

Strongly Interacting Species: Conservation Policy, Management, and Ethics

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Obsolescence of environmental laws and regulations is unavoidable, and policies dealing with endangered species and ecosystem conservation often lag decades behind the relevant science. For example, endangered species laws and regulations and other conservation statutes typically fail to consider the interactions of strongly interacting species, probably because the importance of such interactions was not well understood when the laws were drafted. By failing to consider current knowledge, therefore, natural resource scientists and managers may be harming the species and systems they are charged with protecting. Most ecologists agree that the conservation of biodiversity is facilitated by maintaining population densities and distributions of strongly interactive species above estimable thresholds for ecological effectiveness. Assuming that conservation biologists and natural resource managers are “physicians to nature,” we therefore propose they are obligated to adhere to a doctrine of “best conservation practices based on the best science,” applying a more rigorous standard for the management of relatively interactive species than may be mandated by older statutes and effected by current practice and convention.

Keywords: interactive species, effective densities, management, Endangered Species Act, ethics

Any legislation or other policy instrument based on empirical science is prone to senescence. Consider the US Endangered Species Act (ESA) of 1973. This was the first federal statute to grant de facto existence rights to species of plants and animals (Varner 1987) and to impose binding, enforceable duties on government agencies and private citizens to protect imperiled species. The ESA was based on the best science of the time (Bean and Rowland 1997), and it still remains in the vanguard of worldwide species protection efforts. However, the ESA, like other environmental laws from the 1970s, was enacted before conservation biology existed as a discipline, before the field of population viability analysis existed, before ecologists understood many of the ecosystem consequences of species interactions and community dynamics (Terborgh et al. 1999), and before the spatial and temporal scale-related complexities of effective protection of vulnerable species were widely understood (Soulé et al. 2003). Although the ESA was revised and reauthorized in 1988, it does not reflect many advances in population biology and community ecology.

Among the scientific anachronisms in this law is the absence of specific reference to species interactions that contribute substantially to the maintenance of ecological and species diversity. Not only has the understanding of interaction webs advanced (Menge 1995), but it is now widely understood that the disappearance of a strongly interactive species can lead to profound changes in ecosystem composition, structure, and diversity (Soulé and Terborgh 1999, Terborgh et al. 1999,

Oksanen and Oksanen 2000, Schmitz et al. 2000, Soulé et al. 2003). For instance, decimation of great whales by industrial whaling substantially altered krill-consumer dynamics in the Southern Ocean, and whaling has been proposed as the main cause of a recent megafaunal collapse in the North Pacific Ocean (Springer et al. 2003). In addition, the disruption of fruit dispersal and seed-set patterns following early Holocene megafaunal extinctions fundamentally altered the species composition of neotropical forests (Janzen and Martin 1982), and the functional dynamics of coastal marine ecosystems worldwide have been grossly altered by overfishing of large herbivores and predators (Jackson et al. 2001).

The functional extinction of species interactions often occurs well before the species themselves have completely disappeared. In the oceans, many large, interactive species persist only as rare adults, or as small or juvenile individuals that do not interact like large adults, qualitatively or quantitatively.

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On land, many large animals and other strongly interactive species are completely missing from vast areas that they occupied a century or two ago (Laliberte and Ripple 2004). Globally, many, if not most, large-bodied, strongly interacting species are increasingly rare, even if they persist in parts of their former range. A reasonable hypothesis is that ecosystems that have lost one or more strongly interactive species are destined to undergo profound degradation and simplification over time.

Nevertheless, most conservation laws, including the ESA, fail to reflect the effects of widespread ecological disappearances of strongly interacting species and the resulting ecosystem perturbations. For example, the current criteria for recovery of endangered mammal species under the ESA generally ignore interspecies interactions altogether (Soulé et al. 2003), emphasizing short-term, single-species, demographic viability in only a few circumscribed areas. Indeed, many current recovery plans, at least for mammals, call for no increase in numbers of individuals, numbers of populations, or geographic range (Tear et al. 1995; but see USFWS 1998, Jennings 1999).

Here we propose that population densities of strongly interactive species must not be permitted to fall below thresholds for ecological effectiveness, and that the geographic ranges of such species should be as large as possible (Conner 1988, Soulé et al. 2003). Before this proposal can be implemented, however, two issues must be clarified: (1) the definition of strongly interactive species and (2) the achievement of ecologically effective densities of such species.

What are strongly interactive species?

