



UNIVERSITY OF CALIFORNIA PRESS
JOURNALS + DIGITAL PUBLISHING



What Is Conservation Biology?

Author(s): Michael E. Soulé

Reviewed work(s):

Source: *BioScience*, Vol. 35, No. 11, The Biological Diversity Crisis (Dec., 1985), pp. 727-734

Published by: [University of California Press](#) on behalf of the [American Institute of Biological Sciences](#)

Stable URL: <http://www.jstor.org/stable/1310054>

Accessed: 07/10/2012 20:23

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



University of California Press and American Institute of Biological Sciences are collaborating with JSTOR to digitize, preserve and extend access to BioScience.

<http://www.jstor.org>

What is Conservation Biology?

A new synthetic discipline addresses the dynamics and problems of perturbed species, communities, and ecosystems

Michael E. Soulé

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 information. A conservation biologist may have to make decisions or rec-

Michael E. Soulé is an adjunct professor in the Wildland Management Center, University of Michigan School of Natural Resources. He is coauthor with Otto H. Frankel of *Conservation and Evolution*, published by Cambridge University Press. Address correspondence to 4747 Black Mountain Road, San Diego, CA 92130. © 1985 American Institute of Biological Sciences.

**Although crisis oriented,
conservation biology
is concerned with
the long-term viability
of whole systems**

ommendations 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 structure. 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 nation-

