Ecological Effectiveness: Conservation Goals for Interactive Species

MICHAEL E. SOULÉ,* JAMES A. ESTES,† JOEL BERGER,‡ AND CARLOS MARTINEZ DEL RIO§

*P.O. Box 2010, Hotchkiss, CO 81419, U.S.A., email rewild@tds.net
†U.S. Geological Survey, University of California, Santa Cruz, CA 95060, U.S.A.
‡Wildlife Conservation Society, Moose, WY 83012, U.S.A.
§Department of Zoology, University of Wyoming, Laramie, WY 82071–3166, U.S.A.

Abstract: *The rarity or absence of highly interactive species leaves a functional void that can trigger linked changes leading to degraded or simplified ecosystems. A preliminary analysis indicates a relatively high frequency of such interactive species among endangered mammals. Rapid environmental change is likely to increase the interactivity of some species and reduce that of others over relatively short intervals. The current implementation of environmental policies and laws, such as the U.S. Endangered Species Act, generally ignores interspecific effects; recovery goals are autecological, short term, and numerically and spatially minimalistic. Moreover, by failing to account for interspecific interactions, recovery objectives are becoming indefensible in light of increasing knowledge from community ecology. Using the sea otter (*Enhydra lutris*) and wolf (*Canis lupus*) as examples, we argue that conservation plans should call for recovery or repatriation of such interactive species at ecologically effective densities in as many places as are currently realistic. It will be prudent and beneficial to estimate ecologically effective densities where there is disagreement among experts and interested parties about the desirability of restoring an interactive species to a particular region and to a particular density.*

Efectividad Ecológica: Metas de Conservación para Especies Interactivas

Resumen: *La rareza o ausencia de especies altamente interactivas deja un vacío funcional que puede desencadenar cambios que conducen a ecosistemas degradados o simplificados. Un análisis preliminar indica una frecuencia relativamente alta de esas especies interactivas entre mamíferos en peligro. Es probable que el cambio ambiental rápido incremente la interactividad de algunas especies y reduzca la de otras en períodos relativamente cortos. La actual aplicación de políticas y leyes ambientales, tal como el Acta de Especies en Peligro de E.U.A., generalmente ignora los efectos interespecíficos; las metas de recuperación son autoecológicas, de corto plazo y numérica y espacialmente minimalistas. Más aun, al no tomar en cuenta las interacciones interespecíficas, los objetivos de recuperación se están volviendo indefendibles a la luz del creciente conocimiento de la ecología de comunidades. Utilizando a la nutria marina (*Enhydra lutris*) y al lobo (*Canis lupus*) como ejemplos, argumentamos que los planes de conservación deben considerar la recuperación o repatriación de dichas especies interactivas en densidades ecológicamente efectivas en el mayor número de sitios realistamente posibles. Será prudente y benéfico estimar las densidades ecológicamente efectivas donde hay desacuerdo entre expertos y grupos interesados sobre la conveniencia de restaurar una especie interactiva en una región particular y a una densidad particular.*

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Introduction

Although the first-order effects of the biodiversity crisis—the loss of species—are dire, the second-order consequences—the loss of species interactions—may be more ominous. For instance, Jackson et al. (2001) conclude that, worldwide, the functional dynamics of coastal marine ecosystems were grossly altered decades or centuries ago and that many problems attributed to such recent processes as disease, pollution, and global warming in fact were likely entrained by the historical removal of marine predators. Thus, a primary mission of conservation should be to identify and restore species that interact strongly with others.

We define strongly interactive species operationally because the diversity of potential influences of a strong interactor (sensu Power et al. 1996; Berlow et al. 1999) on other species, species interactions, and ecosystem processes precludes a precise definition. Thus, a species is highly interactive when its virtual or effective absence leads to significant changes in some feature of its ecosystem(s). Such changes include structural or compositional modifications, alterations in the import or export of nutrients, loss of resilience to disturbance, and decreases in native species diversity. Of course, changes in the abundance, distribution, and behavior of other species are likely to underlie those changes detected at the community and ecosystem levels.

At least two typologies have been invented to categorize highly interactive species. Some authors emphasize the type of interactions; among these are mutualists such as pollinators, spore and seed dispersers; consumers (such as large predators), and ecosystem engineers such as beaver (*Castor canadensis*) (Naiman et al. 1986) and elephants (*Loxodonta africana*) (Owen-Smith 1988). Another popular categorization is the distinction between "keystone species" and nonkeystone species. Keystone species (Paine 1969) are defined as having particularly strong, ramifying interactions (Mills et al. 1992), the strength of which are disproportionate to their population densities (Power et al. 1996) and not wholly duplicated by other species (Kotliar 2000). Where the density of a keystone species falls below some threshold, species diversity may decrease, triggering ecological chain reactions ending with degraded or simplified ecosystems (Estes & Palmisano 1974; Jones et al. 1998; Crooks & Soulé 1999; Terborgh et al. 1999; Jackson et al. 2001; Terborgh et al. 2001). Among such "keystones" are large predators (Estes & Palmisano 1974; Carpenter & Kitchell 1993; McLaren & Peterson 1994; Terborgh et al. 1999; Ripple & Larsen 2000). Keystone species can be thought of as having the highest per capita interaction strengths (Berlow et al. 1999).

Clearly, though, the keystone-nonkeystone dichotomy arbitrarily segregates a continuous, multidimensional spectrum of interaction strength (Hurlburt 1997). Moreover, many highly interactive species are too abundant to be classified as keystone species (Soulé & Noss 1998). For these reasons, we suggest using the term *foundation species* for highly interactive species that are often extremely abundant or ecologically dominant, though the earlier use of this term (Dayton 1972) differed from ours. Likely examples of foundation species include bison (*Bison bison*), prairie dogs (*Cynomys* spp. Miller et al. 1994), cottonwood and aspen trees (*Populus* spp.), American chestnut (*Castanea dentata*), cod (*Gadus* spp.), krill (*Euphausia* spp.), bees, and mound-building termites, to name only a few.

