Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems?

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*We investigated how large carnivores, herbivores, and plants may be linked to the maintenance of native species biodiversity through trophic cascades. The extirpation of wolves (*Canis lupus*) from Yellowstone National Park in the mid-1920s and their reintroduction in 1995 provided the opportunity to examine the cascading effects of carnivore–herbivore interactions on woody browse species, as well as ecological responses involving riparian functions, beaver (*Castor canadensis*) populations, and general food webs. Our results indicate that predation risk may have profound effects on the structure of ecosystems and is an important constituent of native biodiversity. Our conclusions are based on theory involving trophic cascades, predation risk, and optimal foraging; on the research literature; and on our own recent studies in Yellowstone National Park. Additional research is needed to understand how the lethal effects of predation interact with its nonlethal effects to structure ecosystems.*

Keywords: wolves, ungulates, woody browse species, trophic cascades, predation risk

The role of predation is of major importance to conservationists as the ranges of large carnivores continue to collapse around the world. In North America, for example, the gray wolf (*Canis lupus*) and the grizzly bear (*Ursus arctos*) have respectively lost 53% and 42% of their historic range, with nearly complete extirpation in the contiguous 48 United States (Laliberte and Ripple 2004). Reintroduction of these and other large carnivores is the subject of intense scientific and political debate, as growing evidence points to the importance of conserving these animals because they have cascading effects on lower trophic levels. Recent research has shown how reintroduced predators such as wolves can influence herbivore prey communities (ungulates) through direct predation, provide a year-round source of food for scavengers, and reduce populations of mesocarnivores such as coyotes (*Canis latrans*) (Smith et al. 2003). In addition, vegetation communities can be profoundly altered by herbivores when top predators are removed from ecosystems, as a result of effects that cascade through successively lower trophic levels (Estes et al. 2001). The absence of highly interactive carnivore species such as wolves can thus lead to simplified or degraded ecosystems (Soulé et al. 2003). A similar point was made more than 50 years ago by Aldo Leopold (1949): "Since then I have lived to see state after state extirpate its wolves.... I have seen every edible bush and seedling browsed, first to anemic desuetude, and then to death" (p. 139).

Increased ungulate herbivory can affect vegetation structure, succession, productivity, species composition, and diversity as well as habitat quality for other fauna. Although the topic remains contentious, a substantial body of evidence indicates that predation by top carnivores is pivotal in the maintenance of biodiversity. Most studies of these carnivores have emphasized their lethal effects (Terborgh et al. 1999). Here our focus is on how nonlethal consequences of predation (predation risk) affect the structure and function of ecosystems. The objectives of this article are twofold: (1) to provide a brief synthesis of potential ecosystem responses to predation risk in a three-level trophic cascade involving large carnivores (primarily wolves), ungulates, and vegetation; and (2) to present research results that center on wolves, elk (*Cervus elaphus*), and woody browse species in the northern range of Yellowstone National Park (YNP).

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Trophic cascades

A trophic cascade is the "progression of indirect effects by predators across successively lower trophic levels" (Estes et al. 2001). In terrestrial ecosystems, top-down and bottom-up effects can occur simultaneously, although their relative strength varies, and interactions among trophic levels can be complex. Here we study top-down processes and associated trophic interactions that potentially have broad ecosystem effects. Although our main purpose is to explore nonlethal effects on ecosystems, we first describe several studies that emphasize the importance of cascading lethal effects.

Predators obviously can influence the size of prey species populations through direct mortality, which, in turn, can influence total foraging pressure on specific plant species or entire plant communities. For example, at the continental scale, Messier (1994) examined 27 studies of wolf–moose (*Alces alces*) interactions and generally found that wolf predation limited moose numbers to low densities (< 0.1 to 1.3 moose per square kilometer [km^2], excluding Isle Royale studies), which resulted in low browsing levels in northern North America, especially in areas where wolves and bears both prey on moose. Comparing total deer (family Cervidae) biomass in areas of North America with and without wolves, Crête (1999) suggested that the extirpation of wolves and other predators has resulted in unprecedentedly high browsing pressure on plants in areas of the continent where wolves have disappeared.

On a smaller scale, islands provide settings for studying predator–prey population dynamics. For example, McLaren and Peterson (1994) studied relationships between wolves, moose, and balsam fir (*Abies balsamea*) in the food chain on Michigan's Isle Royale. As a result of suppression by moose herbivory, young balsam fir on Isle Royale showed depressed growth rates when wolves were rare and moose densities were high. McLaren and Peterson concluded that the Isle Royale food chain appeared to be dominated by top-down control in which predation determined herbivore density through direct mortality and hence affected plant growth rates. Terborgh and colleagues (2001) studied forested hilltops in Venezuela that were isolated by the impounded water of a large reservoir. When predators disappeared from the islands, the number of herbivores increased, and the reproduction of canopy trees was suppressed because of increased herbivory in a manner consistent with a top-down theory. On the islands without predators, Terborgh and colleagues found few species of saplings represented because of a lack of recruitment, even though many more species of trees made up the overstory.

Changes in prey behavior due to the presence of predators are referred to as nonlethal effects or predation risk effects (Lima 1998). These behavioral changes reflect the need for herbivores to balance demands for food and safety, as described by optimal foraging theory (MacArthur and Pianka 1966). They include changes in herbivores' use of space (habitat preferences, foraging patterns within a given habitat, or both) caused by fear of predation (Lima and Dill 1990). Such behaviorally mediated trophic cascades set the foundation for an "ecology of fear" concept (Brown et al. 1999) and provide the basis for this study. Ecologists are now beginning to appreciate how predators can affect prey species' behavior, which in turn can influence other elements of the food web and produce effects of the same order of magnitude as those resulting from changes in predator or prey populations (Werner and Peacor 2003). Interestingly, Schmitz and colleagues (1997) indicate that the effects of predators on the behavior of prey species may be more important than direct mortality in shaping patterns of herbivory.