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

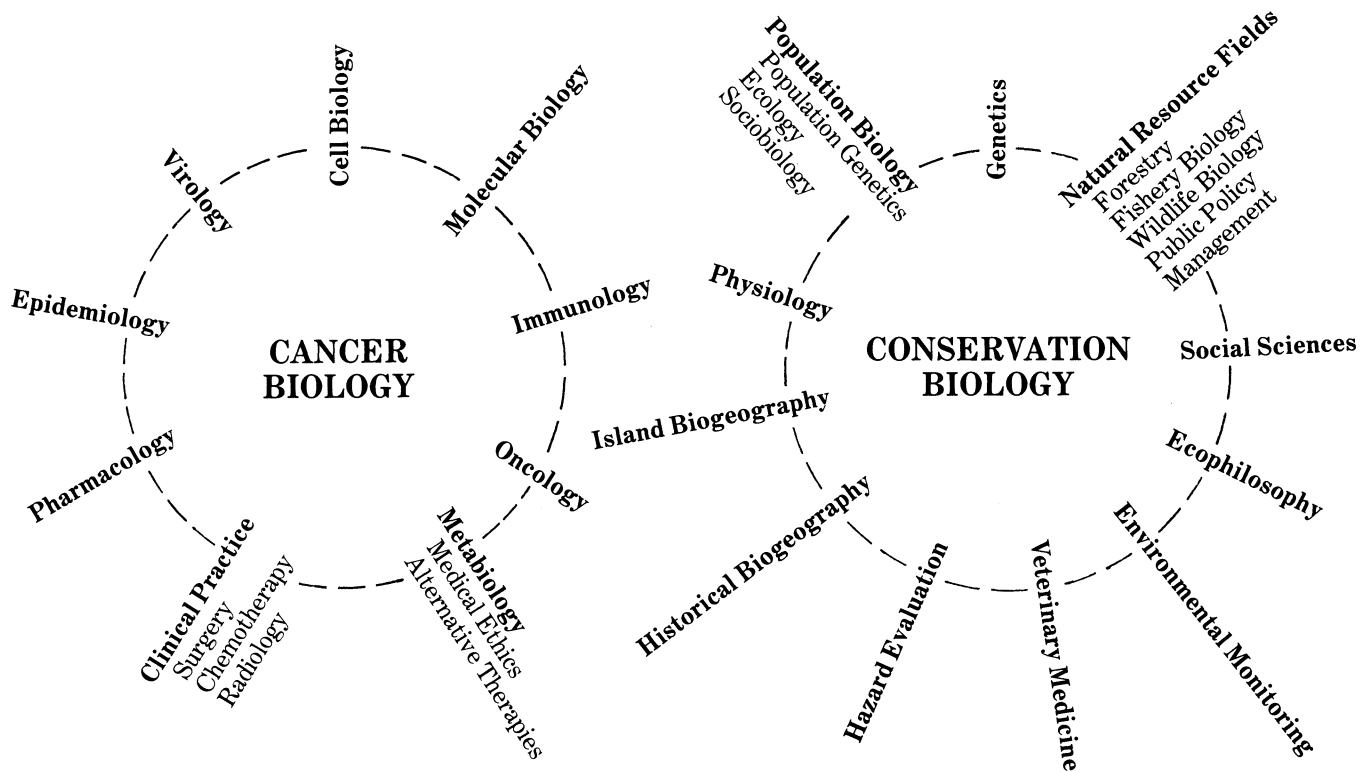


Figure 1. Cancer biology and conservation biology are both synthetic, multidisciplinary sciences. The dashed line indicates the artificial nature of the borders between disciplines and between “basic” and “applied” research. See text.

al 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 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 Soule 1981, Schonewald-Cox et al. 1983, Soule 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 phytophagous 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 impor-

tant 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 geologi-

cal 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 disequilibriumal 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 polymor-

phic population containing unique alleles or genetic combinations has greater value, 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

²Hunters, 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.

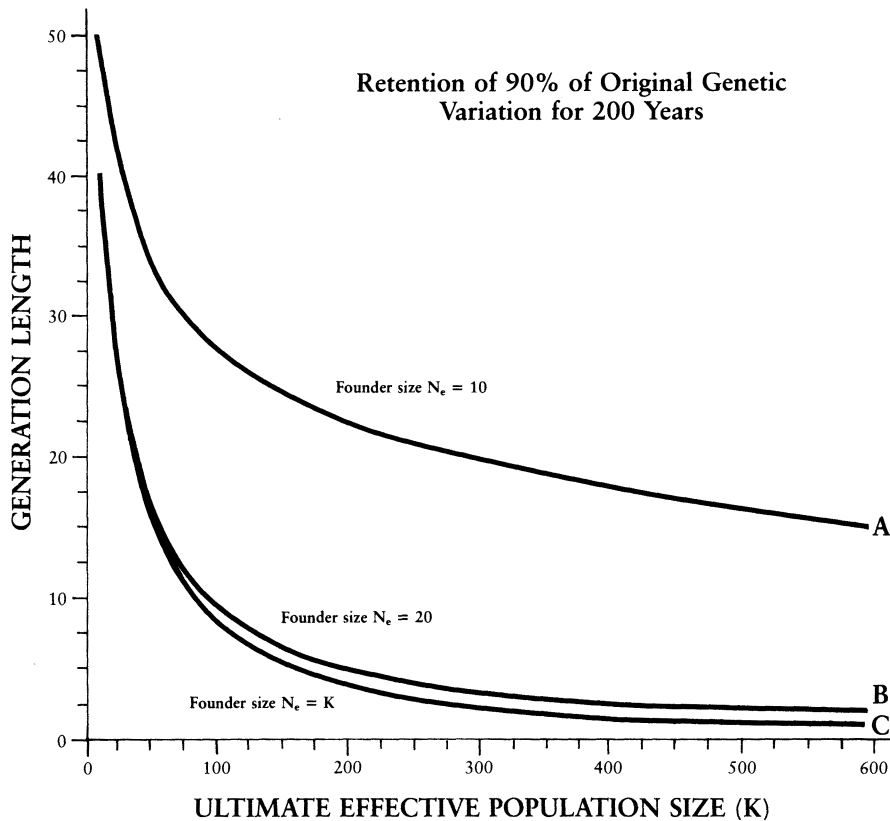


Figure 2. Combinations of effective population sizes and generation lengths (in years) in managed populations required to maintain at least 90% of the genetic variation that existed in the source population; the program lasts 200 years. The calculations on which the curves are based assume an intrinsic 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).

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 captive 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).

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

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

1981, and Mitton and Grant 1984). Russell Lande and George Barrowclough⁴ 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 endan-

gered 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

Michael Gilpin has provided continuing support and advice throughout the evolution of this article. I am also very grateful to Kurt Benirschke, Peter Brussard, John Cairns, William Conway, Paul Dayton, Jared Diamond, Paul Ehrlich, David Hales, Bruce Horwith, Arne Naess, Paul Risser, Hal Salwasser, and especially Patricia Romans for their considerate comments on various drafts of this article.

