

TROPHIC CASCADES

Predators, Prey, and the Changing Dynamics of Nature



Edited by John Terborgh and James A. Estes

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CHAPTER 9



Large Predators, Deer, and Trophic Cascades in Boreal and Temperate Ecosystems

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Historically, humans have modified many boreal and temperate ecosystems by decimating native animal populations and often substituting domesticated stock, thereby influencing food webs and simplifying interactions between species. Large predators, especially, have been subject to worldwide persecution. The profound ecological implications of losing top predators are only now beginning to be understood. Across a variety of environments, predator extirpation can lead via trophic cascades to habitat degradation at multiple trophic levels, species loss, and even ecosystem collapse (Terborgh et al. 1999; Ray et al. 2005).

In the 1800s and early 1900s, gray wolves (*Canis lupus*) and other large predators were the target of widespread eradication efforts throughout much of the United States (Boitani 2003). Extirpation of these predators and subsequent deer irruptions (abrupt population rise) generally occurred earlier in the eastern United States than in the West. The last wolves and cougars (*Puma concolor*) were killed by the 1880s in New York State, and deer subsequently irrupted in the 1890s. By the early 1900s, deer irruptions also occurred in Michigan, Pennsylvania, and Wisconsin (Leopold et al. 1947). In western states, the fate of the wolf was sealed in 1915 when the U.S. Congress authorized eliminating any remaining wolves and other large predators. As part of this program, the U.S. Biological Survey systematically killed wolves, extirpating them from the western United States by the 1930s. Deer irruptions soon followed, with most

population increases in the West taking place between 1935 and 1945 (Ripple and Beschta 2005). Herein we refer to cervids collectively as “deer” in the European manner, unless referring to individual cervid species, which we identify by species name.

Concerns over large predator loss became an important scientific issue in the 1920s and 1930s when leading biologists opposed federal predator extermination programs (Dunlap 1988). Charles Elton created the concept of the food pyramid in his seminal 1927 book *Animal Ecology*, and was the first to hypothesize that wolf extirpation would cause widespread increases of ungulate populations to unsustainable levels. Inspired by Elton (1927), Aldo Leopold (1943) was among the first to investigate how the removal of wolves and cougars across large portions of the United States was a precursor to deer irruptions.

Leopold's views on the importance of large predators were influenced by Charles Elton and by trips in 1935 to Germany and Mexico. In the predator-free forests of Germany, he observed extensive plant damage resulting from overabundant deer (Leopold 1936). In contrast, in the Sierra Madre mountains of northern Mexico he found intact ecosystems, representing reference conditions, where he observed healthy relationships between predators, prey, and their plant communities (Leopold 1937). In 1947 (p. 176), Leopold et al. wrote,

Irruptions are unknown in Mexico, and we know of only two in Canada. Both Canada and Mexico retain wolves or cougars, except in certain settled areas. Since irruptions coincide both in time and space with greatly reduced predation by wolves or cougars, and since they are not known to have occurred in the presence of these predators, there is a strong presumption that over-control of these predators is a predisposing cause.

Leopold argued that predator loss set the stage for deer irruptions, followed by degradation of habitat and eventual reduction in carrying capacity. He supported these views by summarizing reports of irruptions from more than a hundred deer ranges in various portions of the United States where large carnivore populations had been removed or suppressed. From these case studies, Leopold et al. (1947) concluded that irruptions led to overbrowsing and subsequent ecosystem damage, such as reduced biodiversity, habitat loss, and accelerated soil erosion.

To evaluate the Leopold hypothesis, we surveyed a range of studies on trophic cascades related to deer browsing, covering both boreal and temperate ecosystems. In this chapter, we focus on trophic cascades involving relationships

between large mammalian carnivores, deer, plants, and ecosystems. First, we describe several predator–prey systems of the boreal forests of North America and Eurasia. Next, we discuss trophic relationships in the temperate zone where predators have been extirpated, with special emphasis on introduced deer, and finally we recount some case studies from western North America. We close with a discussion of how trophic cascades might facilitate ecological restoration and present conclusions emerging from the synthesis of our field studies and the research of others.

BOREAL FORESTS

The boreal region is one of the world's best for examining trophic dynamics, because large carnivores still abound in much of this vast northern realm. Circumpolar in extent, the boreal region encompasses large portions of northern North America, Russia, and Scandinavia. One of the classic studies of top-down versus bottom-up determinants of population dynamics was conducted in the boreal forest. Krebs et al. (1995) used a large-scale replicated experiment to test the response of an herbivore (the snowshoe hare, *Lepus americanus*) to manipulations of food availability and mammalian predators. The principal mammalian predators (lynx [*Lynx rufus*], coyote [*Canis latrans*]) were excluded by a single strand of electrified wire that allowed hares to pass freely. Hare densities doubled in the predator reduction plots but increased elevenfold when food addition was coupled with predator reduction, indicating a strong interaction between the two variables.

Consistent with Hairston, Smith, and Slobodkin's (HSS 1960) green world hypothesis, Crête (1999) found that deer populations in northern North America remained nonirruptive in the presence of wolves. However, south of the wolf range, deer biomass increased with increasing primary productivity, a relationship predicted by the exploitation ecosystems hypothesis (see Chapter 10, this volume). Crête and Dangle (1999) found that deer biomass in portions of North America that deer share with wolves (British Columbia to southern Quebec) was approximately a fifth of that in areas where wolves are absent (maritime provinces), rare, or recolonizing (northwest United States). Evidence is now mounting that an overabundance of deer is imposing unprecedented browsing pressure on plant communities across much of wolf-free North America (McShea et al. 1997; Crête 1999). Crête and Manseau (1996) found moose (*Alces alces*) densities in eastern North America to be seven times as high

in a region without wolves (1.9 moose per square kilometer) than in one with wolves (0.27 moose per square kilometer), even though primary productivity was higher in the area with wolves. High moose densities in the absence of predation can have a significant impact on forests and biodiversity. In Sweden, after predator extirpation in the twentieth century, high moose densities have also been a significant source of damage to boreal forests (Hörnberg 2001). For example, Angelstam et al. (2000) compared moose densities in the boreal forests without wolves (Sweden) and in those with wolves (Russian Karelia). Both areas have similar climate, vegetation, and timber harvesting history, but moose densities were five times as high in Sweden (1.3 moose per square kilometer) as in Russia (0.25 moose per square kilometer).