Our purpose here is to argue that goals embodied in laws and polices that apply to the conservation of biodiversity should include the protection of ecological interactions, particularly those interspecific interactions critical to the maintenance of ecological complexity at all scales—species, ecosystems, watersheds, landscapes, regions. We propose two such goals. The first is the goal of geographic representation of interactions, which calls for extensive geographic persistence of highly interactive species. Conservation plans and objectives (design, management, and recovery) should provide for the maintenance, recovery, or restoration of species interactions in as many places as feasible, both within the historic range of highly interactive species or in other sites where the consideration of climate change and other factors is appropriate.

The second goal concerns ecological effectiveness within ecosystems, communities, or landscapes. Conservation plans should contain a requirement for ecologically effective population densities; these are densities that maintain critical interactions and help ensure against ecosystem degradation. This goal replaces the de facto nonecological practice of requiring only the attainment of minimum viable populations.

We explore the application of these two goals in the following two case studies: sea otters (*Enhydra lutris*) in North Pacific coastal marine ecosystems, and wolves (*Canis lupus* and *Canis l. lycaon*) in North American terrestrial ecosystems. Although the focus in these cases is carnivores, the principles and conclusions should apply to any highly interactive species. Our choice of examples is limited by space considerations and information availability (e.g., it is unfortunate that the consequences of the disappearance of pollinators are almost unknown; Buchmann & Nabhan 1996; Kearns et al. 1998, Kremen & Ricketts 2000).

Sea Otters and Kelp Forests

Sea otters and kelp forests provide one of the better-known examples of how large predators influence their associated ecosystems. This is because of an unplanned, anthropogenic experiment provided by the Pacific mari-

time fur trade. Abundant sea otter populations inhabited coastal waters of the North Pacific Ocean and southern Bering Sea throughout most of the Pleistocene and recent eras but were reduced to a few remnant colonies by the fur trade. If scientists had viewed the system when otters were either abundant everywhere or nearly extinct everywhere, in all likelihood they would have failed to recognize the species' profound impacts. By the early 1970s, however, populations had returned to high levels in some areas and remained absent in others, at which point the experiment was underway.

But another ingredient was necessary: a conceptual model in which predators are viewed as regulators of herbivore populations. The landmark paper by Hairston et al. (1960) provided this. The sea otter's influences on coastal ecosystems were seen by contrasting places within the species' historical range where they were present or absent, and by following particular areas through time as these places were recolonized by otters and their numbers increased (Estes & Duggins 1995). In all cases these contrasts demonstrate a strong limiting influence of sea otters on their most important prey, sea urchins, which consume kelp. Thus, where sea otters abound so do lush kelp forests, and where sea otters are absent the habitat is typically deforested by hyperabundant sea urchins. Numerous indirect effects also result from this "trophic cascade" (Paine 1980), owing to the importance of kelp as a source of food and habitat for dozens of other coastal species (Duggins et al. 1989; Estes 1996).

These interactions have been known for many years (Estes & Palmisano 1974). But how many sea otters are needed to maintain a healthy kelp forest? This question can be more precisely considered by envisioning the patterns of change in sea urchin populations across the range of possible sea otter densities (from 0 to d_{max}), by envisioning the same relationship between sea urchin and kelp abundance, and ultimately by combining these patterns to illustrate relationships between the abundance of sea otters and the abundance of kelp (Fig. 1).

First, we must know whether the abundance relationships are linear or nonlinear. If they are nonlinear, then we must also know their trajectories and whether these trajectories vary with directionality. This knowledge comes from (1) theoretical studies of consumer-prey interactions (Noy-Mier 1975; May 1977), (2) experimental studies of plant-herbivore dynamics (Konar & Estes 2003), and (3) observations of ecosystem change following the growth (Estes & Duggins 1995) and decline (Estes et al. 1998) of sea otter populations.

Systems dominated by kelp and deforested by sea urchins commonly behave as alternate stable-state communities (sensu Lewontin 1969; Sutherland 1974; Scheffer et al. 2001). That is, the transitional dynamics between these states is not smooth and continuous but instead is characterized by thresholds and breakpoints. Any consumer-prey system can take multiple stable states if, as prey becomes more abundant, consumers become satiated and prey production rate grows and falls as a standard yield curve (Fig. 2). In addition, the deforested state resists invasion by kelp because hungry sea urchins actively move across the sea floor, consuming new kelp recruits (Harrold & Reed 1985). Only when sea urchins either stop moving or occur in low numbers can kelp become reestablished (Konar 2000). Similarly, established kelp populations slow sea urchin invasion by physically beating back the invaders (accomplished through an interplay between water motion and the plants' supple morphology) and by producing enough detrital food to cause the otherwise mobile urchins to become sessile, sit-and-wait consumers. For these reasons, intermediate ecosystem configurations between the kelp-dominated and deforested states are unstable and highly transitory (Estes & Duggins 1995; Konar & Estes 2003).

Consequently, the functional relationship between kelp abundance and sea urchin density is not linear, with the precise functional form differing depending on whether it starts from the kelp-dominated or deforested state (Fig. 1). Abrupt phase shifts between kelp-dominated and deforested states thus occur with changing abundance of sea otters. We refer to the number of otters required to affect this change as the breakpoint density, d_{bp} (Fig. 1). An ecologically effective population density for sea otters must be $\geq d_{bp}$. As we will show, d_{bp} depends both on the consumer-prey dynamics between sea otters and sea urchins and on the replenishment of sea urchins (by immigration and recruitment) to exploited populations.