Predation risk can also have population consequences for prey by increasing mortality, according to the "predation-sensitive food" hypothesis (Sinclair and Arcese 1995). This hypothesis states that predation risk and forage availability jointly limit prey population size, because as food becomes more limiting, prey take greater risks to forage and are more likely to be killed by predators as they occupy riskier sites. Wolves have been largely absent from most of the United States for many decades; hence, little information exists on how adaptive shifts in ungulate behavior caused by the absence or presence of wolves might be reflected in the composition and structure of plant communities.

Prey and plant refugia. Prey refugia are areas occupied by prey that potentially minimize their rate of encounter with predators (Taylor 1984). For example, in a wolf–ungulate system, ungulates may seek refuge by migrating to areas outside the core territories of wolves (migration) or survive longer outside the wolves' core use areas (mortality) (Mech 1977). The relative contributions of migration versus mortality in these ecosystems remain unclear. However, both of these processes can result in low populations of ungulates in the wolves' core use areas and travel corridors, thus creating potential "plant refugia" by lowering herbivory in areas with high wolf densities (Ripple et al. 2001).

Predation risk effects involving wolves and elk were reflected in aspen (*Populus tremuloides*) growth in Jasper National Park. White and colleagues (1998) reported new aspen growth (trees 3 to 5 meters [m] tall) following the recolonization of wolves in the park, with particularly vigorous regeneration in areas of high predation risk (i.e., near wolf trails). The population dynamics of moose in the presence and absence of wolves was studied in Quebec by Crête and Manseau (1996). They found moose densities seven times greater in a region without wolves compared with the moose–wolf region. In Grand Teton National Park, Berger and colleagues (2001) found that the loss of both wolves and grizzly bears allowed an increase in moose density within the park, followed by an increase in moose herbivory on willows (*Salix* spp.).

Historically, aboriginal human hunters in North America affected the distribution of ungulate species (Kay 1994). Laliberte and Ripple (2003) used the journals of Lewis and Clark to assess the influence of aboriginal humans on wildlife distribution and abundance. They found that areas with greater human population density had lower species

diversity and abundance of both large carnivores and ungulates. In today's ecosystems, in which humans have eliminated large carnivores, predation risk effects may occur because of human sport hunting; both prey and plant refugia have been documented where elk are hunted by humans. For example, in Montana, St. John (1995) concluded that elk adjusted their foraging behavior by browsing far from roads to avoid human contact and possible predation. As a result, aspen stands within 500 m of roads were browsed by elk less than stands farther away. In Colorado, McCain and colleagues (2003) found that aspen was heavily browsed and used year-round by elk on land where sport hunting was excluded. In surrounding national forest land where hunting was allowed, aspen stands were minimally browsed. In national parks where both recreational hunting and large carnivores have been removed, dramatic changes in mammal and plant populations have been described (White et al. 1998, Soulé et al. 2003).

Terrain fear factor. The "terrain fear factor" (Ripple and Beschta 2003) represents a conceptual model for assessing the relative predation risk effects associated with encounter situations. This concept indicates that prey species will alter their use of space and their foraging patterns according to the features of the terrain and the extent to which these features affect risk of predation (e.g., avoid sites with high predation risk; forage or browse less intensively at high-risk sites). On landscapes with both open and closed habitat structure, ungulates may use a strategy of hiding in forest cover to lower predator encounter rates, or they may seek open terrain to see predators from afar (Kie 1999). In the latter scenario, the relative level of predation risk at a given site is influenced both by the probability of a prey animal detecting a predator (i.e., visibility) and by the probability of the prey escaping if attacked. For example, Risenhoover and Bailey (1985) found that bighorn sheep (*Ovis canadensis*) preferred open habitats and avoided habitats in which vegetation obstructed visibility. When sheep occasionally used high-risk habitats with poor visibility, they moved more while foraging, and forage intake per step was lower than for habitats with good visibility. Even when high-quality forage occurred at low elevations, Festa-Bianchet (1988) found that pregnant bighorn sheep moved away from predators to higher elevations with low-quality forage.

Altendorf and colleagues (2001) concluded that mule deer (*Odocoileus hemionus*) responded to predation risk by biasing their feeding efforts at the scale of both microhabitats and habitats; the perceived predation risk was lower in open areas than in forested areas. This matches well with the findings of Kunkel and Pletscher (2001), who found that wolves were most successful when they could closely approach ungulates without detection and that the element of surprise appeared to be an important factor in their predation success. Kolter and colleagues (1994) suggested that ibex (*Capra ibex*) reduce their predation risk by foraging most often near "escape terrain" of extremely steep slopes or cliffs, which are difficult or impossible for wolves and other predators to negotiate. Caribou (*Rangifer tarandus*) move to higher elevations to increase the distance between themselves and wolves traveling in valley bottoms (Bergerud and Page 1987).

All of the behavior changes identified above have the potential to influence plant composition and structure by creating local plant refugia at sites whose terrain and landscape characteristics result in high levels of predation risk. These refugia typically have a lower percentage of plants browsed or a smaller amount of the current year's growth removed by ungulates than low-risk sites. Furthermore, since factors affecting predation risk probably occur at specific sites, habitat patches, and other terrain features across larger landscapes, ungulates most likely assess predation risk at multiple spatial scales (Kie 1999, Kunkel and Pletscher 2001).

Predation risk in a dynamic environment. Environmental variables that may influence the degree of predation risk include winter weather, wildfire, and the depth and spatial distribution of snowpacks. Snowpack conditions can greatly influence ungulates' access to vegetation (both herbaceous and woody species) and thus their starvation rates. Variations in snow depth can also affect the ability of ungulates to escape predators (Crête and Manseau 1996). For example, wolves have been found to have higher ungulate kill rates when snow is deep compared with times when snow is shallow (Huggard 1993, Smith et al. 2003). Similarly, winter snowpack accumulation can affect the relationship between wolves, moose, and vegetation. In years that produced deep snow cover, moose predation increased and browsing on firs decreased, affecting both plant litter production and nutrient dynamics (Post et al. 1999). Large snowpack accumulations in broken terrain may preclude elk foraging and affect herd distributions, whereas more open landscapes offer opportunities for snow to melt or blow away from foraging areas. Such open areas also offer good visibility and provide escape terrain with little snow to slow ungulates fleeing from predators. In mountainous terrain, winters with little snowfall may allow ungulates to remain at higher elevations, thus resulting in reduced levels of browsing on woody species in valley bottoms. Conversely, high-snowfall winters are likely to increase browsing pressure on low-elevation plant communities.

