Rewilding and Biodiversity:

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Complementary Goals for Continental Conservation

isputes about goals and methodology are nothing new in the nature conservation movement. Gifford Pinchot's insistence on responsible use and John 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—sometimes 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.

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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 (Terborgh 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 bears 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

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.)

of large, unmanaged wilderness landscapes to represent all of North America'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 sequestering 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 1986). 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 nature 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 defining 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 was 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 wideranging 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 are 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 herbivores (tapir, monkeys, rodents, insects) can precipitate a rapid loss of plant species diversity. Construction of a reservoir in Venezuela caused flooding of a vast area, now known as Lago Guri. Many of the islands thus created 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 (leafeating 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 hyperabundance 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 via-

Glossary

Genetic and demographic rescue The arrival of immigrants into a small population can sometimes be beneficial by slowing the rates of loss of genetic variation and inbreeding and by lowering the chance of extinction caused by small numbers of individuals.

Succession The (sometimes) predictable and sequential change in species composition within a habitat.

Beta diversity The amount of change (turnover) in species composition in a local landscape when sampling across habitats.

Focal species Organisms whose requirements for survival represent factors important to maintaining ecologically healthy conditions; types of focal species include keystone species, umbrella species, flagship species, and indicator species. Focal species are helpful in planning and managing reserves.

Keystone species Organisms whose influence on ecosystem function and diversity are disproportionate to their numerical abundance.

The greatest impediment to rewilding is an unwillingness to imagine it.

bility 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 ani-

mals 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 regions. 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 fishes.

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 systems or processes that have suffered from mismanagement; abuses of this land-scape 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 naïve, 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 that 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.

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References

- Arita, H.T., F. Figueroa, A. Frisch, P. Rodríquez, and K. Santos-del-Prado. 1997. Geographical range size and the conservation of Mexican mammals. *Conservation Biology* 11:92-100.
- Arrhenius, O. 1921. Species and area. Journal of Ecology 9:95-99.
- Bedward, M., R.L. Pressey, and D.A. Keith. 1992. A new approach for selecting fully representative reserve networks: Addressing efficiency, reserve design, and land suitability with an iterative analysis. *Biological Conservation* 62:115-125.
- Church, R.L., D.M. Stoms, and F.W. Davis. 1996. Reserve selection as a maximal covering location problem. *Biological Conservation* 76:105-112.
- Côté, I. M., and W.J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11:395-405.
- Crooks, K. 1997. Tabby go home: House cat and coyote interactions in southern California habitat remnants. *Wild Earth* 7(4):60–63.
- Csuti, B., S. Polasky, P.H. Williams, R.L. Pressey, J.D. Camm, M. Kershaw, A.R. Kiester, B. Downs, R. Hamilton, M. Huso, and K. Sahr. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* 80:83-97.
- DeMalynadier, P. and M. Hunter, Jr. 1997. The role of keystone ecosystems in landscapes. Pages 68-76 in M.S. Boyce and A. Haney, eds.

- Ecosystem Management: Applications for Sustainable Forests and Wildlife Resources. New Haven and London: Yale Univ. Press.
- Diamond, J.M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural preserves. *Biological Conservation* 7:129-146.
- Diamond, J. 1986. The design of a nature reserve system for Indonesian New Guinea. Pages 485-503 in M.E. Soulé, ed. *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA: Sinauer.
- Estes, J.A., N.S. Smith and J.F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59:822-833.
- Faith, D.P., P.A. Walker, J.R. Ive, L. Belbin. 1996. Integrating conservation and forestry production: Exploring trade-offs between biodiversity and production in regional land use assessment. Forest Ecology and Management 85:251.
- Fox, S.R. 1981. John Muir and His Legacy: The American Conservation Movement. Boston, MA: Little, Brown and Co.
- Flather, C.H., K.R. Wilson, D.J. Dean, and W.C. McComb. 1997. Identifying gaps in conservation networks: Of indicators and uncertainty in geographic-based analyses. *Ecological Applications* 7:531-542.