In Isle Royale National Park in Lake Superior, wolves have not prevented periodic moose irruptions and resulting damage to balsam firs (McLaren and Peterson 1994). Moose colonized the island around 1900, with wolves colonizing it 50 years later. The balsam fir component of forests on the island has been reduced from 40 percent in 1848 to less than 5 percent today. The absence of bears on the island could be important, as the coexistence of wolves and bears may prevent the irruptions of ungulate populations (Gasaway et al. 1992; Messier 1994).

Overall, studies of boreal ecosystems have shown that deer irruptions are extremely rare where predator populations remain intact (Gasaway et al. 1983; Flueck 2000; Peterson et al. 2003). Deer irruptions in boreal forests typically occur only after wolf extirpation (Corbett 1995; Peterson et al. 2003).

TEMPERATE ECOSYSTEMS

The temperate region is found in the northern and southern hemisphere. The temperate region's climates are milder, human populations are higher, and predator ranges are more fragmented than in the boreal zone.

Deer Introductions

Researchers investigating why invasive species are so successful often highlight the absence of natural enemies. Within its native range, any species of deer contends with a suite of factors, such as predators, hunters, pathogens, and primary productivity, that can limit population densities. When released in a new region without its coevolved competitors and disturbance regimes, a species can reach unprecedented densities. The "enemy release hypothesis" (Keane and Crawley

2002) appears to accurately characterize such invasions and represent a specific case of trophic cascades.

New Zealand provides a renowned example. Although native deer (and, by extension, native deer predators) were originally absent, since 1800 eight species of deer have been introduced. After subsequent irruptions, New Zealand began aggressively culling them in the 1930s (Caughley 1983). Hunting of wild deer there (and elsewhere) probably prevented outright starvation and subsequent population crashes. Over time, even reduced numbers of deer continued to alter species composition in forests, creating plant communities dominated by both browse-tolerant and unpalatable species (Veblen and Stewart 1982; Stewart and Burrows 1989; Husheer et al. 2003). Even where deer densities have been reduced, regeneration of palatable trees remains limited. In some cases, unpalatable ferns and other plants create an environment inhospitable to seedling establishment and growth of trees (Bellingham and Allan 2003; Coomes et al. 2003). Deer-induced changes have altered New Zealand's forests to such an extent that it may no longer be possible to restore plant community composition to a pre-deer state (Coomes et al. 2003). Similar impacts have been observed on Patagonia's Isla Victoria, where introduced red deer (*Cervus elaphus*) have significantly depressed maqui (*Aristotelia chilensis*) while favoring recruitment of the thorny shrub Darwin barberry (*Berberis darwinii*) and sedges (*Uncinia* spp.) (Veblen et al. 1989).

Black-tailed deer (*Odocoileus hemionus*) have been introduced to several islands in British Columbia's Haida Gwaii (Queen Charlotte) archipelago. Because other islands still lack deer, this archipelago provides an ideal natural laboratory to evaluate deer impacts within these temperate coastal rainforests. Stockton et al. (2005) reported that predator-free islands with deer for more than 50 years have 85 percent less shrub and herbaceous cover and 20–50 percent fewer plant species than deer-free islands. This dramatic transformation has cascaded to birds and invertebrates. Bird densities were greatly diminished on islands with deer, and ground-dwelling invertebrates were reduced by 90 percent (Allombert et al. 2005a, 2005b). Deer influence has been so strong in the archipelago that it upended a central tenet of island biogeography. The smallest islands furthest from the mainland have the greatest species richness, because they are the least likely to have introduced deer (Gaston et al. 2006).

On Quebec's Anticosti Island, introduced white-tailed deer (*Odocoileus virginianus*) have greatly depressed regeneration of balsam fir (*Abies balsamea*) (Potvin et al. 2003) and eliminated nearly every deciduous shrub or seedling in the browse zone (Tremblay et al. 2005). Through excessive browsing of

berry-producing shrubs, deer may have triggered the local extinction of the black bear (*Ursus americanus*) (Côté 2005). Arboreal lichens and broken balsam fir twigs that make up winter litterfall increasingly serve as an alternative food source for deer (Tremblay et al. 2005).

Hyperabundant Native Deer

Consistent with HSS, the decimation or extirpation of natural enemies enables deer to thrive, which in turn reshapes plant communities and generates far-reaching effects that ripple through the ecosystem. Even where deer are native, predator reduction or elimination can generate many of the same effects observed with introduced deer.

Sika deer (*Cervus nippon*) is indigenous to eastern Asia, including the Japan archipelago. After the extinction of Japanese gray wolves more than a century ago, sika deer populations greatly increased and now are altering forest composition. On Kinkazan Island for example, densities of more than sixty sika deer per square kilometer have adversely affected Japanese beech (*Fagus crenata*) such that seedlings can now only grow where protected from herbivory (Takatsuki and Gorai 1994). On Honshu Island's Kii Peninsula, overabundant sika deer are favoring the spread of sasa grass (*Sasa nipponica*) and inhibiting tree regeneration (Ando et al. 2006; Itô and Hino 2007). If this process continues, sasa-dominated grasslands could gradually replace forests.

In Britain, the wolf was extirpated south of Scotland in the 1500s, effectively releasing native red and roe deer (*Capreolus capreolus*) from predation. Simultaneously, gamekeepers guarded deer against poachers because game animals were owned by the Crown and commoners had no hunting rights (Munsche 1981). In their study of the New Forest in southern England, Peterken and Tubbs (1965) found a perplexing age structure: Canopy trees all dated to the 1750s, 1850s, and 1930s. It turns out that these periods corresponded to three periods of release from browsing pressure. In the 1750s, oak was planted to provide timbers for the British Navy, and plantations were fenced to keep deer out. An 1851 act of Parliament mandated removal of all deer from royal forests. Lastly, the Great Depression of the 1930s brought increased hunting pressure on deer (Putman 1996). Deer populations again increased in the latter half of the twentieth century, augmented by the introduction and spread of Chinese muntjac deer (*Muntiacus reevesi*) and sika deer (Fuller and Gill 2001). Today, the combined effects of native and exotic deer in British woodlands are depressing numbers of woodland herbs (Kirby 2001) and altering forest structure, whereas deer exclusion results in an increase in density and cover of understory herbs, shrubs, and saplings and leads to a threefold increase

in migratory bird densities and a fourfold increase of birds that nest or feed in the shrub layer (Gill and Fuller 2007).

