Are ecosystems structured from the top-down or bottom-up: a new look at an old debate

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Abstract Whether ecosystems are structured from the top-down (i.e., predator driven) or bottom-up (i.e., food limited) has been debated by ecologists for nearly a century. Many marine and freshwater aquatic systems appear to be under top-down control, but less evidence exists that predators have had a similar effect in terrestrial systems, especially those systems involving large ungulates. Earlier research, however, omitted any serious discussion of Native Americans. Contrary to prevailing beliefs, Native Americans were not conservationists, and they had dramatic impacts on wildlife populations. Native Americans were the ultimate keystone predator and the ultimate keystone species through activities such as aboriginal burning. Moreover, the idea that North America was a "wilderness" untouched by the hand of man prior to 1492 A.D. is incorrect, as recent population estimates indicate that native people may have numbered as many as 100 million, or more, before they were decimated by introduced diseases and other colonial processes. Until the importance of aboriginal land management is recognized and modern management practices change accordingly, our ecosystems will continue to lose the biological diversity and ecological integrity they once had, even in national parks and other protected areas.

Key words aboriginal overkill, aspen, beaver, bison, elk, fire, keystone predation, keystone species, national park management, Native Americans, predation, willows

Estes (1995, 1996) recently discussed whether ecosystems are structured from the top-down, predator driven, or from the bottom-up, food- or resource-limited. This debate has a long history in ecology (Hairston et al. 1960, Hunter and Price 1992), and its solution is critical if biologists are to implement ecosystem management, especially in national parks and other protected areas (Estes 1996). Many marine and freshwater aquatic systems appear to be under top-down control, but there is less evidence that predators have a similar effect in terrestrial systems (Estes 1995, 1996). Earlier studies, however, omitted any serious discussion of Native Americans, who, I suggest, were the ultimate keystone predator (Mills et al. 1993, Power et al. 1996) that structured North American ecosystems from ca. 12,000 before present (BP) to ca. 1870, especially in the western United States and Canada, where I have conducted most of my research. My views challenge the conventional belief that the impacts of native people on wildlife is unimportant or that they were conservationists (Arcese and Sinclair 1997, Vale 1998). Moreover, I suggest that through practices like aboriginal burning, Native Americans were the ultimate keystone species, creating the very ecosystems that we now consider "natural." I present various lines of evidence and reasoning that support my hypothesis. Because this is a synthesis paper, individual publications should be consulted for the methods that were used in those studies and for the details of their findings.

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Evidence historical and pre-Columbian ungulate populations were not food limited

There are several lines of evidence that suggest from ca. 1750 to 1870 ungulate populations were not food limited across the Intermountain West. These include, but are not limited to, first-person historical accounts, photographs from ca. 1870, berry-utilization data, and the abundance of beaver (*Castor canadensis*; Kay and Wagner 1994; Kay and White 1995; Kay 1995*b,c*, 1996*b*, 1997*a,b,c,d,f,g*;). In addition, archaeological data indicate that pre-Columbian ungulate populations were not food limited (Kay 1990, 1994*a*, 1997*e*; Kay et al. 1994; Allen 1996; Truett 1996).

First-person historical accounts

During the early 1990s, there were an estimated 100,000 elk (*Cervus elaphus*) in the Yellowstone ecosystem and an estimated 4,000 bison (*Bison bison*) in Yellowstone National Park (Harting and Glick 1994). According to the National Park Service, these large ungulate populations are assumed to be "natural" and to represent the "pristine" state of the ecosystem (Houston 1982, Despain et al. 1986). If that were true, then early explorers should have reported an abundance of game. Between 1835 and 1876, 20 different expeditions spent 765 days in the Yellowstone Ecosystem, yet they reported seeing elk only once every 18 party-days, and bison were seen on only 3 occasions, none of which were in Yellowstone Park itself (Kay 1990). In addition, no one reported seeing or killing even a single wolf (*Canis lupus*), another indication that game was scarce (Kay 1995*b*). Moreover, while the explorers were in Yellowstone, their journals contain 45 references to a lack of game or a shortage of food (Kay 1990). Recently, Schullery and Whittesey (1992) published an exhaustive compendium of early wildlife observations in Yellowstone, but their per-party sighting rates were actually only half those reported in first-person journal accounts (Kay 1990).

Similarly, elk are now the most abundant ungulate in Banff National Park and other parts of the Canadian Rockies. Between 1792 and 1872, however, 26 different expeditions spent 369 days traveling through the mountains on foot or horseback yet reported seeing elk on only 12 occasions, or once every 31 party-days (Kay and White 1995). Thus, contrary to popular perception, first-person historical accounts provide no evidence that ungulates were once common in the Intermountain West (Koch 1941, Rawley 1985, Davis 1986, Allen 1996, Truett 1996).

Historical photographs

Historical photographs can also be used to judge the number of ungulates that occupied areas in the past and to determine whether those animals were food limited. If elk, for example, were as abundant historically as they are today in various western national parks (Hess 1993, Wagner et al. 1995, Allen 1996), then favored forage species, like aspen (*Populus tremuloides*) and willows (*Salix* spp.), should show that those communities were as heavily browsed during the 1800s as they are at present (Kay 1990, Kay et al. 1994, Kay and White 1995). If aspen and willows depicted in historical images do not show evidence of repeated browsing, that would indicate that fewer ungulates used the range in the past and that factors other than food limited those herbivores.

