

BIODIVERSITY AND BEARS – A CONSERVATION PARADIGM SHIFT

DANIEL SIMBERLOFF, Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA, email: dsimberloff@utk.edu

Abstract: Burgeoning conservation problems and shrinking resources to deal with them have fostered an ongoing paradigm shift from single-species management to ecosystem management. Simultaneously, the main conservation goal has become maximization of biodiversity. The fact that both ecosystem management and biodiversity have various meanings is ominous for conservation of some species, such as charismatic large mammals. The focus on processes rather than species, and on species richness rather than identity, could detract from conservation of bears (Ursidae). On the other hand, management of large blocks of habitat can be helpful. Bears are highly symbolic to humans in many contexts and thus are natural flagship species, capable of attracting attention and resources to large conservation efforts. There is currently insufficient information to qualify them as keystone species—species whose fate directly determines those of many other species in a system. However, because they have large and often well-defined habitat requirements and some species have been well-studied, they may be excellent umbrella species: their maintenance would require habitat management that would also maintain populations of many other species. The facts that ecosystem management is currently heralded as the governing paradigm for much conservation and that bears may serve as umbrella species to assist ecosystem management pose an enormous challenge to researchers. There are few empirically tested methods in the ecosystem management toolbox, and developing and testing such methods will require testing insightful hypotheses and conducting intensive monitoring, some of which will have to be long-term. Without such research and monitoring, “ecosystem management,” “biodiversity conservation,” and “umbrella species” will remain catchphrases rather than operational terms.

Ursus 11:21–28

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Resource managers are faced with a drastic increase in the number of threatened populations and communities and with tremendously increased competition for funds to deal with them. So it is unsurprising that they have sought new and more efficient conservation approaches. In an age when, for example, one in every 8 plant species worldwide and one in every 3 in the United States is threatened with rapid extinction (Stevens 1998), traditional conservation, emphasizing management of populations and species of particular concern, seems hopeless. Many refuges in the U.S. and elsewhere were established to save dwindling populations of single species—Kirtland’s warbler (*Dendroica kirtlandii*) and the saguaro cactus (*Carnegiea gigantea*), among others. Similarly, the Endangered Species Act (16 U.S.C. 1531–1544) mandates the drafting of a recovery plan to arrest or reverse the decline of any listed species. With about 1,000 listed species already, and, for plants alone in the U.S., about 5,000 species that fulfill the criteria for listing, it is small wonder that the species-by-species method seems increasingly hopeless, difficult, and costly.

Further, the growing emphasis on biodiversity has fostered a shift in conservation goals and methods. The terms “biological diversity” and “biodiversity” first appeared in the conservation literature around 1980 (Norse 1993) and by 1992 had virtually exploded in terms of numbers of publications (Haila and Kouki 1994). They now dominate the popular and scientific literature, highlighted by the proceedings of the National Forum on Biodiversity, *Biodiversity* (Wilson 1986).

BIODIVERSITY AND ECOSYSTEM MANAGEMENT

The new method proposed for conservation is thus ecosystem management, and its goal is to conserve biodiversity. But both the method and the goal are problematic (Simberloff 1998, 1999). With respect to the goal, there is confusion about what biodiversity really means. It is a buzzword, but a pseudocognate one, in that, despite many meanings, most users think that everyone is using the same definition (Gaston 1996). Most lay persons construe “biodiversity” as the number of species in a system (species richness), and this is what conservation biologists usually mean when they speak informally. Technically, however, it has other components. Often it is viewed as having 3 levels: genetic, species, and ecosystem diversity (e.g., Office of Technology Assessment [U.S. Congress] 1987). More recently, there is frequent reference to structural and process diversity as crucial components of biodiversity (e.g., Franklin 1988). The processes and structures may initially be seen as key to maintaining species and ecosystems, but they can come to be the valued elements themselves (Simberloff 1998).

These various definitions of biodiversity lead to major problems. First, of course, different people may be talking about different things. If we are primarily concerned with saving species, we might be surprised and uneasy to see a management plan aimed specifically at preserving structural diversity of a forest. Second, it is not at all obvious how to measure diversity other than at the spe-

cies and perhaps genetic levels (Simberloff 1998, 1999), yet most people assume that biodiversity is not just an abstract concept and can be readily made operational. If we cannot measure something unambiguously, disputes are bound to arise. For example, is a particular forest a unique type, or is it simply another representative of a type already found in a reserve system?