In Scotland, more than 99 percent of the Caledonian pinewoods have been lost (Baines et al. 1994), in part because Scots pine (*Pinus sylvestris*) is failing to regenerate (Palmer et al. 2007). Although pine seedlings are often abundant, they fail to recruit into larger size classes because of excessive browsing by red deer. Watson (1983) notes that recruitment failure dates to the late 1700s, when wolves were extirpated (Nilsen et al. 2007) and the local earl enacted draconian policies to deter deer poachers. Using exclosure experiments in Scotland's native pinewoods, Baines et al. (1994) determined that deer browsing resulted in a fourfold reduction in caterpillar larvae and raised questions about potential cascading effects to insect-feeding birds.

In the eastern United States, the wolf was relentlessly persecuted and effectively extirpated by 1900. These efforts coincided with the felling of the last old-growth forests and hunting of white-tailed deer to very low levels (Whitney 1994). By the mid-twentieth century, forests had regrown and deer populations had recovered to levels that supported recreational hunting in most eastern states (Warren 1991). However, since then deer populations have continued to increase (Ripple and Beschta 2005; Figure 9.1), suggesting that contemporary hunting pressure (combined with other sources of mortality, such as vehicular

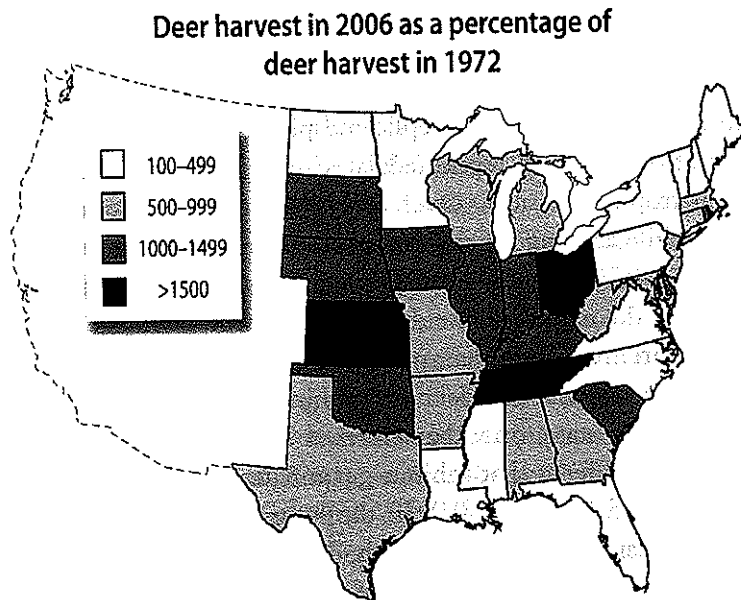


Figure 9.1. Eastern United States showing 2006 deer harvest, by state, relative to harvest levels in 1972. Data from Shead (2005) and unpublished agency deer harvest records.

collisions) has been insufficient to keep irrupting deer populations in check or to preserve biodiversity.

Changes in vegetation over the past century on the Allegheny Plateau in northwestern Pennsylvania provide an important case study of hyperabundant native deer. Old-growth eastern hemlock (*Tsuga canadensis*) and northern hardwood forest once covered this area. Because of its rot-resistant wood, high whole-tree transpiration rates, and influence on soil acidity and moisture, hemlock is a keystone species that contributes to regional biodiversity (Ellison et al. 2005). After wolf and cougar extirpation in the late 1800s, heavily hunted deer populations reached a record low around 1900 (Redding 1995). Deer protection allowed deer densities to exceed sixteen animals per square kilometer by the 1930s. Between 1935 and 1942, deer eliminated most regenerating eastern hemlock and deciduous shrubs from remaining old-growth stands, opening up the forest understory (Hough 1965). Whitney (1984) found that between 1929 and 1978 the recruitment of eastern hemlock saplings more than 30 centimeters tall declined to essentially zero, a decline that coincided with increasing deer densities. The ecological impacts of increased numbers of deer extended beyond eastern hemlock to biodiversity in general. For example, in 1995 Rooney and Dress (1997) replicated a 1929 floristic survey (Lutz 1930) and found a 75 percent decline of shrub and herbaceous species richness in an old-growth stand located in a national scenic area.

Perhaps the most damning findings come from a Pennsylvania study that used large-scale (13- or 26-hectare) deer enclosures. Density control treatments maintained deer at four levels (four, eight, fifteen, and twenty-five deer per square kilometer) for 10 years in replicated plots. Like Krebs et al. (1995) this study is one of the few well-replicated, large-scale, and long-term experiments on terrestrial trophic cascades. Over time, deer reduced sapling density and growth rates while altering species composition in favor of browse-tolerant or -resistant species (Horsley et al. 2003). Furthermore, shrub-nesting birds present at the end of the experiment exhibited the lowest richness and abundance in plots with more than eight deer per square kilometer (de Calesta 1994). Increasing evidence suggests that deer are pushing Allegheny Plateau forests into an alternative stable state, one characterized by a dense cover of regionally common grasses and ferns that inhibits germination and establishment of tree seedlings (Royo and Carson 2006). In the long term, these forests could become similar to bracken grasslands, largely devoid of trees (Stromayer and Warren 1997) and the terrestrial equivalent of sea urchin barrens.

The large predator and deer history of northern Wisconsin parallels that of northwestern Pennsylvania. Predators were extirpated, deer densities declined from intensive hunting, deer received protection, and deer populations ir-

rupted. In 1945, researchers surveyed more than 3,000 plots widely distributed throughout Wisconsin's northern forests to examine potential deer damage to regenerating trees (De Boer 1947; Swift 1948). They found eastern hemlock recruitment only on tribal lands, the only part of the region where deer were subject to greater year-round hunting pressure. Similar trends occurred with northern white cedar (*Thuja occidentalis*), as 70 percent of observed stems exhibited browse damage.

Both enclosure and comparative studies relying on tribal lands as reference areas indicated that the absence of eastern hemlock recruitment in Wisconsin was a consequence of excessive deer browsing (Anderson and Loucks 1979; Anderson and Katz 1993). Similarly, a geographically extensive multivariate analysis revealed deer browsing to be the primary cause of seedling mortality in the 30- to 100-centimeter height class (Rooney et al. 2000). Even if browsing pressure were eliminated, it would take more than 70 years to eliminate the eastern hemlock recruitment gap (Anderson and Katz 1993). Large, long-lived species are vulnerable to deer browsing only for the brief seedling stage of the life cycle, and because they can produce seed for hundreds of years, populations can persist for centuries with no recruitment. Other palatable species with shorter life cycles do not have this advantage.