Ungulates in Yellowstone National Park have reportedly been food limited for many years under what is termed "natural-regulation" management (Houston 1982, Despain et al. 1986). According to this paradigm, predation is an assisting but nonessential adjunct to the regulation of ungulate populations by food limitation. If wolves are present, they will only take the ungulates slated to die from other causes, such as starvation, and, hence, predation will not cause population declines of ungulates (Houston 1982, Despain et al. 1986). In the current debate over reintroduction of wolves to Yellowstone, the Park Service has denied that wolves are needed to control the park's elk herds or that wolves will have any significant impact on the number of ungulates (Boyce 1992, Kay 1996*a*). Instead, the Park Service believes that it is natural for thousands of elk and other ungulates to starve to death during winter. The agency contends that those animals have always heavily impacted the vegetation, including high-lining conifers, which is now widespread (Houston 1982, Despain et al. 1986, Kay 1990).

Historical photographs, however, show no evidence of ungulate browsing (Kay and Wagner 1994; Fig. 1). In addition, photographs taken over time of tall willows ($n = 44$) and aspen ($n = 81$) indicate that the areas occupied by those species have declined 95% since the late 1800s due to repeated ungulate browsing, not other factors (Chadde and Kay 1988, 1991; Kay and Chadde 1992; Kay 1994*b*, 1995*c*, 1996*b*, 1997*d,g*; Kay and Walker 1997). Thus, ungulate high-lining of conifers and repeated browsing of other woody vegetation represent a departure from conditions that existed prior to the establishment of Yellowstone National Park (Kay and Wagner 1994). Moreover, because conifers and other woody species

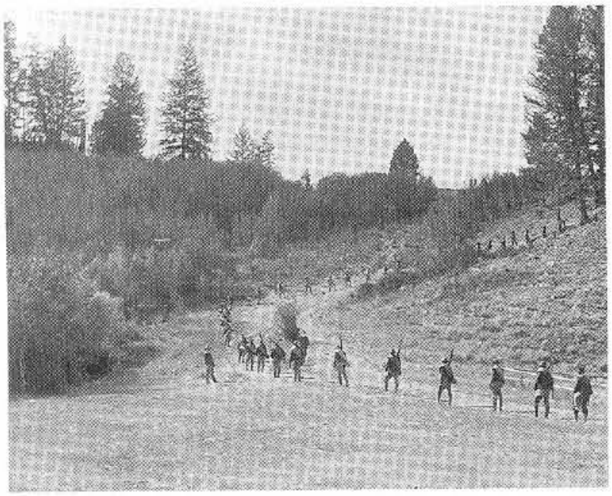

Fig. 1. Unbrowsed condition of aspen in Yellowstone Park during the late 1800s. The aspen in this and other early photographs show no evidence of ungulate browsing. Repeated browsing has now eliminated the aspen shown here. In the foreground, Company D of the Minnesota National Guard is on patrol—the military administered Yellowstone from 1886 until 1916, when the National Park Service was created. Photo (ca. 1893) by F. J. Haynes (H-3069), courtesy of the Montana Historical Society, Helena, Montana.

depicted in early images were 50–100 years old when they were photographed and because they show no evidence of ungulate use, this would suggest that few, if any, elk wintered in Yellowstone from the late 1700s through the 1870s (Kay and Wagner 1994).

Historical photographs taken in the Canadian Rockies show the same pattern (Kay et al. 1994; Kay and White 1995), as do photos taken ca. 1870 throughout the West (Kay 1997*a*; historical and repeat-photo studies in progress for the Agric. Res. Serv., U.S. For. Serv., and Ut. Div. of Wildl. Resour.; Kay and Walker 1997). Early photographs show no evidence of ungulate browsing, the exact opposite of conditions today, especially in national parks and preserves where ungulate populations are food limited.

Use of berries

Berry production and utilization data also suggest that historical ungulate populations were low. Ethnographic accounts and archaeological studies reveal that Native Americans routinely consumed large quantities of berries, such as serviceberries (*Amelanchier alnifolia*) and chokecherries (*Prunus virginiana*; Lowie 1909, Chamerlin 1911). In September 1869, for instance, the Cook–Folsom–Peterson Expedition met Native Americans who were gathering and drying large quantities of chokecherries at the mouth of Tom Miner Creek just north of Yellowstone Park (Haines 1965). The Washburn Expedition of 1870 reported that near Yellowstone Park "we crossed a small stream bordered with black cherry trees [chokecherries], many of the smaller ones broken down by bears, of which animal we found many signs" (Langford 1972:13). Because shrubs have to be ≥2 m in height before branches are commonly broken down by feeding bears (*Ursus* spp.), Yellowstone's chokecherry plants in 1870 not only produced abundant berries, but were apparently rather robust, tall shrubs.

Conditions today are quite different. Serviceberry and chokecherry plants in Yellowstone now average <50 cm tall and produce virtually no berries because they are repeatedly browsed by elk and other resource-limited ungulates (Kay 1990, 1995*c*). At the Lamar-West exclosure on Yellowstone's northern range, 100 protected serviceberry plants produced 111,047 berries, while 100 browsed plants produced no berries, and 100 protected chokecherry plants produced 212,178 berries, while 100 browsed plants produced none (Kay 1995*a,c*, 1997*d*).

Resource-limited ungulate populations and large quantities of berries are mutually exclusive on western ranges. Even moderate numbers of ungulates curtail berry production because those shrubs provide highly preferred forage, especially during winter (Kay 1995*c*). Ungulate-induced berry reduction is even reflected in grizzly bear (*Ursus arctos*) diets. While bears in other ecosystems commonly consume large quantities of berries (Le Franc et al. 1987), grizzlies in Yellowstone eat virtually none (Mattson et al. 1991; Kay 1995*c*, 1997*d,f*). In historic and prehistoric times, peoples in the West consumed large quantities of berries; this suggests that ungulate populations were small and that those animals were not limited by food (Kay 1994*a*, 1995*a,c*, 1996*b*).