Sea otters feed in a size-selective manner, targeting the larger urchins (VanBlaricom 1988; Estes & Duggins 1995; Watt et al. 2000) and avoiding the smaller ones. In the Aleutian Islands, where recruitment of urchins is frequent and strong, enough small urchins remain uneaten to prevent kelp-bed establishment. In contrast, where sea urchin recruitment is weak or episodic, as it often is along the western continental margin of North America (Pearse & Hines 1987; Ebert & Russell 1988; Estes & Duggins 1995), sea urchin populations are constituted of large individuals so that even relatively few sea otters can prevent destructive herbivory by sea urchins. This is why the otter-urchin recovery functions differ so strongly between the Aleutian Islands and southeastern Alaska (Fig. 1, middle panels). The combined result of these herbivore-plant and carnivore-herbivore relationships is a striking interregional difference in the recovery dynamics of sea otters and kelp forests (Fig. 1, bottom panels). Sea urchin barrens persist in the Aleutian Islands following the reestablishment of even large numbers of sea otters, whereas lower densities of sea otters and shorter time periods are sufficient to affect the phase shift in southeast Alaska and British Columbia. In British Columbia, the phase shift is accelerated by a sea urchin "flight response," which occurs when debris from urchin tests is discarded by foraging sea otters and falls to the sea

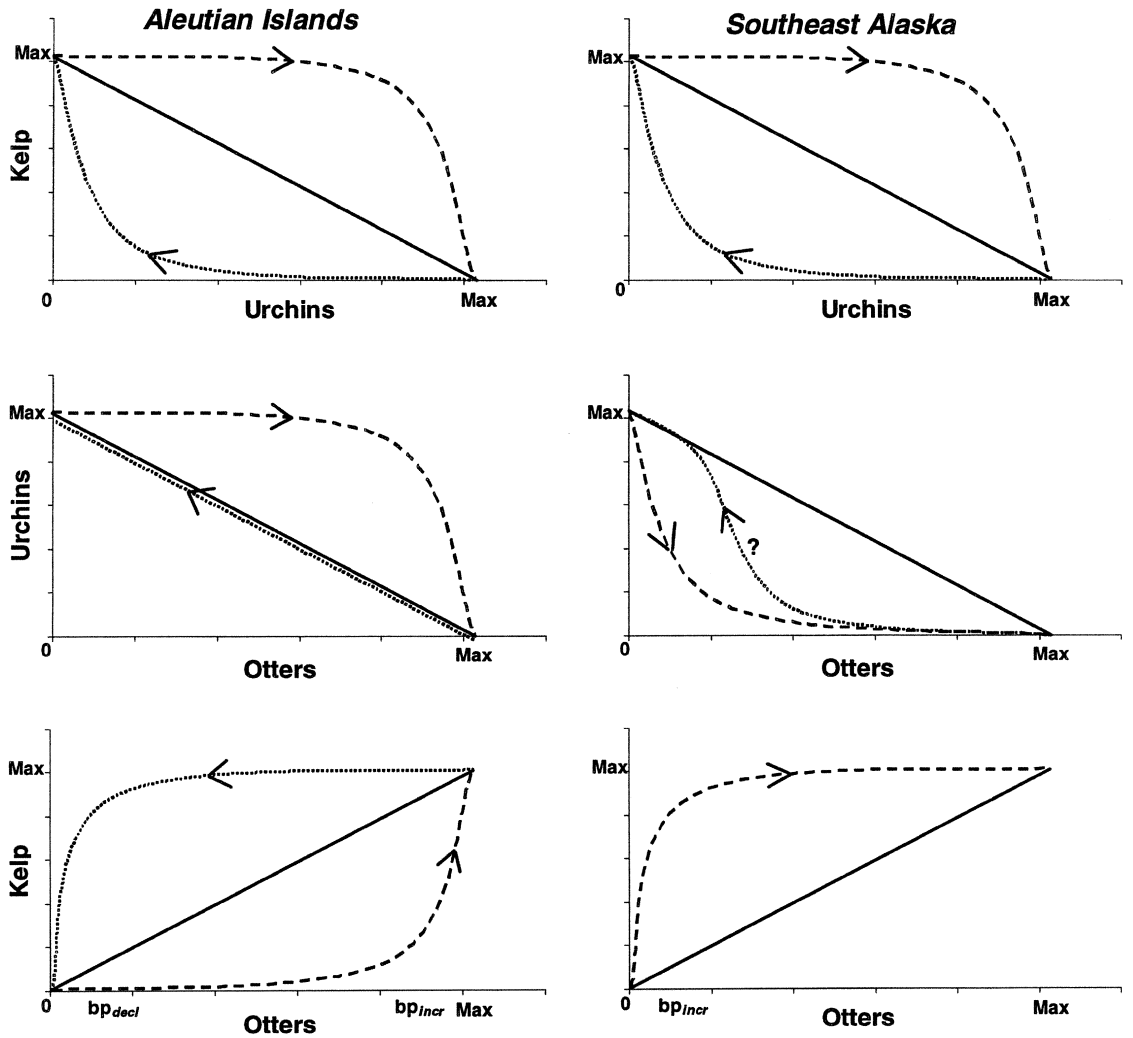

Figure 1. Functional relationships between population abundances of the drivers (horizontal axes) and passengers (vertical axes) in kelp-forest ecosystems of the North Pacific Ocean. Solid lines indicate hypothetical linear response functions and broken lines the known or suspected functional relationships. Dashed and dotted lines portray the respective response functions for increasing and declining driver populations. Functional relations between the abundance of kelp and sea urchins are shown in the top panels; between sea urchins and sea otters in the middle panels; and the resulting relationships between sea otters and kelps in the bottom panels. Sea urchin recruitment is strong and continuous in the Aleutian Islands and episodic in southeast Alaska. The functional relationships between sea urchin and kelp abundance (top panels) and their differing trajectories for increasing or declining urchin populations are both nonlinear. Sea urchin abundance in the Aleutian Islands varies linearly with declining otter numbers (middle, left panel). The varying dynamics between sea otters and sea urchins on the one hand and between sea urchins and kelp on the other result in differing breakpoint densities (bottom panels) for increasing (bp_{incr}) and declining (bp_{decl}) otter populations in the Aleutian Islands and southeast Alaska. The dynamic details for establishing the bp_{decl} for the kelp-otter relationship (bottom, right panel) are unknown.

floor. Urchin-free patches develop around this debris. Kelps rapidly recruit into these patches, creating a mosaic of kelp-dominated and deforested patches (Watson 1993).

