Exhibit N

Linking Wolves and Plants: Aldo Leopold on Trophic Cascades

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Aldo Leopold, perhaps best known for his revolutionary and poignant essays about nature, was also an eloquent advocate during the 1930s and 1940s of the need to maintain wolves and other large carnivores in forest and range ecosystems. He indicated that their loss set the stage for ungulate irruptions and ecosystem damage throughout many parts of the United States. We have synthesized the historical record on the potential effects of wolf extirpation in the context of recent research. Leopold's work of decades ago provides an important perspective for understanding the influence of large carnivores, via trophic cascades, on the status and functioning of forest and range plant communities. Leopold's personal experiences during an era of extensive biotic changes add richness, credibility, and even intrigue to the view that present-day interactions between ungulates and plants in the United States have been driven to a large degree by the extirpation of wolves and other large carnivores.

Keywords: Aldo Leopold, wolves, ungulates, irruptions, trophic cascades

Wolves (*Canis* spp.), once found in all of the conterminous 48 United States, have been largely absent from their original range for many decades (Mech and Boitani 2003, Musiani and Paquet 2004). However, recent wolf reintroductions and range expansions have increased the need to better understand the potential ecological role of wolves and other large carnivores in forest and rangeland ecosystems (Berger et al. 2001, Mech and Boitani 2003, Smith et al. 2003, Soulé et al. 2003).

When the presence of top trophic-level predators significantly affects herbivores (the next lower trophic level), and this interaction alters or influences vegetation (e.g., species composition, age structure, or spatial distribution), a trophic cascade occurs (Pace et al. 1999). The conceptual foundation for top-down forcing and trophic cascades is rooted in a landmark paper published by Hairston and colleagues (1960). Robert T. Paine, originator of the term "trophic cascades," conducted an early experiment showing that predators have effects that permeate food webs from the top down (Paine 1966). More recently, researchers have indicated that predation by large carnivores, through the progression of effects across successively lower trophic levels, may be crucial for the maintenance of biodiversity (Estes 1996, Terborgh et al. 1999). In addition to the classic top-down linkages of predators to herbivores to plants, many other interaction pathways resulting from predator effects are known (e.g., increased species interactions, improved nutrient cycling, limited mesopredator populations, food web support for scavengers), and far more are possible and even likely (Rooney and Waller 2003, Smith et al. 2003, Soulé et al. 2003, Côté et al. 2004).

Once the most widely distributed carnivores in the continental United States, gray wolves (*Canis lupus*) were largely eradicated during and following Euro-American settlement. However, in the last decade, gray wolves have been reintroduced in portions of the western United States (Idaho, Montana, and Wyoming), and their range is expanding in the upper Great Lakes states (Minnesota, Wisconsin, and Michigan). In addition, the Mexican gray wolf (*C. lupus baileyi*) in New Mexico and an experimental population of red wolves (*Canis rufus*) in North Carolina have been recently reintroduced. Although most research involving wolves and trophic cascades has emphasized ecosystem changes resulting from wolf recolonizations and reintroductions (McLaren and Peterson 1994, White et al. 2003), a few recent studies have described ecosystem impacts that resulted from wolf extirpation in the United States during the early 20th century (Ripple and Larsen 2000, Beschta 2003, Ripple and Beschta 2004a, 2004b). While much of our focus in this article will be on wolves in multipredator systems characteristic of many forest and range

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settings, we recognize that cougars (*Felis concolor*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and wolverines (*Gulo gulo*) may also have a significant influence on ungulate densities.

Given the current expansions of gray wolf ranges in various areas of the United States (figure 1), we have a unique opportunity to reconsider Aldo Leopold's (figure 2) pioneering work on wolves and other predators. We compiled historical records of wolf kill estimates, by year, from the records of the US Department of Agriculture and obtained information on case studies of ungulate irruptions, by year, for these same western states from Leopold and colleagues (1947). These two data sets were used to compare the timing of wolf kills (and ultimate extirpation) with the timing of deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) irruptions to evaluate any temporal patterns in these two variables. Our hope is that a synthesis of the potential cascading effects of wolf extirpation documented by Leopold, within the context of recent research, will provide relevant insights on the reemerging role of wolves in forest ecosystems.

