ABORIGINAL OVERKILL
The Role of Native Americans in Structuring Western Ecosystems

Charles E. Kay
Utah State University

Prior to European influence, predation by Native Americans was the major factor limiting the numbers and distribution of ungulates in the Intermountain West. This hypothesis is based on analyses of (1) the efficiency of Native American predation, including cooperative hunting, use of dogs, food storage, use of nonungulate foods, and hunting methods; (2) optimal-foraging studies; (3) tribal territory boundary zones as prey reservoirs; (4) species ratios, and sex and age of aboriginal ungulate kills; (5) impact of European diseases on aboriginal populations; and (6) synergism between aboriginal and carnivore predation. Native Americans had no effective conservation practices, and the manner in which they harvested ungulates was the exact opposite of any predicted conservation strategy. Native Americans acted in ways that maximized their individual fitness regardless of the impact on the environment. For humans, conservation is seldom an evolutionarily stable strategy. By limiting ungulate numbers and purposefully modifying the vegetation with fire, Native Americans structured entire plant and animal communities. Because ecosystems with native peoples are entirely different than those lacking aboriginal populations, a "hands-off" or "natural regulation" approach by today's land managers will not duplicate the ecological conditions under which those ecosystems developed. The modern concept of wilderness as areas without human influence is a myth. North America was not a "wilderness" waiting to be discovered, instead

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Address all correspondence to Charles E. Kay, Institute of Political Economy, Utah State University, Logan, UT 84322.

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it was home to tens of millions of aboriginal peoples before European-introduced diseases decimated their numbers.

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LESSONS FROM YELLOWSTONE

This research began as a study of elk *(Cervus elaphus)* and vegetation in Yellowstone National Park.[1] When Yellowstone was established as the world's first national park in 1872, government officials did not think that there were enough game animals, so they fed wintering elk, bison *(Bison bison)*, and other ungulates, and they killed predators such as wolves *(Canis lupus)* and mountain lions *(Felis concolor)*. By the late 1920s, however, concerns grew that an unnaturally large elk population was severely overgrazing the park, and in particular Yellowstone's northern winter range. In fact, the Park Service was so convinced elk were destroying Yellowstone that from 1949 to 1968 rangers shot more than 13,500 elk to reduce the northern herd. Faced with mounting political opposition, though, the Park Service abandoned its control program in 1968 and by the early 1970s switched to "natural regulation" or "hands-off," "let-nature-take-its-course" management (Despain et al. 1986; Houston 1982). Agency biologists initially based "natural regulation" on the logistic-growth equation and a presumed balance of nature, but recently the Park Service has cited Caughley's (1976) plant-herbivore model to support its paradigm (Boyce 1991; Coughenour and Singer 1991).

Under "natural regulation," predation is assumed to be an assisting but nonessential adjunct to the regulation of ungulates through density-dependent homeostatic mechanisms. The population and distribution of elk and other wild ungulates are limited by food, and according to the Park Service, it is natural for thousands of animals to starve to death. If wolves or other predators were present, they would only kill animals slated by nature to die of other causes and would not limit or lower ungulate numbers. In the current debate over reintroducing wolves to Yellowstone, the Park Service has never said wolves are needed to control the elk herd, and in fact, the agency adamantly denies that wolves will have any significant impact on Yellowstone's game populations.[2]

The Park Service also denies that Yellowstone was ever or is now overgrazed. Today, the agency contends that large numbers of elk

(12–15,000+) have wintered on the park's northern range for the past 8–10,000 years and that those animals have been in equilibrium with Yellowstone's plant communities. According to the Park Service, any recent (1872–1990) vegetation changes are due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. Under "natural regulation," elk browsing and high-lining (stripping of lower branches for food) of Yellowstone's vegetation are natural and represent the pristine condition of the park. The agency also steadfastly maintains that Yellowstone's elk have not competitively excluded sympatric herbivores, such as smaller ungulates or beaver *(Castor canadensis)*.

Recent studies, however, have failed to find any evidence supporting the "natural regulation" paradigm. Since 1872, tall willows (*Salix* spp.) and aspen *(Populus tremuloides)* have declined by 95% owing to repeated ungulate browsing, not other factors (Kay 1985, 1987, 1990, 1993a; Chadde and Kay 1988, 1991; Kay and Chadde 1992; Patten 1993). Beaver were once exceedingly common on Yellowstone's northern range, as they were throughout the West ca. 1800, but they are now ecologically extinct because elk have eliminated willows and aspen beaver need for food and dam building materials (Kay 1990, 1994; Chadde and Kay 1991). Today, even Engelmann spruce *(Picea engelmannii)*, one of the least palatable species, have been high-lined by starving elk. Historical photographs, though, show that in 1871 Yellowstone's conifers had branches down to the ground, and aspen and willows were unbrowsed (Kay and Wagner 1991). In fact, willows and aspen inside ungulate-proof exclosures today look like those plants did when Yellowstone Park was established, another indication that few elk or other ungulates inhabited Yellowstone during the 1800s, a conclusion supported by the park's early explorers.

