Roundtable

Conserving nature at regional and continental scales—a scientific program for North America

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

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October 1999
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 mainland islands (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, coatis, 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 hares 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 Austra-
lia and North and South America (Martin and Klein 1984), most of the earth’s ecosystems contained mega-
herbivore species whose adult mem-
bers, like today’s elephants, were
too large to be killed by the largest
predators. Herbivore–plant interac-
tions must have dominated these eco-
systems, assuming that Pleistocene as well as modern megaherbivores exerted top-down controls on vege-
tation (Kortlandt 1984, Owen-
Smith 1988, Frank et al. 1998). For
some smaller herbivores (e.g., wilde-
beest, caribou, and bison), herd-
forming, migratory behavior effect-
viv limits the impact of predators on herd numbers, leaving a signifi-
cant regulatory role for plant pro-
ductivity (Fryxell et al. 1988).

Neither megaherbivores nor large
herds of migratory ungulates, how-
ever, 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 carnivores play
a major role in maintaining the di-
versity in many of today’s truncated
terrestrial ecosystems, the preserva-
tion or reintroduction of viable popu-
lations 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 depend-
ence on such factors as productivity,
volume, 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 car-
vivores. Big and secure areas are
obviously necessary but are not suf-
ficient. 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 con-
servation programs is the mainte-
nance or restoration of the population
dynamics, interchange, and migrations
in the natural, pre-agricultural, and
pre-industrial landscape.

The restoration of historical dis-
turbance regimes across landscapes
is also essential. Because many abi-
otic forces, including hurricanes and
wildfires, are uncontrollable, wild-
lands must be large enough and appro-
prately configured to as-
sure that no single disturbance event
can eliminate most of a certain habi-
tat 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 per-
turb interactions among trophic lev-
els (Menge and Sutherland 1976).

Although it has proven difficult to
demonstrate rigorously that any spe-
cific 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 frag-
mants can increase the persistence of
populations and local survival of spec-
ies (Forney and Gilpin 1989,
Fahrig and Merriam 1994, Sjogren
and Wyoni 1994, Hanks et al. 1995,
Beier and Noss 1998). Species differ
in how they “see” and use a de-
graded or fragmented landscape; con-
sequently, 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, reconnec-
ting isolated core protected areas may
be necessary just to achieve the big-
ness required to maintain ecological
diversity and resilience (Scott et al.
1999). On a larger scale, inter-re-
gional linkages, such as those envi-
sioned by the Yellowstone to Yukon
project (Yellowstone to Yukon Con-
servation Initiative 1998), are needed
to accommodate gene flow and dis-
persal of grizzly bears and other wide-
ranging species between the north-
ern Rocky Mountains in the United
States and northern Canada (Merrill
and Mattson 1998). Landscape link-
ages on that scale also offer the best
hope for ensuring the persistence of
species in the face of predicted cli-
mate change (Hunter et al. 1988,
Peters 1988). Parenthetically, we
wish to point out that the term “cor-
rider” 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, util-
ity 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, wilder-
ness 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 distur-
bance regime, and that will that mini-
mize invasions by exotic plants and
animals. The need for roadlessness
and the exclusion of motorized ve-
cillars, particularly on federal or
crown lands, displeases “wise-use”
opponents of conservation values. In
fact, these opponents have success-
fully defeated many proposals for
new protected areas in the US Con-
gress and other legislative bodies by
incorrectly caricaturing core reserves
as human exclusion zones that for-
bid hunting, fishing, and other recre-
ational uses (Chase 1995).

On the other hand, it is not essen-
tial that core areas be pristine at the
time of selection to qualify for protec-
tion as cores. One of the more contro-
versial 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 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 (Crumpler 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 semi-natural 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 enhances 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 (Soule 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 cows, 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 non-human. 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 communities 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 (Figure 1) 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 program 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

We wish to acknowledge the invaluable editorial assistance of Yvonne Baskin in the preparation of this manuscript. The ideas summarized here owe much to the perspectives of the 30 biologists who participated in a Wildlands Project Science Workshop, which was held 20–23 November 1997 in Tucson, Arizona, under the sponsorship of The Wildlands Project; see Soulé and Terborgh (1999) for a more detailed account of the proceedings. We thank Kevin Crooks, Jim Estes, Dave Foreman, and Brian Miller for many helpful comments.

References cited


Peters RL. 1988. The effect of global climatic


Rooney TP, Dress WJ. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart’s Content, and old-growth forest in Pennsylvania, USA. Natural Areas Journal 17: 297–305.


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