The aforementioned examples involve growing sea otter populations. Kelp forest phase shifts also occur in the Aleutian Islands, where otter populations have declined, purportedly because of killer whale predation (Estes et al. 1998). The declines began in the late 1980s. By 1993 otter numbers had been reduced to about 50% of equilibrium density (Doroff et al. 2003), and sea urchin abundance had approximately doubled (Watt et al. 2000). By 1997 otter numbers had stabilized at about 10% of equilibrium density, urchin abundance had increased about eightfold, and kelp populations had collapsed throughout most of the shallow sublittoral zone (Estes et al. 1998).

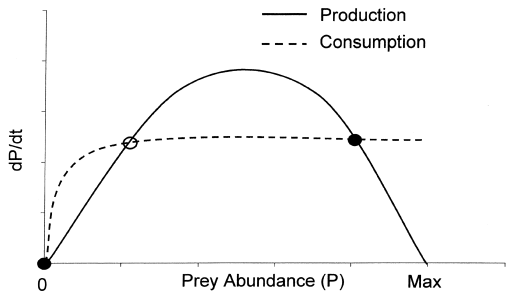

Figure 2. Dynamic model for the maintenance of multiple stable equilibria in prey abundance when prey production and consumption rates (dP/dt) vary with prey abundance (P), as shown (i.e., production rate varies as a standard yield curve and consumption rate satiates). The intersections between production and consumption define equilibria. Solid circles are stable equilibria; open circle is unstable (after May 1977; Noy-Mier 1975).

These data indicate a linear response function between declining sea otters and increasing sea urchins (Fig. 1, middle left panel).

The absence of any apparent lag in this function is at first perplexing, given the slow growth rate of sea urchins in the Aleutian Islands (Estes & Duggins 1995). In this region, however, urchin populations are enhanced by the migration of post-metamorphosis individuals from source populations in deep water. These migrating urchins are probably attracted to shallow water by the more abundant food. Casual observations made by divers in the early 1990s and measurements of the rate of kelp tissue loss to herbivory by sea urchins (Steinberg et al. 1995) indicate that sea otter density was still greater than d_{bp} at that time. In the declining case, therefore, the phase shift occurred when the sea otter population was reduced to somewhere between one-half and one-tenth of equilibrium density. The breakpoint density for declining sea otter populations along the continental margin of North America is unknown but may be even lower than this, given the more episodic recruitment of sea urchins and the more extensive occurrence of soft-sediment habitats (which are unsuitable for sea urchins) in deeper water.

In summary, the sea otter–kelp forest system provides a glimpse into some of the functional complexities of the relationship between carnivore population abundance and ecosystem function. Strong nonlinearities in the nature of plant-herbivore interactions at the base of the food web result in distinct breakpoints in the number of sea otters required to maintain the kelp forest ecosystem. In reference to the goal of ecologically effective densities, these breakpoints serve as conveniently discrete metrics for an ecologically effective population density of sea otters. In reference to the goal of geographic representation, however, ecologically effective densities will depend on context: they are not the same everywhere and under all circumstances. The ecologically effective population density for sea otters may vary by an order of magnitude or even more, depending on geographic locale and whether it is approached from low or high density. In all situations observed, however, otters attain ecologically effective densities if they are not harassed by human beings or eaten by killer whales.

Wolves, Herbivores, and Vegetation

Overbrowsing by ungulates is now recognized as a factor in the structural alteration, the simplification, and even the disappearance of forests throughout the world (Oksanen & Oksanen 2000). In the United States, overbrowsing by native ungulates, particularly white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*), is causing observable changes in the plant species composition in many ecosystems (Miller et al. 1992; Waller & Alverson 1997; Ripple & Larsen 2000) and is a likely consequence of the absence of effective predation by formerly widespread native carnivores and in some places by aboriginal human hunters (Kay 1994).

The impacts of white-tailed deer in the U.S. Midwest and in the deciduous forests of the eastern United States are well known. Among the influences frequently observed are changes in the composition of forests, local extirpation or inhibition of many herbs and tree seedlings, transformation of understories from mixed herbaceous species to park-like assemblages dominated by ferns and grasses (Waller & Alverson 1997), and negative impacts on breeding songbirds (DeCalesta 1994; McShea & Rappole 1997). Among the tree and shrub species for which recruitment failure has been documented (Waller & Alverson 1997) are oaks (*Quercus* spp.), white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), northern white cedar (*Thuja occidentalis*), and Canada yew (*Taxus canadensis*).

Moose (*Alces alces*) are effecting similar changes in vegetation in parts of Canada and the United States in places where wolves are absent (Connor et al. 2000; Berger et al. 2001). In several such localities moose populations are five to seven times higher than in more productive systems with wolves (Cederlund & Sand 1991; Crête & Manseau 1996; Berger et al. 2001). For all three of the large ungulates mentioned above, the virtual absence of predation by wolves and the failure of conservation to achieve their broad ecological representation (goal 1) have contributed to ecological degradation.