When wildfire resets stand dynamics of upland plant communities (e.g., aspen), combined changes in visibility and escape potential are also likely to occur. For example, fire typically stimulates prolific aspen suckering and the growth of dense aspen thickets, reducing visibility and browsing rates and increasing predation risk, and thus promoting even more aspen growth and less visibility (Ripple and Larsen 2000, White et al. 2003). When fire leaves behind coarse woody debris on the ground, predation risk effects are likely to be more pronounced if the debris serves as an escape impediment (e.g., jackstrawed trees [trees that have fallen in tangled heaps]). Thus, while both severe winter weather and wildfire can directly influence ungulate survival through increased or decreased forage availability, these events also

shift the relative importance of predation risk in affecting local and landscape-scale herbivory. Because environmental factors related to predation risk are episodic, efforts at modeling future ecosystem responses to predator–prey interactions are likely to remain imprecise. However, in the long term, relatively high ungulate populations may be reduced to lower densities through periodic die-offs caused by lack of forage (associated with deep snowpacks or extensive wildfire) in combination with the lethal effects of predation and hunting (NRC 2002a, Smith et al. 2003).

Ecosystem responses. Ecosystem responses to trophic cascades can be many and complex (Estes 1996, Pace et al. 1999), but for simplicity we focus on riparian functions and on beaver (*Castor canadensis*) and bird populations. We acknowledge that trophic cascades can affect many other aspects of ecosystem structure and function, both abiotic and biotic, including habitat for numerous species of vertebrates and invertebrates, food web interactions, and nutrient cycling (Rooney and Waller 2003).

Although riparian systems typically occupy a small proportion of most landscapes, they have important ecological functions that affect a wide range of aquatic and terrestrial organisms as well as hydrologic and geomorphic processes of riverine systems. For example, riparian plant communities provide root strength for stabilizing stream banks and hydraulic roughness during overbank flows, maintain hydrologic connectivity between streams and floodplains, sustain carbon and nutrient cycling, moderate the temperature of riparian and aquatic areas, and offer habitat structure and food web support (NRC 2002b). Thus, where riparian systems are heavily altered by excessive herbivory, as in periods of wolf extirpation, the ecological impacts on these systems and their ecological functions can be severe.

Beaver play important roles in riparian and aquatic ecosystems by altering hydrology, channel geomorphology, biochemical pathways, and productivity (Naiman et al. 1986). Beaver dams flood topographic depressions and floodplains, creating more habitat for aspen and willow; hence, beaver can control to some degree the amount of surface water available. Beaver can also increase plant, vertebrate, and invertebrate diversity and biomass and alter the successional dynamics of riparian communities (Naiman et al. 1988, Pollock et al. 1995). The occurrence of predators such as wolves can have direct consequences for beaver populations, since wolves have been shown to frequent riparian areas, travel along stream corridors, and prey on beaver (Allen 1979).

If the presence or absence of wolves in a riparian area has important effects on ungulate herbivory, then these carnivores may represent an indirect control on beaver populations. With wolves present, ungulates may avoid some riparian areas (Ripple and Larsen 2000, Ripple and Beschta 2003), thus reducing herbivory on woody browse species (e.g., aspen, willow, cottonwood) and sustaining the long-term recruitment of these species as well as providing food for beaver. Furthermore, risk-sensitive behavior by ungulates may contribute to relatively high levels of aspen, willow, or cottonwood recruitment in portions of a riparian zone where the capability of ungulates to detect carnivores and escape from them is low (e.g., tributary junctions, mid-channel islands, point bars, areas adjacent to high terraces or steep banks, deep snow) (Ripple and Beschta 2003). Without wolves in the ecosystem, reduced predation risk may allow ungulate herbivory to increase. Where such herbivory is sufficiently severe and sustained, it may ultimately cause the loss of woody browse species on which various riparian functions and beaver depend.

Researchers have recently made connections between the loss of large carnivores and decreases in avian populations. The local extinction of grizzly bears and wolves in Grand Teton National Park caused an increase in herbivory on willow by moose and ultimately decreased the diversity of Neotropical migrant birds (Berger et al. 2001). Avian species richness and abundance were found to be inversely correlated with moose abundance for sites in and near the park. In the absence of large carnivores, mesocarnivore release (i.e., an overabundance of small predators) has been implicated in the decline of bird and small vertebrate populations throughout North America (Crooks and Soulé 1999).

The Yellowstone experiment

In the discussion below of recent research results from YNP, we describe the northern winter range ecosystem, historical predator–prey–vegetation dynamics, and changes in the northern range environment since wolf reintroduction in 1995. Not only is the northern range a sufficiently large ecosystem for assessing trophic cascade effects, the role of elk relative to woody browse species has been a topic of concern over many decades.

