.

The ecological argument for rewilding is buttressed by research on the roles of large animals, particularly top carnivores and other keystone species, in many continental and marine systems (Terborgh et al. 1999, Estes et al. 1978). Studies are demonstrating that the disappearance of large carnivores often causes these ecosystems to undergo dramatic changes, many of which lead to biotic simplification and species loss (Mills et al. 1993). On land, these changes are often triggered by exploding ungulate populations. For example, deer, in the absence of wolves and cougars, have become extraordinarily abundant and emboldened in many rural and suburban areas throughout the United States, causing both ecological and economic havoc (McShea et al. 1977, Nelson 1997, McLaren and Peterson 1994).

Following extirpation of the wolves in Yellowstone National Park, large populations of elk over-browsed riparian vegetation in many areas. Beaver, having nothing to eat, abandoned large valleys, and beaver ponds and riparian habitat greatly diminished, impoverishing the local biodiversity. Where wolves have returned, elk herds don't dally as long near streams, and one might hope for the return of the missing beaver ponds, an ecological irony given that beaver are a prey item of wolves.

Current studies in South America by John Terborgh and his colleagues are showing that the absence of carnivore control on herhivores (tapir, monkeys, rodents, insects) can precipitate a rapid loss of plant species diversity. Construction of a resevoir in Venezuela caused flooding of a vast area, now known as Lago Guri. Many of the islands created thus lack the larger predators (jaguar, puma, Harpy Eagle), and on these islands the reproduction and replacement of many species of canopy trees has come to a halt. On middle-sized islands, even though 60–70 species of trees coexist in the canopy, only a handful of species are represented in young recruits. Terborgh et al. believe that the primary factor in the failure of canopy trees to reproduce is the superabundance of herbivores (leaf-eating monkeys

and ants, rodent seed predators). The herbivores have apparently been "released" from the population control imposed, directly or indirectly, by large predators. As a result, the entire island ecosystem is crashing.

Another frequent consequence of the absence of large carnivores is a remarkable increase in abundance of smaller predators (mesopredators), largely because the top carnivores would normally prey upon and inhibit the foraging of their smaller counterparts. Several studies have suggested that this "demographic release" of mesopredators such as house cats, foxes, and opossums causes severe declines in many songbirds and other small prey animals (Soulé et al. 1988, Palomares et al. 1995, Côté and Sutherland 1997, Terborgh et al. 1999). Studies by Crooks (1997 and pers. comm.) in isolated remnants of scrub habitat in southern California are showing that the presence of coyotes, the top carnivore in these fragments, is associated with the restriction of house cats to the edges of the fragments.

Finally, in some situations the absence of top predators can lead to intense competition among former prey species for space or food, eventuating in one species of competitor eliminating many others (Terborgh et al. 1999). Often referred to as the "Paine effect" (after R. Paine, who first demonstrated the keystone effects of predatory starfish; Paine 1966), this is yet another example of the indirect, but profound, consequences of eliminating large predators.

Prior to the megafauna overkill in the Pleistocene, the role of large carnivores as top-down regulators may not have been as important as it is today. At that time in North America, huge herbivores (including mammoths, mastodons, giant camels, and giant ground sloths) dominated many ecosystems, and probably controlled the distribution and abundance of many plant species and habitat types, as megaherbivores such as elephants still do in Africa. Moreover, highly social, migratory ungulates, such as bison, grazed and browsed in huge numbers. Carnivores were probably not effective regulators of the megaherbivores and the migratory ungulates. Today, however, top predators appear to regulate many ecosystems

(Terborgh et al. 1999), preventing hyperbundance in herbivores and mesopredators.

Our principal premise is that rewilding is a critical step in restoring self-regulating land communities. Recall that viable populations of large predators require both large core areas and connectivity, thus bolstering the resilience and viability of reserve networks. Also, large predators initiate chains of far-reaching and manifold ecological interactions; in the absence of these keystone species, many ecosystems will become degraded and simplified. Extensive networks of cores and habitat linkages also sustain a vast range of natural processes, thus minimizing the need for human management. Once large predators are restored, many if not most of the other keystone and "habitat-creating" species (e.g., beavers, prairie dogs), "keystone ecosystems" (deMaynadier and Hunter 1997), and natural regimes of disturbance and other processes will recover on their own.

Rewilding as a Responsibility

In addition to the scientific justifications for rewilding there are ethical and aesthetic justifications, although some are specific to the North American situation. First, there is the ethical issue of human responsibility. In many regions the deliberate government policy has been to exterminate large carnivores. Unfortunately, this practice continues. The federal agency charged with this task, Animal Damage Control (recently renamed Wildlife Services) still exists. Because carnivores are generally long-lived, produce few young, and nurture those young over a long period of time, their capacity to recover from over-hunting or extirpation campaigns is relatively limited (Noss et al. 1996, Weaver et al. 1996). This underlines the need, if only temporary, for benign human intervention in the form of reintroduction or augmentation of carnivores.

Second, by insuring the viability of large predators, we restore the subjective, emotional essence of "the wild" or wilderness. Wilderness is hardly "wild" where top carnivores, such as cougars, jaguars,

wolves, wolverines, grizzlies, or black bears, have been extirpated. Without these components, nature seems somehow incomplete, truncated, overly tame. Human opportunities to attain humility are reduced.

Nonetheless, rewilding is not the only goal of most regional reserve design efforts. The Wildlands Project encourages planning groups to address the major "wounds" or ecological insults caused by abusive land uses of the past that require redress, a notion that is easily traced to Aldo Leopold and other early ecologists (Foreman, in prep.). Among the most common of these wounds to wildlands is the extirpation of large predators, but there are several others that often require treatment, including overgrazing and destruction of riparian habitats, irrigation and hydroelectric projects, poor forestry practices, over-fishing, habitat abuse and stress in animals from mechanized recreation, introduction of exotic species, draining or pollution of wetlands, and habitat changes stemming from decades of fire suppression. Rewilding does not address all of these, but it is one essential element in most efforts to restore fully functioning ecosystems. Repairing all past insults requires a comprehensive effort. We encourage the use of focal species (Miller et al. in press) when addressing these wounds.

Biodiversity Protection Plus Rewilding Equals Conservation

Ecosystems are constituted of species arrayed along environmental gradients in a shifting mosaic of vegetation. This means that if one protects representative samples of all features, landforms, or vegetation types and successional stages in the reserve network, then most of the biodiversity must also be sequestered—a kind of habitat umbrella effect or "coarse filter" (Noss 1987). The major argument for representation of vegetational or habitat diversity is that it captures and, we would like to think, protects most of a region's species. Certainly, the representation of all vegetation types in a reserve system would seem more efficient than preparing a protection strategy, one by one, for each of the thousands of species that occur in most re-

gions. This is why many regional conservation groups are using a representational methodology as a first stage in the design of reserve proposals, particularly if data on the kinds and geographic distributions of ecosystems, vegetation types, and special biotic elements already exist (for instance, from gap analysis projects; Scott et al. 1993). Such data also can provide the framework on which to hang other kinds of information, and on which to base other studies.

A reserve system based on representation requires several kinds of scientific knowledge, including knowledge of the distribution of vegetation types or physical habitats—or species groups used as surrogates—and knowledge of the frequency and geographic distribution of large-scale disturbances. A more inclusive strategy incorporates special elements and phenomena such as hotspots of endemism, important migratory stopovers or breeding areas, old-growth patches, or roadless areas (Noss 1996). Many of these elements have such restricted distributions that they would not be captured by a representational approach alone.

It does not necessarily follow, however, that the representation of vegetation types or protection of special elements, for which data can easily be accommodated in a geographic information system (GIS) methodology, is the only way to design a reserve system. Several situations allow for non-representational methodologies, at least in preliminary stages. In unpopulated or sparsely settled "frontier" areas, such as most of Canada, for example, reserve planning is proceeding from a basis of securing entire unlogged or undeveloped watersheds, in part because such large, topographically diverse watersheds will contain virtually all of the vegetational diversity within the region (Diamond 1986). Another justification for large watershed protection in the temperate rainforests of North America is the premise that commercial logging in such watersheds can contribute to the local extirpation of a keystone species guild—anadromous fish.

In one region, at least, reserve design has emphasized rewilding and ecological restoration rather than representation or other biodiversity-focused goals. Conservationists designing a nature reserve network for the Sky Island-Greater Gila region of the southwestern

US have based their work on the needs of focal species, some of which are large carnivores and ungulates, and some of which are indicators of the ecological resilience and restoration of particular systens or processes that have suffered from mismanagement; abuses of this landscape include the extirpation of some ungulates and large carnivores, the suppression of fire, and extensive overgrazing, particularly in riparian zones. It remains untested, however, whether such reserve networks will capture a similar proportion of species and habitat diversity as would those based on a representational methodology.

Several authors have codified procedures for securing representation of biodiversity (Pressey and Nicholls 1989, Bedward et al. 1992, Pressey et al. 1993, 1996, Church et al. 1996, Noss 1996, Faith et al. 1996. Csuti et al. 1997). One trend has been the development of algorithms for quantifying the degree of representation in any particular system of reserves and for achieving representation most efficiently (see above references). In the hands of the ecologically naive, however, such powerful technologies can produce myopic dependence on spatially explicit, quantitative data. Moreover, some of the researchers who employ linear programming and economic models for the selection of reserves ignore population viability concerns and rely on ecologically dubious assumptions about the long-term consequences of habitat fragmentation.

The current emphasis on quantitative analysis and GIS mapping in conservation planning often leads to the exclusion of other important considerations. We know of situations where certain carnivore species were excluded from consideration because "a database" or "layer" for that species was lacking. A case in point is the oft-heard question from activists, "How can we include grizzly bears (or jaguars, cougars, wolves) in our model if we lack information on their demography?" "Besides," they continue, "our region is too small to sustain a viable population of such large animals." These concerns can be symptoms of letting the tail of technology wag the dog of common sense. Both ethics and science require the large carnivores be included in conservation planning, even if the needs of these species can only be considered qualitatively at first.

Insufficiency of wildlands in a region is not justification for ignoring large carnivores. Granted, few places south of the 50th parallel are large enough to maintain viable populations of large carnivores at present. This is all the more reason why each regional planning group must be responsible for its link in the chain of nature protection. It is only by coordination of planning in the entire, continental network that full return of land vitality is achievable. The point is that each reserve design group in the network (Soulé 1995) has an obligation to all of the land, not only to their particular region, province, or state.

Politics can also wag the dog. For instance, some activists are excessively anxious about the attitudes of certain stakeholders, particularly those with negative perceptions of wolves or other carnivores. There is a danger in granting too much weight during the design phase to such considerations, and letting politics interfere prematurely with reserve planning. A conservation plan cannot give equal weight to biocentric and socioeconomic goals, or the former will never be realized. Biology has to be the "bottom line." We acknowledge that rewilding is thought by some conservationists to be impractical, particularly in relatively built-up regions of North America. Moreover, many people are uncomfortable in proposing the reintroduction of large and politically troublesome carnivores. But this is no excuse. Timidity in conservation planning and implementation is a betrayal to the land. Even in relatively populated regions like most of the eastern United States, the land cannot fully recover from past and present insults and mismanagement unless its bears, cougars, and wolves return. The greatest impediment to rewilding is an unwillingness to imagine it.

Conclusions

Biodiversity and rewilding are not competing paradigms; rather, they are complementary strategies. Just as a pure representation approach to conserving nature, if it ignored the issue of long-term viability of wide-ranging keystone species, would be unsatisfactory, a

pure rewilding approach might miss some ecosystems and special elements, thus sacrificing significant ecological and species diversity. The Wildlands Project has always emphasized a comprehensive, yet flexible, strategy for the protection of living nature. The representation of ecosystems can be an excellent starting point, but without the consideration of the ecological context, the history of land use in the region, top-down interactions, plus the requirements for large connected spaces, we have little confidence in the long-term viability of ecological reserves.

Moreover, there may be situations where a representational approach might not be adequate because it does not justify the protection of sufficient space for a viable, regional network of natural areas. In locations where vegetation diversity is low, a system of ecological reserves based only on vegetational diversity could end up being small, fragmented, and vulnerable (Flather et al. 1997). In Idaho, for example, a reserve system that protects samples of all vegetation types might sequester just eight percent of the state, much of it highly fragmented (Noss and Cooperrider 1994, Kiester et al. 1996). This is not sufficient area for the persistence of large carnivores, nor for the buffering of edge effects and area effects. On the other hand, a network of connected reserves in Idaho (or elsewhere) that maintains the viability of wide-ranging predators might require one-third or more of the landscape (Noss and Cooperrider 1994, Noss et al. 1996).

Other factors may militate against too much reliance on vegetation as a coarse filter. One of these is the pattern in which species are distributed across the land. For example, in much of Mexico, the mammalian faunas are quite dissimilar over relatively short distances (Arita et al. 1997), an example of high beta diversity. In such places, vegetational diversity may seriously underestimate biodiversity at the species level in some taxa.

Because ecological and cultural contexts differ, local conservationists and biologists are in the best position to develop tactics for the recovery of wilderness and ecological values in their regions. In practice, this means that many grassroots conservation groups will

emphasize representation of habitats or protection of special elements in their reserve designs, at least in the preliminary stages. But it is a mistake to stop there. Sooner or later it is necessary to find the resources to incorporate wilderness and the entire pre-Columbian set of carnivores and other keystone species into reserve designs. Absent these, the long-term success of the continental conservation network in North America is doubtful.

A cynic might describe rewilding as an atavistic obsession with the resurrection of Eden. A more sympathetic critic might label it romantic. We contend, however, that rewilding is simply scientific realism, assuming that our goal is to insure the long-term integrity of the land community.

Rewilding with extirpated carnivores and other keystone species is a means as well as an end. The "end" is the moral obligation to protect wilderness and to sustain the remnants of the Pleistocene—animals and plants—not only for our human enjoyment, but because of their intrinsic value. The "means" refers to the vital roles of keystone species in maintaining the ecological structure, diversity, and resilience of the entire fabric of living nature. It is not helpful, however, to claim that rewilding, or any other conservation tool, is the only means we have to protect and heal the wounds of the land. In a project as complex as saving living nature, a diversity of approaches, often complementary and context dependent, will be needed.

Notes

1   In addition to the four arguments emphasized here (monumentalism, biological conservation, island biogeography, and rewilding), other rationales and strategies for conservation have been employed, particularly in Europe, Africa, and Latin America; these include creating reserves designed to preserve particular cultural forms, and those that emphasize "sustainable" land uses including harvesting of products such as Brazil nuts, chicle, and rubber.

2 Everglades National Park, established in 1947, was the first American park founded for an explicitly biological purpose—to preserve aquatic wildlife (Unfortunately, the ecosystem "preserved" was far too small).

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Introduction to *Conserving Nature at Regional and Continental Scales: A Scientific Program for North America*

In this 1999 paper, John Terborgh and I asserted that to be effective conservation must be carried out on a large geographic scale. The fundamental argument is that without extensive wildlands, large predators cannot persist and fire patterns and other natural disturbance regimes will change, thereby degrading ecosystems. This reminds me of the parable:

> For want of a nail the shoe was lost;
> For want of a shoe the horse was lost;
> For want of a horse the battle was lost;
> For failure of battle the kingdom was lost.

In our case the nail is large predators and the kingdom is ecosystem integrity. When wolves, jaguars, and other large predators are removed, ecosystems degrade as described in paper 10. Consider the Pacific Coast sea otter. When the fur trade reduced hundreds of thousands of otters to a relative handful, their sea urchin prey exploded, destroying kelp forests and replacing them with "urchin barrens." Other species dependent on the kelp disappeared, includ-

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ing many invertebrates, fish, and seabirds. Based on these and other examples, we concluded that when top predators are removed, the effects cascade down the trophic levels to ultimately affect plants and insects, and most likely soil microorganisms too. We call the controlling actions of these top carnivores *top-down regulation*.

Of course ecological interactions are often not as linear as the story above suggests. For example, African elephants are megaherbivores too large to be regulated by carnivores, with the exception of man. As "unregulated herbivores" they can decrease tree diversity by killing tasty species, but they can also promote plant diversity at landscape and regional scales by distributing seeds in their dung.

Our paper recognized the difficulty of maintaining large refuges to support predators and natural disturbance regimes. We proposed solutions, the first being "regional connectivity," namely connecting reserves by corridors to allow free movement of species such as wolverines, bears, and wolves.

We also proposed the restoration of degraded areas. Restoration projects can reestablish missing species and mimic natural disturbance regimes, for example, by prescribed burning. Such projects are typically local in scope and often lack coordination among agencies like the Bureau of Land Management and US Forest Service.

A third solution is to modify activities near reserves—in the "human surround"—so that these areas, albeit not entirely natural, can help sustain predator numbers. A major obstacle is people's penchant for killing predators, in part to take retribution for stock killing. For example, in Idaho in 2012 gray wolves were confirmed to have killed 345 domestic animals, while 401 wolves were killed by people. Rural people in nations like Romania and Georgia are more tolerant of predators. I met shepherds in Georgia who tolerated a modest "take" of their sheep; one said "wolves must eat too; we have removed their natural prey."