The idea that some species interact more strongly than others is not new. Paine (1969) first used the term “keystone species” for particularly strong interactors: those, for example, whose activities maintain species and habitat diversity and whose effects are disproportionate to their abundance (Kotliar et al. 1999). It is worth noting that Paine’s idea, one of the most influential in all of modern ecology, is fundamentally a theory of species diversity—that the presence or absence of one or several key species influences the distribution and abundance of many other species. Ecologists recognize, however, that the keystone designation artificially dichotomizes species into groups such as “strongly interactive” (or keystone) and “non-strongly interactive” (Mills et al. 1993). Though such dualisms have limited utility in science, this particular one is helpful in education and advocacy.

Species that are relatively interactive have been categorized according to the kind of ecological interaction that is most evident. Among these interactions are *habitat enrichment*, *mutualisms*, *predation*, and *competition*. Species whose activities affect and enhance physical or biological habitat structure have been referred to as “ecological engineers” (Jones et al. 1994). Ecological engineers significantly modify their habitat in ways that increase local species diversity. Beavers (*Castor canadensis*), for instance, create wetlands by building dams in streams. Other examples of ecological en-

gineering include mound building by termites, burrowing and grazing by prairie dogs (*Cynomys* spp.), and habitat conversion by elephants (*Loxodonta africana*) and bison (*Bison bison*) (Naiman et al. 1988, Owen-Smith 1988, Detling 1998, Kotliar et al. 1999).

Mutualist species, by virtue of their interactions, can also maintain species diversity. An example is the relationship between the whitebark pine (*Pinus albicaulus*) and Clark’s nutcracker (*Nucifraga columbiana*). Clark’s nutcracker is strongly dependent on the seeds of the whitebark pine, and the pine depends on the nutcracker for the dispersal of its seeds into caches. These seed caches are also a major food source for both small vertebrates and grizzly bears (*Ursus arctos*) in the Greater Yellowstone ecosystem (Mattson et al. 1992).

Terborgh and colleagues (1999) describe how the loss of apex mammalian predators can precipitate ecological chain reactions that lead to profound degradation and species loss. Although top-down forcing through three or more trophic levels has been demonstrated for nonvertebrate taxa (Strong et al. 1996, Terborgh et al. 2001), space constraints and immediate policy relevance preclude a detailed review here. Many predator-mediated chains of reaction have been described or postulated (Estes and Palmisano 1974, Pace et al. 1999, Terborgh et al. 2001); some of these (ecological cascades) are summarized in figure 1 and further elaborated in figure 2. Figure 2a illustrates the familiar case of gray wolves (*Canis lupus*) in Yellowstone, representing the scenario in which the extirpation of a large carnivore leads to the ecological release of large terrestrial ungulates and other herbivores, causing changes in vegetation structure, species composition, and diversity.

Crooks and Soulé (1999) demonstrated the behavioral release of mesopredators in patches of coastal sage scrub and chaparral in southern California, where the local absence of coyotes (*Canis latrans*) led to an increase in the activity of the house cat (*Felis catus*), in turn causing reductions of native, scrub-requiring bird species (figure 2b). An impressive case of competitive release (Paine 1966) was described by Henke and Bryant (1999) and is illustrated in figure 2c. They documented a reduction of rodent diversity from 12 species to just 1 as a result of coyote removal; the survivor was the competitively dominant kangaroo rat, *Dipodomys ordii*. The fourth example (figure 2d)—the case of sea otters (*Enhydra lutris*) and kelp forest—is described below.

The fifth example (figure 2e) of a predator-mediated ecological cascade is hypothesized to have begun with the decimation of the great whales by industrial whaling following World War II. Springer and colleagues (2003) suggest that a series of ecological extinction events affecting pinnipeds and sea otters in the northern Pacific Ocean and the Bering Sea was initiated when killer whales (*Orcinus orca*), following the effective disappearance of large baleen whales, expanded their diets. Though baleen whales are themselves carnivores, they are not considered to be apex predators because of the relatively small size of their prey and because they are preyed on by killer whales.