The National Park Syndrome

One pattern of ungulate-caused landscape simplification, now common enough to be called a syndrome, is occurring in some national parks in the Rocky Mountain

region of the United States. The symptoms include the virtual disappearance of some vegetation types—notably riparian habitat and beaver (*Castor canadensis*) wetlands—and the failure of aspen to recruit into the canopy for the last 80 years, particularly in Yellowstone National Park (YNP) (Ripple & Larsen 2000). This syndrome likely has several interacting causes, but in YNP the two most important appear to be (1) the effective elimination of wolves by around 1925 and (2) the termination of elk population limitation by artificial means after 1968 (Hess 1993; Singer et al. 1998*a*). Similar changes have occurred in Rocky Mountain National Park (RMNP) (Singer et al. 1998*b*). One consequence of these perturbations has been the ecological release of elk (e.g., Ripple & Larsen 2000), but climate change and the suppression of fire during most of the twentieth century probably exacerbated the vegetational changes (Romme et al. 1995; Romme et al. 1997; Singer et al. 1998*b*).

After artificial control of Yellowstone elk ended, the northern range population grew from about 4500 in 1968 to about 20,000 by 1995, reaching winter densities of 12/km^2 by the 1990s, among the highest known densities of elk anywhere. One of the consequences has been heavy browsing by elk on willows (*Salix* spp.), a favored food of beavers. Riparian habitat formerly dominated by willows in parts of YNP has declined 60% in the last 70 years. Consequently, beavers and the beaver pond wetland ecosystem disappeared, and this has triggered other landscape changes. Beaver ponds enhance willow growth by increasing the height of water tables, enhancing productivity by increasing the inputs of nitrogen and phosphorus (Naiman et al. 1986), and preventing erosion. Compared with a century ago, runoff is more concentrated, and many streams are now downcut more than 1 m below levels when beavers were present, further lowering water tables. In addition, stream channels are now straighter and less complex (Singer et al. 2003).

A similar situation occurs in RMNP, where willow patches have declined (Singer et al. 1998*b*; Singer et al. 2002) and beaver numbers have decreased about 80–90% on the winter elk range (Peinetti et al. 2001). After wolves and grizzly bears were extirpated in Grand Teton National Park (GTNP), moose populations irrupted and riparian willow communities were significantly reduced in contrast to outlying regions beyond park borders, where sport hunting of moose remains legal (Berger et al. 2001). Thus, in YNP, RMNP, and GTNP, the modification of vegetation and linked changes in animal communities is likely attributable, at least in part, to the anthropogenic eradication of large carnivores (Berger et al. 2001).

Hansen and Rotella (1999) found that 25% of breeding birds surveyed in the Yellowstone region specialize on cottonwood, aspen, and willow communities. They refer to these areas as "hotspots" and "source areas" for some species and note that they are "critical for maintaining population viability over the local region." Berger et al. (2001) attribute a similar decrease in Neotropical migrant bird diversity in GTNP to overbrowsing by moose in riparian willow communities. They found that control areas outside the park that supported lower moose densities had higher bird diversity. It is ironic that national parks have suffered greater damage from ungulate herbivory than lands that are less protected, such as those managed by the U.S. Forest Service. The apparent reason for this is that sport hunting of ungulates is permitted outside these parks.

Will the parks recover ecologically with the return of the wolf? Wolf reintroduction started in 1995 in YNP, and it is expected that wolves, in combination with other carnivores, will reduce elk populations by about 20–30% below food- and weather-limited carrying capacity in both YNP and RMNP (Singer et al. 2002). The current wolf population in YNP is >200, and the wolves, along with other predators, are killing about 2000 elk annually (M. K. Phillips, personal communication). The elk population (currently about 12,000 in the northern range) is thought to be about 15% below what is expected without wolves.

Just as for sea otters, ecologically effective densities of wolves depend on several interacting factors that vary geographically. For wolves, these include (1) coexistence of predator species, (2) weather, and (3) interactions between forage quality and quantity, productivity, and the number and abundance of prey species. Sympatry with other carnivore species may decrease the effective density of wolves (Gasaway et al. 1992; Messier 1994; Crête & Manseau 1996; Sinclair & Pech 1996; Orians et al. 1997; Mech et al. 1998; Boyce & Anderson 1999). For example, grizzly bears (*Ursus horribilis*) may increase their meat intake by usurping prey killed by wolves, thus forcing the wolves to kill more frequently. Multiple predators limited moose populations in boreal forests to about one-fifth of food-limited carrying capacity (Messier & Crête 1985; Gasaway et al 1992; Messier 1994), a clear indicator of ecological effectiveness. According to Crête and Manseau (1996), where bears are preying on moose calves in the presence of wolves, the density of moose can drop as low as 0.5 moose/km^2, which is seven times lower than in areas with worse forage and harsher winter conditions but lacking wolves. In YNP, several carnivore species are undoubtedly contributing to the limitation of elk (Orians et al. 1997; Peterson 1999), although bears, cougars, and coyotes had little noticeable impact prior to wolf introduction (Coughenour & Singer 1995).

Prey behavior as well as prey numbers are affected by predators, further reducing herbivory in some plant communities (Brown et al. 1999; Terborgh et al. 1999). Wolves, for example, can change the distribution of ungulates in time and space (deer, Nelson & Mech 1981; moose, Berger et al. 2001*b*) and affect group sizes (musk ox [*Ovibos moschatus*], Heard 1992). Although elk numbers per se have yet to decline dramatically in YNP, some

patches of sapling aspen and some patches of willow have been increasing in height since about 1997 (Ripple & Larsen 2000; Singer et al. 2002), suggesting that wolves have reached ecologically effective densities in small parts of Wyoming (in the vicinity of YNP and GTNP) and possibly in Montana and Idaho.

Geographic and temporal variation in weather affects the local distribution of prey species and their ability to escape predators. For example, deep snow (Crête & Manseau 1996) or episodic, severe storms can increase the vulnerability of large ungulates, facilitating their capture (Peterson 1999; Mech et al. 1998; Post et al. 1999) and thereby lowering the effective density of their predators.