Conserving Nature at Regional and Continental Scales: A Scientific Program for North America

MICHAEL E. SOULÉ AND JOHN TERBORGH

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With the closing of the frontier a century ago, visionaries such as John Muir and Theodore Roosevelt sought to ensure the preservation of samples of the most monumental and scenic landscapes of wild America—its grandest vistas and most impressive creatures. As the twentieth century unfolded, however, and as the science of ecology developed, conservation biologists such as Victor Shelford recognized another conservation imperative: the need to protect less spectacular but biologically richer habitats, such as marshes and prairies. The national parks, wildlife refuges, nature reserves, and wilderness areas that today cover approximately 4 percent of the land area of the United States represent the legacy of these two distinct but complementary traditions of nature protection.

Now, as the end of the century approaches, ecologists are documenting unprecedented worldwide habitat conversion driven by rapidly expanding human populations, powerful technologies, and irresistible economic incentives, including the relaxation of international trade barriers. The accelerated conversion of wildlands to croplands, pastures, tree plantations, and sprawling cities; the

mechanized exploitation of natural resources, such as fresh water, forage, timber, and minerals; and the quiet invasion of alien species that is exacerbated by habitat degradation threaten to produce an unprecedented wave of extinctions—a wave that could sweep away as many as half the earth's plant and animal species (Ehrlich and Wilson 1991).

Even as the biodiversity crisis has become more apparent, however, the scale of conservation planning and implementation has remained largely unchanged. That is, conservation efforts are still relatively local, emphasizing islandlike preserves; the implicit premise is that biotic diversity can persist in isolated habitat reserves. Although ecologists recognize the long-term instability of islandlike wildlands, this strategy has gone virtually unchallenged as a matter of policy and implementation. In part, reliance on isolated preserves results from the widespread but mistaken belief that the matrix of semi-developed lands between reserves can sustain the full range of ecological processes and human services, including animal migration, dispersal, and pollination. In actuality, however, the result of this policy is that protected lands are a fragmented patchwork of mostly small wildlands threatened by an inexorable tide of exotic species, edge effects, and increasing human disturbance and encroachment.

Over the past two decades, the science of conservation biology has shown that the island strategy, by itself, is inadequate to the formidable challenge of conserving most living species into the next millennium. The evidence that isolated reserves—a category that includes some of the largest national parks in the United States—gradually lose native species, especially large mammals and carnivores (Newmark 1995), is overwhelming. Such gradual degradation can only accelerate as human activity and development increase on surrounding lands. The elements of the solution are known: bigness and connectivity (e.g., Frankel and Soulé 1981).

These two elements constitute the foundation for any meaningful program of wildlands or biodiversity conservation on a regional or continental scale. Notwithstanding the inevitable and formidable political resistance to the application of these simple principles, a

transformation in conservation philosophy is occurring. On-the-ground realization of a program of large core areas and landscape connectivity will, however, require research, planning, and bold advocacy at unprecedented scales. In this article, we describe the scientific bases for this new stage in the protection of nature. Our major points include recognition of top-down regulation in ecosystems and the need for large core areas and regional connectivity, recognition of the need for ecological restoration on unprecedented scales, and a critique of fashionable alternatives, such as sustainable development.

The Recent History of Science in Nature Conservation

Although several major conservation organizations, including The Wildlands Project, The Nature Conservancy, and the World Wildlife Fund, are now analyzing biodiversity issues on ecosystem or regional scales, the biological theory that justifies geographically extensive conservation projects has, until recently, lagged behind. In the past, appeals for large, connected systems of wildlands have relied mainly on three bodies of evidence that have supported, but not rigorously justified, such an approach. The first argument comes from descriptive biogeography; its major element is the species-area curve (Wilcox 1980)—the larger the patch, the more species it contains. The second argument is based on the spatial and temporal distributions of diversity-enhancing disturbances, such as fire and flood: the larger the area, the more that spatial and temporal distributions of disturbance events and amplitudes approach historic levels, reducing the need for active management. The third argument is based on demographic and genetic considerations, namely, that population viability is proportional to population size; hence, wide-ranging or rare species require big spaces lest they become locally extirpated or ecologically ineffective.

To bolster these arguments for bigness and connectivity, conservationists have relied on a fourth concept—the "umbrella effect" of large, wide-ranging, charismatic animals such as bears, canids, large

cats, herding ungulates, and raptors. Because viable populations of such appealing animals need big, ecologically diverse areas for year-round water, forage, and shelter, these species also provide, indirectly, an umbrella of resources for many other, perhaps less appealing species. But the basis of the umbrella argument is not science. Rather, it is an ethical or aesthetic justification for large areas based on a form of ecological justice or reparation or on the intrinsic value or appeal of big, charismatic species. For example, many environmental ethicists and conservationists argue that society is obligated to redress policies that nearly cleansed the United States of animal competitors such as grizzly bears, mountain lions, bobcats, coyotes, and wolves for the benefit of livestock owners during the first three-quarters of this century. Moreover, many conservationists argue that a defining characteristic of wilderness is the presence of powerful predators (Matthiessen 1977, Lopez 1978, Peacock 1990, Foreman 1991, Wolke 1991). In addition, some "umbrella species" participate in critical ecological interactions, as discussed below, providing a strong ecological argument for bigness and connectivity.

The umbrella idea and the three empirical bodies of evidence already mentioned certainly justify large reserves, but they do not, by themselves, provide an unassailable scientific case for extensively connected systems of wildlands. This lack of compelling evidence exposes conservation to criticism by developers and others hostile to the expansion of wildlands and the protection of nature. An additional argument for extensive—regional to continental—networks of wildlands is based on the ecological roles of large carnivores (Soulé and Noss 1998, Soulé and Terborgh 1999). The major conceptual theme and the underlying argument is that stable, functional wildland networks require keystone species, particularly large carnivores, to stabilize prey and smaller predator populations and to help maintain ecological diversity and resilience in many ecosystems. And if large carnivores are essential, then connected landscapes are the most natural and effective way to achieve conservation. As we describe in more detail below, there is increasing evidence of top-down ecological regulation by carnivores in a variety of ecosystems (Terborgh

et al. 1999). Similar arguments can be made for other critical species and processes. Thus, we propose that, for most ecosystems, effective conservation policies and programs must provide for robust populations of native keystone species—particularly carnivores—at regional and continental scales.

Top-down Regulation

As already noted, one key scientific justification for large core reserves is that the architecture of viable regional conservation networks must, in most parts of North America, reflect the needs of keystone species, meaning those species whose influence is out of proportion to their abundance (Power et al. 1996). Whether top predators play keystone roles in terrestrial ecosystems has long been a contentious issue, although such roles have been unequivocally demonstrated in aquatic (Power 1990) and marine (Paine 1966, Estes et al. 1978, 1989, Carpenter and Kitchell 1993) systems. The paucity of controlled comparisons has made it difficult to evaluate whether terrestrial carnivores are keystone species. Large carnivores have been eliminated from many land areas around the world and persecuted extensively in others. Even in regions where they still persist, carnivores are notoriously difficult to observe and thus have been little studied. Furthermore, indirect effects caused by their presence or absence may take decades to appear, particularly for terrestrial vegetational changes (McLaren and Peterson 1994). For all of these reasons, it is not surprising that, as recently as 1996, a literature review concluded that "trophic cascades and top-down community regulation as envisioned by trophic-level theories are relatively uncommon in nature" (Polis and Strong 1996).

Yet mounting evidence contradicts that conclusion and is consistent with the premise that top-down regulation is a common and predictable feature of many terrestrial as well as aquatic communities. Numerous empirical studies support the view that predation is a key process that regulates the numbers of both herbivores and "mesopredators" (mid-sized carnivores) and thereby stabilizes the

trophic structure of many terrestrial ecosystems (Terborgh 1988, Marquis and Whelan 1994, Crooks and Soulé 1999, Schoener and Spiller 1999, Terborgh et al. 1999). One type of evidence derives from uncontrolled manipulations, such as the introduction or removal of predators or their prey. In an oft-repeated scenario, early seafarers released sheep, goats, pigs, rabbits, horses, cattle, caribou, and other grazing animals on predator-free islands, both oceanic and continental. The almost universal result was the devastation of native vegetation, a top-down effect that seldom occurs in the presence of top predators. The implication is that predators normally regulate herbivores on mainlands (Hairston et al. 1960). An alternative explanation is possible, namely, that island plants that evolved in the absence of herbivores might be unusually vulnerable when grazers are introduced (Carlquist 1974, Bowen and van Vuren 1997), but this explanation is not as relevant on continental islands.

Prima facie evidence of top-down interactions can also be found in the many mainland ecosystems around the globe from which humans have eliminated wolves, bears, lions, tigers, and other carnivores. In most such places, a keystone role for carnivores is masked by human hunting or large-scale replacement of native herbivores with livestock. Yet in parts of suburban and rural North America, the extirpation of large carnivores, in combination with prohibitions on hunting, appears to have caused dramatic changes in mammal and plant populations. In the absence of wolves and cougars, for instance, deer, opossums, raccoons, feral cats, beavers, and other mammals have become notoriously abundant, to the point of becoming nuisances in many areas (Garrott et al. 1993, McShea et al. 1997). In some eastern forests, overbrowsing of acorns and tree seedlings by white-tailed deer is clearly altering the pattern of tree regeneration and threatening some endangered plants (Alverson et al. 1994, McShea et al. 1997). In the South, feral pigs are equally destructive to forests and to the wildflowers that contribute 80 percent of the plant diversity of many temperate forests. Overbrowsing by ungulates, both native and exotic, is so widespread that wildflowers are disappearing, even in some of the most carefully protected old-

growth forests, such as the Heart's Content grove in Pennsylvania (Miller et al. 1992, Rooney and Dress 1997).

An overabundance of raccoons, opossums, house cats, foxes, skunks, and other small to mid-sized predators in the absence of dominant carnivores is a phenomenon known as mesopredator release (Soulé et al. 1988). The ripple effects of this phenomenon go far beyond an urban nuisance factor. Mesopredator release has been blamed for declines in or losses of gamebirds, songbirds, and other small vertebrates across a wide range of North American ecosystems, including grasslands (Vickery et al. 1994), arid scrub (Crooks and Soulé 1999), and eastern deciduous forest (Peterjohn et al. 1995).

One of the classic examples of a carnivore-mediated keystone effect has been the recovery of the native sea otter from near-extinction along the Pacific Coast of North America and the otters' subsequent predation on sea urchin populations. In the absence of control by otters, grazing urchins had stripped kelp forests and turned vast stretches of coastal waters into "urchin barrens." The resurgence of otters reduced urchin numbers and allowed the recovery of kelp forests and their associated invertebrate, fish, and seabird fauna (Estes et al. 1978, 1989). The existence of this trophic cascade was recently confirmed when killer whales again reduced sea otter populations by approximately 90 percent (Estes et al. 1998). Similarly, long-term observations of the interactions among moose, balsam fir, and colonizing gray wolves on Isle Royale, Michigan, show that when wolves are rare and moose abundant, the growth rates of balsam fir trees (on which moose browse) are depressed (McLaren and Peterson 1994, Messier 1994).

Other dramatic top-down effects, including the collapse of native fauna, have accompanied the introduction of alien predators to numerous aquatic and terrestrial ecosystems around the globe. Examples include the introductions of Nile perch to Africa's Lake Victoria, sea lamprey to the Great Lakes, mongooses to several tropical islands, the brown tree snake to Guam, and foxes to boreal and arctic regions (Zaret and Paine 1973, King 1984, Savidge 1987, Kaufman 1992, Bailey 1993).

Similar results are now coming from studies in tropical forests. Comparison of a relatively pristine site in the neotropics, Cocha Cashu Biological Station in Peru's Manu National Park, with Barro Colorado Island in Panama, which was isolated from the mainland by construction of the Panama Canal more than 80 years ago, reveals that although the two sites are similar in climate and original fauna, Barro Colorado Island, due to its small size, lost its top predators—jaguar, puma, and harpy eagle—half a century ago (John Terborgh, unpublished data). Today, Barro Colorado Island harbors markedly greater abundances of mammal species, such as agoutis, coatimundis, sloths, and howler monkeys, than Cocha Cashu, where predators occur at undiminished natural abundance. The contrast has been interpreted as signaling the absence of top-down control on Barro Colorado Island (Terborgh and Winter 1980, Terborgh 1988, 1992), although even in this case alternative explanations have been suggested (Wright et al. 1994).

A more tightly controlled comparison of predator-free and predator-containing landmasses is currently underway in and around Lago Guri, Venezuela, where hundreds of forested hilltops have been isolated by the impounded waters of an enormous hydroelectric reservoir. Within 8 years after the water reached its final stage in 1986, 75–90 percent of the vertebrate species found in the same forest type on the nearby mainland had disappeared from islands less than 15 hectares in area (Terborgh et al. 1997). Currently, a majority of the vertebrate species that persist on these islands have increased by at least an order of magnitude over mainland levels, a result that is consistent with release from top-down control.

Ongoing studies indicate that strong destabilizing forces have been unleashed by the hyperabundance of persistent animals on Lago Guri islands. Among the species showing pronounced hyperabundance are seed predators (small rodents) and herbivores (howler monkeys, common iguanas, and leaf-cutter ants). Elevated levels of seed predation and folivory attributable to these species have markedly suppressed the reproduction of canopy trees in a manner that is

consistent with a top-down trophic cascade (Terborgh et al. 1997, John Terborgh, unpublished data).

In a final example, a series of fenced enclosures was constructed nearly a decade ago in the southern Yukon, Canada, to ascertain the effects of various treatments on snowshoe hare populations. Results so far show that hare continue to follow the classic 10-year cycle of peak and decline. However, on average, hare density doubles under partial predator exclusion, triples with food supplementation, and is 11 times greater with both food supplements and protection from terrestrial (but not avian) predators (Krebs et al. 1995), showing that bottom-up and top-down processes are likely to interact.

Taken together, the results from aquatic, marine, and terrestrial ecosystems at many latitudes strongly suggest that top predators play a major regulatory role in many ecosystems. The precautionary principle compels conservationists to apply such inferences to the design and management of protected areas (Dayton 1998).

There may be a variety of situations in nature, of course, in which consumers or consumer populations are not controlled by predation. For instance, before the late Pleistocene overkill of large mammals in Australia and North and South America (Martin and Klein 1984), most of the earth's ecosystems contained megaherbivore species whose adult members, like today's elephants, were too large to be killed by the largest predators. Herbivore–plant interactions must have dominated these ecosystems, assuming that Pleistocene as well as modern megaherbivores exerted top-down controls on vegetation (Kortlandt 1984, Owen-Smith 1988, Frank et al. 1998). For some smaller herbivores (e.g., wildebeest, caribou, and bison), herd-forming, migratory behavior effectively limits the impact of predators on herd numbers, leaving a significant regulatory role for plant productivity (Fryxell et al. 1988).

Neither megaherbivores nor large herds of migratory ungulates, however, occupy much of the earth's terrestrial habitats today, making these types of ecological regulation little more than Pleistocene relics. Therefore, given the preponderance of evidence that top car-

nivores play a major role in maintaining the diversity in many of today's truncated terrestrial ecosystems, the preservation or reintroduction of viable populations of large carnivores must rank high in conservation programs for the new millennium (Soulé and Noss 1998, Miller et al. 1999, Soulé and Terborgh 1999). Much more research is needed, however, to more clearly establish the degree and limits of top-down regulation and its dependence on such factors as productivity, scale, habitat dimensionality, and types of landscape disturbance (Brian Miller, Denver Zoological Society, personal communication).

Regional Connectivity

Assuming that top-down regulation is a critical ecological phenomenon in many ecosystems, it is essential to define the conditions that support robust populations of large top carnivores. Big and secure areas are obviously necessary but are not sufficient. Indeed, isolated core areas, regardless of their size, are rarely, if ever, big enough to provide for the long-term demographic and genetic viability of these animals. Therefore, a vital element of region-based conservation programs is the maintenance or restoration of the population dynamics, interchange, and migrations in the natural, pre-agricultural, and pre-industrial landscape.

The restoration of historical disturbance regimes across landscapes is also essential. Because many abiotic forces, including hurricanes and wildfires, are uncontrollable, wildlands networks must be large enough and appropriately configured to assure that no single disturbance event can eliminate most of a certain habitat type, such as old-growth forest (Trombulak 1996, White and Walker 1997); prevent recolonization of sites from which particular species have been extirpated; or permanently perturb interactions among trophic levels (Menge and Sutherland 1976).