Researchers have also documented 50-year changes in the forest herb and shrub layers in northern Wisconsin, largely attributable to excessive deer browsing. Sixty-two presettlement-like reference stands showed an 18 percent decline in native species richness between 1949 and 1999, with declines four times higher in state parks and other properties without deer hunting (Rooney et al. 2004). Many of the declining species were known to be susceptible to deer browsing, whereas many of the increasing species were either tolerant or resistant to browsing (Wiegmann and Waller 2006).

Throughout the 1970s and 1980s, wildlife biologists believed that recreational hunting could control deer populations in most places (Warren 1991). They observed excessive deer impacts in some regions, such as northern Wisconsin and Michigan (Figure 9.2) and parts of Pennsylvania, and in state and national parks where deer hunting was prohibited, but at that time they viewed these effects as anomalous. Little research on deer impacts was conducted outside these areas (Russell et al. 2001), so broader generalizations were elusive. However, evidence of widespread deer damage continues to accumulate (Côté et al. 2004). Wildlife managers are increasingly recognizing that control of deer numbers through hunting is limited by declines in hunter numbers, increases in areas off limits to hunting, and a reluctance of hunters to engage in antlerless harvests or other population control strategies (Brown et al. 2000). Indeed, white-tailed deer harvest rates have increased dramatically in the eastern



Figure 9.2. A 16-year-old white-tailed deer exclosure in Vilas County, Wisconsin reveals a recovery of deciduous shrub and tree species inside the fence. Note also the high proportion of grasses and sedges that make up the ground-layer community outside the fence.

United States over the past 30 years (Figure 9.1), even with a decline in the number of deer hunters over the same interval (U.S. Fish and Wildlife Service 2006). In addition, hunting by humans is typically not functionally equivalent to predation by large carnivores due to factors involving risk and the ecology of fear (Berger 2005; Chapter 14, this volume). Human hunters exhibit a Type 1 functional response to deer numbers, whereas large carnivores exhibit Type 2 or Type 3 functional responses (Van Deelen and Etter 2003).

Wolf eradication in the western United States took place a half-century or more later than in the East, not being completed until the 1930s. Although the problem of deer overabundance has often been considered an eastern phenomenon, recent studies have begun to reveal the extent to which predators indirectly structure plant communities and ecosystem processes in the western United States. In the sections that follow, we summarize results of two case studies that took advantage of unplanned landscape-scale natural experiments spanning more than a century. The focus of these studies was to evaluate the status of ecosystems where large mammalian predators had been extirpated or

their populations greatly diminished. The first is a wolf–elk (*Cervus elaphus*) system in Yellowstone National Park; the second, a cougar–mule deer (*Odocoileus hemionus*) system in Zion National Park. In both instances, comparisons occurred across temporal (predator removal) and spatial (browsing refugia) treatments. Additionally, these investigations extended beyond the classic three-level trophic cascade of predator–consumer–producer by evaluating the indirect influence of predators on the physical integrity of riparian streambanks and channel morphology. Cascades involving the overbrowsing of streamside vegetation can degrade riparian and aquatic ecosystems and can eventually cause the loss of beaver.

Yellowstone's Wolves and Elk

Long-term trophic linkages have been identified in the northern range of Yellowstone National Park (Wyoming, USA) between wolves, elk, and deciduous tree species—aspens (*Populus tremuloides*) and cottonwood (*Populus* spp.)—via the use of tree ring analyses to establish the age structure of remnant stands. Tree recruitment occurred regularly in the northern elk winter range when wolves were present but became extremely rare after wolf elimination. However, growth of young aspen within exclosures and young cottonwoods within browsing refugia (areas with little browsing) indicated that climate, fire regimes, or other factors probably had little influence on long-term patterns of recruitment (Ripple and Larsen 2000; Beschta 2005).

In an attempt to replicate findings in the northern range studies, Ripple and Beschta (2004b) evaluated the status of wolves, elk, and woody browse species in the upper Gallatin elk winter range in the northwestern corner of Yellowstone National Park. As in the northern range, wolves were present here until about the mid-1920s and generally absent until reintroduction in the mid-1990s. Analysis of historical reports and a chronosequence of photographs along the Gallatin River indicated that willows (*Salix* spp.) eventually began to die after the removal of wolves, apparently because of unimpeded browsing by elk.

More recently, Halofsky and Ripple (2008b) investigated potential trophic cascades by evaluating aspen recruitment during two time periods in the upper Gallatin winter range: an intact tritrophic cascade of wolf–elk–aspen (pre-1930s and post-1995) and a bitrophic cascade of elk–aspen (1930s to 1995). Abundant aspen recruitment occurred throughout the early period with wolves present, followed by a sharp decline in aspen recruitment subsequent to wolf extirpation (Figure 9.3b). In contrast, aspen recruitment occurred continuously within a fenced exclosure after its construction in 1945 (Figure 9.3a), confirming