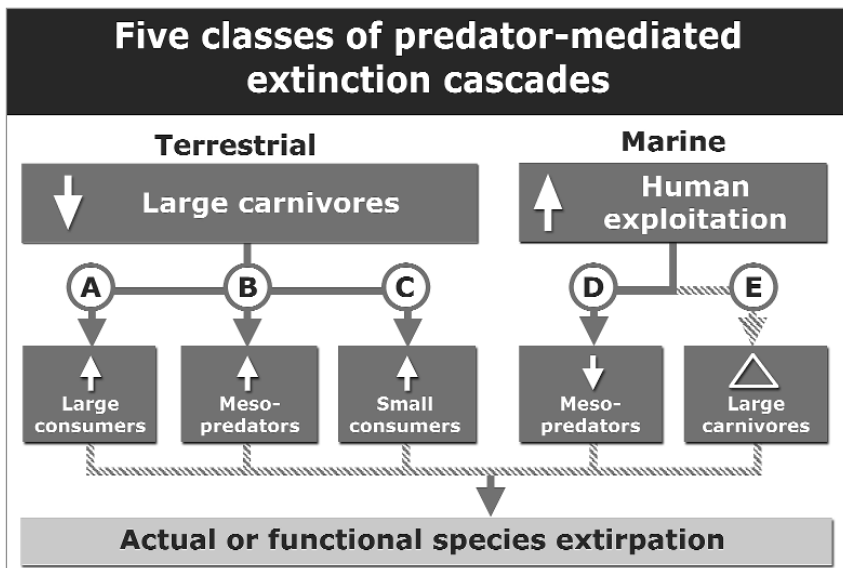


Figure 1. Five classes of predator-mediated trophic cascades leading to local extinction (extirpation) in terrestrial and marine ecosystems. Arrows in shaded boxes indicate an increase or decrease in population. Solid lines between boxes indicate direct effects; broken lines indicate complex, indirect effects; the delta (Δ) indicates a behavioral change (prey switching). The letters (a) through (e) refer to the individual graphics in figure 2.

We know little about the distribution of interaction strength among species in most ecosystems. Nor do we know the morphological, physiological, behavioral, or ecological correlates of strong interactivity. Paine (1992) showed experimentally that the interaction strengths of seemingly similar species can vary substantially; he also argued that mammals are especially strong interactors in many terrestrial ecosystems (Paine 2000). One of us (M. E. S.) surveyed all mammal species listed as threatened or endangered under the ESA for which recovery plans are written (about 44 species or subspecies). It appears that nearly half of these vulnerable mammals are relatively interactive, according to the criteria listed below, though this estimate may be low because the question is unstudied for many of the species (Soulé et al. 2003). Sala and Graham (2002) provide the most comprehensive analysis to date on species-specific variation in interaction strength. They estimate that roughly half of the macroinvertebrate herbivore species in kelp forest ecosystems are strong interactors. Based on limited information, therefore, it appears that a significant proportion of invertebrate and vertebrate species are sufficiently interactive to warrant attention if recovery criteria are an issue. Parenthetically, there are exceptions to the view that strong interactors are universally beneficial. Invasive exotic species and some native carnivores, particularly in highly perturbed ecosystems, can exacerbate management problems. For example, coyotes can devastate smaller, endangered predators such as captive-bred black-footed ferrets (*Mustela nigripes*), particularly if the coyotes are uncontrolled by wolves and if their prey occur in reduced, disturbed, or fragmented habitats (Miller et al. 1996).

The question of how interactivity is distributed in ecosystems has yet another dimension, namely variability within species. Like all ecological variables, interaction strength is contingent on place, time, and history (Power et al. 1996). Just as it would be futile to assign species-wide, fixed values for age-specific fecundity, population growth rate, coefficients of competition, or other context-dependent variables, it would be unreasonable to assign a fixed value for interactivity to a widespread species.

Arguably, the related goals of (a) categorizing the kinds of interspecific interactions and (b) assigning species to these categories trivialize the variability of species and environments in space and time. Interactivity is obviously a complex, context-dependent variable, and no species trait or feature is universally associated with it across all taxonomic groups and ecosystems. Nevertheless, the ESA contains wording that justifies attending to species interactions: "The purposes of this Act [the ESA] are to provide a means whereby the ecosystems upon which threatened and endangered species depend may be con-

served" (16 U.S.C. § 1531 [b]). This leaves us with a practical question: How can agencies and managers, in the face of this uncertainty and variability, determine whether a vulnerable species in a particular locality or region is sufficiently interactive to warrant special consideration with regard to recovery goals?

Guidelines for assessing interactivity

Operationally, a given species should receive special attention for recovery—beyond mere demographic viability—if its absence or unusual rarity causes cascading, dissipative transformations in ecosystems, including alterations or simplifications in ecological structure, function, or composition. The following questions may assist in determining whether there are grounds to warrant the creation of appropriate management prescriptions and actions that guarantee its ecological effectiveness.

Does the absence or decrease in abundance of the species lead directly or indirectly to a reduction in local species diversity? For example, the absence of coyotes from arid ecosystems can lead to a reduction in bird species diversity via mesopredator release (Crooks and Soulé 1999) or to a reduction in rodent species diversity via competitive exclusion (Henke and Bryant 1999), as noted above.