Although it has proven difficult to demonstrate rigorously that any specific small-scale landscape linkage increases the movement of target animal species (Rosenberg et al. 1997), the evidence suggests

that, overall, promoting the movement of individuals between habitat fragments can increase the persistence of populations and local survival of species (Forney and Gilpin 1989, Fahrig and Merriam 1994, Sjogren and Wyoni 1994, Hanski et al. 1995, Beier and Noss 1998). Species differ in how they "see" and use a degraded or fragmented landscape; consequently, solutions for connectivity must differ with the setting and the species. When designing landscape linkages, therefore, a crucial first step is identifying which species the linkage is intended to benefit (Soulé 1991). In many regions, reconnecting isolated core protected areas may be necessary just to achieve the bigness required to maintain ecological diversity and resilience (Scott et al. 1999). On a larger scale, inter-regional linkages, such as those envisioned by the Yellowstone to Yukon project (Yellowstone to Yukon Conservation Initiative 1998), are needed to accommodate gene flow and dispersal of grizzly bears and other wideranging species between the northern Rocky Mountains in the United States and northern Canada (Merrill and Mattson 1998). Landscape linkages on that scale also offer the best hope for ensuring the persistence of species in the face of predicted climate change (Hunter et al. 1988, Peters 1988). Parenthetically, we wish to point out that the term "corridor" has been adopted for so many land-use goals that its use can be misleading. It evokes the image of a linear passageway between two places and is popularly applied to many small-scale land-use features that have little if any ecological value: greenbelts, hike and bike paths, utility corridors, and railroad right-of-ways (Beier and Noss 1998, Dobson et al. 1999).

Restoration

Core protected areas, as mentioned earlier, are vital elements in regional reserve networks (Noss et al. 1999). Some current national parks, wilderness areas, and other protected lands qualify as cores, but many others do not. A distinguishing feature of core areas is the absence of motorized access—ideally, roadlessness—a characteristic that will serve the needs of space-demanding and persecution-

sensitive species, that will facilitate the return of a more natural disturbance regime, and that will minimize invasions by exotic plants and animals. The need for roadlessness and the exclusion of motorized vehicles, particularly on federal or crown lands, displeases "wise-use" opponents of conservation values. In fact, these opponents have successfully defeated many proposals for new protected areas in the US Congress and other legislative bodies by incorrectly caricaturing core reserves as human exclusion zones that forbid hunting, fishing, and other recreational uses (Chase 1995).

On the other hand, it is not essential that core areas be pristine at the time of selection to qualify for protection as cores. One of the more controversial tenets of regional conservation programs is that most core areas will require restoration of some kind, and some will require active management in perpetuity. The irony is that many lands in North America have been so poorly managed for so long that it will take decades or longer to achieve a system of protected areas in which natural fire regimes, water flows, predator–prey interactions, and other ecological processes prevail. This situation will not please those grassroots conservation activists who oppose "hands-on" management.

Another problematic aspect of this conclusion is that the restoration that will be required in many regions to reconstitute the full array of native species, habitats, and processes represents a novel endeavor on a fundamentally different and grander scale than any past efforts in ecological restoration. In fact, the design and restoration of viable regional networks of nature reserves will require no less than a revolution in restoration ecology (Simberloff et al. 1999).

The required restoration paradigm must focus on large-scale, top-down processes. This focus is in sharp contrast to the methodological traditions in restoration ecology, which are modest in scale and ambition and are oriented toward plants and bottom-up processes. Restoration ecology to date has relied largely on empirical tools developed to achieve specific effects on local, often devastated sites, such as the reestablishment of green plant cover over mine tailings (Daniels and Zipper 1988, Smith 1988) or the reclamation of

degraded or filled wetlands and tidal marshes (Zedler 1988, Middleton 1995). Furthermore, the tools developed in such local projects have not been studied in controlled, replicated experiments. Partly as a consequence, the field of restoration ecology has evolved relatively slowly despite its vital importance to conservation (Jordan et al. 1987, Dobson et al. 1997a, Janzen 1998). For example, it cannot yet provide a set of models and tools that assures restoration of a full range of native species and ecosystems (Simberloff et al. 1999).

The need for a large-scale vision in restoration does not negate the importance of small, localized restoration efforts. Such projects have many benefits, but they should not continue to be planned and implemented in isolation, with vague or unstated goals, little monitoring, and no consideration of regional priorities. Otherwise, they run the risk of creating one-of-a-kind "ecological museum pieces" with little functional role in wildlands conservation. Effective restoration requires the development of a unified conceptual framework to guide local efforts so that each project contributes to the maintenance of regionally important habitats, species, and processes.

Although restoration needs will vary from one region to the next, three key factors must be addressed in all restoration efforts: control of invasive exotic species, reintroduction or recovery of native species, and provision for the reestablishment of natural processes and disturbances. Removal or partial control of aggressive exotic species is vital to restoration because of the well-documented ability of invasive plants, animals, fungi, and microbes to disrupt ecological communities through indirect as well as direct interactions (Simberloff et al. 1997). The restoration of native species, especially keystone species, restores top-down regulatory processes. Effective restoration also requires encouraging or actively restoring periodic natural disturbances, such as fires and floods, which have proven necessary for maintaining the integrity of ecological communities (Kirkman and Sharitz 1994, Moreno and Oechel 1994, Minnich et al. 1995).

Few previous restoration efforts have dealt with the complex interplay of these three elements that shape ecological communities and species population dynamics. Rather, the most commonly used

restoration method has been the introduction of one or more plant species (not always natives) in an attempt to mimic or accelerate succession (Bradshaw 1987). The conscious manipulation of these three elements constitutes a new marriage of conservation biology and restoration ecology.

In recent decades, controversies over efforts to reintroduce wolves and grizzly bears, restore natural fire and flood regimes, and control exotic invaders such as feral pigs and horses have made it clear that all three central elements of regional-scale restoration can be expected to generate social and political opposition. Yet without the restoration of natural conditions over large areas, achieving full or effective protection for biodiversity will not be possible.

The Human Surround

Another land-use element that may be required to maintain biological diversity is buffer zones, multiple-use areas that can serve as habitat to some species and insulate core reserves from intensive human activities. A compelling argument for buffer zones is that it is impossible to secure enough public land to protect all biodiversity. In the United States and elsewhere, the majority of rare and endangered species do not exist within nature reserves, and many ecosystems are not well represented in reserves (Crumpacker et al. 1988, Hummel 1989, Dobson et al. 1997b). Although strictly protected areas are by far the most effective conservation strategy, preservation of the full array of biodiversity will require attention to species in the seminatural matrix outside reserves.

The difference between buffer zones and other exploited lands (such as industrial farmlands) is that the economic activities in the former allow the persistence of wildlife habitat that benefits the flora and fauna of adjacent core areas. In other words, the management of economic activities in buffer zones, including the exploitation of natural resources, is conducted so that the birth and death rates of native species in these zones enhance the ecological values of the region. We hasten to add, however, that most exploited multiple-

use lands are unlikely to provide effective security for ecosystems in many regions of the world (Soulé and Sanjayan 1998, Groom et al. 1999). Buffer zones will have to be carefully managed if they are not to become "ecological sinks," particularly for large animals.

Human activities in matrix lands often support unnaturally high population densities of potentially harmful species, such as crows, cowbirds, deer, raccoons, skunks, and opossums, not to mention feral dogs, house cats, and introduced species such as pigs, squirrels, rats, starlings, and house sparrows. On the other hand, the extra territory and resources in matrix lands can benefit some vulnerable species, such as migratory birds that feed in agricultural fields. Ideally, even carnivores can benefit from noncore public lands. Yellowstone National Park, for instance, is not large enough to sustain viable grizzly bear, wolverine, or wolf populations over the long term, yet the surrounding public lands, if properly managed and connected, could provide the additional needed space, as long as human-caused mortality is minimal.

Land-use planners have seldom addressed the issue of which human activities are compatible with, and sustainable, in the lands that border protected areas—in part because the mix of public and private ownership and competing land uses in these areas makes for volatile politics. The best interests of grizzly bears and wolves in the national forests surrounding Yellowstone National Park, for instance, often conflict with the perceived or short-term interests of loggers, ranchers, hunters, outfitters, and off-road vehicle enthusiasts. Education, negotiation, and incentives are partial remedies, although it is easy to be glib about the ease of resolving the competing interests among interested parties.

As already suggested, however, buffer zones may do more harm than good for wildlands, depending on the nature and interactions of the stakeholders, both human and nonhuman. For example, intensive agriculture and dense housing developments seldom make good neighbors for cores because the proximity of humans and wildlife can lead to harmful interchanges in both directions. Wild ungulates can be a serious nuisance amid crops. Exotic species, including

diseases of domestic animals, can pass into native ecosystems and populations. Native predators may prey on pets, livestock, or even human beings and be put at risk by roads or more direct forms of persecution. Frequently, a "hard edge" in the form of a fence or barrier may serve nature and society better than a buffer zone, depending on the kinds and intensities of human activity outside the protected area.

In all cases, however, attention to the culture, economy, and expectations of local people is essential for long-term success of biodiversity preservation in lands surrounding reserves. Landowners, public land managers, elected officials, and conservation organizations must all cooperate, a difficult task given their often disparate goals (Knight and Landres 1998). It also must be recognized that the nature of buffer zones and their inhabitants can change over time. Buffer zones are inherently dynamic, and their conservation values will vary with the density of the human populations and the nature and intensity of human activities. Managing these areas effectively will always require tact and patience.

Implementing the New Conservation Program

The principles espoused in this article—regional and continental networks of wildlands containing the full array of native species, including large carnivores—although biologically justified, will not be welcomed by all sectors of society. Notwithstanding the documented long-range economic and social benefits of such a continental restoration of wilderness and biodiversity (Baskin 1997, Daily 1997), energetic resistance from development exponents is predictable, even if it is based on groundless fears. Yet we believe that efforts that fall short of the program we have proposed will do little more than slow the rate of nature's demise in North America.

Alternatives to the proposed program exist and are being tried, but they are not adequate to prevent a major crisis for biodiversity and nature. Consider the Endangered Species Act (ESA). A retrospective review of the ESA undertaken 20 years after enactment (FWS 1994) revealed that at the time of listing, animals had declined

to a median population of fewer than 1000 individuals, and plants to fewer than 120 individuals. Partly because remedial action comes so late, the status of only 9 percent of listed species was judged to be improving at the time of the review, whereas that of 33 percent was still declining. The rest were either stable (27 percent) or of indeterminate status because of a lack of current information (31 percent). These numbers call for a more aggressive regional land-use planning approach, especially in light of the thousands of species waiting in the political limbo of candidacy for listing.

Although the ESA (or the threat of its implementation) has rescued some species from the brink of extinction, it is a reactive measure. Its protective provisions, for example, are not triggered until species are formally listed as threatened or endangered, by which time recovery is problematic at best. And proposed legislative amendments to make the ESA more "landowner friendly" threaten to weaken it further because they lack provisions for scientific review and cumulative, regional impact analysis. The ESA was a noble experiment, but even before it was weakened by legislative tinkering it was not up to the task of protecting native biodiversity on a landscape scale. Indeed, it was never intended to be a total solution for nature protection.

A second approach, which we refer to loosely as "sustainability," became prominent following the report of the Brundtland commission (WCED 1987) and has sought to harmonize human economic ambition with nature protection. These strategies go by various names: sustainable development, integrated conservation and development, community-based conservation, ecosystem management, and sustainable forest management (Soulé and Sanjayan 1998, Terborgh 1999). Although such development-based programs have been represented as alternatives to strict nature protection, the ascendance of the notion of sustainable development has actually slowed efforts to increase the size and number of strictly protected areas worldwide.

Underlying the emphasis on sustainable development is the assumption that non-industrialized communities currently use resources sustainably (McNeely 1988) and will continue to do so. This premise, however, ignores the recent changes in these commu-

nities due to the adoption of Western technologies and rapid population growth. Moreover, retrospective evaluations of sustainable development projects show that most have achieved neither sustainability nor conservation (Redford and Sanderson 1992, Robinson 1993, Kramer et al. 1997, Bowles et al. 1998, Wells et al. in press). Similar trends are apparent in the United States. Land management concepts currently in vogue, such as ecosystem management, have allowed land managers and resource agencies to argue against setting aside more wilderness areas. Instead, some public lands managers favor a "landscape without lines" (Everett and Lehmkuhl 1997), wherein, it is hypothesized, multiple-use management can protect the full range of biodiversity and ecological processes. There is, however, no empirical justification for the assumption that multiple-use management is an adequate substitute for strict protection. For example, motorized access and relatively high road densities, which are a virtual management imperative for multiple use, are detrimental to the viability of large carnivores (e.g., Green et al. 1997).

A third tactic for improving the protection of biodiversity worldwide has been the setting of target percentages by nations or international conservation organizations. For instance, many conservation groups worldwide have endorsed a guideline that calls for protection of 10–12 percent of each nation's total land area, a target acknowledged to be based more on political expediency than on scientific principles. But because current conservation targets are not based on science, they could actually exacerbate the problem. Popularization of such numbers may lead the public to believe that adequate steps are being taken to prevent the predicted mass extinction, whereas, in fact, scientific studies suggest that much greater percentages of land area must be protected to achieve conservation (Soulé and Sanjayan 1998). Where such science-based targets have been adopted, such as in some provinces in Canada, the political process has often subverted the biologically based goals by emphasizing the protection of unproductive lands that are already well represented in the system of protected areas (Hummel 1996, Soulé and Sanjayan 1998).

A central concept of the new program for conservation that we have described is that large, interconnected core protected areas are critical elements in regional wildland networks and that, in these areas, the needs of large carnivores, other keystone species, and large-scale natural processes, such as fire, must be given priority over capital-intensive economic activity. Fortunately, it appears that nature protection benefits local communities materially and spiritually more in the long run than most economic development schemes that ultimately destroy environmental values and erode the communal bonds that bind people to the land and to each other.

The program proposed here complements existing currents in the conservation movement (Soulé and Noss 1998, Soulé and Terborgh 1999). The elaboration of this progam by the fields of conservation biology and restoration ecology can help conservationists implement effective measures to maintain critical species, ecosystems, and landscape connectivity before the human enterprise overtakes all.

Acknowledgments

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Introduction to *Ecological Effectiveness: Conservation Goals for Interactive Species*

In this paper we defined the category of "strongly interactive species," which are species that have major impacts and whose removal causes changes in ecological structure or function, loss of resilience to disturbance, or decreased native species diversity. Within strongly interactive species we identified two classes, keystone and foundation species.

Keystone species are those that strongly affect ecosystems at low densities. These are often top predators like wolves, which are effective hunters of large herbivores like elk. By limiting elk numbers and distribution, wolves may indirectly affect the abundance and distribution of plants.

Foundation species also have profound ecological effects, but do so by virtue of abundant numbers. Examples include bison, prairie dogs, willows, cod, krill, bees, and mound-building termites. Prairie dog colonies, which in North America once occupied a half million square kilometers with 50 individuals per acre, greatly increase plant and vertebrate diversity. Some vertebrates like the black-footed ferret subsist on prairie dogs and others, like burrowing owls, shelter in

their burrows. Prairie dogs also decrease woody shrubs and increase grasses and forbs, and their browsing causes forbs to increase nitrogen fixation over large areas.

A sad reality is that the federal Endangered Species Act focuses on preventing extinction but places little importance on protecting enough individuals over a wide-enough area to ensure ecological effectiveness. For it is not enough to maintain a few "symbolic" populations of gray wolves; there must be enough wolves to meaningfully decrease the white-tailed deer population. We argued that in order to maintain well-functioning ecosystems, strongly interacting species should be restored to effective numbers throughout all their historic range. An interesting question is whether strongly interacting species that have become extinct should be replaced with ecological analogues, for example, reintroducing rhinos and elephants to North America (paper 6).

What do we know about how many individuals constitute an ecologically effective population? How many wolves are enough? Studies of wolves and sea otters show that the answer depends on factors that vary over space and time. For example, wolves are more effective at reducing elk numbers when bears and other predators are present, and when deep snow makes it harder for elk to escape.

Sea otters do a better job at keeping sea urchins from destroying kelp forests in southeastern Alaska than they do in the Aleutian Islands, where there are deep-water populations of urchins that can replace inshore urchins eaten by otters. The sea otter–urchin interactions also show that as top predators like otters are progressively reduced in number, a tipping point may be reached where prey numbers explode. These facts lead to two conclusions: (1) estimates of ecologically effective population sizes should be based on local data, and (2) a species may be strongly interactive at one location or one time, but not at others. Nature can be inconveniently complex. This is why I tell audiences that the answer to all ecological questions is "it depends."

Ecological Effectiveness: Conservation Goals for Interactive Species

Michael E. Soulé, James A. Estes, Joel Berger, and Carlos Martinez Del Rios

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Introduction

Although the first-order effects of the biodiversity crisis—the loss of species—are dire, the second-order consequences—the loss of species interactions—may be more ominous. For instance, Jackson et al. (2001) conclude that, worldwide, the functional dynamics of coastal marine ecosystems were grossly altered decades or centuries ago and that many problems attributed to such recent processes as disease, pollution, and global warming in fact were likely entrained by the historical removal of marine predators. Thus, a primary mission of conservation should be to identify and restore species that interact strongly with others.

We define strongly interactive species operationally because the diversity of potential influences of a strong interactor (sensu Power et al. 1996; Berlow et al. 1999) on other species, species interactions, and ecosystem processes precludes a precise definition. Thus, a species is highly interactive when its virtual or effective absence

leads to significant changes in some feature of its ecosystem(s). Such changes include structural or compositional modifications, alterations in the import or export of nutrients, loss of resilience to disturbance, and decreases in native species diversity. Of course, changes in the abundance, distribution, and behavior of other species are likely to underlie those changes detected at the community and ecosystem levels.