The abundance of beaver

Beaver also provide evidence that historical ungulate populations were not food limited. Millions of beaver inhabited western North America prior to the fur trade (Johnson and Chance 1974, Kay 1994*b*). Beaver commonly inhabited mountain streams, but large numbers were also found along water courses on the Canadian and United States prairies, especially in Canada's aspen parklands. One Hudson Bay Company fur brigade, for instance, caught 511 beaver from a small northern Utah drainage in just 5 days (Kay 1994*b*). To support these large numbers of beaver, woody vegetation that beaver need for food and dam building materials, like aspen, willows, and cottonwoods (*Populus* spp.), must have been plentiful. Moreover, those plants could not have been subjected to repeated browsing by large numbers of resource-limited ungulates, because those species are quickly eliminated by high levels of herbivory (Keigley 1997).

Yellowstone provides an excellent example of the impact food limited ungulates have on beaver populations. During the early 1800s, Russell (1965) spent weeks trapping beaver on what is now the park's northern range. Even after Yellowstone was established as the world's first national park in 1872, there were hundreds, if not thousands, of beaver on the northern range (Kay 1990, 1997*d*). Today, however, beaver are ecologically extinct on Yellowstone's northern range because repeated browsing by the park's resource-limited ungulates has eliminated the tall willows and aspen beaver need for food (Chadde and Kay 1988, 1991; Kay and Chadde 1992; Kay 1997*e*; Kay and Walker 1997). Ungulate populations have also had a negative impact on beaver in Rocky Mountain National Park (Hess 1993) and in Banff National Park (Flook 1964). Thus, if large numbers of beaver were once common in the past, then ungulates must have been limited by factors other than food.

Archaeological data

Archaeological evidence indicates that pre-Columbian ungulate populations were also not resource limited. In food limited intermountain systems, large ungulates such as elk, bison, and moose (*Alces alces*) competitively exclude smaller, less efficient herbivores like deer (*Odocoileus hemionus* and *O. virginianus*) and bighorn sheep (*Ovis canadensis*; Cliff 1939, Cowan 1947, Flook 1964, Olmsted 1979, Parker et al. 1984, Telfer and Kelsal 1984). If pre-Columbian intermountain ungulate populations were food limited and native people randomly harvested those animals, then archaeologically recovered ungulate faunal remains should be dominated by elk, bison, and moose, whereas deer and bighorn sheep should be less abundant (Kay 1990, 1994*a*). The opposite pattern, however, has been observed.

Of nearly 60,000 ungulate bones unearthed at >400 archaeological sites in the United States and Canadian Rockies, <3% were elk, and only about 10% were bison (Kay 1990, 1994*a*, 1997*e*; Kay et al. 1994; Kay and White 1995). Only 1 moose bone has been recovered in the western United States, an area now inhabited by an estimated 25,000 moose (Kay 1997*e*). Instead, at intermountain archaeological sites in the southern Canadian and United States Rockies, deer and bighorn sheep are the most frequently recovered ungulates (Kay 1990, 1994*a*, 1995*a*, 1997*e*; Kay et al. 1994; Kay and White 1995). Even in the Greater Yellowstone Ecosystem, where elk presently constitute around 80% of the total ungulate fauna, elk are rare to nonexistent in archaeological sites (Wright 1984; Kay 1990, 1992, 1994*a*). Elk currently dominate ungulate communities in Idaho's River of No Return Wilderness and in Oregon's Blue Mountains, but few elk bones have ever been recovered from archaeological sites in those areas (Kay 1990). Similarly, elk now dominate the ungulate fauna in Banff, Jasper, Yoho, and Kootenay national parks, but elk is among the least frequent ungulate species recovered from archaeological remains (Kay et al. 1994, Kay and White 1995, Kay 1997*c*). Similar situations occur in other western states, including Arizona and New Mexico (Allen 1996, Truett 1996). Bandelier National Monument, for instance, now supports high densities of largely resource-limited elk, yet only 9 elk bones have been recovered from 45 archaeological sites (Allen 1996).

Many ecologists harbor a mistaken belief that aboriginal diets were primarily meat (McCabe and McCabe 1984, Reeves and McCabe 1997). Anthropologists, though, have long argued that native people should more appropriately be called gatherer–hunters, instead of hunter–gatherers, because ≥90% of most historic and prehistoric diets were non-ungulate foods (Lee and DeVore 1968, Sahlins 1972). This was especially true in the Intermountain West (Hunn and French 1981, Wright 1984). According to optimal-foraging models, plant foods, small mammals, and fish are lower ranked diet items (i.e., they provide lower caloric return rates per unit time) than ungulates (Smith 1983, Simms 1984, Smith and Winterhalder 1992), which implies that, historically and prehistorically, ungulate population levels were low; i.e., those animals were not food limited (Kay 1990, 1994*a*, 1997*e*). Optimal-foraging theory (Stephens and Krebs 1986) predicts that ungulates will be taken by aboriginal peoples whenever those animals are encountered; a diet of low-ranked items, such as that experienced by Native Americans in the West for >10,000 years, indicates that high-ranked ungulates were rare or absent (Smith 1983; Simms 1984; Broughton 1994*a*, 1994*b*, 1995, 1997; Janetski 1997).

As noted above, elk in Yellowstone National Park are food limited and now winter at densities of 20–40 elk/km^2 (Houston 1982, Singer and Norland 1994, Singer et al. 1997). If this was true in earlier times, optimal-foraging models predict that aboriginal diets should have been nearly 100% elk, but archaeological finds indicate that was not the case (Kay 1990). Thus, it is likely that few elk were actually available to prehistoric hunters and that today's ungulate populations are not representative of pre-Columbian conditions (Kay 1994*a*, 1997*e*). This was true in Yellowstone, and throughout the Intermountain West (Kay 1994*a*, 1997*e*).