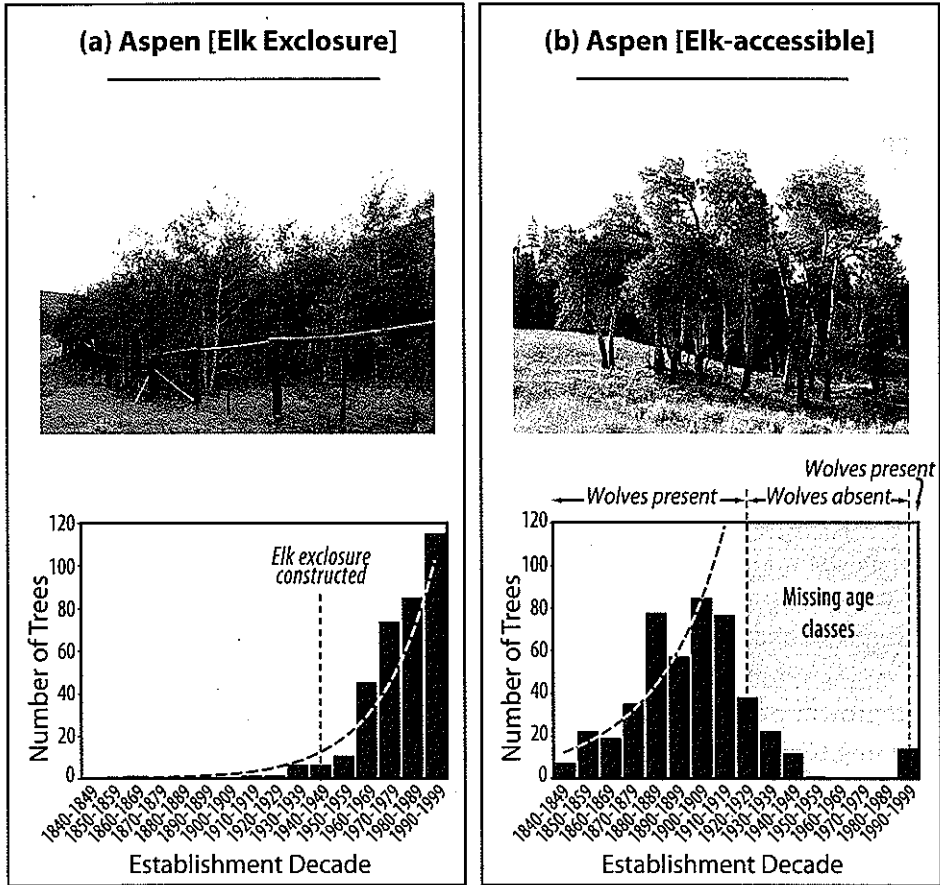


Figure 9.3. Photographs of aspen stands and corresponding age structure: (a) inside the Crown Butte elk exclosure and (b) outside the exclosure in an area accessible to elk browsing. Both locations are in the upper Gallatin elk winter range, southwest Montana. An exponential function (dashed line) was fitted to all tree frequencies in (a) and only to frequencies when wolves were present in (b). “Missing age classes” in (b) indicates the difference between expected (exponential function) and observed tree frequencies (bars) after the 1920s, when wolves were absent.

many decades of exclosure studies in Yellowstone’s northern range, where, in the absence of elk herbivory, recruitment of woody browse species continued to occur regardless of weather and climatic fluctuations (Singer 1996; Kay 1990, 2001; Barmore 2003). Since wolf reintroduction, young aspen in the Gallatin have been growing taller at some sites perceived as high risk by elk. Such high-risk sites benefit from reduced elk foraging and more plant growth (Ripple and Beschta 2004a; Halofsky and Ripple 2008a; see Chapter 14, this volume).

Cascading effects of predator exclusion may propagate widely through an ecosystem and result in some surprising consequences. In Yellowstone, senescing stands of aspen, unreplenished by recruitment, are replete with snags that support an enhanced abundance and diversity of cavity-nesting birds (Hollenbeck and Ripple 2008). However, as these stands continue to age, currently standing snags will fall and will not be replaced by regenerating stems for many decades. Even if aspen stem regeneration significantly increases after wolf re-introduction (Ripple and Beschta 2007b; Halofsky et al. 2008), cavity-nesting birds will probably decline until new snags arise from currently recruiting young aspen saplings.

Research in Yellowstone National Park is yielding new insights into the ecosystem-wide implications of tritrophic cascades. Moreover, the findings from Yellowstone are consistent with those from other sites in western North America, including several additional national parks: Grand Teton (Berger et al. 2001a), Banff (Hebblewhite et al. 2005), Jasper (Beschta and Ripple 2007b), Wind Cave (Ripple and Beschta 2007a), Rocky Mountain (Binkley 2008), and Olympic (Beschta and Ripple 2008).

Zion's Cougar and Mule Deer

Investigation of a cougar–mule deer system in Zion National Park (Utah, USA) provides additional insights into large predator trophic cascades in terrestrial ecosystems. Areas in the park were designated as “cougars common” or “cougars rare” (Ripple and Beschta 2006a). Spatial proximity of study sites helps minimize potentially confounding variation in climate or other factors.

Cougar have remained common in the roadless North Creek drainage, but since the mid-1930s they have largely avoided areas of high tourist visitation in Zion Canyon, only about 15 kilometers east of the North Creek drainage. Visitor numbers increased dramatically in Zion National Park in the 1920s and 1930s when park biologists noted a reduced frequency of cougar sign in Zion Canyon. Mule deer densities increased from less than four per square kilometer in 1930 to a peak of about thirty per square kilometer in 1942. Since then, the canyon deer population has declined to about ten per square kilometer, still considered high.

The relative strength of top-down trophic cascades in Zion Canyon and North Creek were assessed by evaluating the age structure of Fremont cottonwood (*Populus fremontii*) trees along watercourses (Ripple and Beschta 2006a). In North Creek, with uninterrupted cougar presence, cottonwood recruitment had occurred continuously over time, with more young trees than old (Figure 9.4a), a normal feature of a healthy riparian forest. In contrast, little cottonwood