References cited

- Beardmore, J. A. 1983. Extinction, survival, and genetic variation. Pages 125–151 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. *Genetics and Conservation*. Benjamin-Cummings Publishing, Menlo Park, CA.
- Benirschke, K. 1983. The impact of research on the propagation of endangered species in zoos. Pages 402–413 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. *Genetics and Conservation*. Benjamin-Cummings Publishing, Menlo Park, CA.
- Bercovitz, A. B., N. M. Dzekala, and B. L. Lasley. 1978. A new method of sex determination in monomorphic birds. *J. Zoo Anim. Med.* 9: 114–124.
- Carson, R. 1962. *Silent Spring*. Houghton Mifflin, Boston.
- Cody, M. L., and J. M. Diamond, eds. 1975. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, MA.
- Devall, B., and G. Sessions. 1985. *Deep Ecology: Living as if Nature Mattered*. Peregrine Smith Books, Layton, UT.
- Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7: 129–146.
- . 1984. Historic extinctions: their mechanisms, and their lessons for understanding prehistoric extinctions. Pages 824–862 in P. S. Martin and R. Klein, eds. *Quaternary Extinctions*, University of Arizona Press, Tucson.
- Dubos, R. 1980. *The Woeing of the Earth*. Charles Scribner's Sons, New York.
- Ehrenfeld, D. 1981. *The Arrogance of Humanism*. Oxford University Press, London.
- Ehrlich, P. R., and A. H. Ehrlich. 1981. *Extinction*. Random House, New York.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Erwin, T. L. 1983. Tropical forest canopies: the last biotic frontier. *Bull. Entomol. Soc. Am.* 29: 14–19.
- Frankel, O. H. 1974. Genetic conservation: our evolutionary responsibility. *Genetics* 99: 53–65.
- Frankel, O. H., and M. E. Soule. 1981. *Conservation and Evolution*. Cambridge University Press, Cambridge, UK.
- Franklin, I. A. 1980. Evolutionary change in small populations. Pages 135–149 in M. E. Soule and B. A. Wilcox, eds. *Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Futuyma, D. J., and M. Slatkin, eds. 1983. *Coevolution*. Sinauer Associates, Sunderland, MA.
- Gilbert, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pages 11–33 in M. E. Soule and B. A. Wilcox, eds. *Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Gilbert, L. E., and P. H. Raven, eds. 1975. *Coevolution of Plants and Animals*. University of Texas Press, Austin.
- James, F. C., and W. J. Boecklen. 1984. Interspecific morphological relationships and the densities of birds. Pages 458–477 in D. R. Strong, Jr., D. S. Simberloff, L. G. Abele, and A. B. Thistle, eds. *Ecological Communities*. Princeton University Press, Princeton, NJ.
- Janzen, D. H. 1975. *Ecology of Plants in the*