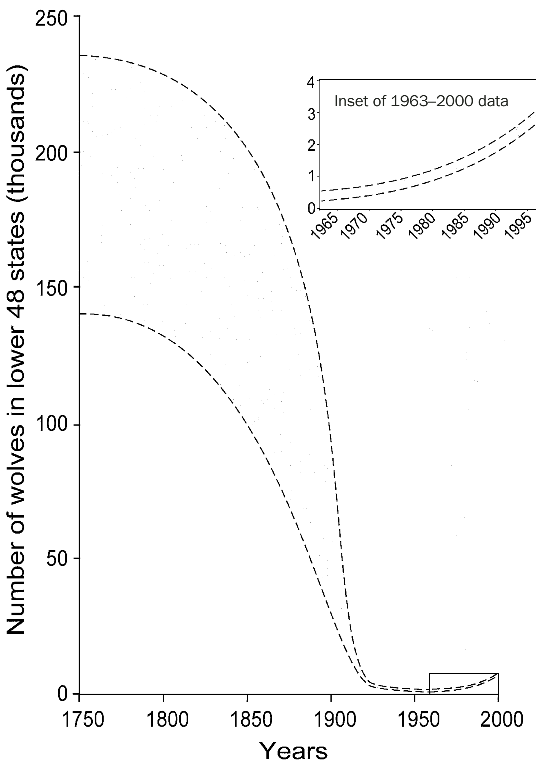

Figure 1. Historical and recent gray wolf population trends in the conterminous 48 United States. The historical population estimate was adapted from prehistoric wolf density estimates made by Hampton (1997), assuming one wolf per 24 square miles (62.1 square kilometers [km^2]), excluding the central Great Plains (4,500,000 km^2), and one wolf per 6 square miles (15.5 km^2) on the central Great Plains (1,800,000 km^2), for the geographic range of the gray wolf (Mech and Boitani 2003, p. 325). This resulted in 72,000 gray wolves in the 48 states excluding the Great Plains, and 116,000 wolves on the Great Plains, for an overall estimate of 188,000 total gray wolves in the 48 states in the year 1750 (the width of the gray band represents ± 25 percent, to account for uncertainty). Gray wolf population estimates from 1963 to 2002 were obtained from Musiani and Paquet (2004).

Early in his professional career, Leopold actively advocated wolf extirpation. At a National Game Conference in 1920, he stated, "It is going to take patience and money to catch the last wolf or lion in New Mexico. But the last one must be caught before the job can be called fully successful. This may sound like a strong statement, but if any of you have lived in the West and see how quickly a piece of country will restock with wolves or lions, you will know what I mean" (Meine 1988, p. 181).

In subsequent years, Leopold studied and observed forest and range ecosystems where wolves had been removed and where they remained. During these latter years, his understanding of wolves and their potential effects on big game production, habitats, and ecosystem conditions changed dramatically. In his widely recognized essay "Thinking Like a Mountain," Leopold (1949) describes how he first began to question his own views after watching a shot female wolf die: "We reached the old wolf in time to watch a fierce green fire dying in her eyes.... I thought that because fewer wolves meant more deer, that no wolves would mean hunter's paradise. But after seeing the green fire die, I sensed that neither the wolf nor the mountain agreed with such a view" (p. 130).

The evolution of Leopold's attitude from "antipredator" to "pro-ecosystem" has been well documented by others (Flader 1974, Meine 1988). In fact, the focus of Flader's (1974) book is the evolution of Leopold's ecological attitude toward wolves, deer, and forests. Although in the 1930s and 1940s Leopold ultimately became a persistent and outspoken advocate of the need to maintain large carnivores in forest and range ecosystems (Estes 2002), his views were perhaps too little and too late, given that wolves, by then, had been functionally extirpated throughout nearly all of the continental United States.

Large carnivores and ungulate irruptions in forest and range ecosystems

In the late 1800s and early 1900s, wolves and other large predators in the western United States were besieged by widespread hunting, trapping, and poisoning efforts. By 1915, the destiny of the wolf in the western United States was sealed when Congress authorized the Bureau of Biological Survey to eliminate the remaining wolves and other predators. As part of this program, federal hunters and trappers systematically killed wolves in western states starting in 1915, functionally extirpating them by the 1930s (figure 3a; Leopold et al. 1947). Ungulate irruptions, primarily of deer, began to occur following the occurrence of wolf extinctions, with most of the western irruptions (80 percent) taking place between 1935 and 1945 (figure 3b).

Scientific interest and concern about predator loss coalesced during the mid-1920s to early 1930s, when several leading mammalogists began to oppose the Bureau of Biological Survey's predator extermination programs. Led by Joseph Grinnell, Joseph Dixon, C. C. Adams, and Adolph and Olaus Murie, these scientists expressed concern about the widespread loss of predators (Dunlap 1988). Their work provided some of the scientific underpinnings Leopold used to develop and champion his visionary hypothesis that the killing of wolves was a predisposing cause of deer and elk irruptions in the United States. Such irruptions ultimately led to overbrowsing of woody species (figure 4a) and subsequent ecosystem damage, such as reduced diversity of flora and fauna, widespread loss of habitat for nongame species, and accelerated soil erosion (Leopold 1937, 1939, 1944, 1949). Leopold formulated his hypothesis from observations, reports, and studies of more than 100 ungulate ranges in various areas of the United States after large carnivores had been suppressed and overbrowsing had ensued (Leopold 1943, Leopold et al. 1947). The conceptual framework Leopold thus created helped develop and refine the then-emerging science of wildlife management.