Northern winter range. The northern winter range comprises more than 1500 km^2 of mountainous terrain, of which approximately two-thirds occurs within the northeastern portion of YNP in Wyoming (NRC 2002a). The remainder lies immediately north of the park and consists of various private lands and Gallatin National Forest lands in Montana (Lemke et al. 1998). Nearly 90% of the winter range within YNP lies between 1500 and 2400 m in elevation, with the remainder at elevations above 2400 m (Houston 1982). The northern winter range typically has long, cold winters and short, cool summers; annual precipitation varies from about 30 centimeters (cm) at lower elevations to 100 cm at higher elevations. Snowpack water equivalent on 1 April averages only 7 cm at the Lamar Ranger Station (1980 m elevation), increasing to 50 cm or more at higher elevations; snowpack depths can vary considerably from year to year. Much of the winter range is shrub–steppe, with patches of intermixed Douglas fir (*Pseudotsuga menziesii*) and aspen. Multiple species of willow, cottonwood, and other woody browse species are common within riparian zones. Seven species of ungulates—elk, bison (*Bison bison*), mule deer, white-tailed deer (*Odocoileus virginianus*), moose, pronghorn antelope

Table 1. Approximate animal densities for the northern range of Yellowstone National Park (YNP).

Species	Density[a]
Carnivores	
Grizzly bear (*Ursus arctos*)	Unknown
Black bear (*Ursus americanus*)	Unknown
Cougar (*Felis concolor*)	< 20
Gray wolf (*Canis lupus*)	50
Coyote (*Canis latrans*)	200–250
Ungulates[b]	
Moose (*Alces alces*)	< 0.05
Bighorn sheep (*Ovis canadensis*)	0.10–0.14
Pronghorn antelope (*Antilocapra americana*)	0.15
Bison (*Bison bison*)	0.4–0.5
Mule deer (*Odocoileus hemionus*)	1.3–2.0
Elk (*Cervus elaphus*)	8–10

a. Number per 1000 km^2 for carnivores, per km^2 for ungulates.
b. White-tailed deer (*Odocoileus virginianus*) have been infrequently observed in Yellowstone's northern range, because this habitat is at the "extreme upper limit of marginal winter range" for this species (YNP 1997).
Source: Adapted from Smith and colleagues (2003), except for pronghorn antelope, which was adapted from YNP (1997).

(*Antilocapra americana*), and bighorn sheep—are found in northeastern YNP, along with gray wolves, cougars (*Felis concolor*), grizzly bears, black bears (*Ursus americanus*), and additional smaller predators (table 1).

Yellowstone from the 1800s to 1995. Relatively little is known about the occurrence of carnivores and ungulates in northwestern Wyoming in the early 1800s or the effects of hunting and fire use by Native Americans. Even with the advent of Euro-American beaver trappers in the mid-1800s, little information about the biota of the northern range was systematically recorded. Although YNP was established in 1872, uncontrolled market hunting inside and adjacent to the park had significant effects on both carnivore and ungulate populations in the early years of park administration. To help curtail impacts on wildlife and other resources, in 1886 the US Army assumed responsibility for protecting resources within the park. Ungulates, bears, and beaver were generally protected during the period of army administration, which ended in 1918; however, predators other than bears were typically killed.

The early 1900s marked an exceptionally important period in the ecological ledger of YNP's northern range. When the National Park Service (NPS) assumed management responsibility in 1918, carnivores other than bears continued to be hunted. For example, recorded kills included 121 mountain lions from 1904 through 1925, 136 wolves from 1914 through 1926, and 4350 coyotes from 1907 through 1935 (Schullery and Whittlesey 1992). This effort ultimately resulted in the extirpation of wolves in 1926 (figure 1a).

Before 1920, elk populations were probably increasing, owing to protection efforts by the US Army and the NPS. Although northern range elk populations of more than 25,000 animals (17 elk per square kilometer) were reported in the early 1900s (Barmore 2003), the accuracy of these estimates and the role of winter die-offs before the mid-1920s may never be known (Houston 1982). The annual census of elk on the winter range began in the mid-1920s (figure 1b) and has

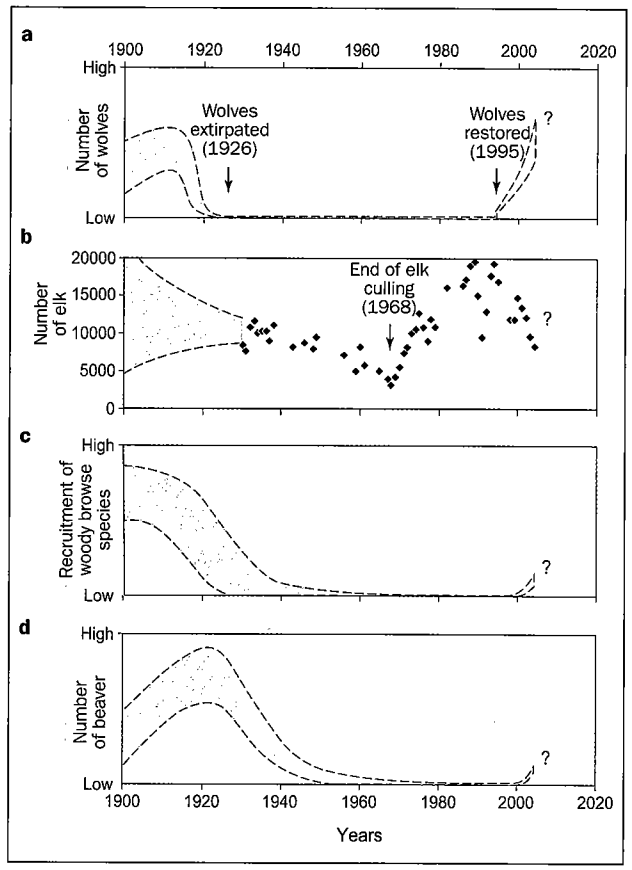

Figure 1. Historical trends for the northern range of Yellowstone National Park since 1900: (a) relative numbers of wolves (Weaver 1978, Smith et al. 2003); (b) annual elk numbers (indicated with diamond shapes) for the northern range herd (Houston 1982, YNP 1997, Barmore 2003, Smith et al. 2003); (c) relative recruitment of woody browse species (Barmore 2003, Beschta 2003, Larsen and Ripple 2003); and (d) relative numbers of beaver (Warren 1926, Jonas 1955, Kay 1990, Smith et al. 2003). The width of the gray tone represents the uncertainty of animal or plant numbers over the period of record, based on the information for each species in the literature citations. Elk populations shown in (b) were not censused during the winters of 1996/1997 and 1997/1998; however, mortality due to winter weather, and not wolf predation, is thought to be the primary reason for the general decrease in elk numbers following the winters of 1996/1997 and 1997/1998. The general increase in beaver from about 1900 to 1920 is thought to be a recovery of depressed populations following heavy trapping pressure in the late 1800s. The increase in beaver also occurred at a time when predators were increasingly being removed from the park.