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

- Tropics*. Edward Arnold, London.
- _____. 1983. No park is an island. *Oikos* 41: 402–410.
- Kushlan, J. A. 1979. Design and management of continental wildlife reserves: lessons from the Everglades. *Biol. Conserv.* 15: 281–290.
- Leigh, E. G., Jr. 1981. The average lifetime of a population in a varying environment. *J. Theor. Biol.* 90: 213–239.
- Leopold, A. 1953. *The Round River*. Oxford University Press, New York.
- _____. 1966. *A Sand County Almanac*. Oxford University Press, New York.
- Levins, R., and R. Lewontin. 1985. *The Dialectical Biologist*. Harvard University Press, Cambridge, MA.
- MacArthur, R. H. 1972. *Geographical Ecology*. Harper & Row, New York.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Marsh, G. P. 1864. *Man and Nature*. Scribners, New York.
- May, R. M. 1984. An overview: real and apparent patterns in community structure. Pages 3–16 in D. R. Strong, Jr., D. S. Simberloff, L. G. Abele, and A. B. Thistle, eds. *Ecological Communities*. Princeton University Press, Princeton, NJ.
- Mitton, J. B., and M. C. Grant. 1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. *Annu. Rev. Ecol. Syst.* 15: 479–499.
- Myers, N. 1984. Genetic resources in jeopardy. *Ambio* 13: 171–174.
- Naess, A. 1973. The shallow and the deep, long-range ecology movement. *Inquiry* 16: 95–100.
- _____. 1985. Identification as a source of deep ecological attitudes. Pages 256–270 in M. Tobias, ed. *Deep Ecology*. Avant Books, San Diego, CA.
- Orians, G. H. 1980. Habitat selection: general theory and applications to human behavior. Pages 49–66 in J. S. Lockard, ed. *The Evolution of Human Social Behavior*. Elsevier North Holland, New York.
- Passmore, J. 1974. *Man's Responsibility for Nature*. Duckworth, London.
- Price, P. W. 1980. *Evolutionary Biology of Parasites*. Princeton University Press, Princeton, NJ.
- Ralls, K., and J. Ballou. 1983. Extinction: lessons from zoos. Pages 164–184 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. *Genetics and Conservation*. Benjamin-Cummings Publishing, Menlo Park, CA.
- Raven, P. R. 1976. Ethics and attitudes. Pages 155–179 in J. B. Simmons, R. I. Bayer, P. E. Branham, G. L. Lucas, and W. T. H. Parry, eds. *Conservation of Threatened Plants*. Plenum Press, New York.
- Rolston, H. 1985. Duties to endangered species. *BioScience* 35: 718–726.
- Ryder, O. A., and E. A. Wedemeyer. 1982. A cooperative breeding programme for the mongolian wild horse *Equus przewalskii* in the United States. *Biol. Conserv.* 22: 259–271.
- Salwasser, H., S. P. Mealey, and K. Johnson. 1984. Wildlife population viability: a question of risk. *Trans. N. Am. Wildl. Nat. Resource Conf.* 49.
- Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. 1983. *Genetics and Conservation*. Benjamin-Cummings Publishing, Menlo Park, CA.
- Seifert, R. P., and F. H. Seifert. 1979. A *Heliconia* insect community in a Venezuelan cloud forest. *Ecology* 60: 462–467.
- Senner, J. W. 1980. Inbreeding depression and the survival of zoo populations. Pages 209–224 in M. E. Soulé and B. A. Wilcox, eds. *Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31: 131–134.
- Shaffer, M. L., and F. B. Samson. 1985. Population size and extinction: a note on determining critical population sizes. *Am. Nat.* 125: 144–151.
- Simberloff, D. S. 1980. Community effects of introduced species. Pages 53–83 in M. H. Nitecki, ed. *Biotic Crises in Ecological and Evolutionary Time*. Academic Press, New York.
- Simberloff, D. S., and L. G. Abele. 1976. Island biogeography theory and conservation practice. *Science* 191: 285–286.
- Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151–169 in M. E. Soulé and B. A. Wilcox, eds. *Conservation Biology*. Sinauer Associates, Sunderland, MA.
- _____. 1983. What do we really know about extinction? Pages 111–125 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. *Genetics and Conservation*. Benjamin-Cummings Publishing, Menlo Park, CA.
- Soulé, M. E., M. E. Gilpin, W. Conway, and T. Foose. 1986. The millenium ark. *Zoo Biol.*, in press.
- Soulé, M. E., and D. S. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biol. Conserv.*, in press.
- Soulé, M. E., and B. A. Wilcox, eds. 1980. *Conservation Biology: An Ecological-Evolutionary Perspective*. Sinauer Associates, Sunderland, MA.
- Strong, D. R., Jr., D. S. Simberloff, L. G. Abele, and A. B. Thistle, eds. 1984. *Ecological Communities*. Princeton University Press, Princeton, NJ.
- Templeton, A. R., and B. Read. 1983. The elimination of inbreeding depression in a captive herd of Speke's gazelle. Pages 241–262 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. *Genetics and Conservation*. Benjamin-Cummings Publishing, Menlo Park, CA.
- Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction-prone species. *BioScience* 24: 715–722.
- Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119–134 in M. E. Soulé and B. A. Wilcox, eds. *Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Tobias, M. 1985. *Deep Ecology*. Avant Books, San Diego, CA.
- Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 in D. R. Strong, Jr., D. S. Simberloff, L. G. Abele, and A. B. Thistle, eds. *Ecological Communities*. Princeton University Press, Princeton, NJ.
- Wilcox, B. A. 1980. Insular ecology and conservation. Pages 95–117 in M. E. Soulé and B. A. Wilcox, eds. *Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Wilson, E. O. 1984. *Biophilia*. Harvard University Press, Cambridge, MA.