Between 1835 and 1876, 20 different parties spent a total of 765 days traveling through the Yellowstone ecosystem on foot or horseback, yet they reported seeing bison only three times—now there are 3,000 to 4,000 bison in the park. Elk were seen by explorers on average only once every 18 days—today there are nearly 60,000 elk in the ecosystem. The fact that many parties broke into small groups and spread out to hunt makes these observation rates all the more meager (Kay 1990). Moreover, while these explorers were in Yellowstone, their first-person journals contain 45 references to a lack of game or a shortage of food. In addition, none of the early parties reported seeing or killing even a single wolf, another indication that ungulates were scarce (Kay 1992a).

Archaeological data suggest that elk were also rare prehistorically. As outlined above, the Park Service's "natural regulation" paradigm assumes that large numbers of elk wintered on Yellowstone's northern range for the past several thousand years and that the relative abundance of ungulate species has not changed over time; that is, elk always dominated the ungulate community. Eighty percent of the ungulates in the Yellowstone ecosystem today are elk, with 15,000 to 25,000 animals on the park's northern range at winter densities of 20 to 40 elk per square kilometer. Assuming that Native Americans killed ungulates in proportion to their abundance and that precolumbian ungulate communities had the same composition as today, then Yellowstone's archaeological sites should be dominated by elk. Elk, however, are rare or even absent from archaeological sites in the Yellowstone area (Table 1) and throughout the Intermountain West, representing only 3% of more than 52,000 unearthed ungulate bones (Wright 1984; Kay 1990, 1992b).[3]

At least six possible factors can be advanced to account for the scarcity of elk in the archaeological record. (1) Perhaps Native Americans could not kill elk, or (2) they may have chosen not to kill elk. (3) Or perhaps elk bones were not brought to sites, inferring a transportation problem. (4) Or conceivably this could have been caused by differential preservation or other taphonomic factors. (5) Then too, special elk processing sites could exist but have never been excavated by archaeologists. (6) And finally, perhaps elk were not present in the mountains simply because they were a plains animal.

First, no evidence exists that Native Americans could not kill elk. Their technology has been more than sufficient to kill all ungulate species for the past 10,000 or so years. Second, optimal-foraging theory and human preferences for meat dispel any notion that native people in the Intermountain West chose not to kill elk. (Both of these findings are discussed below.) Third, the relative scarcity of elk bones in archaeological sites does not appear to be the result of differential transportation. Binford (1978, 1981) and others have suggested that aboriginal hunters, faced with carrying portions of a large ungulate back to distant campsites, would often leave behind lower quality bones in favor of transporting meat. It is unlikely, however, that this factor skewed intermountain archaeological bone deposits for at least three reasons. *(a)* Many archaeological sites are found in close proximity to known ungulate wintering areas so "ditching" bones would probably not have been an overriding consideration. *(b)* Bison bones outnumber elk bones in archaeological sites. Since bison are nearly twice as large as elk, it is improbable that aboriginal hunters would have brought back bones from bison kills but "ditched" elk bones. *(c)* Studies of modern hunter-gatherers have shown that only the largest bull elk fall within the size of animals commonly subject to differential transportation (e.g., O'Connell et al. 1988).

Fourth, the suggestion that differential preservation may somehow

Table 1. The Relative Abundance of Present Ungulate Populations Compared with the Relative Abundance of Ungulate Faunal Remains Unearthed from Archaeological Sites in the Same Areas.

	Species Percentage of Total					
Area, Data Set	*Elk*	*Bison*	*Mule deer*	*Antelope*	*Bighorn sheep*	*Moose*
Greater Yellowstone Ecosystem						
Current ungulate population	79	4	9	1	4	4
Archaeological sites (MNI)	5	15	29	4	46	0
Sunlight Basin[a]						
Current ungulate population	72	0	10	0	14	4
Dead Indian Creek site (NISP)	1	4	67	2	26	0
North Fork of Shoshone[a]						
Current ungulate population	65	0	19	0	14	2
Mummy Cave site (MNI)	1	1	14	0	84	0
Intermountain West						
Archaeological sites (MNI=3,345)	4	11	37	17	30	0.030
Archaeological sites (NISP=52,624)	3	8	56	9	23	0.002

[a]Sunlight Basin and the North Fork of the Shoshone are within the Yellowstone ecosystem just east of Yellowstone Park. See Frison and Walker (1984) and Harris (1978).