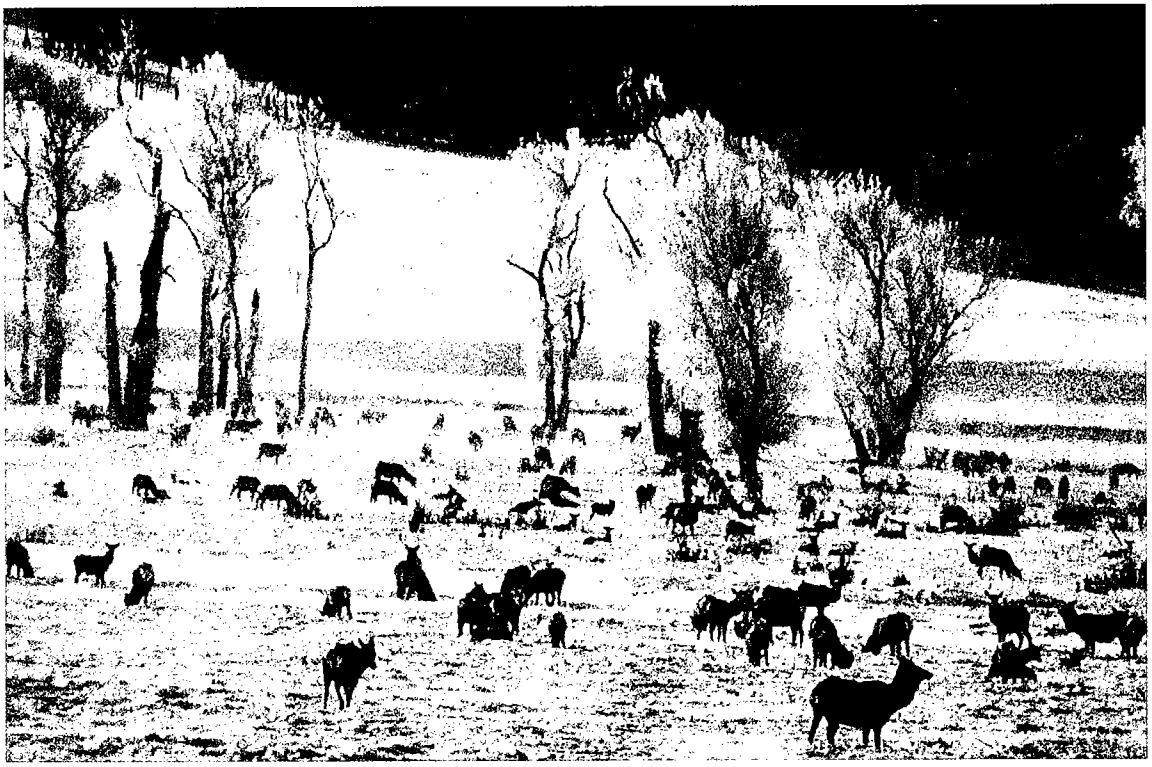

Figure 2. Elk browsing among cottonwood trees in the wintertime along the Lamar River in the northern range of Yellowstone National Park during the period when wolves had been extirpated. Note the lack of recruitment of small and intermediate-sized cottonwood trees that has occurred over many decades and the general lack of vigilance indicated by the elk. Photograph: Yellowstone National Park.

continued until the present, with data missing for some years. With the removal of predation and associated predation risk effects following the extirpation of wolves, elk in the northern range had a significant impact on the recruitment of deciduous woody species. As a consequence, recruitment of upland aspen and riparian cottonwood soon crashed (figure 1c). This loss of recruitment continued over multiple decades, even though sport hunting of elk occurred each winter when some of the elk left the park, and park administrators deliberately sought to reduce the elk population from the mid-1920s to 1968 (figure 1b).

Ripple and Larsen (2000) evaluated aspen overstory recruitment in YNP over the last 200 years, using increment core data collected in 1997 and 1998 and aspen diameter data collected by Warren (1926). Successful aspen overstory recruitment occurred on the northern range of YNP from the mid-1700s to the 1920s, after which it essentially ceased. They found that aspen recruitment ceased during the same years (1920s) that gray wolves were extirpated from the park. In a later study, Larsen and Ripple (2003) concluded that the lack of recruitment was not correlated with indices of climate.

In a study of cottonwoods in the Lamar Valley portion of the northern range, Beschta (2003) evaluated recruitment over the last two centuries and found reduced recruitment in the 1920s and 1930s, with little cottonwood recruitment after the 1930s. The recruitment gap occurred independently of fire history, flow regimes, or other factors affecting normal stand development. Beschta (2003) concluded that the extirpation of wolves allowed elk to browse highly palatable cottonwood seedlings and suckers unimpeded during winter months and prevented any recruitment from occurring for nearly a half-century (figure 2). An exception to the general lack of cottonwood recruitment in the Lamar Valley occurred adjacent to the Lamar Ranger Station, where elk-culling operations were centered from the 1930s to 1968. Apparently the predation risk from humans at this facility allowed a few young cottonwoods to establish after 1933 and ultimately to grow above the browse level of elk.