In the eastern United States, the extirpation of large carnivores and subsequent deer irruptions generally occurred earlier than in the West. For example, Mount Desert Island, Maine, exhibited the earliest recorded irruption in North America, with wolves disappearing between 1863 and 1880 and deer irrupting in 1880 (Leopold et al. 1947). Wolves and cougars disappeared in the Adirondacks between 1882 and 1889, with deer first irrupting in 1895 (Leopold et al. 1947). Other major deer irruptions in the East occurred in the early 20th century in the states of Michigan, New York, Pennsylvania, and Wisconsin (figure 4b), each irruption taking place after the functional extirpation of wolves and cougars (Leopold et al. 1947).

Leopold's thinking about the importance of large carnivores began to crystallize after his 1935 trips to Germany and Mexico. In Germany he gained important insights concerning the role and value of predators when he saw extensive forest damage resulting from overabundant deer populations in predator-free, highly managed forests (Leopold 1936). As an astute naturalist with an exceptionally open and inquiring mind, Leopold also searched for reference conditions representing intact ecosystems. His field trips to the mountains of northern Mexico, where he observed healthy predator–prey–ecosystem relationships (figure 4c), made a profound impression on him. In the Sierra Madre Occidental of Mexico, he noted that wolves and cougars were common and white-tailed deer (*Odocoileus virginianus*) abundant, but not excessive (Leopold 1937). After observing the persistence of large carnivores in Mexico and Canada, and the extirpation of these predators in the United States, Leopold and colleagues (1947) 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

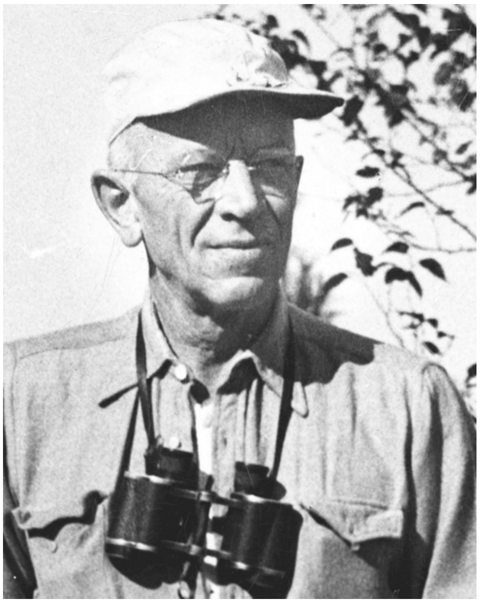

Figure 2. Photograph of Aldo Leopold with his binoculars. Leopold was a both an astute observer of nature in the field and a masterful synthesizer of information and ecological concepts. Photograph courtesy of Robert McCabe, University of Wisconsin Archives, and the Aldo Leopold Foundation.

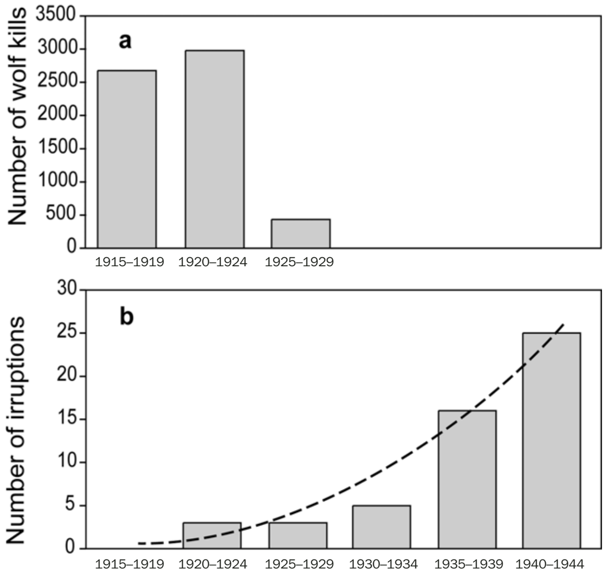

Figure 3. (a) Number of wolf kills by the US Bureau of Biological Survey after 1915 in the western United States and (b) number of deer irruptions in the western United States (1915–1944). Dashed line represents general trend. No wolf kills were reported by the US Bureau of Biological Survey after the 1925–1929 period. Source: (a) annual reports of the US Bureau of Biological Survey and (b) Leopold and colleagues (1947).