- Foreman, D., and H. Wolke. 1989. *The Big Outside*. Tucson, AZ: Ned Ludd Books.
- Foster, R.B. 1980. Heterogeneity and disturbance in tropical vegetation. Pages 75-92 in M.E. Soulé and B.A. Wilcox, eds. *Conservation Biology: An Evolutionary-Ecological Perspective*. Sunderland, MA: Sinauer.
- Frankel, O.H., and M.E. Soulé. 1981. Conservation and Evolution. Cambridge, UK: Cambridge University Press.
- Franklin, I.R. 1980. Evolutionary change in small populations. Pages 135-149 in M.E. Soulé and B.A. Wilcox, eds. *Conservation Biology: An Evolutionary-Ecological Perspective*. Sunderland, MA: Sinauer.
- Gilbert, L.E. 1980. Food web organization and conservation of Neotropical diversity. Pages 11-34 in M.E. Soulé and B.A. Wilcox, eds. Conservation Biology: An Evolutionary-Ecological Perspective. Sunderland, MA: Sinauer.
- Harris, L.D. 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. Chicago: University of Chicago Press.
- Hummel, M. and S. Pettigrew. 1991. Wild Hunters. Toronto, Canada: Key Porter Books.
- Kendeigh, S.C., H.I. Baldwin, V.H. Cahalane, C.H.D. Clarke, C. Cottam, I.M. Cowan, P. Dansereau, J.H. Davis, F.W. Emerson, I.T. Haig, A. Hayden, C.L. Hayward, J.M. Linsdale, J.A. MacNab, and J.E. Potzger. 1950-51. Nature sanctuaries in the United States and Canada: A preliminary inventory. *The Living Wilderness* 15(35):1-45.
- Kiester, A.R., J.M. Scott, B. Csuti, R.F. Noss, B. Butterfield, K. Sahr, and D. White. 1996. Conservation prioritization using GAP data. Conservation Biology 10:1332-1342.
- McLaren, B.E. and R.O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. *Science* 266:1555-1558.
- McShea, W.J., H.B. Underwood, and J.H. Rappole. 1997. The Science of Overabundance: Deer Ecology and Population Management. Washington, DC: Smithsonian Institution Press.
- Miller, B.R. Reading, J. Stritthold, C. Carroll, R. Noss, M.E. Soulé, O. Sanchez, T. Terborgh, and D. Foreman. In press. Focal Species in the Design of Reserve Networks. *Wild Earth*.
- Mills, L.S., M.E. Soulé, and D.F. Doak. 1993. The history and current status of the keystone species concept. *BioScience* 43:219224.
- Nash, R.F. 1982 (1967). Wilderness and the American Mind. New Haven, CT: Yale University Press.
- Nash, R.F. 1989. The Rights of Nature. Madison, WI: University of Wisconsin Press.
- Nelson, R. 1997. *Heart and Blood: Living with Deer in America*. New York: Knopf. Inc.
- Newmark, W.D. 1985. Legal and biotic boundaries of western North American national parks: A problem of congruence. *Biological Conservation* 33:197-208.
- Newmark, W.D. 1995. Extinction of mammal populations in western North American national parks. *Conservation Biology* 9:512-526.
- Noss, R.F. 1983. A regional landscape approach to maintain diversity. *BioScience* 33:700-706.
- Noss, R.F. 1987. From plant communities to landscapes in conservation inventories: A look at The Nature Conservancy (USA). *Biological Conservation* 41:11-37.
- Noss, R.F. 1991. From endangered species to biodiversity. Pages 227-246 in K.A. Kohm, ed. *Balancing on the Brink of Extinction: The Endangered Species Act and Lessons for the Future.* Washington, DC: Island Press.
- Noss, R.F., and A. Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Washington, DC: Defenders of Wildlife and Island Press
- Noss, R.F., and B. Csuti. 1994. Habitat fragmentation. Pages 237-264 in G.K. Meffe and R.C. Carroll, eds. *Principles of Conservation Biology*. Sunderland, MA: Sinauer Associates.
- Noss, R.F., and L.D. Harris. 1986. Nodes, networks, and MUM's: Preserving diversity at all scales. *Environmental Management* 10:299-309.
- Noss, R.F., H.B. Quigley, M.G. Hornocker, T. Merrill, and P.C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.
- Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65-75.
- Paine, R.T. 1980. Food webs: Linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49:667-685.
- Palomares, F. et al. 1995. Positive effects on game species of top predators by controlling smaller predator populations: An example with lynx, mongooses, and rabbits. *Conservation Biology* 9(2):295-305.