Does the absence, decrease in abundance, or range contraction of the species directly or indirectly reduce reproduction or recruitment of other species? For example, the number of forest tree species that successfully reproduced on

islands in a Venezuelan reservoir lacking large predators dropped from about 65 to about 10 because of a superabundance of herbivores (Terborgh et al. 2001). Likewise, ungulate herbivory prevented aspen (*Populus tremuloides*) clones from recruiting sprouts into the overstory after extirpation of wolves in the northern range of Yellowstone National Park (Romme et al. 1995, Ripple and Larsen 2000, Ripple and Beschta 2004).

Does the absence or decrease in abundance of the species lead directly or indirectly to a change in habitat structure or composition of ecosystems? For example, excessive elk (*Cervus elaphus*) herbivory on willow (*Salix* spp.) in the absence of wolves in Rocky Mountain National Park (Peinetti et al. 2002) and Yellowstone National Park (Ripple and Beschta 2004) was apparently the major factor in the disappearance of beaver and associated wetlands.

Does the absence or decrease in abundance of the species lead directly or indirectly to a change in productivity or nutrient dynamics in or between ecosystems? For example, prairie dog colonies shape nutrient cycling, soil chemistry, soil porosity, and the productivity and nutrient content of vegetation through their burrowing and grazing activities (Whicker and Detling 1993, Kotliar et al. 1999, Miller et al. 2000), and sea otters strongly influence algal productivity (Duggins et al. 1989) and food resource availability to herbivores (Konar and Estes 2003).

Does the absence or decrease in abundance of the species change an important ecological process in the system? For example, beavers have a profound effect on stream dynamics, water tables, flooding, and the extent of wetlands (Naiman et al. 1988).

Does the absence or decrease in abundance of the species reduce the resilience of the system to disturbances such as fire, drought, flood, or exotic species? For example, the extirpation of the dingo (*Canis lupus dingo*) in some regions of Australia indirectly degrades habitat quality because dingoes prey effectively on exotic rabbits (*Oryctolagus cuniculus*), red kangaroos (*Macropus rufus*), and other herbivores (Newsome 2001). In addition, dingoes may benefit native fauna, including small, endangered marsupials, by reducing population densities of the introduced red fox (*Vulpes vulpes*) (Newsome 2001), a major predator of small animals (O'Neill 2002).

These questions cannot eliminate the need for informed judgment, because interactivity of species is a multidimensional continuum, not a simple dichotomy. In addition, the interaction strength of species is usually not susceptible to rigorous empirical tests, in part because many appropriate experiments would be manipulative (involving the removal of species), long-term, and geographically extensive. With such a small portion of nature protected, it is difficult to justify

experimental removal of a putatively critical species to prove a point. There are, however, a number of powerful approaches that can often be used to make inferences about interaction strengths. Recovery of ecosystems following the reappearance of species is one such approach that has been used effectively to establish that predators such as gray wolves and sea otters are strongly interactive (see the cases described below). Interaction strength has been modeled on the basis of demographic and energetic parameters (Williams et al. 2004), even where data are limited. Ecological reconstructions based on historical records (Jackson et al. 2001), in conjunction with the comparative approach, provide yet another powerful means of assessing the ecological importance of species.

The estimation of ecologically effective densities

If persistence of species diversity is a management objective, it is essential to consider the densities or population levels that maintain interaction effectiveness rather than mere persistence at minimal numbers. Once it is determined that a species has relatively strong interspecies interactions, the proper management of such a species may require the estimation of the minimum threshold of ecological effectiveness. We define an ecologically effective density as the population level that prevents undesired changes in a defined ecological setting. As stated above, however, the estimation of effective density is strongly contextual, depending on locality, season, productivity, and other variables that fluctuate spatially and temporally (Estes and Duggins 1995, Soulé et al. 2003). Although a challenge, this problem may not be more intractable than the estimation of population viability. For example, many of the relevant parameters in population viability analysis, including age-specific fecundity and mortality, are similarly sensitive to local conditions. To illustrate some of the factors that must be considered in the estimation of ecologically effective densities, we present three examples of strongly interactive genera or species: the sea otter, the gray wolf, and the prairie dog.