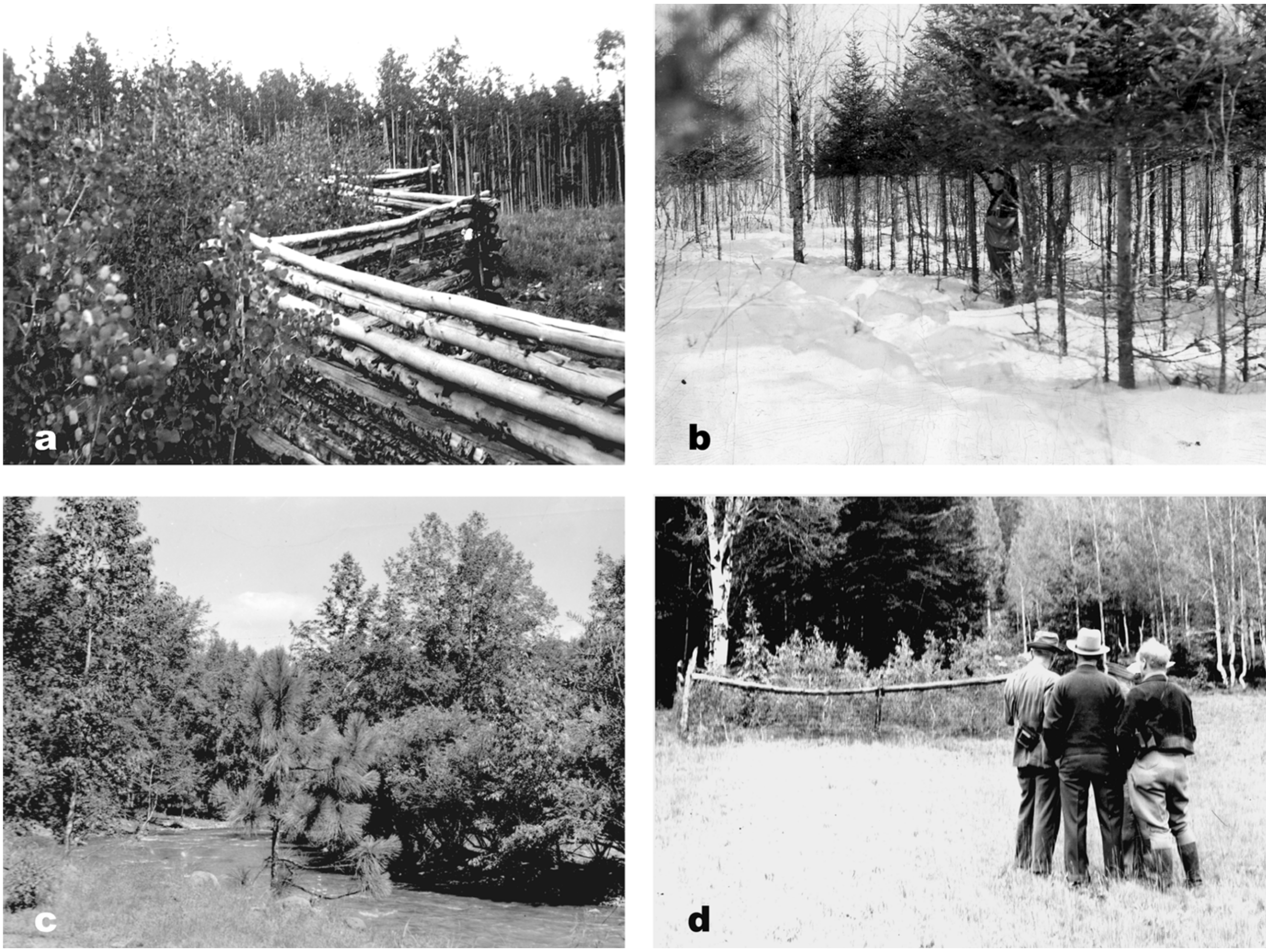

Figure 4. Photographs from Aldo Leopold's collection: (a) Aspen inside and outside a deer-proof fence in the Dixie National Forest, Utah, 1941; (b) "high lining" of balsam fir by deer in Bayfield County, Wisconsin, 1943; (c) flourishing riparian vegetation along the Gavilan River in an area of abundant wolves, Chihuahua, Mexico, 1948; and (d) aspen exclosure on the Kaibab Plateau, Arizona, 1941. Panels a, b, and d show locations with suppressed populations of wolves or cougars, or both. Photographs courtesy of the University of Wisconsin Archives and the Aldo Leopold Foundation.

> 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. (p. 176)

To further investigate Leopold's hypothesis, we considered two case studies of ungulate irruptions in forest ecosystems and their potential linkages to the presence or absence of large carnivores.

Kaibab Plateau, Arizona. One of the most widely publicized examples of an ungulate irruption in the West occurred on the Kaibab Plateau of northern Arizona during the early 20th century (Dunlap 1988). Settlers started grazing sheep and cattle on the Kaibab Plateau in the 1870s, with livestock numbers increasing in the 1880s. Livestock use continued into the early 1900s, but little is known about stocking rates. Between 1906 and 1917, hundreds of mountain lions and the last of the wolves (30 individuals) were reportedly killed (Rasmussen 1941). During this period of predator control, the number of mule deer (*Odocoileus hemionus*) increased dramatically, from approximately 4000 animals in 1906 to many times that number by the mid-1920s (Rasmussen 1941). As a consequence of deer overabundance, aspen, other deciduous woody plants, and conifers were extensively browsed, and range conditions deteriorated (figure 4d).