Furthermore, the condition of archaeologically recovered faunal remains supports the interpretation that pre-Columbian ungulate populations were low (Broughton 1994*a*,*b*, 1995; Potter 1995). Most bone recovered from intermountain archaeological sites is highly fragmented due to processing by the native peoples who left those cultural deposits (Kay 1990); i.e., Native Americans broke-up the bones and then extracted the grease via boiling (Leechman 1951; Vehick 1977; Binford 1978, 1981). Bone-grease processing, however, is labor intensive and may have been done at a net loss of energy (Kay et al. 1994). Thus, native peoples may have been experiencing nutritional stress, or at least a shortage of critical animal fats (Binford 1978, 1981; Olson 1983; Schalk and Mierendorf 1983), which, in turn, indicates that ungulates were not abundant (Broughton 1994*a*, *b*, 1995; Potter 1995). That bone-grease processing was the norm throughout much of western North America suggests that ungulate populations were being kept at low levels by factors other than food limitation (Kay et al. 1994, Kay and White 1995).

Aboriginal overkill

Carnivore predation (Estes 1995, 1996; Kay 1996*a*) and native hunting are factors that may once have limited ungulate numbers. The presence of aboriginal buffer zones, however, indicates that predation by wolves and other carnivores was not the primary factor limiting pre-Columbian ungulate populations. Hickerson (1965:45) noted that "Warfare between members of the two tribes had the effect of preventing hunters from occupying the best game region intensively enough to deplete the [deer] supply... In the one instance, in which a lengthy truce was maintained between certain Chippewas and Sioux, the buffer, in effect a protective zone for the deer, was destroyed and famine ensued." Lewis and Clark (1893:1179) noted that "With regard to game in general, we observe that the greatest quantities of wild animals are usually found in the country lying between two nations at war." Similarly, Palliser (1969:266–267) reported that game on the Canadian prairies was more abundant in aboriginal buffer zones: "... I must admit, we ran some risk of being surprised by an Indian war-party... As a general rule, the more dangerous the country the greater the probability of finding [an] abundance of game, showing in more ways than one the truth of the old sportsmen's adage, the more danger the more the sport. This part of the country is so evidently the line of direction [demarcation] between the three hostile tribes, that none of them dare venture into it for hunting, except when driven to desperation by hunger ... Much therefore as I enjoyed the [present] locality for a hunting camp, seeing buffalo on all sides, elk feeding in the distance, and fresh deer tracks in every direction ... Boucharville [my guide] did not relish it at all, and began already to calculate how soon we were to go away."

Thus, historical sources indicate that aboriginal hunting tended to extirpate or to drive-out game animals, and resource depletion around camps and villages has frequently been reported in studies of modern hunter-gatherers (Smith and Winterhalder 1992; Kay 1994*a*). This pattern would be expected if people pursued an optimal-foraging strategy with no effective conservation practices. Tribal territory boundary zones also explain how early explorers could encounter an abundance of game in a few locations and lack of game elsewhere (Steffian 1991, Hammett 1992). Many aboriginal buffer zones were ≥200 km wide. During the 1800s, for instance, all the land between the Yellowstone and Missouri rivers on the Montana prairies was an aboriginal buffer zone, where game was relatively more abundant (but not food limited), and native use was low due to constant warfare between the Blackfoot Confederation (5 tribes); the Shoshone; the Crow; the Salish, Flatheads, and their Kootenay allies; and the Sioux and their Cheyenne allies (C. E. Kay, unpubl. data). Similarly, West (1995) concluded that bison would not have survived on the central Great Plains without aboriginal buffer zones.

In addition, the age of their respective kills indicates that Native Americans were more efficient predators than wolves. The more difficult it is for a predator to capture a particular prey, the more that predator will take substandard individuals and young (Temple 1987, Kunkel 1997). So, if ≥2 predators are preying upon the same species, the least efficient predator will tend to kill fewer prime-age animals (Okarma 1984). Whereas wolves and other carnivores kill primarily young-of-the-year and old animals, Native Americans killed mostly prime-age ungulates (Stiner 1990).

Ungulates recovered from intermountain archaeological sites invariably exhibit mortality profiles dominated by prime-age animals (Kay 1994*a*, 1995*a*, 1997*e*), which suggests that Native Americans were more efficient predators than wolves or other carnivores (Stiner 1990; Fig. 2). Killing mostly prime-age animals, however, runs contrary to any maximum sustained-yield strategy (Hastings 1983, 1984) and suggests that Native Americans had a major impact on pre-Columbian ungulate populations, especially when one considers that Native Americans also killed a disproportionate number of females, a preference that runs counter to any conservation strategy (Kay 1994*a*, 1995*a*, 1997*e*).