As for the method of ecosystem management, as with biodiversity, there is no consensus definition of "ecosystem management" (Grumbine 1994, 1997; Simberloff 1999). In the U.S., for example, various government agencies define ecosystem management differently (or forswear a definition, as does the Department of Commerce), even though all have adopted it as the governing management method (Morrisey et al. 1994, Simberloff 1999).

At least 2 features of many definitions of ecosystem management have potentially grave consequences for conservation (Simberloff 1999). First, a key aspect of most resource management agency definitions is that humans are typically part of ecosystems. Thus, natural areas from which human activity is excluded are de-emphasized as antithetical to the notion of a normal ecosystem. Second, most definitions of ecosystem management focus on ecological processes rather than species (Meffe and Carroll 1994). Sometimes the processes are desired to maintain the entire ecosystem and the species in it, but often the processes themselves seem to be the *raison d'être* of ecosystem management. For example, a consensus definition of ecosystem management produced by representatives of many government agencies and private organizations (Keystone Center 1993) listed maintaining processes as the first goal. The focus on processes and de-emphasis of natural areas has led to concern that ecosystem management could become a tool for species-bashing (Soulé 1994). Procedures, even effective ones, based on single-species management could be discarded on the grounds that they represent an outmoded paradigm. Further, many ecosystem processes can be preserved even as the species normally responsible for them decline or disappear (Tracy and Brussard 1994). For example, low-diversity second-growth forest often has greater primary productivity than diverse primary forest. Many flagship species might well disappear from an ecosystem without appreciable changes in some key processes. This is especially true of some charismatic large vertebrates that typically have low total biomass and total productivity. The emphasis on substitutability of various species (Ehrlich and Mooney 1983) and on functional equivalence and redundancy, in an ecological sense (Walker 1992), also renders individual species less important.

Bears and Nature

But what does all this have to do with bears? Bears are archetypal flagship species—species so charismatic that they can become the symbol and leading feature of an entire conservation program. Bears captivate our imagination—why else would a bear represent the U.S. Forest Service, and a bear-like panda become the symbol of a leading conservation organization? Children play with teddy bears, not teddy owls. Among 1,247 4-year colleges and universities in the U.S., no fewer than 33 chose bears as their emblems, second only to eagles (39), which have religious connotations and are used primarily by church-supported and religious schools (Simberloff, unpublished data). At least 3 species and one subspecies of bears are represented. Some are cute and cuddly, some are funky, others are fierce. Bears are the focus of numerous Native American and other ceremonies and myths (e.g., Hallowell 1971, Snyder 1990, Moret 1994, Black 1998). Bears are a complex, exploded metaphor, as epitomized most forcefully by Faulkner's "The Bear," essentially a nature myth (Lydenberg 1952). A main interpretation of "The Bear" is that it symbolizes the relationship of humans to the land, and the hunt for the bear, Old Ben, represents the conquest of the South and the destruction of wilderness (Lydenberg 1952).

It is clear that bears have come to represent nature and wilderness—big wilderness—in the modern conservation movement and among conservation biologists as well, probably for the same complex reasons they play such key anthropological, religious, and literary roles. They are big and fierce, yet sufficiently anthropomorphic to engender our sympathy and concern. The vision of the Wildlands Project begins thus: "Our vision is simple: we live for the day when Grizzlies in Chihuahua have an unbroken connection to Grizzlies in Alaska..." (Wildlands Project 1995/1996:1). The Yellowstone-to-Yukon project under the umbrella of the Wildlands Project insists on the need for continuity and large areas for bears to thrive in the entire region. Conservation biologists have similarly focused on bears in many areas of academic and applied research, from theoretical studies of genetic deterioration (e.g., Shaffer 1983, Allendorf 1994) and metapopulation dynamics (e.g., Doak 1995) through studies of wildlife roadkill (e.g., Brody and Pelton 1989).