Leopold (1943) argued that the loss of predators set the stage for an irruption of the Kaibab deer population, followed by a degradation of habitat and an eventual reduction in carrying capacity. This study, considered a classic, was widely reported in early ecology textbooks. More recently, the Kaibab story was deleted from textbooks and alternative hypotheses for deer irruptions were suggested, involving such potentially interacting factors as Native American hunting, livestock grazing, and fire control, among others (Caughley

1970). However, new analyses of aspen tree rings from the Kaibab are consistent with Leopold's hypothesis of extreme deer herbivory following predator removal, as well as the importance of predation in controlling deer populations on the Kaibab (Binkley et al. forthcoming).

Yellowstone National Park, Wyoming. Long-term databases and recent studies in the mountains of northern Yellowstone National Park (YNP) have provided important new perspectives regarding the potential role of wolves in ecosystems. In the late 1800s and early 1900s, elk and other wild ungulates in YNP were generally protected, while wolves experienced the effects of long-term control efforts and were finally extirpated in the mid-1920s (Ripple and Larsen 2000). Following the loss of wolves from YNP, park biologists became concerned about observed impacts of elk browsing on vegetation and soils in the northern winter range. Thus, the Park Service undertook a long-term program of herd reduction that lasted from the mid-1920s until 1968. After 1968, the Park Service curtailed elk culling, and elk numbers rapidly increased from an estimated low of just over 3000 to a high of approximately 19,000 by 1994 (NRC 2002).

During the seven decades of wolf absence, from the 1920s to the mid-1990s, the recruitment of woody browse species (e.g., aspen, willow, cottonwood) quickly ceased, with concurrent impacts on soils, beaver, and other ecosystem conditions (Ripple and Larsen 2000, NRC 2002, Beschta 2003, Ripple and Beschta 2004a). With the removal of wolves, ungulates could browse their winter range largely unimpeded by predation, regardless of climate, fire regimes, or other factors. The removal of this keystone predator effectively eliminated any wolf-driven trophic cascades that had historically influenced elk numbers and foraging patterns, which, in turn, maintained a healthy distribution and structure of deciduous woody plant communities. Results from YNP are consistent with other documented cases of trophic cascades in the Rocky Mountains, involving wolves, moose, willow, and birds in Grand Teton National Park (Berger et al. 2001) and wolves, elk, and aspen in the Canadian Rocky Mountains (White et al. 2003).

Leopold was among the first to suggest that the lack of wolves on the northern range of Yellowstone was the direct reason for vegetation damage resulting from high levels of browsing by elk: "Thus the Yellowstone has lost its wolves and cougars, with the result that elk are ruining the flora, particularly on the winter range" (Leopold 1949, p. 196). As far as we know, this statement, published in *A Sand County Almanac* more than five decades ago, has not been cited in the extensive scientific debate regarding ungulate browsing and grazing impacts in Yellowstone. Conversely, a variety of other hypotheses have been suggested in an attempt to explain the decline of woody vegetation, including climate change or fluctuation, lower water tables, wildfire suppression, chemical defenses of plants, loss of beaver (*Castor canadensis*), Native American influences, changes to the northern range outside the park, ungulate migration patterns, and various combinations of these factors (NRC 2002). However, it now appears that Leopold's original insights provide the most compelling explanation of vegetation impacts, since recent research in Yellowstone has provided strong evidence of trophic cascades through linkages among wolves, elk, and multiple woody browse species (figure 5).

Even earlier, in 1943, YNP superintendent Edmond Rogers considered but rejected the idea of hiring Leopold to do a study of the elk population and potential overgrazing on the park's northern range. Rogers decided against inviting Leopold, believing that the only issue pending was deciding how many elk needed to be shot to protect the northern range ecosystem (Schullery 1997). A year later Leopold (1944) advocated the need for wolves in YNP: "Probably every reasonable ecol-