It is often claimed, however, that Native Americans' religious beliefs prevented those peoples from overutilizing their resources (Speck 1939; Nelson 1982, 1983). Native Americans tended to view wildlife as their spiritual kin where success in the hunt was obtained by following prescribed rituals and

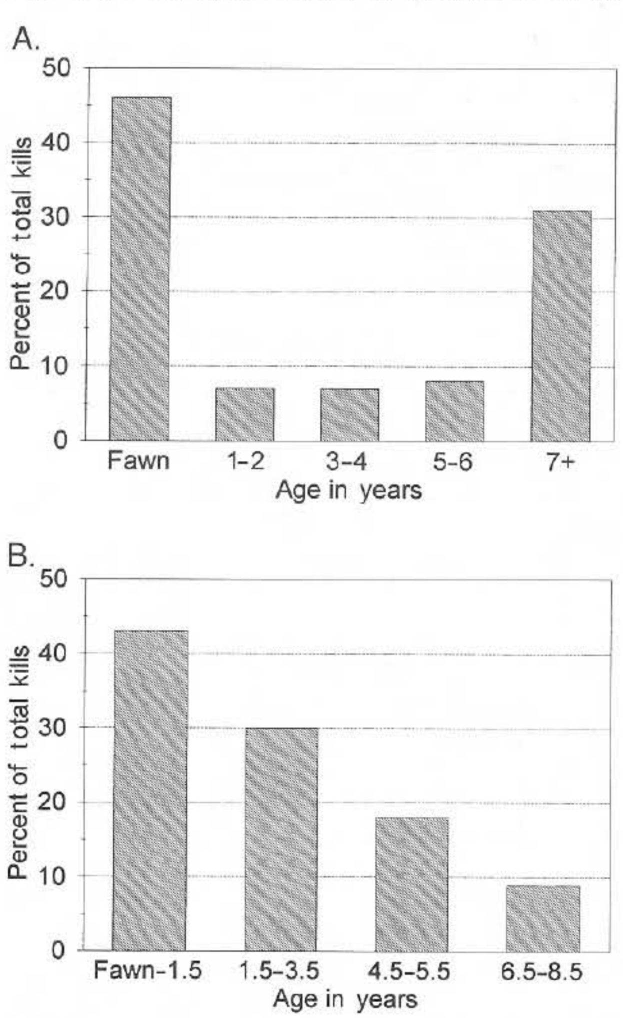

Fig. 2. Age structure of ungulates killed by wolves and Native Americans. (A) Age of white-tailed deer ($n = 48$) killed by wolves in Minnesota (Fritts and Mech 1981). (B) Age of mule deer ($n = 60$) unearthed from the 4,200-year-old Dead Indian Creek archaeological site in northwest Wyoming just east of Yellowstone Park (Simpson 1984). Unlike carnivores, which tend to select prey among young and old animals, Native Americans killed predominantly prime-age ungulates—an indication that Native Americans were more efficient predators. Moreover, the deer at this archaeological site were killed with spears or atlatls, which are less efficient hunting instruments than the bow and arrow that came into use around 1,500 BP (Blitz 1988).

atonement after the kill (Feit 1987). A scarcity of animals or failure in the hunt were not viewed as biological or ecological phenomena, but rather as a spiritual consequence of social events or circumstances (Reeves and McCabe 1997). If a Native American could not find any game, it was not because his people had overharvested the resource, but because he had done something to displease his gods. Because Native Americans saw no connection between their hunting and game numbers, their system of religious beliefs actually fostered the overexploitation of ungulate populations (Kay 1994*a*, 1995*a*, 1996*b*, 1997*e*).

Native hunters were opportunistic and tended to take high-ranking ungulates, regardless of the size of the prey populations or the likelihood of those animals becoming extinct (Alvard 1993, 1994, 1995; Broughton 1994*a*, 1994*b*, 1995, 1997). Native Americans had no concept of maximum sustained yield and did not manage ungulate populations to produce the greatest offtake. In addition, human hunting and predation by carnivores are generally additive and work in concert to reduce ungulate numbers (Walters et al. 1981, Kunkel 1997). Moreover, competition from carnivores would have tended to discourage any possible ungulate conservation practices (Kay 1994*a*, 1995*a*, 1996*b*, 1997*e*). Because Native Americans could prey-switch between trophic levels to small animals, plant foods, and fish, they could hunt their preferred ungulate prey to low levels or extinction without having an adverse effect on human populations. In fact, once Native Americans killed off most of the ungulates, human populations rose (Hawkes 1991, 1992, 1993).

Although the demonstrated lack of elk and other ungulates in archaeological sites may at first appear to refute the aboriginal overkill hypothesis, the opposite is true. Optimal-foraging theory (Smith 1983, Simms 1984, Smith and Winterhalder 1992, Broughton 1997, Janetski 1997) predicts that high-ranked items, like elk and other ungulates, are more susceptible to overexploitation than low-ranked items, such as plant foods, small mammals, or fish. According to optimal-foraging models, high-ranked items will seldom appear in the diet if they are being overexploited (Broughton 1994*a*, 1994*b*, 1995, 1997). So, ungulate species unearthed with the lowest frequency in archaeological sites, such as moose and elk, were probably subjected to extreme overexploitation (Kay 1994*a*, 1997*e*).

Birkedal (1993) reported that Native Americans, armed with no more than spears and hunting dogs, once kept grizzly bear populations at very low levels throughout much of Alaska, and Taulman and Robbins (1996) suggested that native hunters limited the distribution and abundance of the 9-banded armadillo (*Dasypus novemcinctus*) in the southern United States. Moreover, aboriginal effects were not limited to terrestrial communities. Broughton (1997), for example, found that Native Americans had a significant impact on the population of white sturgeon (*Acpenser transmontanus*) in San Francisco Bay, and Hewes (1973) and Schalk (1986) suggested that aboriginal fishing had a detrimental effect on the number of salmon in the Columbia Basin. Archaeological information also indicates that native hunters significantly reduced pinniped populations along the California and Oregon coasts (Hildebrandt and Jones 1992, Jones and Hildebrandt 1995) and that native peoples had a significant effect on freshwater and marine shellfish populations (Botkin 1981). Adler (1970) found that the eastern box turtle (*Terrapene carolina*) was eliminated from many areas by aboriginal peoples.