- Pickett, S.T.A., and J.N. Thompson. 1978. Patch dynamics and the design of nature reserves. *Biological Conservation* 13:27-37.
- Pickett, S.T.A., and P.S. White. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, FL: Academic Press.
- Power, M.E., D. Tilman, J.A. Estes, B.A. Menge, W.J. Bond, L.S. Mills, G. Daily, J.C. Castilla, J. Lubchenco, and R.T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609-620.
- Pressey, R.L., and A.O. Nicholls. 1989. Application of a numerical algorithm to the selection of reserves in semi-arid New South Wales. Biological Conservation 50:263-278.
- Pressey, R.L., C.J. Humphries, C.R. Margules, R.I. Vane-Wright, and P.H. Williams. 1993. Beyond opportunism: Key principles for systematic reserve selection. *Trends in Ecology and Evolution* 8:124-128.
- Pressey, R.L., H.P. Possingham, and C.R. Margules. 1996. Optimality in reserve selection algorithms: When does it matter and how much? *Biological Conservation* 76:259-267.
- Runte, A. 1987. *National Parks: The American Experience*. Second Edition. Lincoln, NE: University of Nebraska Press.
- Scott, J.M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, J. Anderson, S. Caicco, F. D'Erchia, T.C. Edwards, J. Ulliman, and R.G. Wright. 1993. Gap analysis: A geographical approach to protection of biological diversity. Wildlife Monographs 123:1-41.
- Shaffer, M.L. 1981. Minimum population sizes for species conservation. BioScience 31:131-134.
- Shelford, V.E. (ed.). 1926. *Naturalist's Guide to the Americas*. Baltimore, MD: Williams and Wilkins.
- Shelford, V.E. 1933a. Ecological Society of America: A nature sanctuary plan unanimously adopted by the Society, December 28, 1932. *Ecology* 14:240-245.
- Shelford, V.E. 1933b. Conservation versus preservation. Science 77:535.Simberloff, D., and L.G. Abele. 1976. Island biogeography theory and conservation practice. Science 191:285-286.
- Soulé, M.E. and B. M. Wilcox (eds.). 1980. Conservation Biology: An Ecological-Evolutionary Perspective. Sunderland, MA: Sinauer Associates.
- Soulé, M.E. 1986. Conservation biology and the "real world." Pages 1-12 in in M.E. Soulé, ed. *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA: Sinauer.
- Soulé, M.E., and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation* 35:19-40.
- Soulé, M.E. (ed.). 1987. Viable Populations for Conservation. Cambridge, UK: Cambridge University Press.
- Soulé, M.E. 1995. An unflinching vision: Networks of people defending networks of lands. Pages 1-8 in D. Saunders, J.L. Craig, and E.M. Mattiske, eds. Nature Conservation 4: The Role of Networks. Sydney: Surrey Beatty, Inc.
- Soulé, M.E., B. Wilcox and C. Holtby. 1979. Benign neglect: A model of faunal collapse in the game reserves of East Africa. *Biological Conservation* 15:259-272.
- Soulé, M.E., D.T. Bolger, A.C. Alberts, R. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75-92.
- Terborgh, J. 1974. Preservation of natural diversity: The problem of extinction prone species. *BioScience* 24:715-722.
- Terborgh, J. 1988. The big things that run the world—A sequel to E. O. Wilson. *Conservation Biology* 2:402-403.
- Terborgh, J., J.A. Estes, P. Paquet, K. Ralls, D. Boyd, B. Miller and R. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. In Soulé, M. and J. Terborgh, Continental Conservation: Design and Management Principles for Long-term, Regional Conservation Networks. Covelo, CA and Washington, DC: Island Press. In press.
- Thrupp, L. 1995. Bittersweet Harvests for Global Supermarkets. Washington, DC: World Resources Institute.
- Ward, P.D. 1997. *The Call of the Distant Mammoths*. New York: Copernicus.
- Weaver, J.L., P.C. Paquet, and L.F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10:964-976.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229-299.
- Wilson, E.O., and E.O. Willis. 1975. Applied biogeography. Pages 522-534 in M.L. Cody and J.M. Diamond. *Ecology and Evolution of Communities*. Cambridge, MA: Belknap Press of Harvard University.