Adapted from Kay (1990). MNI = minimum number of individuals, NISP = number of identified specimens

explain the scarcity of elk in archaeological contexts is also not supported by available evidence. Taphonomic studies by Binford (1981) and others have shown that, in general, large dense bones preserve better than small light bones. Based on these considerations, differential preservation should favor elk and work to the detriment of mule deer *(Odocoileus hemionus)* and bighorn sheep *(Ovis canadensis)* bones, the exact opposite of the species-abundance patterns observed at intermountain sites. Based on butchering marks and breakage patterns, there is also no evidence that aboriginal peoples treated elk bones differently from those of other ungulates.

Fifth, although the idea that special elk-processing sites exist but have never been excavated or found by archaeologists cannot be summarily dismissed, the large number of documented habitation sites strongly suggests that this cannot account for the observed pattern. Furthermore, the many types of archaeological sites—from temporary camps to kill sites to base camps and permanent villages—that have been excavated make a bias against elk processing sites doubtful even if the latter existed.

Sixth, based on their archaeological experience in western Wyoming, both Frison (1991) and Wright (1984) conclude that large numbers of elk did not inhabit the mountains in prehistoric times because the species was primarily a plains animal, but this supposition is not supported by ecological data. Biological studies on digestive efficiency, diet breadth, and energetics have all shown that elk are superior competitors to bighorn sheep and mule deer on intermountain winter ranges. Elk will simply outcompete, and outnumber, the smaller ungulates. If elk thrive in the Yellowstone ecosystem and other western mountains today, why were they rare in prehistoric times?

Thus, vegetation data, early photographs, historical first-person journals, and archaeological data all suggest that large numbers of resource-limited ungulates did not inhabit the Yellowstone ecosystem until the onset of European influence. But what is different today, and what could account for this change? Unlike much of North America, the Yellowstone ecosystem has remained relatively intact, except that wolves and Native Americans are no longer present. While early records suggest that wolves were also rare in Yellowstone, first-person journals written between 1835 and 1876 contain 53 references to Native Americans (Kay 1990, 1992a).[4] This led me to consider the role native peoples played in prehistoric ungulate ecology. That research forced me to conclude that prior to European influence, predation by Native Americans limited the numbers and distribution of ungulates in the Yellowstone ecosystem and throughout the Intermountain West.[5]

Although the demonstrated lack of elk in archaeological sites may at first appear to negate my aboriginal overkill hypothesis, in fact, the opposite is true. Optimal-foraging theory (see below) predicts that high-ranked items, like elk or other ungulates, are more susceptible to overexploitation than low-ranked items, such as vegetal foods, small mammals, or fish. According to optimal-foraging models, high-ranked items will seldom appear in the diet if they are being overexploited. So, ungulate species unearthed with the lowest frequency in archaeological sites, such as moose (*Alces alces*, represented by only 1 of more than 52,000 bones) and elk, were probably subjected to extreme overexploitation. Moreover, the small proportion of large mammals in intermountain aboriginal diets, both historically and prehistorically, as well as the highly fragmented nature of archaeologically recovered bone suggest that all species of ungulates were relatively rare for the past 10,000 years.

EVIDENCE THAT PRECOLUMBIAN UNGULATE POPULATIONS WERE LOW

Besides archaeological data, four additional lines of evidence suggest that precolumbian ungulate populations were low and that they were not limited by food: historical journals, aboriginal use of berries such as serviceberry (*Amelanchier alnifolia*), types of wood used for arrow shafts, and tribal buffer zones. First, in addition to the Yellowstone journals discussed above, I have also conducted continuous-time analyses on approximately 100 first-person accounts of the Intermountain West written between 1790 and 1850.[6] Except as noted below, those journals all indicate that game was seldom encountered in the western mountains. For instance, between 1792 and 1871, 21 different parties spent 369 days in the southern Canadian Rockies but reported seeing elk only 12 times (Kay et al. 1994).