At least two typologies have been invented to categorize highly interactive species. Some authors emphasize the type of interactions; among these are mutualists such as pollinators, spore and seed dispersers; consumers (such as large predators), and ecosystem engineers such as beaver (*Castor canadensis*) (Naiman et al. 1986) and elephants (*Loxodonta africana*) (Owen-Smith 1988). Another popular categorization is the distinction between "keystone species" and nonkeystone species. Keystone species (Paine 1969) are defined as having particularly strong, ramifying interactions (Mills et al. 1992), the strength of which are disproportionate to their population densities (Power et al. 1996) and not wholly duplicated by other species (Kotliar 2000). Where the density of a keystone species falls below some threshold, species diversity may decrease, triggering ecological chain reactions ending with degraded or simplified ecosystems (Estes & Palmisano 1974; Jones et al. 1998; Crooks & Soulé 1999; Terborgh et al. 1999; Jackson et al. 2001; Terborgh et al. 2001). Among such "keystones" are large predators (Estes & Palmisano 1974; Carpenter & Kitchell 1993; McLaren & Peterson 1994; Terborgh et al. 1999; Ripple & Larsen 2000). Keystone species can be thought of as having the highest per capita interaction strengths (Berlow et al. 1999).

Clearly, though, the keystone-nonkeystone dichotomy arbitrarily segregates a continuous, multidimensional spectrum of interaction strength (Hurlburt 1997). Moreover, many highly interactive species are too abundant to be classified as keystone species (Soulé & Noss 1998). For these reasons, we suggest using the term *foundation species* for highly interactive species that are often extremely

abundant or ecologically dominant, though the earlier use of this term (Dayton 1972) differed from ours. Likely examples of foundation species include bison (*Bison bison*), prairie dogs (*Cynomys* spp. Miller et al. 1994), cottonwood and aspen trees (*Populus* spp.), American chestnut (*Castanea dentata*), cod (*Gadus* spp.), krill (*Euphausia* spp.), bees, and mound-building termites, to name only a few.

Our purpose here is to argue that goals embodied in laws and policies that apply to the conservation of biodiversity should include the protection of ecological interactions, particularly those interspecific interactions critical to the maintenance of ecological complexity at all scales—species, ecosystems, watersheds, landscapes, regions. We propose two such goals. The first is the goal of geographic representation of interactions, which calls for extensive geographic persistence of highly interactive species. Conservation plans and objectives (design, management, and recovery) should provide for the maintenance, recovery, or restoration of species interactions in as many places as feasible, both within the historic range of highly interactive species or in other sites where the consideration of climate change and other factors is appropriate.

The second goal concerns ecological effectiveness within ecosystems, communities, or landscapes. Conservation plans should contain a requirement for ecologically effective population densities; these are densities that maintain critical interactions and help ensure against ecosystem degradation. This goal replaces the de facto nonecological practice of requiring only the attainment of minimum viable populations.

We explore the application of these two goals in the following two case studies: sea otters (*Enhydra lutris*) in North Pacific coastal marine ecosystems, and wolves (*Canis lupus* and *Canis l. lycaon*) in North American terrestrial ecosystems. Although the focus in these cases is carnivores, the principles and conclusions should apply to any highly interactive species. Our choice of examples is limited by space considerations and information availability (e.g., it is unfor-

tunate that the consequences of the disappearance of pollinators are almost unknown; Buchmann & Nabhan 1996; Kearns et al. 1998; Kremen & Ricketts 2000).

Sea Otters and Kelp Forests

Sea otters and kelp forests provide one of the better-known examples of how large predators influence their associated ecosystems. This is because of an unplanned, anthropogenic experiment provided by the Pacific maritime fur trade. Abundant sea otter populations inhabited coastal waters of the North Pacific Ocean and southern Bering Sea throughout most of the Pleistocene and recent eras but were reduced to a few remnant colonies by the fur trade. If scientists had viewed the system when otters were either abundant everywhere or nearly extinct everywhere, in all likelihood they would have failed to recognize the species' profound impacts. By the early 1970s, however, populations had returned to high levels in some areas and remained absent in others, at which point the experiment was underway.

But another ingredient was necessary: a conceptual model in which predators are viewed as regulators of herbivore populations. The landmark paper by Hairston et al. (1960) provided this. The sea otter's influences on coastal ecosystems were seen by contrasting places within the species' historical range where they were present or absent, and by following particular areas through time as these places were recolonized by otters and their numbers increased (Estes & Duggins 1995). In all cases these contrasts demonstrate a strong limiting influence of sea otters on their most important prey, sea urchins, which consume kelp. Thus, where sea otters abound so do lush kelp forests, and where sea otters are absent the habitat is typically deforested by hyperabundant sea urchins. Numerous indirect effects also result from this "trophic cascade" (Paine 1980), owing to the importance of kelp as a source of food and habitat for dozens of other coastal species (Duggins et al. 1989; Estes 1996).

These interactions have been known for many years (Estes & Palmisano 1974). But how many sea otters are needed to maintain a healthy kelp forest? This question can be more precisely considered by envisioning the patterns of change in sea urchin populations across the range of possible sea otter densities (from 0 to d_{max}), by envisioning the same relationship between sea urchin and kelp abundance, and ultimately by combining these patterns to illustrate relationships between the abundance of sea otters and the abundance of kelp (Fig. 1).

First, we must know whether the abundance relationships are linear or nonlinear. If they are nonlinear, then we must also know their trajectories and whether these trajectories vary with directionality. This knowledge comes from (1) theoretical studies of consumer-prey interactions (Noy-Mier 1975; May 1977), (2) experimental studies of plant-herbivore dynamics (Konar & Estes 2003), and (3) observations of ecosystem change following the growth (Estes & Duggins 1995) and decline (Estes et al. 1998) of sea otter populations.

Systems dominated by kelp and deforested by sea urchins commonly behave as alternate stable-state communities (sensu Lewontin 1969; Sutherland 1974; Scheffer et al. 2001). That is, the transitional dynamics between these states is not smooth and continuous but instead is characterized by thresholds and breakpoints. Any consumer-prey system can take multiple stable states if, as prey becomes more abundant, consumers become satiated and prey production rate grows and falls as a standard yield curve (Fig. 2). In addition, the deforested state resists invasion by kelp because hungry sea urchins actively move across the sea floor, consuming new kelp recruits (Harrold & Reed 1985). Only when sea urchins either stop moving or occur in low numbers can kelp become reestablished (Konar 2000). Similarly, established kelp populations slow sea urchin invasion by physically beating back the invaders (accomplished through an interplay between water motion and the plants' supple morphology) and by producing enough detrital food to cause the otherwise
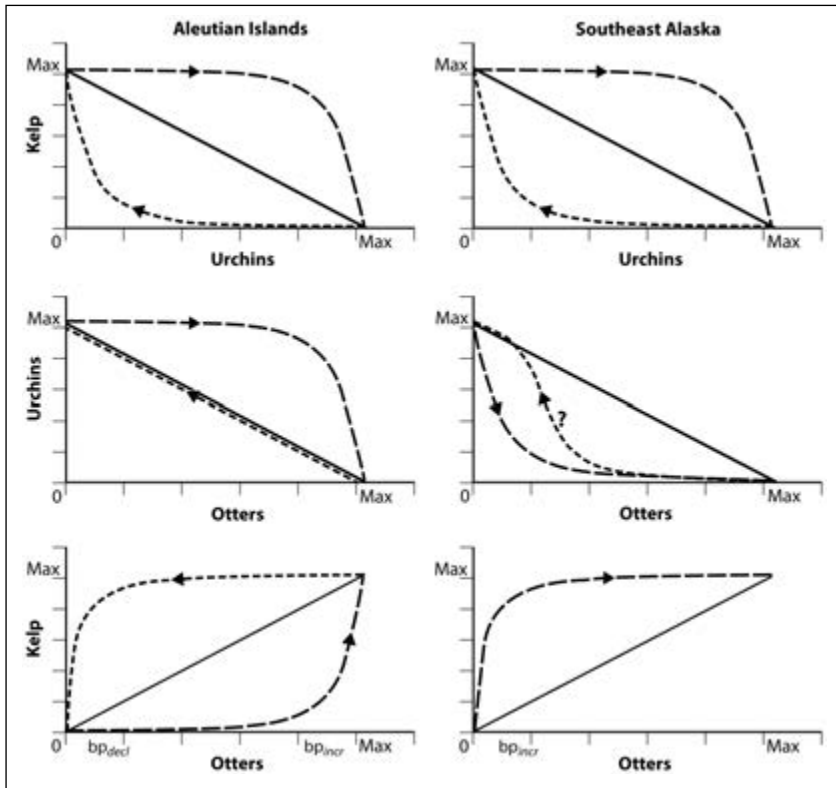
Figure 1. Functional relationships between population abundances of the drivers (horizontal axes) and passengers (vertical axes) in kelp-forest ecosystems of the North Pacific Ocean. Solid lines indicate hypothetical linear response functions and broken lines the known or suspected functional relationships. Dashed and dotted lines portray the respective response functions for increasing and declining driver populations. Functional relations between the abundance of kelp and sea urchins are shown in the top panels; between sea urchins and sea otters in the middle panels; and the resulting relationships between sea otters and kelps in the bottom panels. Sea urchin recruitment is strong and continuous in the Aleutian Islands and episodic in southeast Alaska. The functional relationships between sea urchin and kelp abundance (top panels) and their differing trajectories for increasing or declining urchin populations are both nonlinear. Sea urchin abundance in the Aleutian Islands varies linearly with declining otter numbers (middle, left panel). The varying dynamics between sea otters and sea urchins on the one hand and between sea urchins and kelp on the other result in differing breakpoint densities (bottom panels) for increasing (bp_{incr}) and declining (bp_{decl}) otter populations in the Aleutian Islands and southeast Alaska. The dynamic details for establishing the bp_{decl} for the kelp-otter relationship (bottom, right panel) are unknown.
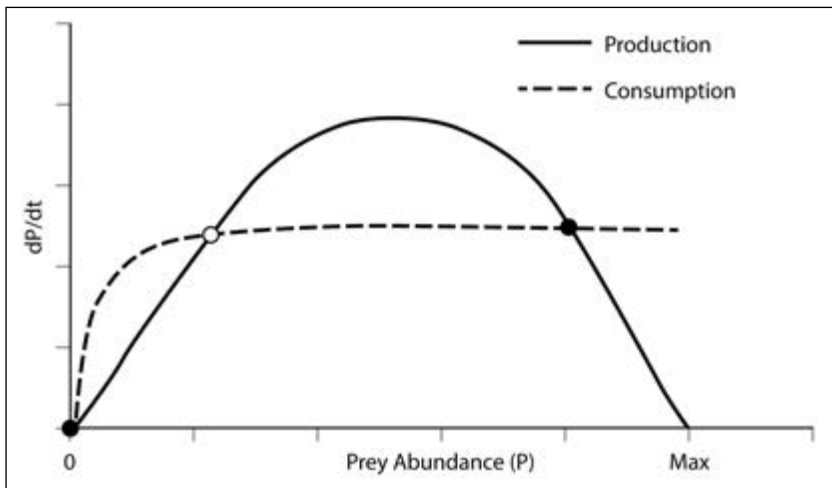
FIGURE 2. Dynamic model for the maintenance of multiple stable equilibria in prey abundance when prey production and consumption rates (dP/dt) vary with prey abundance (P), as shown (i.e., production rate varies as a standard yield curve and consumption rate satiates). The intersections between production and consumption define equilibria. Solid circles are stable equilibria; open circle is unstable (after May 1977; Noy-Mier 1975).

mobile urchins to become sessile, sit-and-wait consumers. For these reasons, intermediate ecosystem configurations between the kelp-dominated and deforested states are unstable and highly transitory (Estes & Duggins 1995; Konar & Estes 2003).

Consequently, the functional relationship between kelp abundance and sea urchin density is not linear, with the precise functional form differing depending on whether it starts from the kelp-dominated or deforested state (Fig. 1). Abrupt phase shifts between kelp-dominated and deforested states thus occur with changing abundance of sea otters. We refer to the number of otters required to effect this change as the breakpoint density, d_{bp} (Fig. 1). An ecologically effective population density for sea otters must be $\geq d_{bp}$. As we will show, d_{bp} depends both on the consumer-prey dynamics between sea otters and sea urchins and on the replenishment of sea urchins (by immigration and recruitment) to exploited populations.

Sea otters feed in a size-selective manner, targeting the larger urchins (VanBlaricom 1988; Estes & Duggins 1995; Watt et al. 2000) and avoiding the smaller ones. In the Aleutian Islands, where recruitment of urchins is frequent and strong, enough small urchins remain uneaten to prevent kelp-bed establishment. In contrast, where sea urchin recruitment is weak or episodic, as it often is along the western continental margin of North America (Pearse & Hines 1987; Ebert & Russell 1988; Estes & Duggins 1995), sea urchin populations are constituted of large individuals so that even relatively few sea otters can prevent destructive herbivory by sea urchins. This is why the otter-urchin recovery functions differ so strongly between the Aleutian Islands and southeastern Alaska (Fig. 1, middle panels). The combined result of these herbivore-plant and carnivore-herbivore relationships is a striking interregional difference in the recovery dynamics of sea otters and kelp forests (Fig. 1, bottom panels). Sea urchin barrens persist in the Aleutian Islands following the reestablishment of even large numbers of sea otters, whereas lower densities of sea otters and shorter time periods are sufficient to affect the phase shift in southeast Alaska and British Columbia. In British Columbia, the phase shift is accelerated by a sea urchin "flight response," which occurs when debris from urchin tests is discarded by foraging sea otters and falls to the sea floor. Urchin-free patches develop around this debris. Kelps rapidly recruit into these patches, creating a mosaic of kelp-dominated and deforested patches (Watson 1993).

The aforementioned examples involve growing sea otter populations. Kelp forest phase shifts also occur in the Aleutian Islands, where otter populations have declined, purportedly because of killer whale predation (Estes et al 1998). The declines began in the late 1980s. By 1993 otter numbers had been reduced to about 50% of equilibrium density (Doroff et al. 2003), and sea urchin abundance had approximately doubled (Watt et al. 2000). By 1997 otter numbers had stabilized at about 10% of equilibrium density, urchin abundance had increased about eightfold, and kelp populations had

collapsed throughout most of the shallow sublittoral zone (Estes et al. 1998). These data indicate a linear response function between declining sea otters and increasing sea urchins (Fig. 1, middle left panel).

The absence of any apparent lag in this function is at first perplexing, given the slow growth rate of sea urchins in the Aleutian Islands (Estes & Duggins 1995). In this region, however, urchin populations are enhanced by the migration of post-metamorphosis individuals from source populations in deep water. These migrating urchins are probably attracted to shallow water by the more abundant food. Casual observations made by divers in the early 1990s and measurements of the rate of kelp tissue loss to herbivory by sea urchins (Steinberg et al. 1995) indicate that sea otter density was still greater than d_{bp} at that time. In the declining case, therefore, the phase shift occurred when the sea otter population was reduced to somewhere between one-half and one-tenth of equilibrium density. The breakpoint density for declining sea otter populations along the continental margin of North America is unknown but may be even lower than this, given the more episodic recruitment of sea urchins and the more extensive occurrence of soft-sediment habitats (which are unsuitable for sea urchins) in deeper water.

In summary, the sea otter–kelp forest system provides a glimpse into some of the functional complexities of the relationship between carnivore population abundance and ecosystem function. Strong nonlinearities in the nature of plant-herbivore interactions at the base of the food web result in distinct breakpoints in the number of sea otters required to maintain the kelp forest ecosystem. In reference to the goal of ecologically effective densities, these breakpoints serve as conveniently discrete metrics for an ecologically effective population density of sea otters. In reference to the goal of geographic representation, however, ecologically effective densities will depend on context: they are not the same everywhere and under all circumstances. The ecologically effective population density for sea otters may vary by an order of magnitude or even more, depending

on geographic locale and whether it is approached from low or high density. In all situations observed, however, otters attain ecologically effective densities if they are not harassed by human beings or eaten by killer whales.

Wolves, Herbivores, and Vegetation

Overbrowsing by ungulates is now recognized as a factor in the structural alteration, the simplification, and even the disappearance of forests throughout the world (Oksanen & Oksanen 2000). In the United States, overbrowsing by native ungulates, particularly white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*), is causing observable changes in the plant species composition in many ecosystems (Miller et al. 1992; Waller & Alverson 1997; Ripple & Larsen 2000) and is a likely consequence of the absence of effective predation by formerly widespread native carnivores and in some places by aboriginal human hunters (Kay 1994).

The impacts of white-tailed deer in the U.S. Midwest and in the deciduous forests of the eastern United States are well known. Among the influences frequently observed are changes in the composition of forests, local extirpation or inhibition of many herbs and tree seedlings, transformation of understories from mixed herbaceous species to park-like assemblages dominated by ferns and grasses (Waller & Alverson 1997), and negative impacts on breeding songbirds (DeCalesta 1994; McShea & Rappole 1997). Among the tree and shrub species for which recruitment failure has been documented (Waller & Alverson 1997) are oaks (*Quercus* spp.), white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), and Canada yew (*Taxus canadensis*).