The NPS initiated efforts in the mid-1920s to reduce the size of elk herds in the northern range because of concerns about overgrazing; those efforts continued until the late 1960s (YNP 1997). From the 1930s to the early 1950s, the elk population on the northern range generally fluctuated between 8000 and 11,000 animals (5.3 to 7.3 elk per square kilometer). By the 1950s and 1960s, live trapping and shooting of elk by NPS personnel, in combination with sport hunting of animals that seasonally migrated outside of park boundaries, reduced the number of elk to between 4000 and 8000 animals (2.7 to 5.3 elk per square kilometer) (figure 1b). For comparison, White and colleagues (2003) indicate that more than four elk per square kilometer is considered a high density in the Canadian Rockies. Of the nearly 75,000 elk removed from the northern range herd over the period 1926–1968, approximately 36% involved culling operations by the NPS and 74%

Figure 3. Photograph taken in 1900 near Tower Junction on the northern range of Yellowstone National Park, showing evidence of elk browsing on the outer stems of a 3- to 5-meter-tall aspen thicket in the foreground and multiple aspen thickets on a distant hillslope (Meagher and Houston 1998). We hypothesize that dense regeneration after wildfire resulted in high levels of predation risk in the interior of aspen thickets; thus, browsing is evident only along the outer edges of the thicket. Even following the widespread fires of 1988, such aspen thickets are not common on the northern range. Photograph: Yellowstone National Park.

represented hunting kills outside the park. Seasonal sport hunting just outside the park boundary may have caused some elk to remain within the park instead of following former down-valley migrations (Barmore 2003). However, by the late 1960s, when the elk population had been reduced, recruitment of woody browse species did not occur (figure 1c).

Following a cessation of culling efforts in 1969, the elk population began to increase rapidly and eventually attained herd sizes ranging from 12,000 to 18,000 animals (8 to 12 elk per square kilometer) between the late 1970s and the mid-1990s (figure 1b). Although the NPS has generally characterized the post-1968 management period as one of "natural regulation" (NRC 2002a), the gray wolf—a keystone predator—and its associated lethal and nonlethal effects remained absent during this period (until its reintroduction in 1995), thus allowing a continuation of high levels of herbivory on woody browse species.

Various other studies (Houston 1982, Kay 1990, Romme et al. 1995, Meagher and Houston 1998) have noted declines in woody browse species (aspen, willows, and berry-producing shrubs) during the 20th century. Willows represent deciduous woody browse species that are commonly found in riparian areas associated with the streams and rivers of YNP. As with aspen and cottonwood, widespread losses of willows have occurred in northern YNP over the past century (Chadde and Kay 1996, Barmore 2003, Singer et al. 2003). However, much of the evidence of willow loss is based on comparisons of paired historical photographs, often taken widely spaced in time (Meagher and Houston 1998). Whereas increment cores from existing aspen and cottonwood stands provide a convenient means of determining when recruitment declines occurred, similar temporal documentation of loss is not available for willow stands.

Historical photographs provide evidence of young aspen and willow thickets on the northern range of YNP in the early 20th century (Houston 1982, Kay 1990, Meagher and Houston 1998). Houston (1973) attributed the common occurrence of aspen thickets on the northern range in the 1800s and early 1900s to the occurrence of frequent fires. Historically, elk may have avoided the interior of aspen thickets because of predation risk effects resulting from a lack of visibility and increased impediments to escape associated with high stem densities (Ripple and Larsen 2000). Then and now, postfire accumulations of coarse woody debris serve as barriers to browsing as well as impediments to escape (Ripple and Larsen 2001).

Meagher and Houston (1998) commented on the visible effects of preferential ungulate browsing along the edge of aspen thickets (figure 3). This type of risk-sensitive foraging has also been observed for caribou in Alaska, which skirt willow thickets to avoid predation by wolves (Roby 1978). The hypothesis that elk typically browse on the edge of aspen thickets to avoid predation by wolves is also supported by empirical

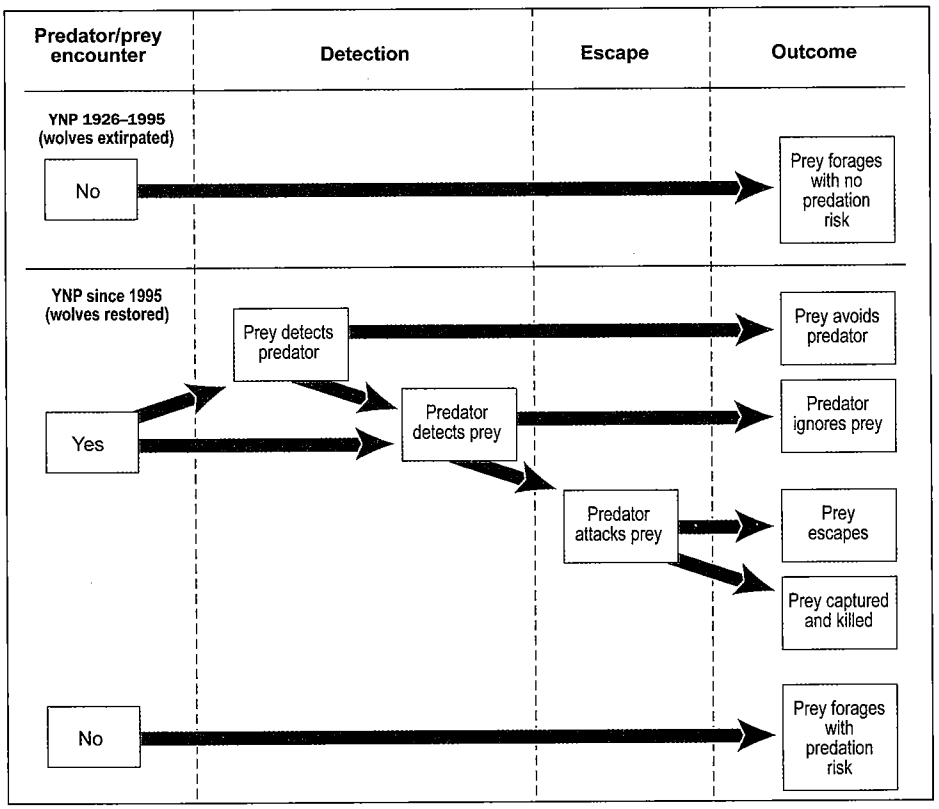

Figure 4. Flow diagram of predator–prey encounters for wolves and elk in Yellowstone National Park (YNP) since 1926. Modified from Lima and Dill (1990).

data from the Canadian Rockies. When elk were under risk of predation by wolves, the number of elk pellets was higher on the edge of aspen thickets than in the interior of aspen patches (White et al. 2003).