BEARS, ECOSYSTEM MANAGEMENT, AND BIODIVERSITY

Bears, with 7 species, certainly do not comprise much species-level biodiversity. So if the main goal of ecosystem management is to maximize biodiversity, the loss of

bears may be seen as a minor issue. Many people, including some who count themselves as conservationists, probably feel this way with respect to bears in their backyards or even regions (Grumbine 1992). I do not believe that our goal should be simply maximizing the number of species, but my point is, if one really does feel this way, what justification is there for worrying about bears? One possibility is that the disappearance of a bear species from an ecosystem might precipitate a cascade of subsequent extinctions, and that these *would* constitute a substantial decrease in biodiversity. I will discuss this proposition below. For now, let us assume that the elimination of a particular bear population would entail no major subsequent species losses in the system.

Some ecologists (e.g., Christensen et al. 1996) simply assume that loss of a species—any species—somehow harms the ecosystem, in the absence of much evidence. However, 2 traditional arguments for saving specific species even in the absence of evidence that they matter to the rest of the system are the rivet-popper hypothesis (Ehrlich and Ehrlich 1981) and the redundancy hypothesis (Walker 1992). The rivet-popper metaphor envisions a maniac randomly removing airplane rivets. Loss of some rivets may not bring the airplane down, but at some point, removal of the next rivet causes a crash. The rivet-popper hypothesis is agnostic about exactly why the plane crashes (Simberloff 1999). It could be the cumulative impact of the absence of many rivets (for example, wing vibration could surpass some threshold), or it could be that the last rivet served some unique function, and, had a different rivet been removed at this point, the plane would still be airborne. The redundancy hypothesis (Walker 1992) states that many species in species-rich ecosystems belong to groups of functional equivalents, and so long as at least one representative of each group remains, the system will continue to function more or less normally as species are lost. Removal of the last species in any functional group, however, will destroy the entire system. Of course, the second interpretation of the rivet-popper metaphor is exactly the redundancy hypothesis. Two recent widely publicized experiments (Hooper and Vitousek 1997, Tilman et al. 1997), though they do not directly test the redundancy hypothesis, certainly give results consistent with it and suggest that plant species diversity is not as crucial to ecosystem function as the number of functional groups.

So if some people think bears are not important to save in their own right, it seems that a justification for them might be that they serve unique functions in their respective ecosystems. What is the function of a bear?

Keystone, Flagship, and Umbrella Species

The concept of a “keystone species” may rationalize concern over an individual species if biodiversity is the main goal. A keystone species is one that affects many others in an ecosystem, far beyond what one would have expected given its biomass or numbers (Paine 1969, 1995). The concept has been assailed on the grounds that there is no clear demarcation of how much impact a species must have to qualify for this status or even an operational way to measure impact (Mills et al. 1993, Hurlbert 1997). However, there are enough instances in which a single species clearly affects the fates of many others (examples and references in Simberloff 1998) that it seems perverse to throw out the entire notion simply because it is difficult to specify a cut-off point. The impacts of some single-species removals (e.g., American chestnut [*Castanea dentata*] and beaver [*Castor canadensis*]) show that some species affect many others. And top carnivores often play key roles in regulating entire ecosystems (Terborgh et al. 1999). Might bears qualify as keystone species?

Many proposed examples of keystone species disproportionately feed on species that would otherwise dominate space or some other resource (e.g., Paine 1969). The introduction of carnivores into new systems has sometimes precipitated trophic cascades—impacts propagated down through the food web and affecting many species, even those not eaten by the carnivore (references in Polis and Strong 1996). It is precisely this top-down impact of some carnivores that suggests to the Wildlands Project that establishment of preserves large enough to maintain them is crucial to the existence of natural ecosystems. However, terrestrial examples of predator-mediated trophic cascades are rare and often rest on isolated systems such as the wolves (*Canis lupus*) and moose (*Alces alces*) of Isle Royale (Peterson and Page 1983). Polis and Strong (1996) argue on several grounds that trophic cascades are generally rare, especially terrestrial ones, but that omnivory by the top carnivore will facilitate them.