Moose (*Alces alces*) are effecting similar changes in vegetation in parts of Canada and the United States in places where wolves are absent (Connor et al. 2000; Berger et al. 2001). In several such localities moose populations are five to seven times higher than in more

productive systems with wolves (Cederlund & Sand 1991; Crête & Manseau 1996; Berger et al. 2001). For all three of the large ungulates mentioned above, the virtual absence of predation by wolves and the failure of conservation to achieve their broad ecological representation (goal 1) have contributed to ecological degradation.

The National Park Syndrome

One pattern of ungulate-caused landscape simplification, now common enough to be called a syndrome, is occurring in some national parks in the Rocky Mountain region of the United States. The symptoms include the virtual disappearance of some vegetation types—notably riparian habitat and beaver (*Castor canadensis*) wetlands—and the failure of aspen to recruit into the canopy for the last 80 years, particularly in Yellowstone National Park (YNP) (Ripple & Larsen 2000). This syndrome likely has several interacting causes, but in YNP the two most important appear to be (1) the effective elimination of wolves by around 1925 and (2) the termination of elk population limitation by artificial means after 1968 (Hess 1993; Singer et al. 1998*a*). Similar changes have occurred in Rocky Mountain National Park (RMNP) (Singer et al. 1998*b*). One consequence of these perturbations has been the ecological release of elk (e.g., Ripple & Larsen 2000), but climate change and the suppression of fire during most of the twentieth century probably exacerbated the vegetational changes (Romme et al. 1995; Romme et al. 1997; Singer et al. 1998*b*).

After artificial control of Yellowstone elk ended, the northern range population grew from about 4500 in 1968 to about 20,000 by 1995, reaching winter densities of 12/km² by the 1990s, among the highest known densities of elk anywhere. One of the consequences has been heavy browsing by elk on willows (*Salix* spp.), a favored food of beavers. Riparian habitat formerly dominated by willows in parts of YNP has declined 60% in the last 70 years. Consequently, beavers and the beaver pond wetland ecosystem disappeared, and

this has triggered other landscape changes. Beaver ponds enhance willow growth by increasing the height of water tables, enhancing productivity by increasing the inputs of nitrogen and phosphorus (Naiman et al. 1986), and preventing erosion. Compared with a century ago, runoff is more concentrated, and many streams are now downcut more than 1 m below levels when beavers were present, further lowering water tables. In addition, stream channels are now straighter and less complex (Singer et al. 2003).

A similar situation occurs in RMNP, where willow patches have declined (Singer et al. 1998b; Singer et al. 2002) and beaver numbers have decreased about 80–90% on the winter elk range (Peinetti et al. 2001). After wolves and grizzly bears were extirpated in Grand Teton National Park (GTNP), moose populations irrupted and riparian willow communities were significantly reduced in contrast to outlying regions beyond park borders, where sport hunting of moose remains legal (Berger et al. 2001). Thus, in YNP, RMNP, and GTNP, the modification of vegetation and linked changes in animal communities is likely attributable, at least in part, to the anthropogenic eradication of large carnivores (Berger et al. 2001).

Hansen and Rotella (1999) found that 25% of breeding birds surveyed in the Yellowstone region specialize on cottonwood, aspen, and willow communities. They refer to these areas as "hotspots" and "source areas" for some species and note that they are "critical for maintaining population viability over the local region." Berger et al. (2001) attribute a similar decrease in Neotropical migrant bird diversity in GTNP to overbrowsing by moose in riparian willow communities. They found that control areas outside the park that supported lower moose densities had higher bird diversity. It is ironic that national parks have suffered greater damage from ungulate herbivory than lands that are less protected, such as those managed by the U.S. Forest Service. The apparent reason for this is that sport hunting of ungulates is permitted outside these parks.

Will the parks recover ecologically with the return of the wolf? Wolf reintroduction started in 1995 in YNP, and it is expected that

wolves, in combination with other carnivores, will reduce elk populations by about 20–30% below food- and weather-limited carrying capacity in both YNP and RMNP (Singer et al. 2002). The current wolf population in YNP is >200, and the wolves, along with other predators, are killing about 2000 elk annually (M. K. Phillips, personal communication). The elk population (currently about 12,000 in the northern range) is thought to be about 15% below what is expected without wolves.

Just as for sea otters, ecologically effective densities of wolves depend on several interacting factors that vary geographically. For wolves, these include (1) coexistence of predator species, (2) weather, and (3) interactions between forage quality and quantity, productivity, and the number and abundance of prey species. Sympatry with other carnivore species may decrease the effective density of wolves (Gasaway et al. 1992; Messier 1994; Crête & Manseau 1996; Sinclair & Pech 1996; Orians et al. 1997; Mech et al. 1998; Boyce & Anderson 1999). For example, grizzly bears (*Ursus horribilis*) may increase their meat intake by usurping prey killed by wolves, thus forcing the wolves to kill more frequently. Multiple predators limited moose populations in boreal forests to about one-fifth of food-limited carrying capacity (Messier & Crête 1985; Gasaway et al 1992; Messier 1994), a clear indicator of ecological effectiveness. According to Crête and Manseau (1996), where bears are preying on moose calves in the presence of wolves, the density of moose can drop as low as 0.5 moose/km², which is seven times lower than in areas with worse forage and harsher winter conditions but lacking wolves. In YNP, several carnivore species are undoubtedly contributing to the limitation of elk (Orians et al. 1997; Peterson 1999), although bears, cougars, and coyotes had little noticeable impact prior to wolf introduction (Coughenour & Singer 1995).

Prey behavior as well as prey numbers are affected by predators, further reducing herbivory in some plant communities (Brown et al. 1999; Terborgh et al. 1999). Wolves, for example, can change the distribution of ungulates in time and space (deer, Nelson & Mech

1981; moose, Berger et al. 2001*b*) and affect group sizes (musk ox [*Ovibos moschatus*], Heard 1992). Although elk numbers per se have yet to decline dramatically in YNP, some patches of sapling aspen and some patches of willow have been increasing in height since about 1997 (Ripple & Larsen 2000; Singer et al. 2002), suggesting that wolves have reached ecologically effective densities in small parts of Wyoming (in the vicinity of YNP and GTNP) and possibly in Montana and Idaho.

Geographic and temporal variation in weather affects the local distribution of prey species and their ability to escape predators. For example, deep snow (Crête & Manseau 1996) or episodic, severe storms can increase the vulnerability of large ungulates, facilitating their capture (Peterson 1999; Mech et al. 1998; Post et al. 1999) and thereby lowering the effective density of their predators.

Wolves are more likely to persist in a region that contains more than one species of prey (Fuller & Murray 1999). Where beavers are relatively abundant, wolf numbers stabilize at higher densities than in places where moose are the only available large herbivore (Messier & Crête 1985). Predators can shift from one prey species to another because the densities of different prey species may be uncorrelated over seasons and years. Therefore, a diversity of prey species is likely to increase the spatial effectiveness (goal 1) of wolves as regulators of prey.

Productivity interacts with the above factors, including the diversity of prey, in a variety of interesting ways affecting predator distribution. Because of low productivity in some boreal or tundra ecosystems, at least two prey species are required to maintain large carnivores (e.g., Crête & Manseau 1996). In fact, large predators cannot exist where productivity is less than about 0.7 kg/m²/year (Oksanen & Oksanen 2000). Finally, in the presence of wolves, cervid (mostly moose) biomass in the boreal zone does not increase with increasing primary production (Crête & Manseau 1996: Oksanen & Oksanen 2000), suggesting that wolves are effectively regulating (goal 2) their prey (Messier 1994).

Conclusions

Our conclusions or working hypotheses about ecologically effective densities for highly interactive species that may be drawn from the sea otter and wolf cases include the following:

(1) The absence of these species from previously occupied regions may result in the simplification of ecosystems.

(2) Ecologically effective densities of strongly interacting species can vary by as much as an order of magnitude and are highly contingent and contextual.

(3) For these carnivores, the ecological variables that may influence determinations of effective densities include primary productivity, weather, prey behavior and its variation in space and time, the presence of multiple (alternative) prey species, competition among herbivore prey, prey life history and its variation in space, and the potential for nonadditive interactions and competition among predators species. A similar list probably applies to many highly interactive species.

(4) If not harassed, predator species (individually or as a local "guild") naturally achieve densities above the threshold for ecological effectiveness, except in regions of exceptionally low or variable primary productivity.

Are these tentative conclusions generally applicable in the practice and science of conservation? The answer depends in large part on the proportion of focal or endangered species that are highly interactive. That is, are the two goals mentioned above—extensive geographic representation and ecologically effective functionality within ecosystems—applicable to many species in many places? This question has not been answered, but a survey being conducted by M.E.S. of recovery plans for endangered species in the United States and its territories gives some preliminary results. Nearly half of the endangered species or subspecies included in the approximately 44 existing plans for mammals could be classified as strong interactors (Table 1). The relevant interactions include predation, parasitism,

TABLE 1. Occurrence of strong interactions among mammals for which recovery plans exist under the U.S. Endangered Species Act.

Species	Ecology/food	Strong Interactions
Marianna (*Pteropus mariannus*) (on Guam) and Little Marianna (*Pteropus tokudae*) fruit bats	frugivorous	none known
Grey bat (*Myotis grisescens*)	insectivorous	none known
Indiana bat (*Myotis sodalis*)	insectivorous	none known
Ozark (*Plecotus townsendi ingens*) and Virginia big-eared (*P. t. virginianum*) bats	insectivorous	none known
Hawaiian hoary bat (*Lasiurus cinereus semotus*)	insectivorous	none known
Lesser long-nosed bat (*Leptonycteris curasoae yerbabuenae*)	pollinator, seed disperser for cacti and agave	yes; important for reproduction of columnar cacti and agave spp. (Nabhan & Fleming 1993)
Mexican long-nosed bat (*L. nivalis*)	pollinator, seed disperser for cacti and agave	yes; important for reproduction of columnar cacti and agave spp. (Nabhan & Fleming 1993)
Grizzly bear (*Ursus arctos*)	omnivore; locally highly carnivorous	yes; habitat disturbance; important nitrogen disperser where feeding on salmon
Louisiana black bear (*Ursus americana luteolus*)	omnivore; locally carnivorous*	probable; as seed disperser and in association with other predators (Gasaway et al. 1992; Jacoby et al. 1999)
Black-footed ferret (*Mustela nigripes*)	specialist on prairie dogs	none known; possible
Southern sea otter (*Enhydra lutris*)	molluscs, urchins, fish	yes; see text
San Joaquin kit fox (*Vulpes macrotis mutica*)	rodents, lagomorphs, insects	possible
Eastern timber wolf (*Canis lupus lycaon*)	predator of deer, moose, beaver	yes; see text
Mexican wolf (*Canis lupus baileyi*)	predator on deer, elk, etc.	yes; see text

TABLE I (CONTINUED). Occurrence of strong interactions among mammals for which recovery plans exist under the U.S. Endangered Species Act.

Species	Ecology/food	Strong Interactions
Northern Rocky Mountain wolf (*C. l. nebulosa*)	predator on elk, deer, moose, etc.	yes; see text
Red wolf (*Canis rufus*)	predator on deer, raccoons, nutria, etc.	yes (Phillips et al. 2003)
Eastern cougar (*Felis concolor*)	predator on deer, smaller animals	yes (Logan & Sweanor 2001)
Florida panther (*Felis concolor coryi*)	predator on deer, smaller animals	yes (Logan & Sweanor 2001)
Ocelot (*Felis pardalis*)	predator on small mammals, brocket deer, birds, fish, reptiles, invertebrates	possible
Hawaiian monk seal (*Monachus schavinslandi*)	piscivorous	possible
Pt. Arena Mountain beaver (*Aplodontia rufa*)	herbivore, strong burrower	yes (Maser 1998); burrows support skunks, salamanders, moles, shrews, chipmunks, weasels
Appalachian northern flying squirrel (*Glaucomys sabrinus fuscus* and *G. s. coloratus*)	feeds on hypogeous fungi	possible (Carey 1991; Carey et al. 1999); possibly important for forest maintenance and productivity based on role in dispersal of ectomycorrhizal and bacterial spores
Delmarva Peninsula fox squirrel (*Sciurus niger cinereus*)	feeds most on fungi, flowers	possible (Steele & Koprowski 2001); possible role in fungal spore dispersal
Mt. Graham red squirrel (*Tarmiasciurus hudsonicus grahamensis*)	feeds on conifer, aspen seeds, macrofungi, rusts, birds, mast, berries	possible (Steele & Koprowski 2001); effective nest predator

TABLE 1 (CONTINUED). Occurrence of strong interactions among mammals for which recovery plans exist under the U.S. Endangered Species Act.

Species	Ecology/food	Strong Interactions
Utah prairie dog (*Cynomys parvidens*)	herbivore	yes (Kotliar 2000; Miller et al. 2000); prairie dogs often considered keystone or foundation species
Pacific pocket mouse (*Perognathus longimembrus pacificus*)	granivore	none known
Giant kangaroo rat (*Dipodomys ingens*)	granivore	yes (U.S. Fish and Wildlife Service [USFWS] 1998); mounds and burrows provide refugia for many other species; strong effects on vegetation; highly competitive with other rodents; important prey of carnivores
Tipton kangaroo rat (*Dipodomys nitratoides nitratoides*)	granivore	yes (USFWS 1998); see *D. ingens* above
Fresno kangaroo rat (*Dipodomys nitratoides exilis*)	granivore	yes (USFWS 1998); see *D. ingens* above
Short-nosed kangaroo rat (*Dipodomys nitratoides brevinasus*)	granivore	yes (USFWS 1998); see *D. ingens* above
Morro Bay kangaroo rat (*Dipodomys heermani morroensis*)	granivore	probable (Goldingay 1997); see *D. ingens* above
Key Largo woodrat (*Neotoma floridana smalli*)	herbivore	none known
Silver rice rat (*Oryzomys palustris hefneri* = *O. argentatus*)	omnivore	none known
Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*)	herbivore	none known
Southeastern beach mouse (*Peromyscus polionotus niveventris*)	herbivore	none known

TABLE 1 (CONTINUED). Occurrence of strong interactions among mammals for which recovery plans exist under the U.S. Endangered Species Act.

Species	Ecology/food	Strong Interactions
Choctawhatchee, Perdido beach mouse and Alabama beach mouse (*P. polionotus subsp.*)	herbivore	none known
Anastasia Island beach mouse and southeastern beach mouse (*P. polionotus phasma*)	herbivore	none known
Hualapai Mexican vole (*Microtus mexicanus hualapaiensis*)	herbivore	none known
Florida salt marsh vole (*Microtus pennsylvanicus dukecampbelli*)	herbivore	none known
Amaragosa vole (*Microtus californicus scirpensis*)	herbivore	none known
Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*)	herbivore	none known
Selkirk Mountain caribou (*Rangifer tarandrus caribou*)	herbivore	none known
Columbian white-tailed deer (*Odocoileus virginianus leucurus*)	herbivore	none known
Key deer (*O. v. clavium*)	herbivore	none known
Sonoran pronghorn (*Antilocapra americana sonoriensis*)	herbivore	none known
Peninsula range bighorn sheep (*Ovis canadensis*)	herbivore	none known
Florida manatee (West Indian manatee) (*Trichechus manatus lativostis*)	herbivore	none known
Puerto Rican West Indian manatee (*Trichechus manatus lativostis*)	herbivore	none known
Humpback whale (*Megaptera novaeangliae*)	krill, small schooling fishes	none known

*Extent of predation and its ecological effects unclear.

pollination, defoliation, seed and spore dispersal, and cavity and burrow construction. The proportion of highly interactive species, however, could be greater given the lack of studies necessary to make such determinations.

Endangered mammals may not be typical, so it would be premature to generalize about the proportion of species, endangered or otherwise, that are highly interactive. For example, data for most species, including plants, are lacking. While the empirical difficulties in answering this question are an obvious challenge, the standards of scientific inference may be an even greater challenge. Even the nomination of the sea otter as a highly interactive species has been questioned (Foster & Schiel 1988). Despite these uncertainties, two important points emerge from Table 1. One is that a substantial proportion of these species are strong interactors. The other is that ecological function is simply unknown for the majority of listed mammals. Thus, the challenge is not only to restore the known strong interactors to ecologically effective population levels (density and range) but to establish which, if any, of the species for which information is lacking are strong interactors, at least in some ecological contexts. Might it be that most species would prove to be strong interactors if we knew more about their ecological functions?

Spatial and Temporal Variation in Interaction Strength

Interaction strength not only varies among species, but it obviously varies spatially, as demonstrated in the otter and wolf cases. We noted above, for example, that predation by wolves on ungulates may be more effective in localities where other large carnivores are present and where alternative prey exist. Brown et al. (2001) identified species that have the potential to alter ecosystems only under restrictive conditions, such as in chronically stressful, marginal habitats. They determined that the stem-boring moth *Diryctrioa albovitella* has insignificant ecological effects on pinyon pine communities inhabiting favorable sandy-loam soils. In stressful cinder soils, however, it has severe effects on dominant pinyon trees. These effects radi-

ate through the ecosystem, influencing the species composition and abundance of organisms ranging from mycorrhizae to seed-eating birds. These considerations lead us to two more conclusions:

(1) globally applicable estimates of ecologically effective densities (or rules of thumb) will likely be meaningless, and

(2) we should be cautious when assuming that a given species is not highly interactive or lacks the potential to become so, particularly because species distributions adjust to changing environments.