There are, however, exceptions to aboriginal overkill. According to predator-prey theory, prey populations will increase if they have a refugium where they are safe from predation (Taylor 1984). Therefore, ungulates that could escape aboriginal hunters in time or in space were more abundant. Moreover, refugia do not have to be complete to be effective. Partial refugia also enable prey populations to survive (Taylor 1984). This may explain why larger numbers of ungulates existed on the Great Plains and in the Arctic. By undertaking long-distance migrations, bison and caribou (*Rangifer tarandus*) were able to outdistance many of their human and carnivorous predators (Bergerud 1990, 1992; Kay 1994*a*, 1995*a*, 1996*b*, 1997*e*); however, even migratory ungulates historically were not food limited.

Aboriginal populations

Aboriginal populations were also much larger than commonly believed. Until recently, it was thought that only about 2,000,000 natives inhabited North America prior to the arrival of Columbus (Stannard 1989, 1992). Dobyns (1983), however, postulated that native people, who were attempting to escape Spanish exploitation in Cuba, fled to Florida in ocean-going canoes and brought European-introduced smallpox with them to the mainland during the early 1500s. This and other diseases, to which aboriginal inhabitants had no immunological resistance, then ravaged native people, reducing aboriginal populations by ≥90% before the Pilgrims landed at Plymouth Rock. Subsequently, Ramenofsky (1987), Smith (1987), and Campbell (1990) tested Dobyns' hypothesis using the archaeological record and concluded that ca. 1550–1600 a major collapse of native populations had occurred in North America—100 to 200 years prior to direct contact of Europeans with native people in many areas, especially the Intermountain West; i.e., European diseases were transmitted from native group to native group across all of North America—termed pandemics. Based on this and other evidence, it is now believed that in 1492 there may have been as many as 100 million native people in North America with perhaps an even larger number in South America (Stannard 1992). Although Dobyns' hypothesis is still debated (Snow 1995), in general, estimates of pre-European native populations have steadily been revised upward.

There was no "wilderness." In fact, the idea that North America was a "wilderness" untouched by the hand of man before 1492 is a myth, a myth that may have been created, in part, to justify appropriation of aboriginal lands and the genocide that befell native peoples (Denevan 1992, Gomez-Pompa and Kaus 1992, Simms 1992, Cronon 1995). Moreover, there is no evidence that native people ever purposefully limited their populations to avoid environmental impacts or that, if they tried, they were successful (Cohen 1977, 1989; Cohen and Armelagos 1984; Blurton-Jones 1986, 1987; Diamond 1992*b*; Smith and Winterhalder 1992). As resource use intensified over the last several thousand years, a parallel increase in the violence within and between prehistoric societies occurred (i.e., people were fighting over scarce resources; Lambert 1997).

The Serengeti myth

Ecologists and wildlife biologists often cite Africa's Serengeti as an example of how North America must have looked before it was despoiled by Europeans (Frank et al. 1998). It has been claimed, for instance, that Yellowstone National Park is the last remnant of North America's Serengeti (Anonymous 1996). Today's Serengeti, however, is not a natural ecosystem, nor is it a vignette of "wilderness" Africa. Instead the Serengeti is a romantic, European, ethnocentric view of how "primitive" Africa should have looked (Adams and McShane 1992); one of the first things that colonial governments did when they created Serengeti and other African national parks was to forcefully remove all of the indigenous peoples. Hominoid predators, however, have existed in Africa for ≥3.5 million years, and it is thought that *Homo sapiens* evolved in Africa about 100,000 years ago (Shreeve 1995, Tattersall 1995). Thus, I suggest that here is nothing more unnatural than an African ecosystem without hominoid predators; the Serengeti, therefore, is not a "natural" ecosystem nor is it an example of how North America teemed with wildlife before the arrival of Columbus.

In all the ecological studies that have been done on the Serengeti, native people have rarely been mentioned, or if they have, it has usually been in the pejorative sense, as "poachers" (Sinclair and Norton-Griffiths 1979, Sinclair and Arcese 1995). Simulation models have indicated that Serengeti's wildlife populations will collapse if present levels of "poaching" increase by 10% (Sinclair and Arcese 1995:617–637). I would suggest, however, that this may simply be a case of native people exercising their aboriginal rights.

The 60 million bison myth

Similarly, it is often claimed that nearly 60 million bison roamed the North American plains until decimated by advancing European civilization (Roe 1951). That 60-million figure, though, was based on maximum carrying capacity (i.e., food limited) and made no allowance for either the impacts of carnivore predation or native hunting (Roe 1951). Shaw (1995) recently questioned this interpretation, and Geist (1996), concluded that the factor driving bison evolution, ecology, and behavior for the last 12,000 years was hunting by native peoples. Both Shaw (1995) and Geist (1996) revised bison population estimates downward to 10–15 million animals, but I believe that number is still too high (Kay 1996*b*).

First, buffer zones, berry use, and beaver populations on the prairies all suggest that early wildlife populations were not food limited. Second, widespread burning of the prairies in historical and pre-Columbian times, provides another line of evidence that large numbers of resource-limited bison did not inhabit the plains. Early historical observations provide ample evidence that during the late 1700s and early 1800s, prairie fires often burned for days, and single fires covered huge areas, often running for 100–200 km (Nelson and England 1971, Thomas 1977, Higgins 1986). Large numbers of ungulates and large prairie fires, however, are mutually exclusive because heavy grazing reduces standing plant biomass, prevents the accumulation of plant litter, and creates discontinuous fuel patterns, all of which prevent the growth and spread of large fires (Norton-Griffiths 1979, McNaughton 1992, Hobbs 1996). If there were large fires on the prairies (Nelson and England 1971, Higgins 1986) bison and other ungulates could not have been food limited. Fidler (1990), who traveled with Piegan natives during 1792–1793, reported virtually no unburnt ground on the Canadian prairies from the Oldman River to Buckingham House, a distance of several hundred kilometers. Fidler (1990) observed that most of those fires had either purposefully or accidentally been set by native people. Much of that burning, in fact, occurred during winter when there was no lightning to start fires.