Viewed from a perspective of trophic cascades and predation risk, the plant community responses experienced in northeastern YNP over the 20th century are consistent with the expected consequences of extirpating gray wolves. The resultant lack of predation and predation risk allowed elk to forage unimpeded on woody browse species, causing much-simplified plant communities of low stature (figure 4). Without the presence of this keystone predator, the only major limitation to accessing woody browse species each winter was snow depth. Since valley bottoms in the northern range typically have relatively shallow snow depths (Barmore 2003), this situation ensured that woody plants in riparian areas were heavily affected by browsing (figure 2).

Even though coyotes, bears, and cougars were present in the park throughout the 20th century, these predators have had no documented effects on winter patterns of elk herbivory. Furthermore, upland (aspen) and riparian (willow, cottonwood) woody browse species were heavily browsed in spite of long-term NPS efforts to reduce elk numbers. The potential long-term sustainability of many woody browse species in the northern range represents a major ecological concern, since the pattern of unimpeded browsing resulting from a lack of predation risk continued from the 1920s to the mid-1990s. For example, aspen clones that may have existed on the northern range for thousands of years, if lost, cannot be restored except through seeding events, which are rare (Kay 1990, Romme et al. 1995, Larsen and Ripple 2003).The persistent overbrowsing and reduction of woody browse species has also had consequences for other faunal species (figure 5a). With fewer aspen and riparian woody plants, the capability of these plant communities to provide food for avian species is greatly diminished (Dobkin et al. 2002). For beaver, although historical details are lacking, the impacts have apparently been severe. The Yellowstone region abounded in beaver in the early 1800s, but extensive trapping by Euro-Americans began in the 1830s and continued through the latter half of the 19th century. The beaver population apparently began to recover by the early 1900s and attained relatively high numbers by the early 1920s (figure 1d; Warren 1926). However, the number of beaver underwent a major decline in the late 1920s (Schullery and Whittlesey 1992), with only scattered colonies of beaver remaining by the early 1950s (Jonas 1955). Numbers of beaver in the northern range remained low over the next five decades; during the 1980s and early 1990s, beaver were essentially absent from streams of the northern range (Kay 1990, YNP 1997). The loss of beaver populations appears to represent an ecological chain reaction to behaviorally mediated trophic cascades involving elk, following the extirpation of wolves. According to the NPS (1961), the decrease in beaver in the northern range, which began in the

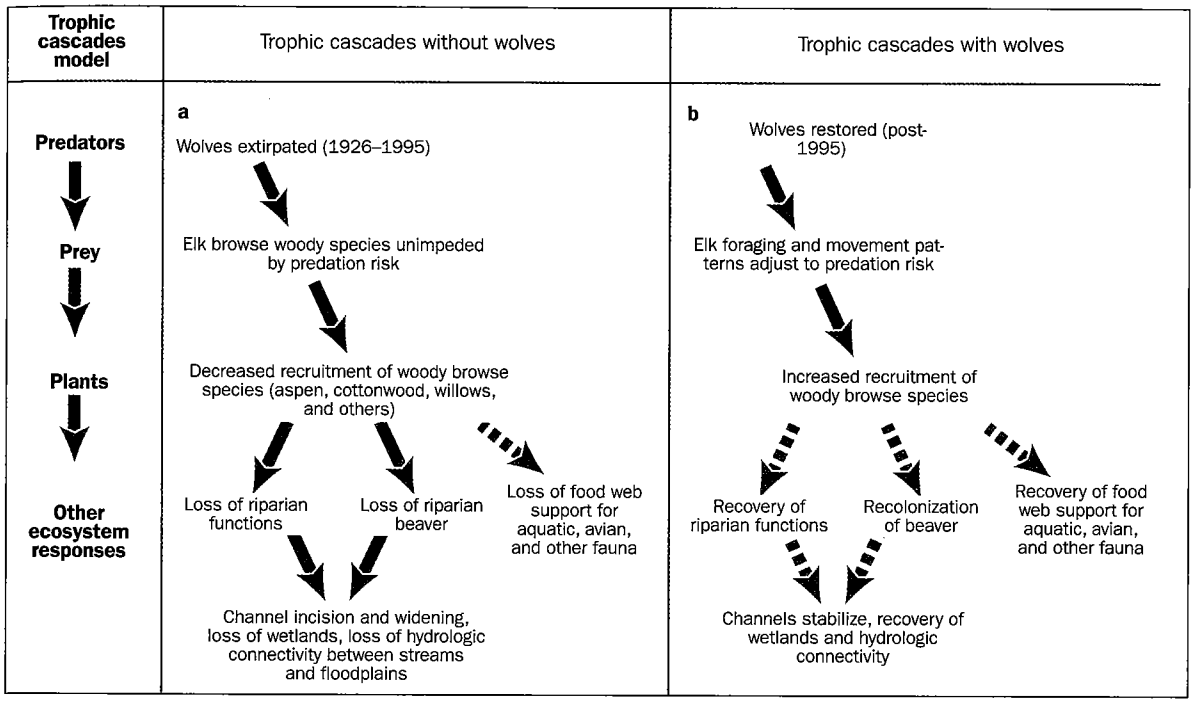

Figure 5. Trophic interactions due to predation risk and selected ecosystem responses to (a) wolf extirpation (1926–1995) and (b) wolf recovery (post-1995) for northern ecosystems of Yellowstone National Park. Solid arrows indicate documented responses; dashed arrows indicate predicted or inferred responses.

late 1920s, resulted from interspecific competition with elk: Beaver would fell the larger stems of aspen, willow, or cottonwood for food and dam material, while elk would consume all new shoots. Thus, unimpeded browsing by elk may have effectively destroyed any food supplies for beaver.