The sea otter. Abundant sea otter populations inhabited coastal waters of the North Pacific Ocean and southern Bering Sea throughout most of the Pleistocene and Holocene, but were reduced to a few remnant colonies by the maritime fur trade of the 18th and 19th centuries. Recovery following the fur trade was spatially and temporally asynchronous, thus providing contrasts between otherwise similar habitats with and without sea otters. These contrasts demonstrate a strong limiting influence of sea otters on their most important prey, kelp-consuming sea urchins (*Strongylocentrotus* spp.). Thus, lush kelp forests abound where sea otters are abundant; where sea otters are absent, the habitat is typically deforested by hyperabundant sea urchins. Because kelp forests are highly productive (Duggins et al. 1989), provide habitat for other coastal species (Dayton 1985), and attenuate water movements (Jackson and Winant 1983), sea otters exert far-reaching influences on many other species (Estes 1996). Without sea otters, some of these kelp-dependent species

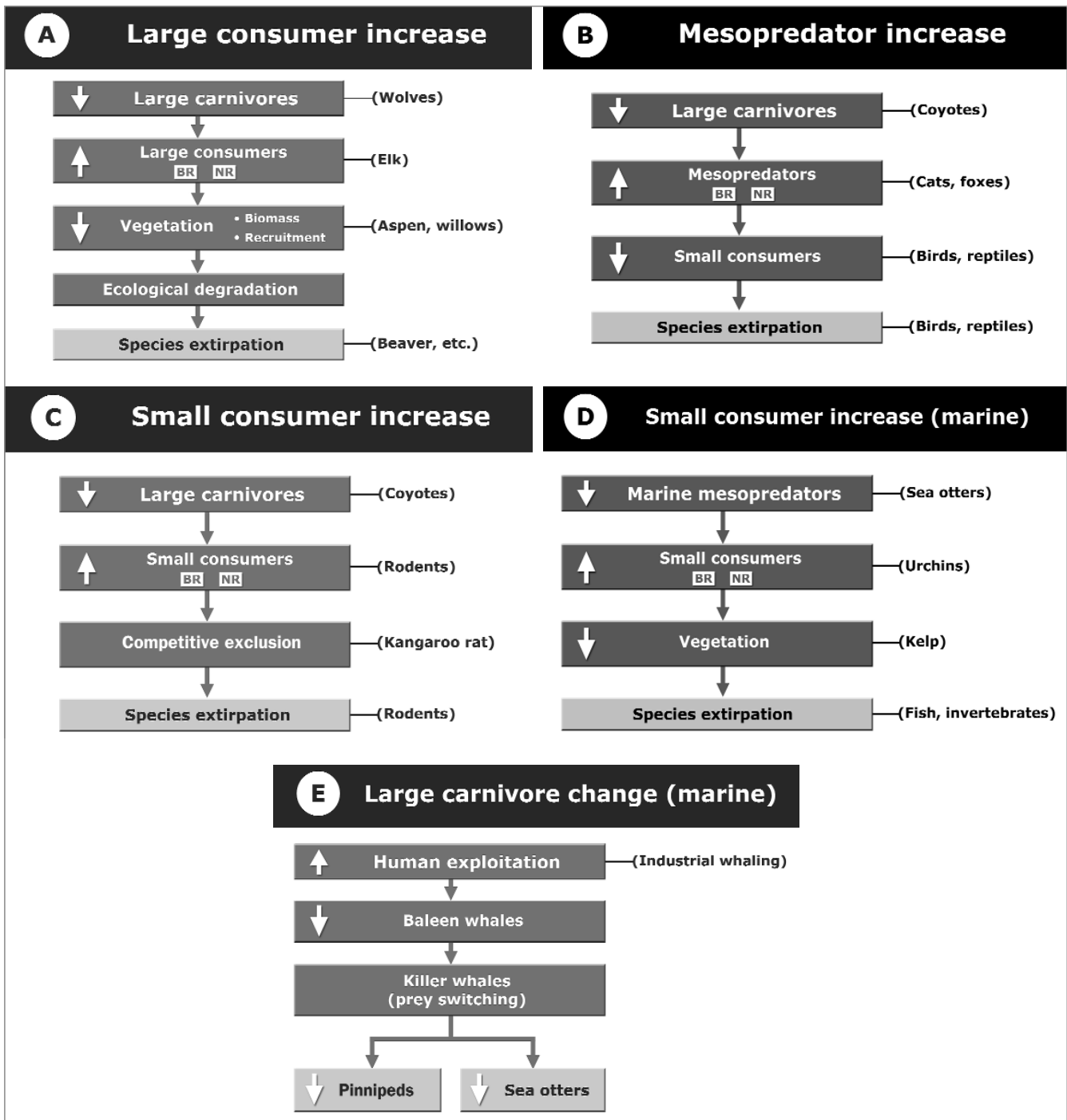


Figure 2. Examples of predator-mediated cascades causing local species extinctions. (a) The extirpation of large carnivores (wolves) in Yellowstone National Park led to an increase in large consumers (elk) and to the local extinction of beavers. (b) In coastal sage scrub and chaparral in southern California, the absence of large carnivores (coyotes) led to mesopredator release (cats, foxes), leading to an increase in predation on small prey. (c) Predator extirpation (coyote removal) can lead to competitive release, or the ecological release of superior competitors (e.g., the kangaroo rat), among rodent species, leading in turn to the local extirpation of competitively inferior species. (d) The extirpation of a marine predator (the sea otter) can cause the disappearance of an entire ecosystem (kelp beds). (e) Prey switching by killer whales, resulting from human exploitation of baleen whales, is postulated to reduce the populations of pinnipeds and sea otters. Arrows in shaded boxes indicate an increase or decrease in population; arrows between boxes indicate cascading trophic effects. Abbreviations: BR, behavioral release; NR, numerical release.

decline or disappear, while others, including urchins, erupt to high levels. The ecologically effective population for sea otters, though regionally variable, is always much larger than minimum viable population sizes based on demography, and in some instances is near the environmental carrying capacity (Estes and Duggins 1995).

Geographic variation in the behavior of predators, competitors, and prey will also affect the population density threshold for ecological effectiveness. For example, the density of sea otters that is effective in suppressing sea urchins differs between sites, because the demography and dispersal of sea urchins vary geographically. In the Aleutian Islands, where urchin recruitment is frequent and strong, a higher density of otters is needed to suppress the urchins and prevent kelp deforestation than in southeast Alaska, where urchin recruitment is weak and episodic, and where just a few otters are enough to maintain the kelp ecosystem (Estes and Duggins 1995).