Uncertainty about future ecological dynamics, including inter-specific interactions, is increasing as a result of rapid environmental change. The profound changes in small-mammal communities that occurred at the close of the last glaciation about 13,000 years ago (Graham & Lundelius 1984; Flannery 2001) attest to this, as does predation on sea otters by killer whales. This means we cannot know exactly which interactions and which species will be most critical for the maintenance of biodiversity in the future. For example, the predatory sea star (*Pisaster orchraceous*), by preying on the competitively dominant mussel (*Mytilus* spp.), enhances species diversity in rocky intertidal communities of the west coast of North America (Paine 1966). However, the per capita interaction strength between sea stars and mussels is strongly influenced by ocean temperature (Sanford 1999), thus raising the possibility of altered community dynamics as the result of global warming or other climatic changes.

These kinds of uncertainty, however, should not discourage managers from establishing operational targets or thresholds for ecosystem recovery. Examples of such qualitative objectives would be (1) the recovery of kelp forests where anthropogenic factors have contributed to the reduction or disappearance of sea otters and other sea urchin predators, (2) the restoration of canopy recruitment of trees and forest understory diversity where plant reproduction has been arrested by excessive herbivore browsing, and (3) the recovery of beaver wetland ecosystems where their disappearance is an indirect consequence of carnivore eradication.

Policy and Management Issues

Neither the interspecies interactions of functionally important species nor interaction strength (Berlow et al. 1999) have been widely recognized in the policy context of conservation laws and regulations, although the goal of management under the U.S. Marine Mammal Protection Act (1977; Section 2) requires that such species and population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part. In contrast, the U.S. Endangered Species Act of 1973 (ESA) hardly refers to interactions among species, though it and many other laws contain vague references to ecological interactions and integrity. The virtual absence of insights from community ecology in conservation management and species recovery is not unexpected given that the ESA and many of its amendments (last ones enacted in 1988) became law before the founding of the Society for Conservation Biology.

Perhaps as a result, recovery goals under the ESA for threatened or endangered species manifest demographic or numerical minimalism. In general, recovery criteria are modest—about three populations with sizes just large enough to prevent disappearance over a short interval such as a century. In several recent recovery plans, the population goals are even more conservative; it is becoming the convention to employ phrases such as "stabilization at existing population size and geographic distribution." Rarely, if ever, is recovery defined in terms of restoration of critical ecological interactions over extensive geographic areas or the propagation of endangered interactions across trophic levels. It has been observed that the formation of recovery goals now leans more heavily on social and economic concerns than biological information (Elphick et al. 2001; Gerber & Schultz 2001).

For all of these reasons the criteria for listing and the concepts of recovery and recovery goals in the ESA rarely if ever take interaction strength into account. Although the ESA states in the "Findings"

section that "The purposes of this Act are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved . . ." This broader goal is never mentioned again, and recovery is usually defined in terms of local (single-species) demographic or genetic viability. Moreover, this language appears to reflect the naive view that species are critically dependent on the preservation of their habitats but that ecosystems are much less dependent on the preservation of their component species.

Until such laws and policies are constructively rewritten and enforced, the current principles of community dynamics and the integrative role of highly interactive species are likely to be ignored in conservation planning and management. One such principle or hypothesis is the idea that wide-ranging and strongly interacting species occur (or once occurred) in many, if not most, ecosystems (MacArthur 1972; Paine 1980; Brown & Heske 1990; Fonseca & Robinson 1990; Henke & Bryant 1999; Pace et al. 1999; Terborgh et al. 1999; Estes et al. 2001). This hypothesis challenges scientists to view the recovery of such species and the restoration of biodiversity from a community perspective and on landscape, regional, and continental scales (Soulé & Noss 1998; Soulé & Terborgh 1999). Specifically, strongly interacting but extirpated species should be restored throughout all those parts of their potential range, where their absence may contribute to ecological degradation or simplification.

Can conservation biology provide the requisite tools and justifications for the maintenance of highly interactive species? It is apparent in the sea otter and wolf cases that estimates of ecologically effective densities are feasible at local to regional scales. In the future, the estimation of this population-community metric may partially supplant the use of more conservative autecological tools such as population viability analysis (Soulé 1987; Beissinger & McCullough 2002).

Proposals by conservationists to repatriate native predators are likely to impel interest in estimates of effective densities. Such pro-

posals often ignite social conflict over the potential impacts of predators on sport hunting and livestock operations, or over polarized public perceptions of carnivores. In such situations, conservation biologists may need to analyze whether the artificial control or geographic restriction of the species, below some estimated threshold of effectiveness, has been ecologically harmful.

Ecosystems are complex and always changing. For these reasons, conservation should facilitate extensive spatial access for highly interactive native species, according to their needs and ecological opportunities. In particular, highly interactive species—present or potential—should be given the benefit of the doubt in our management and recovery efforts. A contemporary example is wolf recovery in the United States. Wolves are still absent from most of the western states and occupy only about 4–5% of their historic range in the United States exclusive of Alaska (M. K. Phillips, personal communication).

In the end, our success in rehabilitating an ecologically degraded world will be judged more on the persistence of interspecies interactions than on the geographically limited persistence of populations based only on causing the least economic burden and ensuring only symbolic survival. Both the science of ecology and our obligations to minimize harm to nature require that land use and conservation policies reflect this higher standard.

Acknowledgments

Note

*Extent of predation and its ecological effects unclear.

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Introduction to *Strongly Interacting Species: Conservation Policy, Management, and Ethics*

As explained in paper 12, conservation plans to protect ecosystems must ensure healthy populations of strongly interacting species. If population sizes drop so low that these species cannot fulfill their ecological roles, then extinctions and disruptions occur throughout the food web.

Examples of strongly interacting species described in this paper include top predators like the gray wolf and sea otter, mutualists like honey bees, and ecological engineers like beavers, elephants, and prairie dogs that maintain specific types of habitat. Although it is difficult to know whether a particular species is strongly interacting until removed from its ecosystem, we know such species are numerous. A review I did shortly before publication of this paper found that nearly half the mammals listed under the federal Endangered Species Act are probably strong interactors.

The Endangered Species Act and other conservation laws were enacted before we knew much about strongly interacting species, so they do not mandate preservation of ecologically effective population sizes. As an example of why this is important, consider prairie

dogs. A population of 1,000 prairie dogs is probably large enough, barring a plague epidemic or human interference, to survive indefinitely, but it is not large enough to be effective. That is, it cannot alter vegetation over any appreciable area; nor is it large enough to sustain a population of black-footed ferrets, which require nearly that many prairie dogs to sustain a single female ferret and her pups.

We developed the following guidelines to help conservationists and land managers identify strongly interacting species. A comprehensive test is to determine whether removing or decreasing the species does the following:

1. Reduces local species diversity
2. Decreases reproductive success of other species
3. Reduces resilience of the ecosystem to fire, drought, flood, or exotic species
4. Changes habitat structure or composition
5. Changes productivity or nutrient dynamics
6. Changes other important ecological processes

Based on case studies of sea otters, gray wolves, and prairie dogs, we stated general conclusions. One bit of good news is that many species are resilient and can increase their numbers to ecologically effective levels once persecution by people ends. A second conclusion is that the ecological effectiveness of a species depends on factors like forage, primary productivity, and the number and abundance of other species. This means that conservationists should base conservation plans on local data.

Finally, absent new legislation and rules from the US Fish and Wildlife Service, litigation demanding enforcement of existing laws, such as the Endangered Species Act, is essential. An example of a poorly enforced law is the National Forest Management Act, which requires that agencies "provide for the diversity of plant and animal communities" in national forest plans. We now know this cannot be done without ensuring ecologically effective populations of the strongly interacting species.

Strongly Interacting Species: Conservation Policy, Management, and Ethics

Michael E. Soulé, James A. Estes, Brian Miller, and Douglas L. Honnold

Any legislation or other policy instrument based on empirical science is prone to senescence. Consider the US Endangered Species Act (ESA) of 1973. This was the first federal statute to grant de facto existence rights to species of plants and animals (Varner 1987) and to impose binding, enforceable duties on government agencies and private citizens to protect imperiled species. The ESA was based on the best science of the time (Bean and Rowland 1997), and it still remains in the vanguard of worldwide species protection efforts. However, the ESA, like other environmental laws from the 1970s, was enacted before conservation biology existed as a discipline, before the field of population viability analysis existed, before ecologists understood many of the ecosystem consequences of species interactions and community dynamics (Terborgh et al. 1999), and before the spatial and temporal scale–related complexities of effective protection of vulnerable species were widely understood (Soulé et al. 2003). Although the ESA was revised and reauthorized in 1988, it does not reflect many advances in population biology and community ecology.

Among the scientific anachronisms in this law is the absence of specific reference to species interactions that contribute substantially to the maintenance of ecological and species diversity. Not only has the understanding of interaction webs advanced (Menge 1995), but it is now widely understood that the disappearance of a strongly interactive species can lead to profound changes in ecosystem composition, structure, and diversity (Soulé and Terborgh 1999, Terborgh et al. 1999, Oksanen and Oksanen 2000, Schmitz et al. 2000, Soulé et al. 2003). For instance, decimation of great whales by industrial whaling substantially altered krill-consumer dynamics in the Southern Ocean, and whaling has been proposed as the main cause of a recent megafaunal collapse in the North Pacific Ocean (Springer et al. 2003). In addition, the disruption of fruit dispersal and seed-set patterns following early Holocene megafaunal extinctions fundamentally altered the species composition of neotropical forests (Janzen and Martin 1982), and the functional dynamics of coastal marine ecosystems worldwide have been grossly altered by overfishing of large herbivores and predators (Jackson et al. 2001). The functional extinction of species interactions often occurs well before the species themselves have completely disappeared. In the oceans, many large, interactive species persist only as rare adults, or as small or juvenile individuals that do not interact like large adults, qualitatively or quantitatively.

On land, many large animals and other strongly interactive species are completely missing from vast areas that they occupied a century or two ago (Laliberte and Ripple 2004). Globally, many, if not most, large-bodied, strongly interacting species are increasingly rare, even if they persist in parts of their former range. A reasonable hypothesis is that ecosystems that have lost one or more strongly interactive species are destined to undergo profound degradation and simplification over time.

Nevertheless, most conservation laws, including the ESA, fail to reflect the effects of widespread ecological disappearances of strongly interacting species and the resulting ecosystem perturbations. For example, the current criteria for recovery of endangered

mammal species under the ESA generally ignore interspecies interactions altogether (Soulé et al. 2003), emphasizing short-term, single-species, demographic viability in only a few circumscribed areas. Indeed, many current recovery plans, at least for mammals, call for no increase in numbers of individuals, numbers of populations, or geographic range (Tear et al. 1995; but see USFWS 1998, Jennings 1999).

Here we propose that population densities of strongly interactive species must not be permitted to fall below thresholds for ecological effectiveness, and that the geographic ranges of such species should be as large as possible (Conner 1988, Soulé et al. 2003). Before this proposal can be implemented, however, two issues must be clarified: (1) the definition of strongly interactive species and (2) the achievement of ecologically effective densities of such species.

What Are Strongly Interactive Species?

The idea that some species interact more strongly than others is not new. Paine (1969) first used the term "keystone species" for particularly strong interactors: those, for example, whose activities maintain species and habitat diversity and whose effects are disproportionate to their abundance (Kotliar et al. 1999). It is worth noting that Paine's idea, one of the most influential in all of modern ecology, is fundamentally a theory of species diversity—that the presence or absence of one or several key species influences the distribution and abundance of many other species. Ecologists recognize, however, that the keystone designation artificially dichotomizes species into groups such as "strongly interactive" (or keystone) and "non-strongly interactive" (Mills et al.1993).Though such dualisms have limited utility in science, this particular one is helpful in education and advocacy.

Species that are relatively interactive have been categorized according to the kind of ecological interaction that is most evident. Among these interactions are *habitat enrichment, mutualisms, predation,* and *competition.* Species whose activities affect and

enhance physical or biological habitat structure have been referred to as "ecological engineers" (Jones et al. 1994). Ecological engineers significantly modify their habitat in ways that increase local species diversity. Beavers (*Castor canadensis*), for instance, create wetlands by building dams in streams. Other examples of ecological engineering include mound building by termites, burrowing and grazing by prairie dogs (*Cynomys* spp.), and habitat conversion by elephants (*Loxodonta africana*) and bison (*Bison bison*) (Naiman et al. 1988, Owen-Smith 1988, Detling 1998, Kotliar et al. 1999).

Mutualist species, by virtue of their interactions, can also maintain species diversity. An example is the relationship between the whitebark pine (*Pinus albicaulus*) and Clark's nutcracker (*Nucifraga columbiana*). Clark's nutcracker is strongly dependent on the seeds of the whitebark pine, and the pine depends on the nutcracker for the dispersal of its seeds into caches. These seed caches are also a major food source for both small vertebrates and grizzly bears (*Ursus arctos*) in the Greater Yellowstone ecosystem (Mattson et al. 1992).

Terborgh and colleagues (1999) describe how the loss of apex mammalian predators can precipitate ecological chain reactions that lead to profound degradation and species loss. Although top-down forcing through three or more trophic levels has been demonstrated for nonvertebrate taxa (Strong et al. 1996, Terborgh et al. 2001), space constraints and immediate policy relevance preclude a detailed review here. Many predator-mediated chains of reaction have been described or postulated (Estes and Palmisano 1974, Pace et al. 1999, Terborgh et al. 2001); some of these (ecological cascades) are summarized in figure 1 and further elaborated in figure 2. Figure 2a illustrates the familiar case of gray wolves (*Canis lupus*) in Yellowstone, representing the scenario in which the extirpation of a large carnivore leads to the ecological release of large terrestrial ungulates and other herbivores, causing changes in vegetation structure, species composition, and diversity.

Crooks and Soulé (1999) demonstrated the behavioral release of mesopredators in patches of coastal sage scrub and chaparral in southern California, where the local absence of coyotes (*Canis*
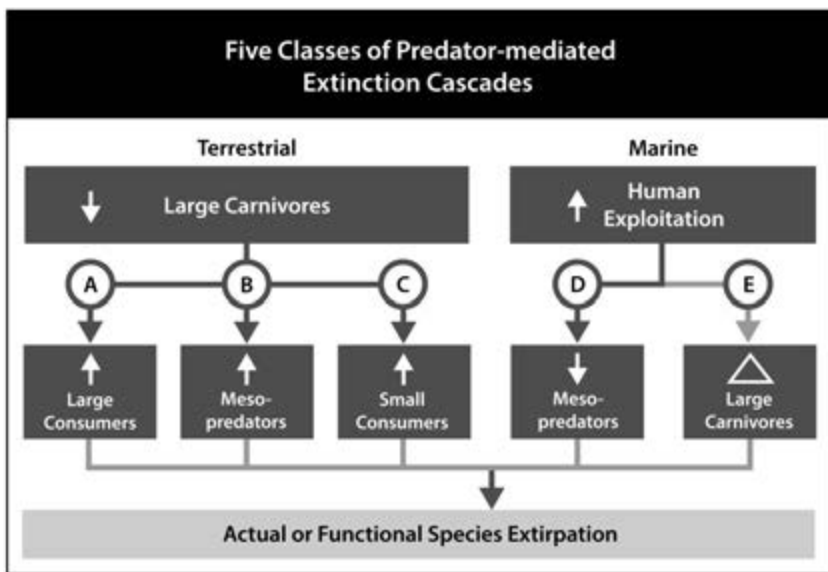
FIGURE 1. Five classes of predator-mediated trophic cascades leading to local extinction (extirpation) in terrestrial and marine ecosystems. Arrows in shaded boxes indicate an increase or decrease in population. Solid lines between boxes indicate direct effects; broken lines indicate complex, indirect effects; the delta (Δ) indicates a behavioral change (prey switching). The letters (a) through (e) refer to the individual graphics in figure 2.

latrans) led to an increase in the activity of the house cat (*Felis catus*), in turn causing reductions of native, scrub-requiring bird species (figure 2b). An impressive case of competitive release (Paine 1966) was described by Henke and Bryant (1999) and is illustrated in figure 2c. They documented a reduction of rodent diversity from 12 species to just 1 as a result of coyote removal; the survivor was the competitively dominant kangaroo rat, *Dipodomys ordii*. The fourth example (figure 2d)—the case of sea otters (*Enhydra lutris*) and kelp forest—is described below.