Circumstances were the same throughout the Intermountain West, historically and prehistorically, for many of those plant communities were also once swept by frequent but low-intensity fires (Kay et al. 1994, Kay 1995*a*, Kay and White 1995). This could not have been true, though, if large numbers of food limited ungulates had been present (Savage and Swetnam 1990; Touchan et al. 1995, 1996; Swetnam and Baisan 1996). In Yellowstone, for instance, grazing by resource-limited elk and bison has created discontinuous fuel patterns that have changed historical burning patterns and limited the spread of fires (Kay 1997*g*; Fig. 3). The area along Blacktail Creek was overrun by wildfires in 1988, yet much of the range did not actually burn because ungulate grazing had prevented the accumulation of plant litter necessary to carry fire through these grassland communities. Instead, 100- to 160-km/hour winds drove the fire from patch of fuel to patch of fuel in swales and on north aspects where snow limited forage removal by elk and other wintering ungulates. Historically, Yellowstone's northern range had a fire frequency of once every 25 years (Houston 1973), yet despite the park's "let-burn" policy, virtually none of the northern range has burnt in the last 30 years, except for 1988, but that is thought to be a 100–300 year event (Romme and Despain 1989), and, thus, similar fires could not have created the original fire-return interval. Despain et al. (1986:109) suggested that the park's grasslands have failed to burn during the past 30 years because "lightning has chosen not to strike very often on the northern range," but that hypothesis is not supported by data from the Bureau of Land Management's Automatic Lightning Strike Detection System which shows that, on average, lightning strikes four times per km2 per year (Kay 1990:136-137). Instead, the range does not burn because the park's food limited elk and bison have overgrazed Yellowstone's grasslands, unlike conditions in the past when native hunting limited ungulate numbers.

The ultimate keystone species

Native people were not only the ultimate keystone predator, they were also the ultimate keystone species

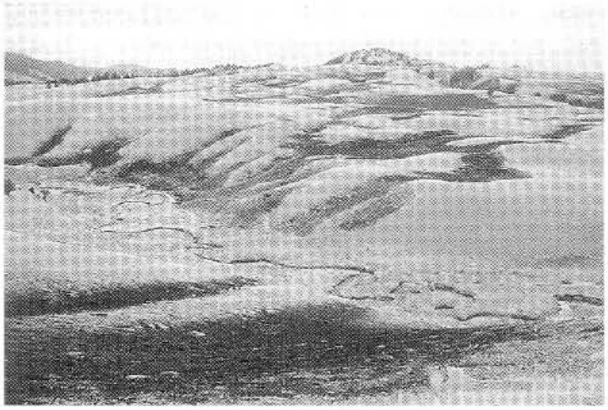

Fig. 3. Ungulate-induced burn pattern in Yellowstone National Park. Photo by C. E. Kay.

(Bonnicksen et al. In press). The Americas, as first seen by Europeans, had largely been created by native peoples, not crafted by nature. Native people modified their environments in many ways (Bonnicksen et al. In press), but I will discuss only competition between humans and wildlife for food and aboriginal burning.

Passenger pigeon myths

Neumann (1984, 1985, 1989, 1995) has written extensively about native people, who, by consuming certain foods, limited various wildlife populations. His most interesting example involves the passenger pigeon (*Ectopistes migratorius*), often cited as an example of how pre-Columbian America teemed with wildlife before Europeans drove that and other species to extinction. But as Neumann (1985) has chronicled, native populations in pre-Columbian times were so large that those people consumed most of the nuts, fruits, and berries that passenger pigeons needed for food. It was only after European diseases decimated Native American populations, and thereby freed the mast crop for wildlife, that the passenger pigeon grew to unprecedented numbers. Thus, the large flocks of passenger pigeons that reportedly darkened the skies during the 1700s and 1800s were an artifact of the "American Holocaust" (Stannard 1992), not an example of how America teemed with wildlife before Europeans arrived.

Aboriginal burning

Native Americans also had a major impact on ecosystems by repeatedly burning the vegetation. They did this to modify plant and animal communities for human benefit and to increase productivity (Pyne 1995). In California, for instance, native peoples had 70 reasons for burning the vegetation (Lewis 1973), and even in northern Canada, where the vegetation is less diverse, Native Americans still set fires for at least 17 different reasons (Lewis and Ferguson 1988). Although aboriginal burning has been widely reported in the anthropological literature (e.g., Lewis 1985; Boyd 1986; Turner 1991; Pyne 1993, 1995; Gottesfeld 1994), those findings have been largely ignored by ecologists (Kay 1995*a*).

Determining how fires started, though, is critical because "fires set by hunter-gatherers differ from [lightning] fires in terms of seasonality, frequency, intensity, and ignition patterns" (Lewis 1985:75). The majority of aboriginal fires were set in the spring, between snowmelt and vegetation greenup, or late in the fall when burning conditions were not as severe (Pyne 1995). Unlike lightning fires, which tend to be infrequent and of high intensity, native burning produced a high frequency of low-intensity fires. Aboriginal burning and lightning fires created different vegetation mosaics, and in many instances, entirely different plant communities (Blackburn and Anderson 1993). Moreover, aboriginal burning reduced or eliminated the number of high intensity, lightning-generated fires (Reid 1987; Pyne 1993, 1995). Once aboriginal fires opened up the vegetation, then subsequent lightning fires behaved like those set by Native Americans (Pyne 1993, 1995).