In summary, the estimation of effective densities of sea otters for preventing kelp deforestation depends, among other things, on whether the state of the system is kelp dominated or deforested, on the recruitment dynamics of urchins to the kelp beds, on whether the substrate is dominated by rocks or mud, and on the mortality rate of otters (see Soulé et al. 2003). For these reasons, the ecologically effective densities of otters can vary by an order of magnitude, but in all situations observed, otters eventually attain such densities if they are not harassed by human beings or preyed on by killer whales.

The gray wolf. Large areas of the United States, including most of the East Coast and Midwest, now lack wolves and other large carnivores, the result of a century of eradication on behalf of livestock growers, hunters, and other interest groups that benefit from the absence of wolf predation on ungulates. Populations of white-tailed deer (*Odocoileus virginianus*), elk, and moose (*Alces alces*) have increased both in numbers and in per capita consumption (Soulé et al. 2003), and these increases are frequently attributed, at least in part, to the absence of wolves (Messier 1994, Crête 1999). Among the many harmful consequences of wolf eradication have been increased costs for agricultural producers in the Midwest and East, the widespread degradation of forests and other ecosystems, and the decline of many species of plants favored by ungulates (Rooney et al. 2004). As noted above, aspen recruitment failed for 80 years in large parts of Yellowstone National Park, reflecting numerical and behavioral release of elk subsequent to wolf eradication. Excessive browsing by elk also affected recruitment of riparian cottonwoods and willows (Beschta 2003), causing the local disappearance of beaver wetlands. These effects are being reversed in Yellowstone National Park since wolves were reintroduced (starting in 1995), and signs of ecological effectiveness were noted before wolves reached their current abundance of about 200 (Ripple and Beschta 2004). A similar trend has been observed in Grand Teton National Park, where a decrease in Neotropical migrant

bird diversity has been attributed to overbrowsing by moose in riparian willow communities in the absence of wolf predation or sport hunting of moose (Berger et al. 2001). It is noteworthy that the recovery of willows in northern Yellowstone National Park is particularly striking in areas where the topography facilitates capture of elk by wolves (Ripple and Beschta 2003). Several factors affect wolves' ecologically effective population density. It is lower where hunters can suppress ungulate numbers; where wolves coexist with other large carnivores, such as bears and cougars; or where deep winter snow or periodically severe storms facilitate capture of prey—for example, El Niño versus La Niña years (Schmitz et al. 2003). We grant that predators do not always control large herbivores, but given alternative prey, multiple carnivore species, or appropriate habitat, wolves can often control superabundant ungulates (Soulé et al. 2003).