Wolves are more likely to persist in a region that contains more than one species of prey (Fuller & Murray 1999). Where beavers are relatively abundant, wolf numbers stabilize at higher densities than in places where moose are the only available large herbivore (Messier & Crête 1985). Predators can shift from one prey species to another because the densities of different prey species may be uncorrelated over seasons and years. Therefore, a diversity of prey species is likely to increase the spatial effectiveness (goal 1) of wolves as regulators of prey.

Productivity interacts with the above factors, including the diversity of prey, in a variety of interesting ways affecting predator distribution. Because of low productivity in some boreal or tundra ecosystems, at least two prey species are required to maintain large carnivores (e.g., Crête & Manseau 1996). In fact, large predators cannot exist where productivity is less than about 0.7 $kg/m^2/year$ (Oksanen & Oksanen 2000). Finally, in the presence of wolves, cervid (mostly moose) biomass in the boreal zone does not increase with increasing primary production (Crête & Manseau 1996: Oksanen & Oksanen 2000), suggesting that wolves are effectively regulating (goal 2) their prey (Messier 1994).

Conclusions

Our conclusions or working hypotheses about ecologically effective densities for highly interactive species that may be drawn from the sea otter and wolf cases include the following:

(1) The absence of these species from previously occupied regions may result in the simplification of ecosystems.
(2) Ecologically effective densities of strongly interacting species can vary by as much as an order of magnitude and are highly contingent and contextual.
(3) For these carnivores, the ecological variables that may influence determinations of effective densities include primary productivity, weather, prey behavior and its variation in space and time, the presence of multiple (alternative) prey species, competition among herbivore prey, prey life history and its variation in space, and the potential for nonadditive interactions and competition among predators species. A similar list probably applies to many highly interactive species.
(4) If not harassed, predator species (individually or as a local "guild") naturally achieve densities above the threshold for ecological effectiveness, except in regions of exceptionally low or variable primary productivity.

Are these tentative conclusions generally applicable in the practice and science of conservation? The answer depends in large part on the proportion of focal or endangered species that are highly interactive. That is, are the two goals mentioned above—extensive geographic representation and ecologically effective functionality within ecosystems—applicable to many species in many places? This question has not been answered, but a survey being conducted by M.E.S. of recovery plans for endangered species in the United States and its territories gives some preliminary results. Nearly half of the endangered species or subspecies included in the approximately 44 existing plans for mammals could be classified as strong interactors (Table 1). The relevant interactions include predation, parasitism, pollination, defoliation, seed and spore dispersal, and cavity and burrow construction. The proportion of highly interactive species, however, could be greater given the lack of studies necessary to make such determinations.

Endangered mammals may not be typical, so it would be premature to generalize about the proportion of species, endangered or otherwise, that are highly interactive. For example, data for most species, including plants, are lacking. While the empirical difficulties in answering this question are an obvious challenge, the standards of scientific inference may be an even greater challenge. Even the nomination of the sea otter as a highly interactive species has been questioned (Foster & Schiel 1988). Despite these uncertainties, two important points emerge from Table 1. One is that a substantial proportion of these species are strong interactors. The other is that ecological function is simply unknown for the majority of listed mammals. Thus, the challenge is not only to restore the known strong interactors to ecologically effective population levels (density and range) but to establish which, if any, of the species for which information is lacking are strong interactors, at least in some ecological contexts. Might it be that most species would prove to be strong interactors if we knew more about their ecological functions?

Spatial and Temporal Variation in Interaction Strength

Interaction strength not only varies among species, but it obviously varies spatially, as demonstrated in the otter and wolf cases. We noted above, for example, that pre-

Table 1. Occurrence of strong interactions among mammals for which recovery plans exist under the U.S. Endangered Species Act.

Species	*Ecology/food*	*Strong interactions*
Marianna (*Pteropus mariannus)* (on Guam) and Little Marianna (*Pteropus tokudae)* fruit bats	frugivorous	none known
Grey bat (*Myotis grisescens*)	insectivorous	none known
Indiana bat (*Myotis sodalis*)	insectivorous	none known
Ozark (*Plecotus townsendi ingens*) and Virginia big-eared (*P. t. virginianum*) bats	insectivorous	none known
Hawaiian hoary bat (*Lasiurus cinereus semotus*)	insectivorous	none known
Lesser long-nosed bat (*Leptonycteris curasoae yerbabuenae*)	pollinator, seed disperser for cacti and agave	yes; important for reproduction of columnar cacti and agave spp. (Nabhan & Fleming 1993)
Mexican long-nosed bat (*L. nivalis*)	pollinator, seed disperser for cacti and agave	yes; important for reproduction of columnar cacti and agave spp. (Nabhan & Fleming 1993)
Grizzly bear (*Ursus arctos*)	omnivore; locally highly carnivorous	yes; habitat disturbance; important nitrogen disperser where feeding on salmon
Louisiana black bear (*Ursus americana luteolus*)	omnivore; locally carnivorous*	probable; as seed disperser and in association with other predators (Gasaway et al. 1992; Jacoby et al. 1999)
Black-footed ferret (*Mustela nigripes*)	specialist on prairie dogs	none known; possible
Southern sea otter (*Enhydra lutris*)	molluscs, urchins, fish	yes; see text
San Joaquin kit fox (*Vulpes macrotis mutica*)	rodents, lagomorphs, insects	possible
Eastern timber wolf (*Canis lupus lycaon*)	predator of deer, moose, beaver	yes; see text
Mexican wolf (*Canis lupus baileyi*)	predator on deer, elk, etc.	yes; see text
Northern Rocky Mountain wolf (*C. l. nebulosa*)	predator on elk, deer, moose, etc.	yes; see text
Red wolf (*Canis rufus*)	predator on deer, raccoons, nutria, etc.	yes (Phillips et al. 2003)
Eastern cougar (*Felis concolor*)	predator on deer, smaller animals	yes (Logan & Sweanor 2001)
Florida panther (*Felis concolor coryi*)	predator on deer, smaller animals	yes (Logan & Sweanor 2001)
Ocelot (*Felis pardalis*)	predator on small mammals, brocket deer, birds, fish, reptiles, invertebrates	possible
Hawaiian monk seal (*Monachus schavinslandi*)	piscivorous	possible
Pt. Arena Mountain beaver (*Aplodontia rufa*)	herbivore, strong burrower	yes (Maser 1998); burrows support skunks, salamanders, moles, shrews, chipmunks, weasels
Appalachian northern flying squirrel (*Glaucomys sabrinus fuscus* and *G. s. coloratus*)	feeds on hypogeous fungi	possible (Carey 1991; Carey et al. 1999); possibly important for forest maintenance and productivity based on role in dispersal of ectomycorrhizal and bacterial spores
Delmarva Peninsula fox squirrel (*Sciurus niger cinereus*)	feeds most on fungi, flowers	possible (Steele & Koprowski 2001); possible role in fungal spore dispersal
Mt. Graham red squirrel (*Tarmiasciurus hudsonicus grahamensis*)	feeds on conifer, aspen seeds, macrofungi, rusts, birds, mast, berries	possible (Steele & Koprowski 2001); effective nest predator
Utah prairie dog (*Cynomys parvidens*)	herbivore	yes (Kotliar 2000; Miller et al. 2000); prairie dogs often considered keystone or foundation species
Pacific pocket mouse (*Perognathus longimembrus pacificus*)	granivore	none known