Except for polar bears (*Ursus maritimus*), bears are remarkably omnivorous (Bunnell 1984a,b,c; Lentifer 1984). However, there is a notable dearth of evidence of the population impact of bears on the species they eat. For black bears (*U. americanus*) and brown bears (*U. arctos*), there is much evidence that the availability of certain prey species affects bear densities rather than vice-versa—classic bottom-up control (e.g., Committee on Management of Wolf and Bear Populations in Alaska [National Research Council] 1997). One might have

expected the polar bear, because of its more restricted diet, to have a great impact on seal (Otariidae) populations, but I know of no evidence that it does. It may well have influenced seal evolution in many ways that could ultimately have ecological effects (Stirling 1988), but current ecological impacts on seal populations are poorly studied. Experiments on black and brown bear removal have been inconclusive with respect to their normal influence on ungulate prey populations that might, in turn, have system-wide impacts (Committee on Management of Wolf and Bear Populations in Alaska [National Research Council] 1997). A black bear removal experiment in east-central Saskatchewan (Stewart et al. 1985) is perhaps the only one even to suggest a population impact on an ungulate (moose), and this result is not definitive.

Species can have enormous system-wide impacts other than through the energy transfer achieved by eating them, of course: beaver dams, rooting by feral hogs (*Sus scrofa*), and uprooting of trees by elephants (Proboscidea) all transform ecosystems. The Asian black bear (*Selenarctos thibetanus*) can do enormous damage to forests by its habit of stripping bark off trees, thus killing as many as 40 trees per family per night (Bunnell 1984a, Moret 1994), though the full ecosystem consequences have not been assessed. Naiman and Rogers (1997) suggest that the grizzly bear (*Ursus arctos horribilis*) can, in concert with several other species, maintain a mosaic of habitats in riparian forests by trampling and digging; again, the crucial measurements have yet to be taken. Bears as well as other carnivores, such as mink (*Mustela vison*), have been implicated in the massive transfer of nutrients, particularly phosphorus and nitrogen, from marine systems to terrestrial ones by virtue of heavy feeding on runs of salmon (*Oncorhynchus* spp.) and subsequent deposition of feces and salmon carcasses on land (Willson et al. 1998, Hilderbrand et al. 1999). The consequences of this fertilization and the role of bears in it have just begun to be assessed.

If bears are not yet known to be keystone species, they are, as noted above, flagship species *par excellence*, and thus may merit protection if only because their presence energizes an entire conservation effort. Would there be as much concern for habitat destruction in western North America if the grizzly bear did not live there? Because of their large sizes, with consequent low densities and large home ranges, bears may also be excellent umbrella species. These are species that require such large amounts of a specified natural habitat that saving them would almost certainly incidentally save many other species requiring the same habitat (Meffe and Carroll 1997). For example, Cox et al. (1994) have shown that proposed

conservation areas for the Florida black bear (*Ursus americanus floridanus*) would include more threatened vertebrates and plants than would those for the Florida panther (*Felis concolor coryi*), a species whose legendary home range size would seem to qualify it as a perfect umbrella.

Using umbrella species is hypothesized to be a shortcut, in that it may lead to effective conservation of biodiversity without the enormous investment of time and money required to study each species in a community and determine its precise habitat requirement. A component of the Wildlands Project advocates using as umbrella species large carnivores that are also flagship species, that have some defined habitat association, and that have already been well-studied, such as black bears (D. Foreman, The Wildlands Project, Tucson, Arizona, USA, personal communication, 1997). It is difficult to imagine a more logical choice.

ECOSYSTEM MANAGEMENT FOR BEARS AND BIODIVERSITY

Ideas on how to manage ecosystems for biodiversity are for the most part just that—ideas that show a commitment to that goal rather than a toolbox of scientifically tested, on-the-ground methods (Simberloff 1999). For example, the “new forestry” (Franklin 1989) consists of suggestions (such as leaving some slash rather than clearing or burning it) that sound reasonable in that they provide resources for species suffering under previous logging systems, but they are largely untested. It has yet to be shown that even conscientious application of all these techniques really would preserve biodiversity, yet allow substantial logging. There is research on some aspects of leaving dead wood (references in Simberloff 1999), but much remains to be done. Similarly, much is known about the impact of various fire regimes on some forest types (e.g., Hermann 1993) and there is a well-developed technology of controlled burns, but much research is needed before it will be possible to say what fire regime in which system will foster which biodiversity and how the optimal regime can be conducted. For single-species management, many techniques have a long history of study and perfection—captive propagation, translocation, supplemental feeding, etc. Ecosystem management is not as mature, at least as concerns effect of various methods on biodiversity.