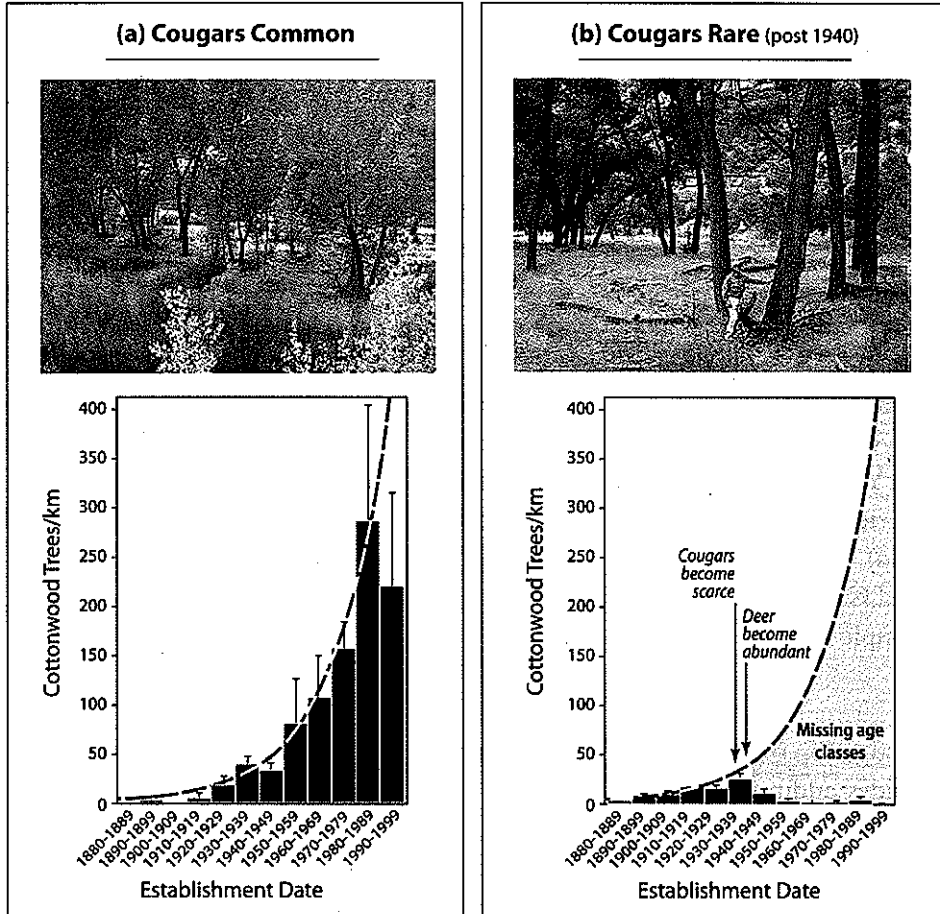


Figure 9.4. Photographs of cottonwoods and corresponding cottonwood age structure for riparian areas in Zion National Park: **(a)** North Creek, where cougars were common (control), and **(b)** Zion Canyon, where they were rare (treatment). The exponential function (dashed line) for tree recruitment cohorts in the control reaches **(a)** was also plotted in **(b)** for comparison after cougar became scarce. “Missing age classes” in **(b)** indicate the difference between expected (exponential function) and observed tree frequencies (bars) after the 1930s, when cougar were scarce. Error bars represent standard error of the means.

recruitment had occurred in Zion Canyon since the 1930s (Figure 9.4b). Post-1940 cottonwoods were forty-seven times more abundant along North Creek than in Zion Canyon.

To assess indirect effects of predator scarcity on biodiversity, Ripple and Beschta (2006a) conducted visual encounter surveys of indicator species on streambanks along North Creek and in Zion Canyon. Markedly higher num-

bers of wildflowers, amphibians, lizards, and butterflies were tallied along streams in the North Creek area than in Zion Canyon: Amphibians were more than 100 times, lizards three times, and butterflies five times more abundant (Figure 9.5). Although none of the censused wildflower species occurred within belt transects in Zion Canyon, they occurred outside the belt transects

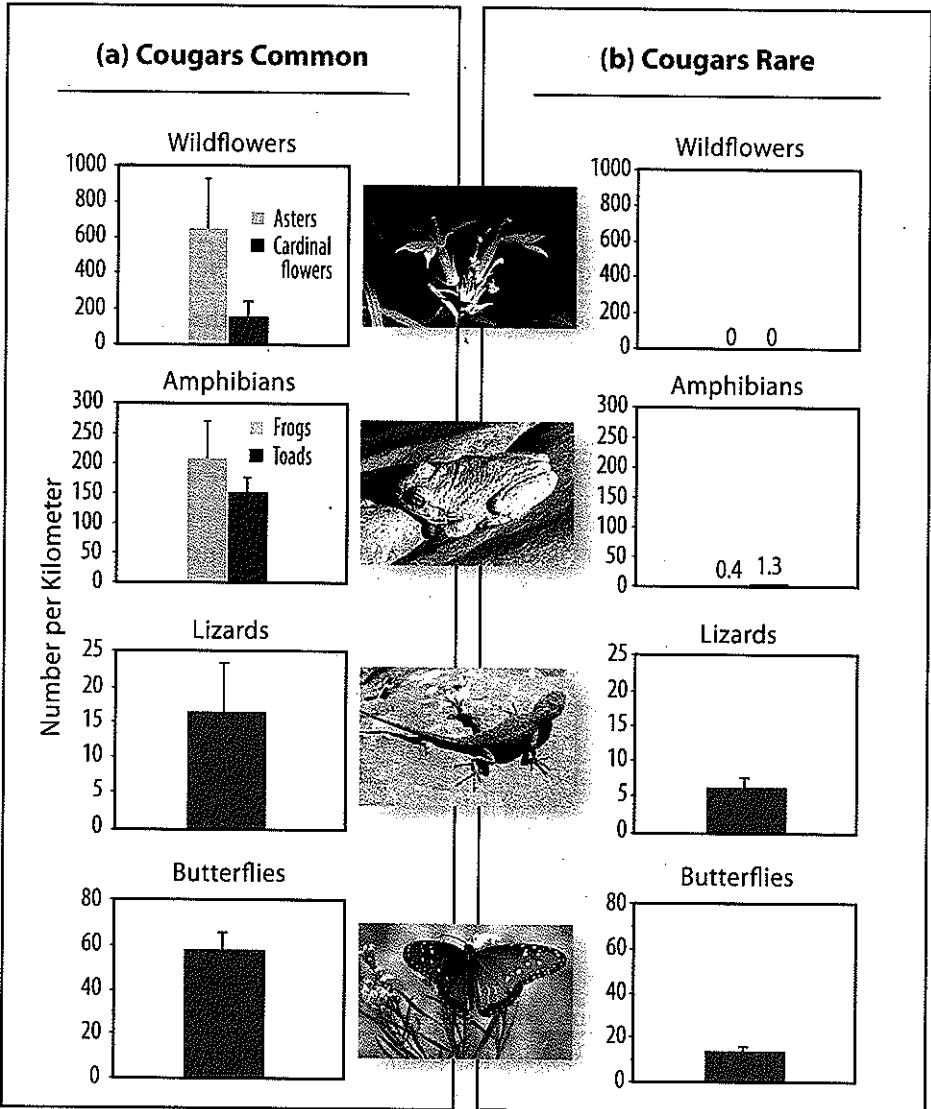


Figure 9.5. Comparison of species abundances in areas where cougars were common (a) and rare (b) for wildflowers, amphibians, lizards, and butterflies. Both locations are in Zion National Park.

in areas physically protected from deer browsing (i.e., plant refugia). Changes in cottonwood age structure and native species abundance indicate a shift to an alternative, low-diversity ecosystem state in Zion Canyon. This regime shift probably has also altered food web linkages between the aquatic and terrestrial components of the riverine system (Baxter et al. 2005).

Results from Zion National Park generally affirm Leopold's (1943) interpretation of the mule deer irruption on the Kaibab Plateau of Arizona and its effect on plant communities after cougar and wolf eradication. Aspen recruitment on the Kaibab subsequently plummeted, just as cottonwood recruitment nearly ceased in Zion Canyon after cougars vacated the area (Binkley et al. 2006). Findings from Yosemite National Park, another cougar–mule deer system, are consistent with those of both the Kaibab and Zion (Ripple and Beschta 2008).