continued

Table 1. Continued

Species	*Ecology/food*	*Strong interactions*
Giant kangaroo rat (*Dipodomys ingens*)	granivore	yes (U.S. Fish and Wildlife Service [USFWS] 1998); mounds and burrows provide refugia for many other species; strong effects on vegetation; highly competitive with other rodents; important prey of carnivores
Tipton kangaroo rat (*Dipodomys nitratoides nitratoides*)	granivore	yes (USFWS 1998); see *D. ingens* above
Fresno kangaroo rat (*Dipodomys nitratoides exilis*)	granivore	yes (USFWS 1998); see *D. ingens* above
Short-nosed kangaroo rat (*Dipodomys nitratoides brevinasus*)	granivore	yes (USFWS 1998); see *D. ingens* above
Morro Bay kangaroo rat (*Dipodomys heermani morroensis*)	granivore	probable (Goldingay 1997); see *D. ingens* above
Key Largo woodrat (*Neotoma floridana smalli*)	herbivore	none known
Silver rice rat (*Oryzomys palustris hefneri* = *O. argentatus*)	omnivore	none known
Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*)	herbivore	none known
Southeastern beach mouse (*Peromyscus polionotus niveventris*)	herbivore	none known
Choctawhatchee, Perdido beach mouse and Alabama beach mouse (*P. polionotus subsp.*)	herbivore	none known
Anastasia Island beach mouse and southeastern beach mouse (*P. polionotus phasma*)	herbivore	none known
Hualapai Mexican vole (*Microtus mexicanus hualapaiensis*)	herbivore	none known
Florida salt marsh vole (*Microtus pennsylvanicus dukecampbelli*)	herbivore	none known
Amaragosa vole (*Microtus californicus scirpensis*)	herbivore	none known
Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*)	herbivore	none known
Selkirk Mountain caribou (*Rangifer tarandrus caribou*)	herbivore	none known
Columbian white-tailed deer (*Odocoileus virginianus leucurus*)	herbivore	none known
Key deer (*O. v. clavium*)	herbivore	none known
Sonoran pronghorn (*Antilocapra americana sonorienesis*)	herbivore	none known
Peninsula range bighorn sheep (*Ovis canadensis*)	herbivore	none known
Florida manatee (West Indian manatee) (*Trichechus manatus lativostis*)	herbivore	none known
Puerto Rican West Indian manatee (*Trichechus manatus lativostis*)	herbivore	none known
Humpback whale (*Megaptera novaeangliae*)	krill, small schooling fishes	none known

**Extent of predation and its ecological effects unclear.*

dation by wolves on ungulates may be more effective in localities where other large carnivores are present and where alternative prey exist. Brown et al. (2001) identified species that have the potential to alter ecosystems only under restrictive conditions, such as in chronically stressful, marginal habitats. They determined that the stem-boring moth *Diryctrioa albovitella* has insignificant ecological effects on pinyon pine communities inhabiting favorable sandy-loam soils. In stressful cinder soils, however, it has severe effects on dominant pinyon trees. These effects radiate through the ecosystem, influencing the species composition and abundance of organisms ranging from mycorrhizae to seed-eating birds.

These considerations lead us to two more conclusions: (1) globally applicable estimates of ecologically effective densities (or rules of thumb) will likely be meaningless, and (2) we should be cautious when assuming that a given species is not highly interactive or lacks the potential to become so, particularly because species distributions adjust to changing environments.

Uncertainty about future ecological dynamics, including interspecific interactions, is increasing as a result of

rapid environmental change. The profound changes in small-mammal communities that occurred at the close of the last glaciation about 13,000 years ago (Graham & Lundelius 1984; Flannery 2001) attest to this, as does predation on sea otters by killer whales. This means we cannot know exactly which interactions and which species will be most critical for the maintenance of biodiversity in the future. For example, the predatory sea star (*Pisaster orchraceous*), by preying on the competitively dominant mussel (*Mytilus* spp.), enhances species diversity in rocky intertidal communities of the west coast of North America (Paine 1966). However, the per capita interaction strength between sea stars and mussels is strongly influenced by ocean temperature (Sanford 1999), thus raising the possibility of altered community dynamics as the result of global warming or other climatic changes.