The fifth example (figure 2e) of a predator-mediated ecological cascade is hypothesized to have begun with the decimation of the great whales by industrial whaling following World War II. Springer and colleagues (2003) suggest that a series of ecological
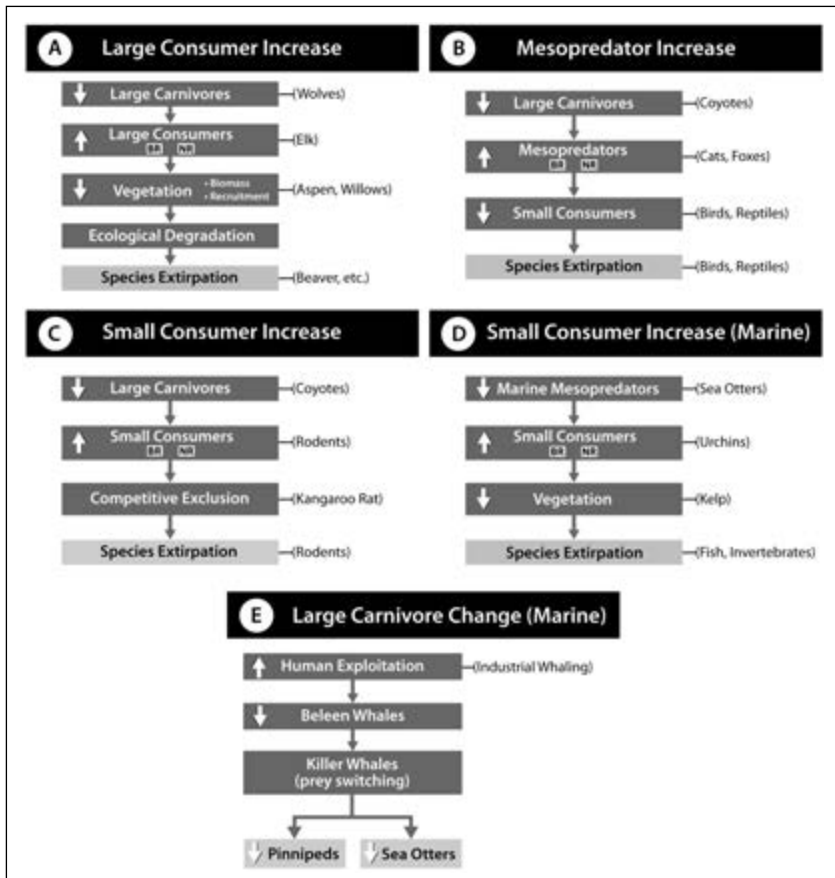
FIGURE 2. Examples of predator-mediated cascades causing local species extinctions. (a) The extirpation of large carnivores (wolves) in Yellowstone National Park led to an increase in large consumers (elk) and to the local extinction of beavers. (b) In coastal sage scrub and chaparral in southern California, the absence of large carnivores (coyotes) led to mesopredator release (cats, foxes), leading to an increase in predation on small prey. (c) Predator extirpation (coyote removal) can lead to competitive release, or the ecological release of superior competitors (e.g., the kangaroo rat), among rodent species, leading in turn to the local extirpation of competitively inferior species. (d) The extirpation of a marine predator (the sea otter) can cause the disappearance of an entire ecosystem (kelp beds). (e) Prey switching by killer whales, resulting from human exploitation of baleen whales, is postulated to reduce the populations of pinnipeds and sea otters. Arrows in shaded boxes indicate an increase or decrease in population; arrows between boxes indicate cascading trophic effects. Abbreviations: BR, behavioral release; NR, numerical release.

extinction events affecting pinnipeds and sea otters in the northern Pacific Ocean and the Bering Sea was initiated when killer whales (*Orcinus orca*), following the effective disappearance of large baleen whales, expanded their diets. Though baleen whales are themselves carnivores, they are not considered to be apex predators because of the relatively small size of their prey and because they are preyed on by killer whales.

We know little about the distribution of interaction strength among species in most ecosystems. Nor do we know the morphological, physiological, behavioral, or ecological correlates of strong interactivity. Paine (1992) showed experimentally that the interaction strengths of seemingly similar species can vary substantially; he also argued that mammals are especially strong interactors in many terrestrial ecosystems (Paine 2000). One of us (M. E. S.) surveyed all mammal species listed as threatened or endangered under the ESA for which recovery plans are written (about 44 species or subspecies). It appears that nearly half of these vulnerable mammals are relatively interactive, according to the criteria listed below, though this estimate may be low because the question is unstudied for many of the species (Soulé et al. 2003). Sala and Graham (2002) provide the most comprehensive analysis to date on species-specific variation in interaction strength. They estimate that roughly half of the macroinvertebrate herbivore species in kelp forest ecosystems are strong interactors. Based on limited information, therefore, it appears that a significant proportion of invertebrate and vertebrate species are sufficiently interactive to warrant attention if recovery criteria are an issue. Parenthetically, there are exceptions to the view that strong interactors are universally beneficial. Invasive exotic species and some native carnivores, particularly in highly perturbed ecosystems, can exacerbate management problems. For example, coyotes can devastate smaller, endangered predators such as captive-bred blackfooted ferrets (*Mustela nigripes*), particularly if the coyotes are uncontrolled by wolves and if their prey occur in reduced, disturbed, or fragmented habitats (Miller et al. 1996).

The question of how interactivity is distributed in ecosystems has yet another dimension, namely variability within species. Like all ecological variables, interaction strength is contingent on place, time, and history (Power et al. 1996). Just as it would be futile to assign species-wide, fixed values for age-specific fecundity, population growth rate, coefficients of competition, or other context-dependent variables, it would be unreasonable to assign a fixed value for interactivity to a widespread species.

Arguably, the related goals of (a) categorizing the kinds of interspecific interactions and (b) assigning species to these categories trivialize the variability of species and environments in space and time. Interactivity is obviously a complex, context-dependent variable, and no species trait or feature is universally associated with it across all taxonomic groups and ecosystems. Nevertheless, the ESA contains wording that justifies attending to species interactions: "The purposes of this Act [the ESA] are to provide a means whereby the ecosystems upon which threatened and endangered species depend may be conserved" (16 U.S.C. § 1531[b]). This leaves us with a practical question: How can agencies and managers, in the face of this uncertainty and variability, determine whether a vulnerable species in a particular locality or region is sufficiently interactive to warrant special consideration with regard to recovery goals?

Guidelines for Assessing Interactivity

Operationally, a given species should receive special attention for recovery—beyond mere demographic viability—if its absence or unusual rarity causes cascading, dissipative transformations in ecosystems, including alterations or simplifications in ecological structure, function, or composition. The following questions may assist in determining whether there are grounds to warrant the creation of appropriate management prescriptions and actions that guarantee its ecological effectiveness.

Does the absence or decrease in abundance of the species lead directly or indirectly to a reduction in local species diversity? For example, the absence of coyotes from arid ecosystems can lead to a

reduction in bird species diversity via mesopredator release (Crooks and Soulé 1999) or to a reduction in rodent species diversity via competitive exclusion (Henke and Bryant 1999), as noted above.

Does the absence, decrease in abundance, or range contraction of the species directly or indirectly reduce reproduction or recruitment of other species? For example, the number of forest tree species that successfully reproduced on islands in a Venezuelan reservoir lacking large predators dropped from about 65 to about 10 because of a superabundance of herbivores (Terborgh et al. 2001). Likewise, ungulate herbivory prevented aspen (*Populus tremuloides*) clones from recruiting sprouts into the overstory after extirpation of wolves in the northern range of Yellowstone National Park (Romme et al. 1995, Ripple and Larsen 2000, Ripple and Beschta 2004).

Does the absence or decrease in abundance of the species lead directly or indirectly to a change in habitat structure or composition of ecosystems? For example, excessive elk (*Cervus elaphus*) herbivory on willow (*Salix* spp.) in the absence of wolves in Rocky Mountain National Park (Peinetti et al. 2002) and Yellowstone National Park (Ripple and Beschta 2004) was apparently the major factor in the disappearance of beaver and associated wetlands.

Does the absence or decrease in abundance of the species lead directly or indirectly to a change in productivity or nutrient dynamics in or between ecosystems? For example, prairie dog colonies shape nutrient cycling, soil chemistry, soil porosity, and the productivity and nutrient content of vegetation through their burrowing and grazing activities (Whicker and Detling 1993, Kotliar et al. 1999, Miller et al. 2000), and sea otters strongly influence algal productivity (Duggins et al. 1989) and food resource availability to herbivores (Konar and Estes 2003).

Does the absence or decrease in abundance of the species change an important ecological process in the system? For example, beavers have a profound effect on stream dynamics, water tables, flooding, and the extent of wetlands (Naiman et al. 1988).

Does the absence or decrease in abundance of the species reduce the resilience of the system to disturbances such as fire, drought, flood, or exotic species? For example, the extirpation of the dingo (*Canis lupus*

dingo) in some regions of Australia indirectly degrades habitat quality because dingoes prey effectively on exotic rabbits (*Oryctolagus cuniculus*), red kangaroos (*Macropus rufus*), and other herbivores (Newsome 2001). In addition, dingoes may benefit native fauna, including small, endangered marsupials, by reducing population densities of the introduced red fox (*Vulpes vulpes*) (Newsome 2001), a major predator of small animals (O'Neill 2002).

These questions cannot eliminate the need for informed judgment, because interactivity of species is a multidimensional continuum, not a simple dichotomy. In addition, the interaction strength of species is usually not susceptible to rigorous empirical tests, in part because many appropriate experiments would be manipulative (involving the removal of species), long-term, and geographically extensive. With such a small portion of nature protected, it is difficult to justify experimental removal of a putatively critical species to prove a point. There are, however, a number of powerful approaches that can often be used to make inferences about interaction strengths. Recovery of ecosystems following the reappearance of species is one such approach that has been used effectively to establish that predators such as gray wolves and sea otters are strongly interactive (see the cases described below). Interaction strength has been modeled on the basis of demographic and energetic parameters (Williams et al. 2004), even where data are limited. Ecological reconstructions based on historical records (Jackson et al. 2001), in conjunction with the comparative approach, provide yet another powerful means of assessing the ecological importance of species.

The Estimation of Ecologically Effective Densities

If persistence of species diversity is a management objective, it is essential to consider the densities or population levels that maintain interaction effectiveness rather than mere persistence at minimal numbers. Once it is determined that a species has relatively strong interspecies interactions, the proper management of such a species may require the estimation of the minimum threshold of ecologi-

cal effectiveness. We define an ecologically effective density as the population level that prevents undesired changes in a defined ecological setting. As stated above, however, the estimation of effective density is strongly contextual, depending on locality, season, productivity, and other variables that fluctuate spatially and temporally (Estes and Duggins 1995, Soulé et al. 2003). Although a challenge, this problem may not be more intractable than the estimation of population viability. For example, many of the relevant parameters in population viability analysis, including age-specific fecundity and mortality, are similarly sensitive to local conditions. To illustrate some of the factors that must be considered in the estimation of ecologically effective densities, we present three examples of strongly interactive genera or species: the sea otter, the gray wolf, and the prairie dog.

The sea otter. Abundant sea otter populations inhabited coastal waters of the North Pacific Ocean and southern Bering Sea throughout most of the Pleistocene and Holocene, but were reduced to a few remnant colonies by the maritime fur trade of the 18th and 19th centuries. Recovery following the fur trade was spatially and temporally asynchronous, thus providing contrasts between otherwise similar habitats with and without sea otters. These contrasts demonstrate a strong limiting influence of sea otters on their most important prey, kelp-consuming sea urchins (*Strongylocentrotus* spp.). Thus, lush kelp forests abound where sea otters are abundant; where sea otters are absent, the habitat is typically deforested by hyperabundant sea urchins. Because kelp forests are highly productive (Duggins et al. 1989), provide habitat for other coastal species (Dayton 1985), and attenuate water movements (Jackson and Winant 1983), sea otters exert farreaching influences on many other species (Estes 1996). Without sea otters, some of these kelp-dependent species decline or disappear, while others, including urchins, erupt to high levels. The ecologically effective population for sea otters, though regionally variable, is always much larger than minimum viable population sizes based on demography, and in some instances is near the environmental carrying capacity (Estes and Duggins 1995).

Geographic variation in the behavior of predators, competitors, and prey will also affect the population density threshold for ecological effectiveness. For example, the density of sea otters that is effective in suppressing sea urchins differs between sites, because the demography and dispersal of sea urchins vary geographically. In the Aleutian Islands, where urchin recruitment is frequent and strong, a higher density of otters is needed to suppress the urchins and prevent kelp deforestation than in southeast Alaska, where urchin recruitment is weak and episodic, and where just a few otters are enough to maintain the kelp ecosystem (Estes and Duggins 1995).

In summary, the estimation of effective densities of sea otters for preventing kelp deforestation depends, among other things, on whether the state of the system is kelp dominated or deforested, on the recruitment dynamics of urchins to the kelp beds, on whether the substrate is dominated by rocks or mud, and on the mortality rate of otters (see Soulé et al. 2003). For these reasons, the ecologically effective densities of otters can vary by an order of magnitude, but in all situations observed, otters eventually attain such densities if they are not harassed by human beings or preyed on by killer whales.

The gray wolf. Large areas of the United States, including most of the East Coast and Midwest, now lack wolves and other large carnivores, the result of a century of eradication on behalf of livestock growers, hunters, and other interest groups that benefit from the absence of wolf predation on ungulates. Populations of white-tailed deer (*Odocoileus virginianus*), elk, and moose (*Alces alces*) have increased both in numbers and in per capita consumption (Soulé et al. 2003), and these increases are frequently attributed, at least in part, to the absence of wolves (Messier 1994, Crête 1999). Among the many harmful consequences of wolf eradication have been increased costs for agricultural producers in the Midwest and East, the widespread degradation of forests and other ecosystems, and the decline of many species of plants favored by ungulates (Rooney et al. 2004). As noted above, aspen recruitment failed for 80 years in large parts of Yellowstone National Park, reflecting numerical and behavioral release of elk subsequent to wolf eradication. Excessive browsing

by elk also affected recruitment of riparian cottonwoods and willows (Beschta 2003), causing the local disappearance of beaver wetlands. These effects are being reversed in Yellowstone National Park since wolves were reintroduced (starting in 1995), and signs of ecological effectiveness were noted before wolves reached their current abundance of about 200 (Ripple and Beschta 2004). A similar trend has been observed in Grand Teton National Park, where a decrease in Neotropical migrant bird diversity has been attributed to overbrowsing by moose in riparian willow communities in the absence of wolf predation or sport hunting of moose (Berger et al. 2001). It is noteworthy that the recovery of willows in northern Yellowstone National Park is particularly striking in areas where the topography facilitates capture of elk by wolves (Ripple and Beschta 2003). Several factors affect wolves' ecologically effective population density. It is lower where hunters can suppress ungulate numbers; where wolves coexist with other large carnivores, such as bears and cougars; or where deep winter snow or periodically severe storms facilitate capture of prey—for example, El Niño versus La Niña years (Schmitz et al. 2003). We grant that predators do not always control large herbivores, but given alternative prey, multiple carnivore species, or appropriate habitat, wolves can often control superabundant ungulates (Soulé et al. 2003).

The prairie dog. A century ago, five species of prairie dog lived in a shifting mosaic of colonies that covered more than 40,000,000 hectares (ha) on the Great Plains. By 1960, prairie dog area had declined to about 600,000 ha (Marsh 1984), largely because of poisoning campaigns, land conversion, and the introduction of plague (*Yersinia pestis*). This is a decline of 98 percent, and the remaining colonies are small and isolated. Prairie dogs are a valuable food for many species of predators. In addition, prairie dogs decrease densities of woody shrubs and increase densities of grasses and forbs, thus creating conditions that large grazers prefer. Prairie dog activities also increase plant productivity, soil nitrogen, nutrient cycling, and digestibility of grasses and forbs (Whicker and Detling 1993, Detling 1998). Their burrowing activity changes soil chemistry; in-

creases soil porosity, soil turnover, and the organic content of soil; and enhances the dimensionality of the habitat for many other species (Whicker and Detling 1993, Outwater 1996). Some species of plants, invertebrates, and vertebrates benefit from prairie dog activities, while other species benefit from the areas outside of the colony (Kotliar et al. 1999). These effects differ among prairie dog species. Furthermore, prairie dogs, unfenced bison, and fire interacted closely on the midgrass prairies, although that triad may not have been as tightly associated on the drought-driven shortgrass prairies or the semidesert grasslands and shrublands.

Estimating ecologically effective densities of prairie dogs is complicated by the introduction of plague. Plague reduces numbers and changes the temporal and spatial characteristics of the historic "shifting mosaic" between prairie dog colonies and grasslands. Despite those ambiguities, it is clear that ecologically effective densities of prairie dogs are far higher than the densities required for population persistence (Miller et al. 2000). As an example, 762 prairie dogs may be required to support each female black-footed ferret and her offspring (Biggins et al. 1993). Thus, conservative recovery goals that consider only population viability could maintain prairie dogs without providing sufficient resources for ferrets.

Summary. What commonalities emerge from these three overviews of ecological effectiveness? First, studies of these mammals demonstrate several pertinent factors, most of which appear to be extrinsic and context specific. Among these extrinsic factors are (a) weather and other abiotic influences, (b) interactions between forage quality and quantity, (c) primary productivity, and (d) the number and abundance of other species—such as prey, predators, pathogens, mutualists, and competitors—with which these species interact. Of course, intrinsic factors, such as the maximum growth rate of the population, are also relevant, but variability in intrinsic variables is partly determined by the extrinsic factors listed above.