From Predators to River Beds: Cascades Extend beyond the Producer Level

Investigations of tritrophic cascades normally conclude at the producer level. Yet in the western United States, as we have seen, highly productive and bio-diverse riparian corridors are especially targeted by large herbivores when predators are scarce or absent. Destruction of riparian vegetation then cascades to the abiotic environment by exposing denuded streambanks to erosion. Channel widths expand, with consequent reduction of stream depth and altered fish habitat. Such chain reactions have been documented for streams in the upper Gallatin winter range, Wyoming (Beschta and Ripple 2006; Figure 9.6), Zion Canyon, Utah (Ripple and Beschta 2006a), and Olympic National Park, Washington (Beschta and Ripple 2008). Broadening of channel widths or channel incision reduces overbank flooding during spring snowmelt. Floodplains consequently fail to store floodwater during periods of high flow, to the detriment of riparian flora and fauna.

RECOVERY OF ECOSYSTEMS

We have summarized some of the ecological consequences of introducing deer into predator-free environments and compared the effects of predator presence and absence on several native species of deer. In each of these cases, large mammalian herbivores in the absence of strongly interacting predators (Soulé et al. 2005) have been found to have major impacts on vegetation, reducing and skewing tree recruitment in forests, transforming understory herbaceous communities, and denuding riparian vegetation. These profound and potentially

devastating effects of large herbivore overabundance are little understood or appreciated by much of the public and many practicing biologists (Pyare and Berger 2003). For example, state cougar management plans in the United States typically overlook the role cougars play in regulating trophic cascades. Similarly, state wolf recovery plans base recovery goals on population size alone and generally ignore the potential biodiversity benefits provided by this keystone predator.

Can ecosystem decline initiated by the loss of a large carnivore be simply reversed if the carnivore is reintroduced to a part of its former range? Where large carnivores are reintroduced into fragmented ecosystems, what role does

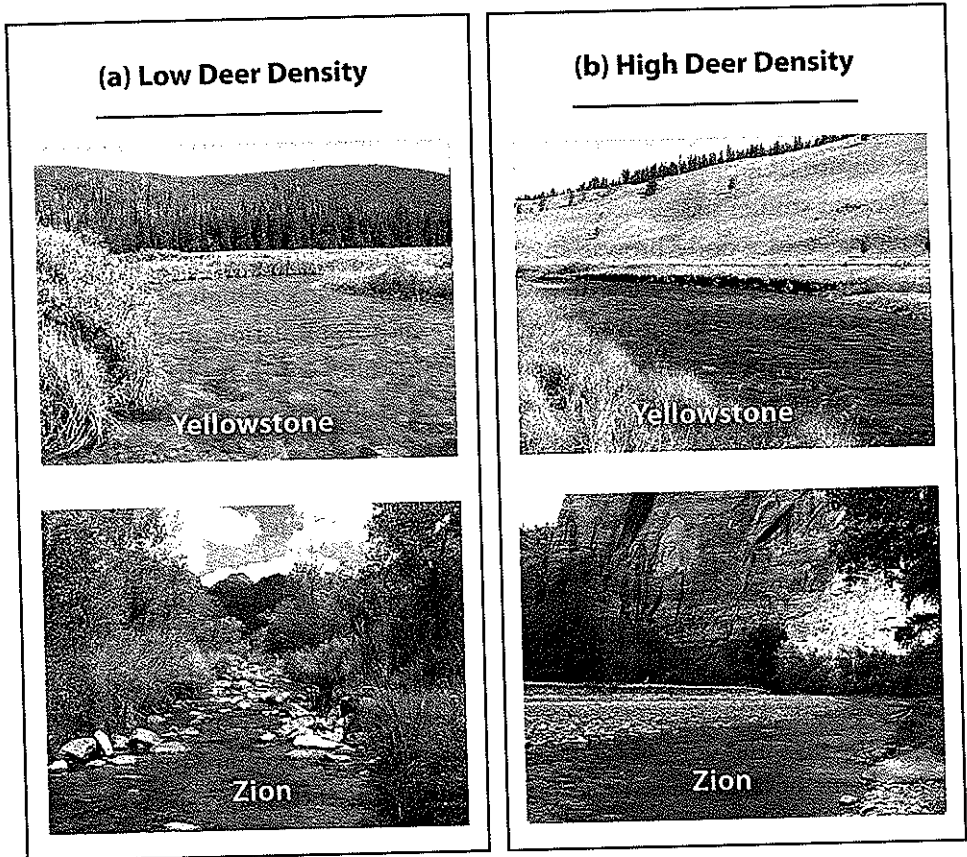


Figure 9.6. Streamside plant communities and streambank conditions for riverine systems with low (a) and high (b) deer densities. The upper two photos are for elk summer range (left) and elk winter range (right) along the upper Gallatin River in Yellowstone National Park; the lower two photos show areas of low (left) and high (right) mule deer densities in Zion National Park.

management of predator and deer populations have on the structure and function of ecosystems? How does continuing human modification of ecosystems affect trophic cascades? And is it possible to apply trophic cascade science effectively to areas outside parks and reserves? These have emerged as key questions to be answered in future research. At present, we can draw only preliminary conclusions based on fragmentary evidence.

Whether ecosystem impacts caused by large carnivore removal can predictably be mitigated or reversed with large carnivore reintroductions remains to be proven, although initial responses to wolf reintroductions in Yellowstone are promising. For example, the diminished stature and density of willows after the extirpation of wolves in the upper Gallatin winter range of Wyoming (Patten 1968; Lovaas 1970; Figure 9.7) began to change when wolves recolonized the area in 1996, after nearly 70 years of absence. Increased heights of young willows began to occur as early as 1999 at sites associated with high predation risk (Ripple and Beschta 2004b; also see Chapter 14, this volume). By 2003, it was difficult to discern a difference between willow height inside and outside an enclosure (Ripple and Beschta 2004b) (Figure 9.7).

Recent studies in Yellowstone's northern range have similarly documented the recovery of woody browse species after wolf reintroduction. Willow, cottonwood, and aspen have begun growing taller in areas of high predation risk. However, heavy browsing by an expanding bison population may be a major factor limiting recovery, especially along main valley bottoms. To date, the release of woody browse species has been spatially patchy and has occurred mostly in riparian zones (Ripple and Beschta 2003, 2004a, 2006b, 2007b; Beyer et al. 2007; Beschta and Ripple 2007a). The extent to which the improving recruitment of these species will continue and perhaps usher in a broader recovery of riparian and upland plant communities is yet to be determined (Fortin et al. 2005).