The prairie dog. A century ago, five species of prairie dog lived in a shifting mosaic of colonies that covered more than 40,000,000 hectares (ha) on the Great Plains. By 1960, prairie dog area had declined to about 600,000 ha (Marsh 1984), largely because of poisoning campaigns, land conversion, and the introduction of plague (*Yersinia pestis*). This is a decline of 98 percent, and the remaining colonies are small and isolated. Prairie dogs are a valuable food for many species of predators. In addition, prairie dogs decrease densities of woody shrubs and increase densities of grasses and forbs, thus creating conditions that large grazers prefer. Prairie dog activities also increase plant productivity, soil nitrogen, nutrient cycling, and digestibility of grasses and forbs (Whicker and Detling 1993, Detling 1998). Their burrowing activity changes soil chemistry; increases soil porosity, soil turnover, and the organic content of soil; and enhances the dimensionality of the habitat for many other species (Whicker and Detling 1993, Outwater 1996). Some species of plants, invertebrates, and vertebrates benefit from prairie dog activities, while other species benefit from the areas outside of the colony (Kotliar et al. 1999). These effects differ among prairie dog species. Furthermore, prairie dogs, unfenced bison, and fire interacted closely on the midgrass prairies, although that triad may not have been as tightly associated on the drought-driven shortgrass prairies or the semidesert grasslands and shrublands.

Estimating ecologically effective densities of prairie dogs is complicated by the introduction of plague. Plague reduces numbers and changes the temporal and spatial characteristics of the historic "shifting mosaic" between prairie dog colonies and grasslands. Despite those ambiguities, it is clear that ecologically effective densities of prairie dogs are far higher than the densities required for population persistence (Miller et al. 2000). As an example, 762 prairie dogs may be required to support each female black-footed ferret and her offspring (Biggins et al. 1993). Thus, conservative recovery goals that consider only population viability could maintain prairie dogs without providing sufficient resources for ferrets.

Summary. What commonalities emerge from these three overviews of ecological effectiveness? First, studies of these mammals demonstrate several pertinent factors, most of which appear to be extrinsic and context specific. Among these extrinsic factors are (a) weather and other abiotic influences, (b) interactions between forage quality and quantity, (c) primary productivity, and (d) the number and abundance of other species—such as prey, predators, pathogens, mutualists, and competitors—with which these species interact. Of course, intrinsic factors, such as the maximum growth rate of the population, are also relevant, but variability in intrinsic variables is partly determined by the extrinsic factors listed above.

Second, the above case studies suggest that strongly interactive species, if not harassed, will often achieve ecologically effective densities without human intervention, though active management will probably be necessary in some highly perturbed situations, including the presence of exotic pathogens and overharvesting. For example, the recovery of sea otters in southwestern Alaska may be contingent on the recovery of great whales (Springer et al. 2003). Populations tend to increase their numbers and energy consumption to levels where ecological resistance due to diminishing resources, disease, or other factors (e.g., territoriality) halts further growth. It is likely, therefore, that thresholds for ecological effectiveness are often below carrying capacity, thus obviating the need in many situations for modeling or specific management prescriptions. But even if particular circumstances, such as conflicts between human interest groups, require the modeling of effective densities, we believe that the modeling will be no more complex than the estimation of single-species population viability.

Conclusions

Mitigating the current anthropogenic mass extinction will require a scientifically rigorous and ecologically comprehensive grasp of its drivers. Among these is the increasing rarity of interactive species, such as plants that provide critical resources (Terborgh 1986), insect pollinators (Dobson et al. 1999), habitat modifiers (Soulé et al. 2003), coral reef herbivores (Jackson et al. 2001), and carnivores, both marine and terrestrial (Terborgh et al. 1999). The activities of relatively interactive species are disproportionately significant for the survival of native species and ecosystems.

It is essential, therefore, that conservation practitioners, whether governmental or nongovernmental, adopt an ecological view that ensures the persistence of interactive species at ecologically effective population densities and maximal spatial occurrence (Soulé et al. 2003). In particular, we believe that natural-resource policymakers and wildlands managers should determine whether the rarity or absence (Hughes et al. 2000) of a species in a region can be expected to trigger ecological degradation, including the disappearances of native species and other elements of biodiversity.

Even though interactivity is a quantitative variable, managers may be forced to make binary determinations, such as

whether to treat a particular species as strongly interactive when formulating recovery goals. Notwithstanding the arbitrariness of such decisions, a commonsense approach will often suffice. One should assume, for instance, that a substantial reduction of tree species that produce mast or invite cavity formation, or of apex predators and many large herbivores—such as wolves, coyotes, sea otters, killer whales, sharks, predatory freshwater fish, and large, predatory or algae-eating reef fish—will trigger cascades of ecological degradation and species loss (Terborgh et al. 1999, Jackson et al. 2001, Soulé et al. 2003, Springer et al. 2003). Other situations may require literature reviews or detailed research to ascertain whether a particular species in a particular place fulfills any of the criteria for relatively strong interactivity given above.