These kinds of uncertainty, however, should not discourage managers from establishing operational targets or thresholds for ecosystem recovery. Examples of such qualitative objectives would be (1) the recovery of kelp forests where anthropogenic factors have contributed to the reduction or disappearance of sea otters and other sea urchin predators, (2) the restoration of canopy recruitment of trees and forest understory diversity where plant reproduction has been arrested by excessive herbivore browsing, and (3) the recovery of beaver wetland ecosystems where their disappearance is an indirect consequence of carnivore eradication.

Policy and Management Issues

Neither the interspecies interactions of functionally important species nor interaction strength (Berlow et al. 1999) have been widely recognized in the policy context of conservation laws and regulations, although the goal of management under the U.S. Marine Mammal Protection Act (1977; Section 2) requires that such species and population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part. In contrast, the U.S. Endangered Species Act of 1973 (ESA) hardly refers to interactions among species, though it and many other laws contain vague references to ecological interactions and integrity. The virtual absence of insights from community ecology in conservation management and species recovery is not unexpected given that the ESA and many of its amendments (last ones enacted in 1988) became law before the founding of the Society for Conservation Biology.

Perhaps as a result, recovery goals under the ESA for threatened or endangered species manifest demographic or numerical minimalism. In general, recovery criteria are modest—about three populations with sizes just large enough to prevent disappearance over a short interval such as a century. In several recent recovery plans, the population goals are even more conservative; it is becoming the convention to employ phrases such as "stabilization at existing population size and geographic distribution." Rarely, if ever, is recovery defined in terms of restoration of critical ecological interactions over extensive geographic areas or the propagation of endangered interactions across trophic levels. It has been observed that the formation of recovery goals now leans more heavily on social and economic concerns than biological information (Elphick et al. 2001; Gerber & Schultz 2001).

For all of these reasons the criteria for listing and the concepts of recovery and recovery goals in the ESA rarely if ever take interaction strength into account. Although the ESA states in the "Findings" section that "The purposes of this Act are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved . . . " this broader goal is never mentioned again, and recovery is usually defined in terms of local (single-species) demographic or genetic viability. Moreover, this language appears to reflect the naive view that species are critically dependent on the preservation of their habitats but that ecosystems are much less dependent on the preservation of their component species.

Until such laws and policies are constructively rewritten and enforced, the current principles of community dynamics and the integrative role of highly interactive species are likely to be ignored in conservation planning and management. One such principle or hypothesis is the idea that wide-ranging and strongly interacting species occur (or once occurred) in many, if not most, ecosystems (MacArthur 1972; Paine 1980; Brown & Heske 1990; Fonseca & Robinson 1990; Henke & Bryant 1999; Pace et al. 1999; Terborgh et al. 1999; Estes et al. 2001). This hypothesis challenges scientists to view the recovery of such species and the restoration of biodiversity from a community perspective and on landscape, regional, and continental scales (Soulé & Noss 1998; Soulé & Terborgh 1999). Specifically, strongly interacting but extirpated species should be restored throughout all those parts of their potential range, where their absence may contribute to ecological degradation or simplification.

Can conservation biology provide the requisite tools and justifications for the maintenance of highly interactive species? It is apparent in the sea otter and wolf cases that estimates of ecologically effective densities are feasible at local to regional scales. In the future, the estimation of this population-community metric may partially supplant the use of more conservative autecological tools such as population viability analysis (Soulé 1987; Beissinger & McCullough 2002).

Proposals by conservationists to repatriate native predators are likely to impel interest in estimates of effective densities. Such proposals often ignite social conflict over

the potential impacts of predators on sport hunting and livestock operations, or over polarized public perceptions of carnivores. In such situations, conservation biologists may need to analyze whether the artificial control or geographic restriction of the species, below some estimated threshold of effectiveness, has been ecologically harmful.

Ecosystems are complex and always changing. For these reasons, conservation should facilitate extensive spatial access for highly interactive native species, according to their needs and ecological opportunities. In particular, highly interactive species—present or potential—should be given the benefit of the doubt in our management and recovery efforts. A contemporary example is wolf recovery in the United States. Wolves are still absent from most of the western states and occupy only about 4–5% of their historic range in the United States exclusive of Alaska (M. K. Phillips, personal communication).

In the end, our success in rehabilitating an ecologically degraded world will be judged more on the persistence of interspecies interactions than on the geographically limited persistence of populations based only on causing the least economic burden and ensuring only symbolic survival. Both the science of ecology and our obligations to minimize harm to nature require that land use and conservation policies reflect this higher standard.

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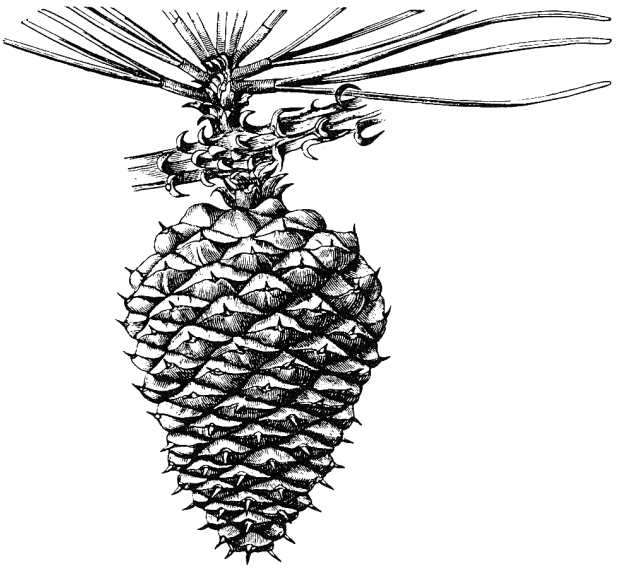
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