Earlier we indicated that the removal of carnivores appears to have resulted in hyperabundant deer populations with subsequent impacts on biodiversity and ecosystems. Policymakers can use an understanding of trophic cascades to analyze the pros and cons of carnivore reintroductions, recolonizations, and the management of large carnivores and deer in boreal and temperate ecosystems around the globe. Where large carnivore reintroductions are impractical, forest managers and others will be able to use trophic cascades science within an adaptive management framework. Deer hyperabundance is only one, but perhaps the most obvious, consequence of large predator loss. Others include deer behavioral changes, mesopredator release, negative indirect effects on small vertebrates, changes in the composition or structure of plant communities, altered

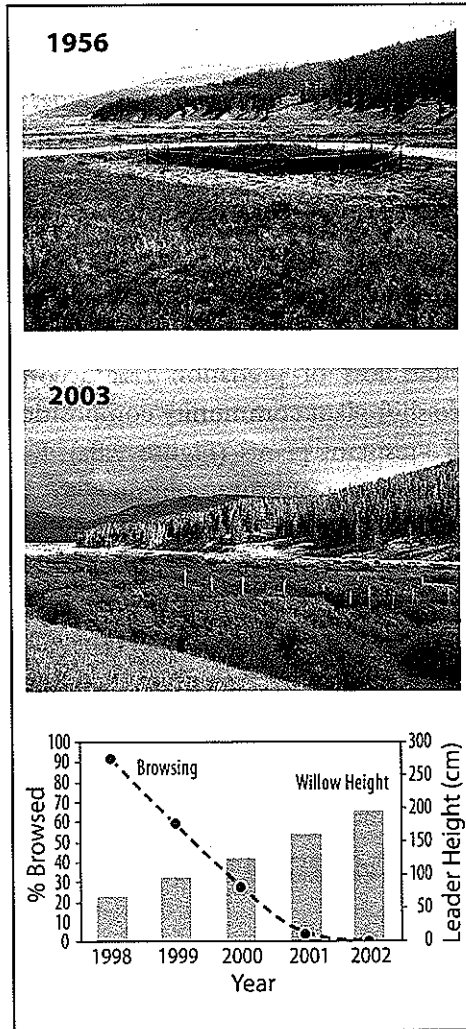


Figure 9.7. Willow suppression outside the Snowflake enclosure in 1956 (upper photo) during the mid-1920s to mid-1990s period of wolf absence and in 2003 (lower photo) after the 1995–1996 reintroduction of wolves. The enclosure was constructed in 1945 along the Gallatin River in the upper Gallatin elk winter range. The graph shows decreased browsing (dashed line) and increased mean willow height (bars) outside the enclosure from 1998 to 2002, after wolves were reintroduced.

hydrologic interactions in riverine systems, and facilitation of the invasion of exotic plants. In the face of so many deleterious consequences of predator loss, there is no simple solution. Simply liberalizing hunting regulations will not suffice to mitigate or reverse so many adverse trends, including the loss of natural predator–prey behavioral dynamics (Berger 2005; Chapter 14, this volume).

CONCLUSIONS

Strong top-down forcing by apex predators appears to be widespread, if not universal, in intact boreal and temperate ecosystems. This is the consistent conclusion of numerous accounts from Asia, Oceania, Europe, and North America. Like Aldo Leopold more than 60 years ago, we found no evidence that deer populations ever irrupt in the presence of intact wolf and bear populations (i.e., a tritrophic cascade). Wherever deer have been released from historic predation pressure (truncated trophic cascade), we observe the same general pattern: high population densities and loss of predation risk accompanied by intensive browsing that begins to shift plant community composition toward domination by browse-tolerant or -resistant plants (Figure 9.8a). Even after an irruptive peak, persistently high foraging pressure continues to drive changes in plant community composition. Over time, the ecological integrity of terrestrial eco-

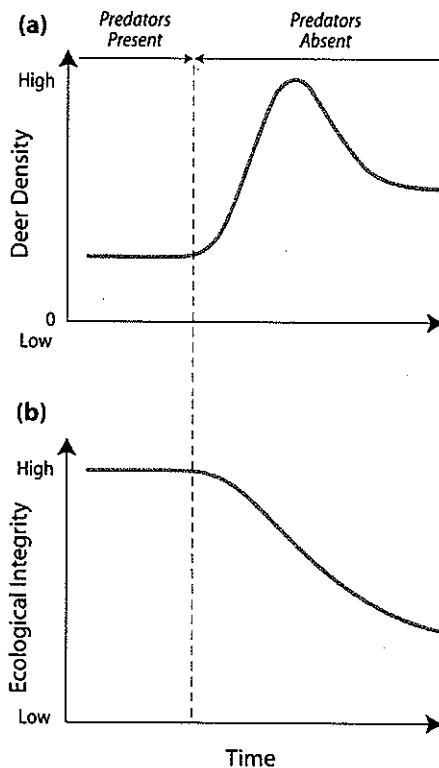


Figure 9.8. Numerical response of deer after the removal of large carnivores (a) and the consequent loss of ecological integrity with increased browsing pressure (b).

systems (Woodley et al. 1993), including native plant communities and wildlife species dependent on them, is invariably affected (Figure 9.8b).

In forested ecosystems, declining species diversity first becomes apparent in understory vegetation, as less palatable ferns or grasses crowd out more palatable herbaceous dicots and inhibit the establishment of tree seedlings. Suppressed tree recruitment opens gaps in the age structure of palatable shrub and tree species, possibly hindering recovery, even when a natural predation regime is restored. With continued intensive browsing, plant communities shift toward an alternative stable state composed of species resistant or resilient to herbivore pressure (see Chapter 10, this volume). Decreased standing biomass and decreased diversity of native species, in turn, may trigger additional ecosystem effects, such as increased soil and streambank erosion, altered terrestrial and aquatic food webs, and changes in nutrient cycling (see Chapter 12, this volume). Thus, the removal or significant reduction of large predators sets in motion a chain of events that initiates a downward spiral toward ecosystem simplification. Although complete loss of forest ecosystems is a possible though still unproven endpoint (Chapter 8, this volume), preventing or reversing the impacts of large herbivores so that diverse native plant communities and dependent wildlife can thrive represents a daunting but pressing challenge for the scientific community and society as a whole.

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