A conundrum for managers is that the ecological effectiveness of strongly interacting species is not specifically addressed in current laws and policies dealing with biodiversity protection and management. Until this perspective has been codified in such laws, conservationists need to consider how best to provide for such species and the processes they mediate in accord with the intent of these laws. Population viability analyses and conservative recovery goals are an inadequate regulatory context for strongly interacting species.

We now understand that the biodiversity of ecosystems will degrade unless the interactions of species are maintained in as many regions as feasible, particularly those areas within the historic range. This more holistic, contemporary view requires that strongly interactive species receive special attention to assure that they are well distributed and abundant, a position consistent with an opinion of the US Ninth Circuit Court of Appeals (*Defenders of Wildlife v. Norton*, 258 F.3d 1136 [2001]). Such a geographic criterion for recovery would require more than scattered or refugial representation of such species. Ecological function and diversity cannot be conserved in a region by maintaining interactive species in only a few protected areas. Rather, it is essential that strongly interactive species be distributed as broadly as possible and be protected within well-distributed, secure areas. Applying this guideline to the wolf in the United States, for example, would mean that effective populations should be restored and protected in the Northeast, the Pacific Northwest, the Great Basin, the Colorado Plateau, the Southwest, and the southern Rockies. Moreover, if the current trend of decreasing sport hunting and the spread of chronic wasting disease in deer and elk continue, the pressure to reinstitute natural control mechanisms will surely increase.

The critical roles of interspecies interactions are rarely considered in recovery planning. For example, the US Fish and Wildlife Service (USFWS) admits that its goals for wolf recovery are “somewhat conservative...and should be considered minimal” (68 Fed. Reg. 15817 [2003]). A recent decision by USFWS (68 Fed. Reg. 15821 [2003]) states that USFWS is not required to restore a species across its available habitat. The decision would limit wolf protection to about 5 percent of its historical range in the lower 48 states. Similarly, the multistate conservation plan for black-tailed prairie dogs (Luce 2003)

sets a 10-year recovery goal for black-tailed prairie dogs (*Cynomys ludovicianus*) at about 2.5 percent of their historical area, essentially the status quo.

We believe that such conservative recommendations are not based on current ecological knowledge about the significance of species interactions. Moreover, minimalist distributional and temporal goals constitute a trivialization of the term “recovery” as it is used in the ESA. In other words, “recovery,” at least for mammals, is typically used to mean the persistence of only a few populations in a limited area for a few generations.

Notwithstanding current policies, most natural-resource and environmental laws require that federal agencies consider new scientific knowledge. Indeed, the ESA’s own mandate is to use “the best scientific and commercial data available” (16 U.S.C. § 1533[b][1][A]). Moreover, implementing regulations for the National Environmental Protection Act of 1969 require that federal agencies disclose and consider “cumulative impacts” and the anticipated environmental impacts of proposed federal agency actions (40 C.F.R. § 1500 et seq. 1995). Any artificially induced reduction in abundance of a strongly interactive species, therefore, must be considered in these environmental analyses. In addition, regulations of the National Forest Management Act of 1976 require that national forest plans “provide for the diversity of plant and animal communities” and that “such diversity shall be considered throughout the process” (36 C.F.R. § 219.3).

Since the recognition of conservation biology as a discipline (Soulé 1985), its practitioners have tacitly assumed that conservation biologists are “physicians to nature.” Indeed, there are many parallels between conservation biology and the fields of medicine and public health—disciplines infused with morality. Following the Hippocratic principle of doing the least harm and the most good for patients and the public, physicians and public health officers are obligated, we think, to consider using new therapies and prophylaxes stemming from peer-reviewed research, even before such practices are generally adopted in canonical documents such as textbooks. We propose, therefore, that conservation practitioners, whether in a public or private (nongovernmental) employ, are similarly obligated to apply new biological knowledge in their work. Such a doctrine of “best conservation practices based on the best science” is tantamount to an ethical obligation of biologists to adopt a higher standard for management than is mandated by existing statutes and regulations, if the evidence warrants it. Environmental codes build the legal and ethical foundation of conservation practice, but the best science of the day creates the walls and ceiling.

In practice, policymakers and managers already have enough flexibility to implement new knowledge while still adhering to relevant statutes and policies, though the exercise of this doctrine may be inhibited by monetary and political constraints. (Setting relatively stringent recovery objectives for strongly interactive species, for example, will be opposed by individuals and organizations who perceive negative consequences of such actions.) Even so, ignoring the interspecific

interactions of strongly interactive species will further impair the diversity and resilience of ecosystems that are already unraveling. In a nation and a world where increasing numbers of species and ecosystems are shoved toward the brink of annihilation, it is more important than ever that environmental policy and management be buttressed by the best available science.

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