Pleistocene considerations

Others, however, contend impacts of Native people were insignificant because these were grazing (i.e., food limited) systems during the Pleistocene (Frank et al. 1998), and, thus, intermountain plant communities are preadapted to withstand high levels of large mammal herbivory (Burkhardt 1996). According to this view, there has not been a long enough period of time since the extinction of the Pleistocene megefauna for plants in the West, and the rest of North and South America as well, to adapt to the low levels of ungulate herbivory caused by native hunters (Burkhardt 1996). However, this contention is incorrect for at least 2 reasons. First, 10,000 years is more than enough time for evolution to work, and second, systems during the Pleistocene were predator limited, not food limited, as is usually assumed.

The rate of evolution depends not on time alone, but on the intensity of selection pressure (Weiner 1994). Evolution can occur quite quickly if natural selection is intense. On the Isle of Jersey off the coast of France, for instance, red deer (*Cervus elephus*) "became reduced to one-sixth of their body weight in less than six thousand years" (Lister 1989:539). On other islands, various poboscideans evolved into forms only 1–2 m tall in <10,000 years (Stuart 1991, 1993). Thus, sufficient time may have passed since the megafauna extinctions for plants to evolve from heavily grazed to lightly grazed forms, especially since heavily grazed plant communities quickly revert to other forms once herbivory is removed (Kay 1990, 1995*c*, 1997*g*; Kay and Chadde 1992).

Moreover, Pleistocene animals were termed megafauna for a reason; they were huge. For herbivores to obtain large body size, however, they must have more than adequate forage intake and nutrition (Geist 1971, 1986, 1987*a*, 1987*b*). Historically, when herbivores reached islands and predators did not, the herbivores invariably became smaller. The reason red deer lost five-sixth of their "normal" body size on the Isle of Jersey was because they were being limited by food, not predation (Lister 1989). As Geist (1987*b*:1067) noted, "Island dwarfs appear to be shaped by efficiency [food] selection in the absence of predation." Thus, if herbivores had been food limited during the Pleistocene, they would not have achieved megafauna size.

Some authors believe that climate change-induced food limitation drove the megafauna to extinction. Others contend that predation, and human predation in particular, caused the megafauna extinctions, not only in the Americas, but around the world (Martin 1967, 1973; Martin and Wright 1967; Martin and Klein 1984; Flannery 1990, 1994; Stuart 1991). Fisher (1996) recently tested the food-extinction and predator-extinction hypotheses by measuring dentinal growth lines in ca. 12,000 BP proboscidean tusks, and found that prehistoric mammoths and mastodons were well fed and had been reproducing at near their maximum theoretical rate, before they went extinct (Fisher 1996, Ward 1997). Not only did native people structure entire ecosystems for the last 12,000 years, but they also may have caused the megafauna extinctions, as well, and, therefore, might be considered the ultimate keystone predator.

Management implications

Whether ecosystems are structured from the top-down or the bottom-up is more than a theoretical debate because it will influence how we manage the Earth's ecosystems, especially in preserves and other protected areas (Diamond 1992*a*, Estes 1996). Most national parks, wilderness areas, and nature reserves, for instance, are supposedly manged to represent the conditions that existed in pre-Columbian times (i.e., so-called natural or pristine conditions; Arcese and Sinclair 1997). But what is natural? If Native Americans determined the structure of entire plant and animal communities by firing the vegetation and limiting ungulate numbers, among other activities, then that is a completely different situation than we have today (Martinez 1993; Wagner and Kay 1993; Kay 1997*a*, 1997*b*). Thus, a hands-off or "natural-regulation" approach by modern land managers will not duplicate the ecological conditions under which those communities developed (Wagner et al. 1995).

Native Americans were not only the ultimate keystone predator but also the ultimate keystone species, whose removal has altered North American ecosystems, even in protected areas. Unless the importance of aboriginal land management is recognized, and modern management practices changed accordingly, our ecosystems will continue to lose the biological diversity and ecological integrity they once had. For, as Aldo Leopold noted >40 years ago, "if we are serious about restoring (or maintaining) ecosystem health and ecological integrity, then we must first know what the land was like to begin with" (Covington and Moore 1994). Native Americans owned, used, and modified nearly all of the New World for ≥12,000 years; to dismiss those people as having had little effect on their environment (Arcese and Sinclair 1997, Vale 1998) is in White's (1995:175) words an act of "immense condescension."

How might these concepts apply to park management? Under the Treaties of 1851 (Kappler 1904:594–596) and 1868 (Kappler 1904:1008–1011), various native people already claim hunting rights in Yellowstone National Park. Thus, 1 way to reduce overgrazing in that park (Wagner et al. 1995) would be to honor the United States' previous commitment to Yellowstone's original owners and to allow them once again to hunt in the park and surrounding areas (Czech 1995, Kay 1997*b*). Native people successfully managed Yellowstone and other North American ecosystems for at least the last 10,000 years, and, although they were not conservationists as that term is commonly used, by keeping ungulate populations low, Native Americans promoted biodiversity, which is the hallmark of a keystone predator (Mills et al. 1993, Power et al. 1996). Similarly, aboriginal burning will have to be reinstated if communities are to retain their ecological integrity (Kay and White 1995). And, finally, it should be remembered that allowing nature to take its course under present conditions (Arcese and Sinclair 1997), so called "natural-regulation" or "hands-off" management, is really a value judgment and a decision that has wide-ranging consequences (Wagner et al. 1995), because areas that today are structured from the bottom-up are entirely different from the ecosystems that were historically and prehistorically structured from the top-down (Wagner and Kay 1993).

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