With respect to bears, a part of the threat faced by at least some populations of all species is that they are hunted, for the gall bladder trade, or because they are seen as pests (Nowak 1991, World Wildlife Fund 1998). This is not a major mortality factor for most species considered as umbrellas, such as the Florida pan-

ther or the northern spotted owl (*Strix occidentalis caurina*). An umbrella species serves as an umbrella by virtue of demanding habitat requirements (see above), and its population trajectory is generally interpreted as reflecting change in habitat quality or amount, rather than rate of harvest. Populations of all bear species are also threatened in this regard (e.g., by deforestation [Nowak 1991]), though the relative importance of harvest and habitat change varies from case to case and is often controversial. However, there is little doubt that habitat change is often crucial, and thus to the extent that ecosystem management will entail managing large blocks of habitat so that they can sustain viable populations of most or all species in region, it can be a useful tool in bear conservation. However, if bears are to be umbrella species for particular communities, specific habitat-centered management procedures that aid both the bear and a substantial component of its community must be tested empirically with enough monitoring to allow a definitive statement about whether they work. A pervasive, crucial shortcoming of current ecosystem management plans is insufficient monitoring to test hypotheses (Yoon 1997). Without such data on a substantial fraction of the community as well as the umbrella species, all we have are clever ideas.

For example, the importance of corridors in maintaining viable populations has rarely been tested empirically; thus the whole notion remains controversial (Hobbs 1992, Simberloff et al. 1992). The absence of data is one problem; another is that corridors need not have the same importance for all species in all systems, yet many discussions of them are generic. The black bear, with its attachment to forests and occasional hesitancy to cross open spaces (Harting 1987, Halioua 1991), as well as its documented problems with cars (Wooding and Brady 1987, Brody and Pelton 1989), may be one animal that actually benefits from corridors. Does it? Do other species in its communities? What sorts of corridors?

CONCLUSIONS

Ecosystem management, ill-defined as it may be, is rapidly becoming entrenched as the dominant mode of conservation activity, both because of perceived economies of scale and because it seems adapted to a goal of maintaining biodiversity. Single species, even charismatic ones like bears, are destined to be de-emphasized in much conservation planning as this shift occurs. However, the manifold human fascination with bears, and their role as symbols for nature, adapt them to the role of flagship species in any kind of conservation effort, including those with biodiversity as the chief goal. There

is currently little evidence that they are keystone species, but several aspects of the biology of some bear species suggest that they might serve as excellent umbrella species in ecosystem management approaches. To test this hypothesis will require extensive monitoring and, where possible, field experiments.

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LITERATURE CITED

- ALLENDORF, F.W. 1994. Genetically effective sizes of grizzly bear populations. Pages 155–156 in G.K. Meffe and C.R. Carroll, editors. *Principles of conservation biology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- BLACK, L.T. 1998. Bears in human imagination and ritual. *Ursus* 10:343–347.
- BRODY, A.J., AND M.P. PELTON. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* 17:5–10.
- BUNNELL, F. 1984a. Small bears. Pages 96–97 in D. Macdonald, editor. *The encyclopedia of mammals*. Facts on File Publications, New York, New York, USA.
- . 1984b. Grizzly bear. Pages 88–91 in D. Macdonald, editor. *The encyclopedia of mammals*. Facts on File Publications, New York, New York, USA.
- . 1984c. American black bear. Pages 94–95 in D. Macdonald, editor. *The encyclopedia of mammals*. Facts on File Publications, New York, New York, USA.
- CHRISTENSEN, N.L., A.M. BARTUSKA, J.H. BROWN, S. CARPENTER, C. D'ANTONIO, R. FRANCIS, J.F. FRANKLIN, J.A. MACMAHON, R.F. NOSS, D.J. PARSONS, C.H. PETERSON, M.G. TURNER, AND R.G. WOODMANSEE. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6:665–691.
- COMMITTEE ON MANAGEMENT OF WOLF AND BEAR POPULATIONS IN ALASKA (NATIONAL RESEARCH COUNCIL). 1997. *Wolves, bears, and their prey in Alaska*. National Academy Press, Washington, D.C., USA.
- COX, J., R. KAUTZ, M. MACLAUGHLIN, AND T. GILBERT. 1994. *Closing the gaps in Florida's wildlife habitat conservation system*. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida, USA.
- DOAK, D.F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. *Conservation Biology* 9:1370–1379.
- EHRlich, P.R., AND A.H. EHRlich. 1981. *Extinction: The causes and consequences of the disappearance of species*. Random House, New York, New York, USA.
- , AND H.A. MOONEY. 1983. Extinction, substitution, and ecosystem services. *BioScience* 33:248–254.