Yellowstone after wolf reintroductions (1995–present). Under the protection of the 1973 federal Endangered Species Act, an experimental population of wolves was reintroduced into YNP during the winter of 1995/1996, following a 70-year period without their presence (figure 1a). Since the reintroduction of 31 wolves into YNP in the mid-1990s, their numbers have steadily increased. By the end of 2001, the population of wolves in Yellowstone's northern range had grown to 77 animals (Smith et al. 2003). Even with the reintroduction of wolves and their subsequent increase in recent years, we are still in the early stages of understanding how their restoration is influencing ungulates, vegetation, riparian functions, or other ecological components in northern Yellowstone (figure 5b).

Following the reintroduction of wolves, Ripple and Beschta (2003) found that predation risk associated with various terrain conditions (and their related fear factors) played a role in the selective release of willow and cottonwood from the browsing pressure caused by elk in the Lamar Valley of northern YNP. In 2001 and 2002, they found willow and young cottonwood plants 2 to 4 m in height, which is in stark contrast with the long-term observations of plants less than 1 m in height during the decades before wolf reintroduction. Willow and cottonwood were found to be subject to less browsing pressure (figure 6) at potentially high-risk sites with limited visibility (i.e., limited opportunities for prey to see approaching wolves) or with terrain features that could impede the escape of prey, such as sites below high terraces or steep cutbanks and near gullies. As an additional indicator of riparian recovery, several new beaver colonies have recently been established on the northern range, a rare occurrence over the last five decades (figure 1d). The number of beaver colonies on the park's northern range increased from one in 1996 to seven in 2003 (YNP files).

Ripple and Beschta (2003) suggested that elk would increasingly forage at sites that allow early detection and successful escape from wolves, since the Lamar Valley has a predominately open habitat structure (figures 3, 4). Had the woody plant communities in the northern range not been so thoroughly simplified and degraded by multiple decades of persistent and unimpeded elk herbivory in the absence of wolves, the differential plant responses to predation risk following wolf reintroductions might not have been readily observed. Conversely, if elk densities in the future are reduced, with concurrent decreases in overall browsing pressure, we envisage that it will be more difficult to detect differential plant responses associated with predation risk. If elk densities become low enough, we expect a more widespread release from browsing of woody plants rather than release only at high-risk sites.

Figure 6. Willow along Blacktail Creek in spring 1996 (left) and summer 2002 (right). Following a 70-year period of wolf extirpation, heavy browsing of willows and conifers is evident in the 1996 photograph. In 2002, after 7 years of wolf recovery, willows show evidence of release from browsing pressure (increases in density and height). Photographs: left, Yellowstone National Park; right, William J. Ripple.

Conclusions

Can predation risk structure ecosystems? Our answer—based on theory involving trophic cascades, predation risk, and optimal foraging, in addition to a developing body of empirical research—is yes. Although some may find the support for this answer equivocal, we find it compelling when all the evidence is combined. Predation risk probably affects ecosystems in both subtle and dramatic ways through various interactions, many of which are unknown. For example, little is known about how elk use scent and sound in conjuction with visual indicators for assessing predation risk. Because many carnivores have been extirpated from their original ranges, there has been little opportunity to study their lethal and nonlethal effects on prey, alone or in combination with episodic abiotic events. Ultimately, researchers and managers need to understand how the interaction of lethal and nonlethal effects structures the ecosystem. In Yellowstone, the role of lethal effects may become increasingly important in the future, as the combined effects of predation by wolves, bears, and hunters, along with periodic severe winter weather events, may ultimately cause lower elk populations.

The concept of trophic cascades provides a basis for understanding, perhaps for the first time, the often conflicting viewpoints regarding interactions between elk (as well as beaver and other fauna) and vegetation in Yellowstone's northern range. Over a period of many decades, the intense ecological and political debate regarding potential overbrowsing effects of elk on the northern range of YNP has almost always centered on numbers of elk (NRC 2002a). In contrast, our assessment of the broader literature and the Yellowstone research indicates that the extirpation of the gray wolf—a keystone predator in this ecosystem—is most likely the overriding cause of the precipitous decline and cessation in the recruitment of aspen, cottonwood, and willow across the northern range. This hiatus in recruitment of woody species is also directly linked to the loss of beaver and the decline in food availability for other faunal species. It is important to note that the loss of recruitment occurred despite long-term variations in winter weather, snowpack, and other climate variables, with or without the occurrence of fire, and independent of efforts by the NPS to control ungulate numbers inside the park (pre-1968) or to let them increase by ceasing control efforts (post-1968).

In terms of future management of the northern range ungulate herds, our assessment suggests that restoration goals should focus on the recovery of natural processes. In the case of Yellowstone, the return of wolves represents an example of active management to recover a lost keystone species. However, passive restoration of other ecosystem processes and components as a result of the combined lethal and nonlethal effects of this restored predator can now play out in ways that we cannot easily predict and perhaps will not fully understand for many decades. In addition to restoring large carnivores such as wolves, it may be important to recover historical ungulate migrations as much as possible, especially in situations where ungulates tend to avoid natural migrations in an effort to lower their risk of predation or other impacts from humans and, as a consequence, reside inside park or reserve boundaries.

Since much of our discussion has focused specifically on the northern range of YNP, we are not sure of the extent to which our conclusions on behaviorally mediated trophic cascades match what has occurred to ungulates, plants, and associated ecosystem responses in other portions of North America where wolves have been extirpated and, in some cases, reintroduced. In the last decade, wolf recovery efforts have been initiated in portions of Montana, Idaho, Arizona, New Mexico, and the upper Midwest. If ecosystem responses similar to those that have occurred historically or that are under way on the northern range are documented in other locations, we may finally understand more fully the observations and concerns of Aldo Leopold from over half a century ago.

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