Second, the above case studies suggest that strongly interactive species, if not harassed, will often achieve ecologically effective densities without human intervention, though active management

will probably be necessary in some highly perturbed situations, including the presence of exotic pathogens and overharvesting. For example, the recovery of sea otters in southwestern Alaska may be contingent on the recovery of great whales (Springer et al. 2003). Populations tend to increase their numbers and energy consumption to levels where ecological resistance due to diminishing resources, disease, or other factors (e.g., territoriality) halts further growth. It is likely, therefore, that thresholds for ecological effectiveness are often below carrying capacity, thus obviating the need in many situations for modeling or specific management prescriptions. But even if particular circumstances, such as conflicts between human interest groups, require the modeling of effective densities, we believe that the modeling will be no more complex than the estimation of single-species population viability.

Conclusions

Mitigating the current anthropogenic mass extinction will require a scientifically rigorous and ecologically comprehensive grasp of its drivers. Among these is the increasing rarity of interactive species, such as plants that provide critical resources (Terborgh 1986), insect pollinators (Dobson et al. 1999), habitat modifiers (Soulé et al. 2003), coral reef herbivores (Jackson et al. 2001), and carnivores, both marine and terrestrial (Terborgh et al. 1999). The activities of relatively interactive species are disproportionately significant for the survival of native species and ecosystems.

It is essential, therefore, that conservation practitioners, whether governmental or nongovernmental, adopt an ecological view that ensures the persistence of interactive species at ecologically effective population densities and maximal spatial occurrence (Soulé et al. 2003). In particular, we believe that natural-resource policymakers and wildlands managers should determine whether the rarity or absence (Hughes et al. 2000) of a species in a region can be expected to trigger ecological degradation, including the disappearances of native species and other elements of biodiversity.

Even though interactivity is a quantitative variable, managers may be forced to make binary determinations, such as whether to treat a particular species as strongly interactive when formulating recovery goals. Notwithstanding the arbitrariness of such decisions, a commonsense approach will often suffice. One should assume, for instance, that a substantial reduction of tree species that produce mast or invite cavity formation, or of apex predators and many large herbivores—such as wolves, coyotes, sea otters, killer whales, sharks, predatory freshwater fish, and large, predatory or algae-eating reef fish—will trigger cascades of ecological degradation and species loss (Terborgh et al. 1999, Jackson et al. 2001, Soulé et al. 2003, Springer et al. 2003). Other situations may require literature reviews or detailed research to ascertain whether a particular species in a particular place fulfills any of the criteria for relatively strong interactivity given above.

A conundrum for managers is that the ecological effectiveness of strongly interacting species is not specifically addressed in current laws and policies dealing with biodiversity protection and management. Until this perspective has been codified in such laws, conservationists need to consider how best to provide for such species and the processes they mediate in accord with the intent of these laws. Population viability analyses and conservative recovery goals are an inadequate regulatory context for strongly interacting species.

We now understand that the biodiversity of ecosystems will degrade unless the interactions of species are maintained in as many regions as feasible, particularly those areas within the historic range. This more holistic, contemporary view requires that strongly interactive species receive special attention to assure that they are well distributed and abundant, a position consistent with an opinion of the US Ninth Circuit Court of Appeals (*Defenders of Wildlife* v. *Norton*, 258 F.3d 1136 [2001]). Such a geographic criterion for recovery would require more than scattered or refugial representation of such species. Ecological function and diversity cannot be conserved in a region by maintaining interactive species in only a few protected areas. Rather, it is essential that strongly interactive

species be distributed as broadly as possible and be protected within well-distributed, secure areas. Applying this guideline to the wolf in the United States, for example, would mean that effective populations should be restored and protected in the Northeast, the Pacific Northwest, the Great Basin, the Colorado Plateau, the Southwest, and the southern Rockies. Moreover, if the current trend of decreasing sport hunting and the spread of chronic wasting disease in deer and elk continue, the pressure to reinstitute natural control mechanisms will surely increase.

The critical roles of interspecies interactions are rarely considered in recovery planning. For example, the US Fish and Wildlife Service (USFWS) admits that its goals for wolf recovery are "somewhat conservative...and should be considered minimal" (68 Fed. Reg. 15817 [2003]). A recent decision by USFWS (68 Fed. Reg. 15821 [2003]) states that USFWS is not required to restore a species across its available habitat. The decision would limit wolf protection to about 5 percent of its historical range in the lower 48 states. Similarly, the multistate conservation plan for black-tailed prairie dogs (Luce 2003) sets a 10-year recovery goal for black-tailed prairie dogs (*Cynomys ludovicianus*) at about 2.5 percent of their historical area, essentially the status quo.

We believe that such conservative recommendations are not based on current ecological knowledge about the significance of species interactions. Moreover, minimalist distributional and temporal goals constitute a trivialization of the term "recovery" as it is used in the ESA. In other words, "recovery," at least for mammals, is typically used to mean the persistence of only a few populations in a limited area for a few generations.

Notwithstanding current policies, most natural-resource and environmental laws require that federal agencies consider new scientific knowledge. Indeed, the ESA's own mandate is to use "the best scientific and commercial data available" (16 U.S.C. § 1533[b][1][A]). Moreover, implementing regulations for the National Environmental Protection Act of 1969 require that federal agencies disclose and consider "cumulative impacts" and the anticipated

environmental impacts of proposed federal agency actions (40 C.F.R. § 1500 et seq. 1995). Any artificially induced reduction in abundance of a strongly interactive species, therefore, must be considered in these environmental analyses. In addition, regulations of the National Forest Management Act of 1976 require that national forest plans "provide for the diversity of plant and animal communities" and that "such diversity shall be considered throughout the process" (36 C.F.R. § 219.3).

Since the recognition of conservation biology as a discipline (Soulé 1985), its practitioners have tacitly assumed that conservation biologists are "physicians to nature." Indeed, there are many parallels between conservation biology and the fields of medicine and public health—disciplines infused with morality. Following the Hippocratic principle of doing the least harm and the most good for patients and the public, physicians and public health officers are obligated, we think, to consider using new therapies and prophylaxes stemming from peer-reviewed research, even before such practices are generally adopted in canonical documents such as textbooks. We propose, therefore, that conservation practitioners, whether in a public or private (nongovernmental) employ, are similarly obligated to apply new biological knowledge in their work. Such a doctrine of "best conservation practices based on the best science" is tantamount to an ethical obligation of biologists to adopt a higher standard for management than is mandated by existing statutes and regulations, if the evidence warrants it. Environmental codes build the legal and ethical foundation of conservation practice, but the best science of the day creates the walls and ceiling.

In practice, policymakers and managers already have enough flexibility to implement new knowledge while still adhering to relevant statutes and policies, though the exercise of this doctrine may be inhibited by monetary and political constraints. (Setting relatively stringent recovery objectives for strongly interactive species, for example, will be opposed by individuals and organizations who perceive negative consequences of such actions.) Even so, ignoring the interspecific interactions of strongly interactive species will fur-

ther impair the diversity and resilience of ecosystems that are already unraveling. In a nation and a world where increasing numbers of species and ecosystems are shoved toward the brink of annihilation, it is more important than ever that environmental policy and management be buttressed by the best available science.

Acknowledgments

Notes

Michael E. Soulé (e-mail: rewild@tds.net) is professor emeritus of Environmental Studies at the University of California, Santa Cruz, CA 95064; he can be reached at PO Box 2010,Hotchkiss, CO 81419. James A. Estes is a research scientist with the US Geological Survey and adjunct professor in the Institute of Marine Sciences at the University of California, Santa Cruz. Brian Miller is with the Wind River Ranch Foundation, PO Box 27, Watrous, NM 87753. Douglas L. Honnold has litigated many cases involving the Endangered Species Act and is an attorney with Earthjustice, Bozeman, MT 59715. © 2005 American Institute of Biological Sciences.

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Introduction to *The "New Conservation"*

I am dismayed by the recent rise of an ideology promoted by some biologists who want to shift the emphasis of conservation science from conserving biological diversity to promoting resource extraction. Although this group calls themselves the "new conservationists," they are really trying to resurrect beliefs of the 1940s and '50s that prevailed before Ed Wilson, Reed Noss, Peter Raven, Paul Ehrlich, and others revolutionized conservation by insisting that it be based on good science.

To understand this ideology, it's helpful to review the history of conservation thought. In the early twentieth century, Teddy Roosevelt, John Muir, and others worked to found national parks and wildlife refuges. These protected areas were created long before we knew much about species and ecosystems, and so they are usually too small, lack resources needed for large predators, and were seen more as playgrounds for people than refuges for wildlife. Bill Newmark's eye-opening paper, "Extinction of Mammal Populations in Western North American National Parks," in 1995 showed that all

parks have lost species since their creation, with the most species lost from the smallest parks.

During the middle decades, state wildlife agencies, the US Forest Service, and others responsible for managing wildlife embraced practices that we now consider misguided. They treated nature as a "natural resource" to be managed for "maximum sustainable yield." For large mammals, this meant extirpating predators so that deer and other game species would be unnaturally abundant for sport hunters. This also meant turning most old-growth forests into timber and overfishing marine fish stocks (in 2013 the National Oceanic and Atmospheric Administration concluded that 26 percent of fish stocks were "subject to overfishing" or "overfished"). The result was a loss of species diversity and degradation of ecosystems. This misguided philosophy lives on in the guise of "multiple use" and "new conservation."

By the 1970s the damage was impossible to overlook. We early conservation biologists began using experiments, observation, and mathematical models to understand how interactions between wild species shape ecosystems, and we laid scientific groundwork for effective conservation plans. Driving much of this work was not only scientific curiosity, but also belief that the natural world is valuable for its own sake. Just as the world was horrified in 1972 when a disturbed man fractured Michelangelo's Pietà with a hammer, so most of us are horrified by the destruction of nature.

Conservationists now find ourselves facing a movement to return conservation to the philosophy of the last century, namely that the purpose of nature is to serve the human economy. In 2012, new-conservation advocates Peter Kareiva and Michelle Marvier wrote "Conservation science has as a key goal the improvement of human wellbeing through the management of the environment," and in another paper Kareiva wrote "Instead of pursuing the protection of biodiversity for biodiversity's sake, a new conservation should seek to enhance those natural systems that benefit the widest number of people." A particularly cogent rebuttal of new conservation can be found in "What Is the Future of Conservation?" a 2014 piece by Daniel Doak, Victoria Bakker, Bruce Goldstein, and Benjamin Hale published in the journal *Trends in Ecology and Evolution*. My own answer follows.

The "New Conservation"

Michael Soulé

Editorial from the journal *Conservation Biology*, 2013

A powerful but chimeric movement is rapidly gaining recognition and supporters. Christened the "new conservation," it promotes economic development, poverty alleviation, and corporate partnerships as surrogates or substitutes for endangered species listings, protected areas, and other mainstream conservation tools. Its proponents claim that helping economically disadvantaged people to achieve a higher standard of living will kindle their sympathy and affection for nature. Because its goal is to supplant the biological diversity–based model of traditional conservation with something entirely different, namely an economic growth–based or humanitarian movement, it does not deserve to be labeled conservation.

Institutional allies and supporters of the new conservation include the Gordon and Betty Moore Foundation, the Long Now Foundation, the Nature Conservancy, and the social-justice organization The Breakthrough Institute (Nordaus & Shellenberger 2011). The latter write—in the style of the Enlightenment—that, "We must open our eyes to the joy and excitement experienced by the newly prosperous and increasingly free [persons]. We must

create a world where every human can not only realize her material needs, but also her higher needs."

The manifesto of the new conservation movement is "Conservation in the Anthropocene: Beyond Solitude and Fragility" (Lalasz et al. 2011; see also Kareiva 2012). In the latter document, the authors assert that the mission of conservation ought to be primarily humanitarian, not nature (or biological diversity) protection: "Instead of pursuing the protection of biodiversity for biodiversity's sake, a new conservation should *seek to enhance those natural systems that benefit the widest number of people, especially the poor*" (emphasis added). In light of its humanitarian agenda and in conformity with Foreman's (2012) distinction between environmentalism (a movement that historically aims to improve human well-being, mostly by reducing air and water pollution and ensuring food safety) and conservation, both the terms *new* and *conservation* are inappropriate.

Proponents declare that their new conservation will measure its achievement in large part by its relevance to people, including city dwellers. Underlying this radically humanitarian vision is the belief that nature protection for its own sake is a dysfunctional, antihuman anachronism. To emphasize its radical departure from conservation, the characters of older conservation icons, such as Henry David Thoreau, John Muir, and Edward Abbey, are defamed as hypocrites and misanthropes and contemporary conservation leaders and writers are ignored entirely (Lalasz et al. 2011).

The new conservationists assume biological diversity conservation is out of touch with the economic realities of ordinary people, even though this is manifestly false. Since its inception, the Society for Conservation Biology has included scores of progressive social scientists among its editors and authors (see also letters in BioScience, April 2012, volume 63, number 4: 242–243). The new conservationists also assert that national parks and protected areas serve only the elite, but a poll conducted by the nonpartisan National Parks Conservation Association and the National Park Hospitality Association estimates that 95% of voters in America want continued government support for parks (National Parks Conservation

Association 2012). Furthermore, Lalasz et al. (2011) argue that it should be a goal of conservation to spur economic growth in habitat-eradicating sectors, such as forestry, fossil-fuel exploration and extraction, and agriculture.

The key assertion of the new conservation is that affection for nature will grow in step with income growth. The problem is that evidence for this theory is lacking. In fact, the evidence points in the opposite direction, in part because increasing incomes affect growth in per capita ecological footprint (Soulé 1995; Oates 1999).

Other nettlesome issues are ignored, including which kinds of species will persist and which will not if the new economic-growth agenda replaces long-term protection in secure protected areas? Related questions include:

Would the creation of designated wilderness areas be terminated? Would the funds to support the new conservation projects be skimmed from the dwindling conservation budgets of nongovernmental and government agencies? Is conservation destined to become a zero-sum game, pitting the lifestyles and prosperity of human beings against the millions of other life forms? Is it ethical to convert the shrinking remnants of wild nature into farms and gardens beautified with non-native species, following the prescription of writer Marris (2011)? Will these garden-like reserves designed to benefit human communities admit inconvenient, bellicose beasts such as lions, elephants, bears, jaguars, wolves, crocodiles, and sharks—the keystone species that maintain much of the wild's biological diversity (Terborgh & Estes 2010; Estes et al. 2011)?

The new conservationists assume the benefits of economic development will trickle down and protect biological diversity. Even if that assumption were borne out, I doubt that children growing up in such a garden world will be attuned to nature or that the hoped-for leap in humanity's love for the wild will occur once per capita consumption reaches a particular threshold.

Most shocking is the dismissal by the new conservationists of current ecological knowledge. The best current research is solidly supportive of the connection between species diversity and the sta-

bility of ecosystems. It has firmly established that species richness and genetic diversity enhance many ecological qualities, including productivity and stability of terrestrial and marine ecosystems, resistance to invasion by weedy species, and agricultural productivity; furthermore, research shows that greater species and genetic diversity reduces transmission rates of disease among species (Tilman 2012).

In contrast, implementation of the new conservation would inevitably exclude the keystone species whose behaviors stabilize and regulate ecological processes and enhance ecological resistance to disturbance, including climate change (Terborgh & Estes 2010). For these reasons and others, conservationists and citizens alike ought to be alarmed by a scheme that replaces wild places and national parks with domesticated landscapes containing only nonthreatening, convenient plants and animals.

The globalization of intensive economic activity has accelerated the frenzied rush for energy and raw materials and is devouring the last remnants of the wild, largely to serve the expanding, affluent, consumer classes in industrialized and developing nations. At current rates of deforestation, dam construction, extraction of fossil fuels, land clearing, water withdrawal, and anthropogenic climate change, it is expected that the 2 major refugia for biological diversity on the globe—the wet, tropical forests of the Amazon, and Congo Basin—will be gone by the end of this century (Mackey et al. 2013).

Is the sacrifice of so much natural productivity, beauty, and diversity prudent, even if some human communities and companies might be enriched? No. The worth of nature is beyond question and our obligation to minimize its gratuitous degradation is no less.

There is no evidence for the proposition that people are kinder to nature when they are more affluent, if only because their ecological footprints increase roughly in proportion to their consumption. We also know that the richer nations may protect local forests and other natural systems, but they do so at the expense of those ecosystems elsewhere in less affluent places. A third thing we know is

that anthropogenic climate change is probably the greatest threat to civilization (Gleick et al. 2010).

I must conclude that the new conservation, if implemented, would hasten ecological collapse globally, eradicating thousands of kinds of plants and animals and causing inestimable harm to humankind in the long run.

Finally, I believe that those who donate to conservation organizations do so in full confidence that their gifts will benefit wild creatures and their habitats. The central issue is whether monies donated to the Nature Conservancy and other conservation nonprofit organizations should be spent for nature protection or should be diverted to humanitarian, economic-development projects such as those proffered by the new conservation on the dubious theory that such expenditures may indirectly benefit biological diversity in the long run.

Traditional conservationists do not demand that humanitarians stop helping the poor and underprivileged, but the humanitarian-driven new conservationists demand that nature not be protected for its own sake but that it be protected only if it materially benefits human beings.

Note

A more literary version of this essay that highlights the intrinsic value of biological diversity can be accessed at www.michaelsoule.com.

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