- FRANKLIN, J.F. 1988. Structural and functional diversity in temperate forests. Pages 166–175 in E.O. Wilson, editor. *Biodiversity*. National Academy Press, Washington, D.C., USA.
- . 1989. Toward a new forestry. *American Forests*, 1989 (Nov/Dec):1–8.
- GASTON, K.J. 1996. What is biodiversity? Pages 1–9 in K.J. Gaston, editor. *Biodiversity. A biology of numbers and difference*. Blackwell, Oxford, U.K.
- GRUMBINE, R.E. 1992. Ghost bears. Exploring the biodiversity crisis. Island Press, Washington, D.C., USA.
- . 1994. What is ecosystem management? *Conservation Biology* 8:27–38.
- . 1997. Reflections on “What is ecosystem management?” *Conservation Biology* 11:41–47.
- HAILA, Y., AND J. KOUKI. 1994. The phenomenon of biodiversity in conservation biology. *Annales Zoologici Fennici* 31:5–18.
- HALIOUA, J. 1991. Baribal. Une invitation chez les ours. *Terre Sauvage* 57:64–81. (In French.)
- HALLOWELL, A.I. 1971. Bear ceremonialism in the eastern Woodlands area. Pages 141–143 in F.L. Utley, L.Z. Bloom, and A.F. Kinney, editors. *Bear, man, and God: Eight approaches to William Faulkner’s “The Bear.”* Random House, New York, New York, USA.
- HARTING, A.L. 1987. Grizzly bear–black bear relationships. Pages 77–78 in M.N. LeFranc, Jr., M.B. Moss, K.A. Patnode, and W.C. Sugg, III, editors. *Grizzly bear compendium*. Interagency Grizzly Bear Committee, Washington, D.C., USA.
- HERMANN, S.M., EDITOR. 1993. Proceedings of the Tall Timbers fire ecology conference No. 18. The longleaf pine ecosystem: Ecology, restoration and management. Tall Timbers Research Station, Tallahassee, Florida, USA.
- HILDERBRAND, G.V., T.A. HANLEY, C.T. ROBBINS, AND C.C. SCHWARTZ. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121:546–550.
- HOBBS, R.J. 1992. The role of corridors in conservation: solution or bandwagon? *Trends in Ecology and Evolution* 7:389–392.
- HOOPER, D.U., AND P.M. VITOUSEK. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- HURLBERT, S.H. 1997. Functional importance vs. keystone: Reformulating some questions in theoretical biocenology. *Australian Journal of Ecology* 22:369–382.
- KEYSTONE CENTER. 1993. National ecosystem management forum meeting summary. Keystone Center, Keystone, Colorado, USA.
- LENTIFER, J.W. 1984. Polar bear. Pages 92–93 in D. Macdonald, editor. *The encyclopedia of mammals*. Facts on File Publications, New York, New York, USA.
- LYDENBERG, J. 1952. Nature myth in Faulkner’s “The Bear.” *American Literature* 24:62–72.
- MEFFE, G.K., AND C.R. CARROLL. 1994. Principles of conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.
- , AND ———. 1997. Principles of conservation biology. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- MILLS, L.S., M.E. SOULÉ, AND D.F. DOAK. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.
- MORET, J. 1994. Un ours-lune au pays du soleil levant. *Terre Sauvage* 81:61–67. (In French.)
- MORRISSEY, W.A., J.A. ZINN, AND M.L. CORN. 1994. Ecosystem management: Federal agency activities. Library of Congress, Congressional Research Service, Washington, D.C., USA.
- NAIMAN, R.J., AND K.H. ROGERS. 1997. Large animals and system-level characteristics in river corridors. *BioScience* 47:521–529.
- NORSE, E.A., EDITOR. 1993. Global marine biological diversity. Island Press, Washington, D.C., USA.
- NOWAK, R.M. 1991. Walker’s mammals of the world, Fifth edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- OFFICE OF TECHNOLOGY ASSESSMENT (U.S. CONGRESS). 1987. Technologies to maintain biological diversity. U.S. Government Printing Office, Washington, D.C., USA.
- PAINE, R.T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103:91–93.
- . 1995. A conversation on refining the concept of keystone species. *Conservation Biology* 9:962–964.
- PETERSON, R.O., AND R.E. PAGE. 1983. Wolf–moose fluctuation in Isle Royale National Park, Michigan, USA. *Acta Zoologica Fennica* 174:251–253.
- POLIS, G.A., AND D.R. STRONG. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- SHAFFER, M.L. 1983. Determining minimum viable population sizes for the grizzly bear. *International Conference on Bear Research and Management* 5:133–139.
- SIMBERLOFF, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biological Conservation* 83:247–257.
- . 1999. The role of science in the preservation of forest biodiversity. *Forest Ecology and Management* 115:101–111.
- , J.A. FARR, J. COX, AND D.W. MEHLMAN. 1992. Movement corridors: conservation bargains or poor investments. *Conservation Biology* 6:493–504.
- SNYDER, G. 1990. *The practice of the wild*. North Point Press, San Francisco, California, USA.
- SOULÉ, M.E. 1994. Normative conflicts and obscurantism in the definition of ecosystem management. Page 20 in W.W. Covington and L.F. DeBano, editors. *Sustainable ecological systems: Implementing an ecological approach to land management*. U.S. Department of Agriculture Forest Service, Fort Collins, Colorado, USA.
- STEVENS, W.K. 1998. One in every eight plant species is imperiled, a survey finds. *New York Times* (9 April):A1, A24.
- STEWART, R.R., E.H. KOWAL, R. BEAULIEU, AND T.W. ROCK. 1985. The impact of black bear removal on moose calf survival in east-central Saskatchewan. *Alces* 21:403–418.
- STIRLING, I. 1988. *Polar bears*. University of Michigan Press,