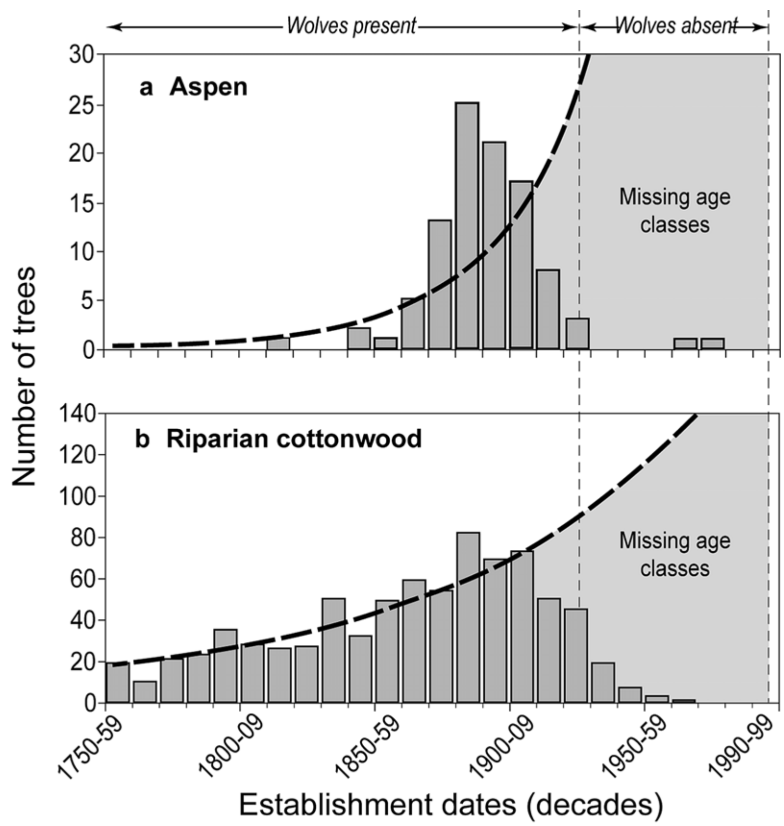

Figure 5. Establishment dates for (a) aspen and (b) riparian cottonwood in the northern elk winter range of Yellowstone National Park, Wyoming, showing loss of recruitment due to unimpeded browsing by elk after the extirpation of wolves. Dashed lines (exponential relationships fitted to the data for the period before wolf extirpation) represent expected patterns of aspen and cottonwood numbers if wolves had remained in the northern Yellowstone ecosystem. Source: Adapted from (a) Larsen and Ripple (2003) and (b) Beschta (2005).

ogist will agree that some of them should lie in the larger national parks and wilderness areas; for instance, the Yellowstone and its adjacent national forests" (p. 929).

With the successful reintroduction of 31 wolves into YNP in the mid-1990s, under the protection of the 1973 federal Endangered Species Act, their numbers have steadily increased; by the end of 2003, the Yellowstone's northern range population of wolves had grown to nearly 100. Following the reintroduction of wolves, top-down trophic cascades have been observed, including altered patterns of ungulate herbivory, declining elk and coyote populations, new recruitment of woody browse species, and increases in the number of active beaver colonies on the northern range (Ripple and Beschta 2003, 2004a, Smith et al. 2003).

Trophic cascades

Leopold was inspired by the work of his British friend and mentor, leading theoretical animal ecologist Charles Elton (1927), in writing his seminal essay "A Biotic View of the Land," which later became part of *A Sand County Almanac* (Leopold 1939). In this essay, Leopold describes a biotic pyramid, composed of layers representing soils, plants, and animal communities, as an energy circuit whereby "each successive layer depends on those below for food and often for other services, and each in turn furnishes food and services to those above." In this essay, he also states that when large predators "are lopped off the cap of the pyramid[,] food chains, for the first time in history, are made shorter rather than longer." While not explicitly using the phrase "trophic cascades," he nevertheless indicates the occurrence of both top-down and bottom-up energy flows in his biotic pyramid.

Nonlethal effects of wolves. In his book *Game Management* (1933), Leopold notes the occurrence of behaviorally mediated trophic cascades. He describes the nonlethal effects of large carnivores on the ungulates of Vancouver Island in Canada as an example of deer reaction to release from predation:

> It is said that a normally distributed herd of deer on Vancouver Island, after the lions and wolves had been killed off for their benefit, suddenly huddled up on a small part of their original range and overgrazed it. Apparently normal depredation had some as yet obscure influence in keeping the deer normally distributed over the range.... The case is cited merely as suggestive of many possible predator influences as yet beyond our vision. (p. 247)

"Perhaps," he suggests, "wolves and cougars originally performed for deer the function of dispersal from congested spots which most species perform for themselves" (Leopold 1943, p. 359).

Decades later, Peek (1980) similarly suggested that large carnivores could influence the distributions of ungulates. Such suggestions have been supported by recent observations of cascading nonlethal effects following the wolf reintroductions into YNP in 1995–1996. Researchers have documented how elk have increased their vigilance (Laundré et al. 2001) and changed their patterns of browsing since wolf reintroduction (Ripple and Beschta 2003). Ecologists now posit that behaviorally mediated trophic cascades may produce effects of the same order of magnitude as those resulting in changes in predator or prey populations (Schmitz et al. 1997, Ripple and Beschta 2004a).

Lethal effects of wolves. While the historic loss of wolves was expected to result in more ungulates, the magnitude of the response in ungulate numbers and impacts to ecosystems was not widely understood or appreciated even within the scientific community. In his review of *The Wolves of North America* (Young and Goldman 1944), Leopold (1944) expresses concern that an important ecosystem response to wolf extirpation had not been discussed:

> Entirely unmentioned in the book is the modern curse of excess deer and elk, which certainly stems, at least in part, from the excessive decimation of wolves and cougars under the aegis of the present authors and of the Fish and Wildlife Service. None of us foresaw this penalty. I personally believed, at least in 1914 when predator control began, that there could not be too much horned game, and that the extirpation of predators was a reasonable price to pay for better big game hunting. Some of us have learned since the tragic error of such a view, and acknowledged our mistake. (p. 929)

Today, the best area for examining wolf–ungulate population dynamics lies north of the conterminous United States, in Canada and Alaska, as large carnivores still abound in much of this northern region. Research since Leopold's time continues to show that ungulate irruptions are extremely rare in ecosystems where wolves coexist with other large carnivores. Studies further show that the coexistence of wolves and bears in Canada and Alaska may prevent the irruptions of ungulate prey populations (Gassaway et al. 1992, Messier 1994). By contrast, wolves moving into Isle Royale were unable, in the absence of other large carnivores, to prevent an overabundance of moose and subsequent vegetation damage (McLaren and Peterson 1994). At the global scale, Flueck (2000) recently reviewed the literature from northern latitudes around the world and found "no reports of repeated deer [cervid] irruptions in unmodified continental environments containing complete large predator and prey communities."