- Ann Arbor, Michigan, USA.
- TERBORGH, J., J.E. ESTES, P. PAQUET, K. RALLS, D. BOYD-HEGER, B.J. MILLER, AND R.F. NOSS. 1999. The role of top carnivores in regulating terrestrial ecosystems. Pages 39–64 in M.E. Soulé and J. Terborgh, editors. *Continental conservation: Scientific foundations for regional conservation networks*. Island Press, Washington, D.C., USA.
- TILMAN, D., J. KNOPS, D. WEDIN, P. REICH, M. RITCHIE, AND E. SIEMANN. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- TRACY, C.R., AND P.F. BRUSSARD. 1994. Preserving biodiversity: species in landscapes. *Ecological Applications* 4:205–207.
- WALKER, B.H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:18–23.
- WILDLANDS PROJECT. 1995/1996. *Wildlands. The Wildlands Project*. *Wild Earth* 5(4):1.
- WILLSON, M.F., S.M. GENDE, AND B.H. MARSTON. 1998. Fishes and the forest. *BioScience* 48:455–462.
- WILSON, E.O., EDITOR. 1986. *Biodiversity*. National Academy Press, Washington, D.C., USA.
- WOODING, J.B., AND J.R. BRADY. 1987. Black bear roadkills in Florida. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 41:438–442.
- WORLD WILDLIFE FUND. 1998. Website <http://www.wwf.org/new/fires/species.htm>
- YOON, C.K. 1997. Many habitat conservation plans found to lack key data. *New York Times* (23 December):B13.