Other ecosystem effects. After a trip to Mexico, Leopold developed a theory regarding the increasingly abundant coyote population in the United States. His observations indicated that coyotes had not invaded the Sierra Madre in Mexico as they had the mountainous areas of the United States. Leopold (1937) wondered if wolves had kept them out:

> There are no coyotes in the mountains, whereas with us there is universal complaint from Alaska to New Mexico that the coyote has invaded the high country to wreak havoc on both game and livestock. I submit for conservationists to ponder the question of whether the wolves have not kept the coyotes out? And whether the presence of a normal complement of predators is not, at least in part, accountable for the absence of irruption? If so, would not our rougher mountains be better off and might we not have more normalcy in our deer herds, if we let the wolves and lions come back in reasonable numbers? (p. 120)

Today we know this phenomenon as a "mesocarnivore release," whereby the removal of large carnivores results in the overabundance of smaller predators, which may have various ecosystem impacts, such as the decline of bird populations (Crooks and Soulé 1999). Conversely, within three years of the wolves' return to Yellowstone's northern range, coyote densities dropped by 50 percent (Crabtree and Sheldon 1999). As a cascading effect of this coyote reduction, pronghorn antelope (*Antilocapra americana*) densities may be increasing, since coyotes prey heavily on young pronghorn (Smith et al. 2003).

Leopold (1949) expresses his thoughts about the cascading effects of wolves on ecosystems in three different sections of his final work, *A Sand County Almanac.* In this landmark publication and in reports published elsewhere, he poetically and passionately addresses the subjects of predator control, ungulate overbrowsing, and subsequent damage to vegetation (box 1).

Alternative hypotheses. In the eastern United States, forest harvest and the release of early seral vegetation, or the increased availability of agricultural crops, have sometimes been proposed as factors contributing to deer irruptions (see the *Wildlife Society Bulletin*'s 1997 special issue on deer overabundance, vol. 25, no. 2). Deer irruptions in the upper Midwest and farther east followed the intensive wave of logging. The regenerating forests made prime conditions for burgeoning herds. However, forest harvest also has occurred in Canadian provinces where wolves and bears coexist, but cervid irruptions have been rare.

In the western United States, cattle and sheep grazing, fire frequency reduction, climate, and other factors represent potentially significant contributions to deer irruptions, but the removal of major predators appears to have been the important precursor. In northern Mexico and Yellowstone, the

Box 1. Aldo Leopold's thoughts on the lethal effects of wolves and their impact on deer populations and browsing levels.

From "Deer Irruptions" (Leopold 1943)

We have found no record of a deer irruption in North America antedating the removal of deer predators. Those parts of the continent which still retain the native predators have reported no irruptions. This circumstantial evidence supports the surmise that removal of predators predisposes a deer herd to irruptive behavior. (p. 360)

In Chihuahua [Mexico], where deer are abundant and organized predator control unknown, irruptions are likewise unknown. No irruptions are clearly recorded for Canada, nor has government predator control prevailed there. (p. 361)

It appears, then, that cougars and wolves are the most effective deer predators. The evidence available supports the surmise that their removal does not cause irruptions, but paves the way for irruptive behavior, either at once or at some future time. (p. 361)

From "A Survey of Over-populated Deer Ranges in the United States" (Leopold et al. 1947)

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. In Europe, likewise, deer troubles began as effective predators ceased. (p. 176)

Prior to the turn of the century, the prevalent population problem in deer was scarcity. Since that time, about a hundred herds of deer, varying in size from a small refuge to half a state, have pyramided their numbers to the point of presenting a problem. (p. 176)

From *A Sand County Almanac, and Sketches Here and There* (Leopold 1949)

Since then I have lived to see state after state extirpate its wolves. I have watched the face of many a newly wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anemic desuetude, and then to death. I have seen every edible tree defoliated to the height of a saddlehorn. ("Thinking Like a Mountain," p. 130)

Damage to plant life usually follows artificialized management of animals—for example, damage to forests by deer. One may see this in north Germany, in northeast Pennsylvania, in the Kaibab, and in dozens of other less publicized regions. In each case over-abundant deer, when deprived of their natural enemies, have made it impossible for deer food plants to survive and reproduce. Beech, maple, and yew in Europe, ground hemlock and white cedar in the eastern states, mountain mahogany and cliff-rose in the West, are deer foods threatened by artificialized deer. The composition of the flora, from wild flowers to forest trees, is gradually impoverished, and the deer in turn are dwarfed by malnutrition. ("Conservation Esthetic," p. 170)

One of the most insidious invasions of wilderness is via predator control. It works thus: wolves and lions are cleaned out of a wilderness area in the interest of big game management. The big game herds (usually deer and elk) then increase to the point of overbrowsing the range. ("Wilderness," p. 191) lack of irruptions before wolf extirpation is consistent with the suggestion that the removal of large carnivores represents a predisposing factor. Leopold reported on more than 100 deer irruptions throughout the United States and recognized that none preceded and all followed the extirpation of large carnivores.

Although reduced market hunting, greater conservation enforcement, and the exemption of does from hunting (buck laws) in many parts of the United States during the early part of the 20th century have been identified as factors contributing to deer irruptions, Leopold believed these effects were secondary to predator removal as causes for deer irruptions. Recent literature describes ungulate hunting by humans as a poor substitute mechanism for controlling ungulate populations (Brown et al. 2000). The periodic hunting of ungulates by humans is also unlikely to replicate the persistent predation risk effects associated with wolves. In addition, other differences between human and carnivore hunting may exist, including differences in the ungulate age and sex classes being killed, as well as resulting differences in mesocarnivore densities and scavenger–carrion relationships (Berger 2005).

Since Leopold's time, deer and elk densities have increased in many areas of the United States and have been implicated in a variety of chronic problems, such as altered structure and function of forest and range plant communities, accelerated soil erosion, negative effects on commercial forest regeneration, increased crop damage and vehicle–ungulate accidents, and reduced habitat for other wildlife species (Rooney and Waller 2003, Côté et al. 2004). Since 1960, the white-tailed deer population alone has increased an estimated five- to sixfold in the conterminous United States (figure 6). Yet the vast majority of the authors citing Leopold (1943) and Leopold and colleagues (1947) in recent decades focus primarily on the topic of deer overabundance, largely ignoring Leopold's hypothesis on the relationships between wolves, deer, and vegetation, despite the landmark contribution of Flader's (1974) book. Comprehensive reviews of studies of overabundant deer in the United States (e.g., Russell et al. 2001, *Wildlife Society Bulletin* special issue, vol. 25, no. 2, 1997) also largely ignore issues associated with the removal of wolves and other large carnivores. It is important to note that the preponderance of research on forest wildlife in this country has occurred since wolves were extirpated; the degree to which the results of that research have been influenced by an absence of large predators is unknown.

Conclusions

In retrospect, it appears that Leopold's visionary and iconoclastic work of decades ago provided important and forward-looking perspectives for understanding the role of large carnivores in affecting the status and functioning of ecosystems. His research results and insights regarding wolves and trophic cascades strongly suggest that the ecological role of wolves and other top predators should receive greater consideration in evaluating the success of wolf restoration efforts and in identifying areas where the restoration of wolves and other predators could be used as a management tool to offset ungulate impacts. We encourage readers to strive to "think like a mountain" and to reread Leopold's 1949 essay, because it now appears that he was accurately describing trophic cascades when he so eloquently portrayed the relationship of the wolf to the deer and the deer to the mountain.

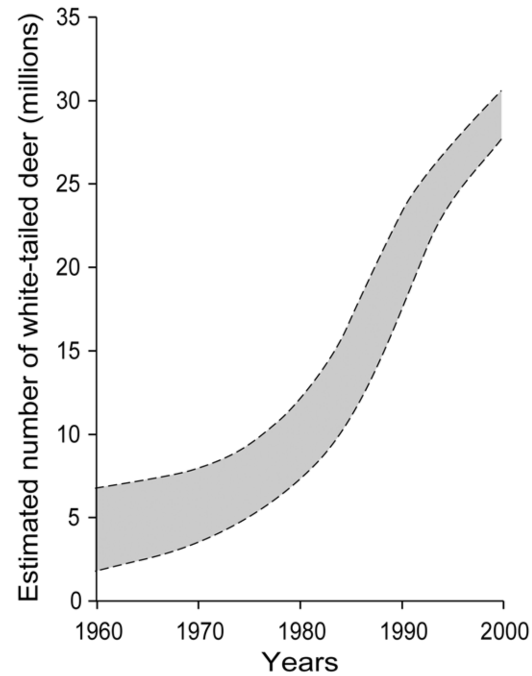

Figure 6. White-tailed deer population in the lower 48 states from 1960 to 2000, exclusive of 11 western states where white-tailed deer are either uncommon or absent. The width of the gray band represents an estimate of uncertainty. Adapted from the **Deer Hunters' Almanac** ***2004, edited by Joe Shead (Iola, WI: Krause Publications).***

Acknowledgments

We thank Cristina Eisenberg, Jim Estes, Werner Flueck, Curt Meine, Mark O'Donoghue, James Peek, Tom Rooney, Douglas Smith, and Michael Soulé for reviewing a draft of this manuscript.

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