A second line of evidence is berry production. Ethnohistoric (e.g., Chamberlin 1911; Lowie 1924) and archaeological studies reveal that Native Americans commonly consumed large quantities of berries, such as serviceberries and chokecherries (*Prunus virginiana*). In September 1869, the Cook-Folsom-Peterson Expedition encountered Native Americans who were gathering and drying large quantities of chokecherries at the mouth of Tom Miner Creek a few kilometers north of Yellowstone Park. "Here we found a wickiup inhabited by two old squaws who were engaged in gathering and drying choke-cherries . . . they had two or three bushels drying in the sun" (Haines 1965:16). 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). Since shrubs have to be at least 2 m tall before branches are commonly broken down by feeding bears, chokecherry plants in 1870 not only produced abundant berries but were also very large.

Conditions today are very different. Serviceberry and chokecherry plants in Yellowstone are now less than 50 cm tall and they produce virtually no berries because the plants are repeatedly browsed by elk and other ungulates (Table 2). Resource-limited ungulate populations and large quantities of berries are mutually exclusive on western ranges. Even moderate numbers of ungulates curtail berry production because these plants provide highly preferred forage, especially in winter. Ungulate-induced berry reduction is even reflected in grizzly bear (*Ursus arctos*) food habits. Whereas grizzlies in Canada and Alaska commonly consume large quantities of berries, bears in the Yellowstone ecosystem do not. From 1977 to 1992 more than 10,000 grizzly bear scats were collected and analyzed in Yellowstone, yet chokecherries were only reported in one scat, serviceberries in two, and buffaloberries (*Shepherdia canadensis*) in 51 (Kay 1993b). The fact that Native Americans in the West consumed large quantities of berries both historically and prehistorically means that ungulate numbers were low and those populations were not limited by food.

A third line of evidence is plant growth form. Ethnographic accounts and archaeological finds indicate that Native Americans preferred to

Table 2. The Effect of Ungulate Browsing on Berry Production in the Yellowstone Ecosystem. The number of berries produced by plants protected from browsing inside ungulate-proof exclosures compared with the number of berries produced by the same species outside the exclosures.

	Number of Berries per 100 Plants		
Exclosure, Species	*Inside*	*Outside*	p
Camp Creek			
Serviceberry	133,307	7	<.001
Lamar-west			
Serviceberry	111,047	0	<.001
Chokecherry	212,178	0	<.001
Uhl Hill			
Serviceberry	10,468	0	<.001
Chokecherry	6,508	0	<.001
Mammoth			
Buffaloberry	119,146	250	<.001
Total	592,654	257	<.001

Adapted from Kay (1993b)

make arrows from serviceberry branches because the wood was very durable and those plants grew straight and tall, especially under aboriginal management such as pruning or burning (e.g., Anderson 1991; Sinopoli 1991). Now, however, repeated browsing of the highly palatable serviceberry makes it difficult to find branches that are long and straight enough for arrows. Even moderate numbers of ungulates severely hedge these plants because serviceberry is so highly preferred. It is impossible to make arrows from any of the serviceberry that exist in Yellowstone today, except where plants are protected from ungulates (Kay 1993b). This is also true on other ranges throughout the West.

A fourth line of evidence is aboriginal buffer zones. Mech (1977, 1994) reported that wolf packs used the edges of their territories less frequently than the central part of their ranges in order to avoid encounters with neighboring wolves. This reduced predation pressure along the territorial edges, which permitted more white-tailed deer *(O. virginianus)* to survive in those areas and to live longer (Hoskinson and Mech 1976). Mech (1977) could find only one other instance of this buffer zone phenomena in the literature, a paper by Hickerson (1965) entitled "The Virginia Deer and Intertribal Buffer Zones in the Upper Mississippi Valley." 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 Chippewa and Sioux, the buffer, in effect a protective zone for the deer, was destroyed and famine ensued.

My research, however, has uncovered frequent references to buffer zones created by Native American hunting. Lewis and Clark (1893: 1197), for instance, 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 nations at war." In 1859, General Raynolds (1868), who led an expedition across the Dakotas and Montana, found an abundance of grass but no game east of the Powder River. Along the Powder River, though, he reported an abundance of game and little grass, whereas to the west he again encountered an abundance of grass and no game. Raynolds (1868:38) noted that

> The presence of these animals [bison] in such large numbers in this barren region [Powder River] is explained by the fact that this valley is a species of neutral ground between the Sioux and the Crows and other bands nearer the mountains, or, more correctly speaking, the common war ground visited only by war parties, who never disturb the game, as they would thereby give notice to their enemies of their presence. For this reason the buffalo remain here undisturbed and indeed would seem to make the valley a place of refuge.

Historical sources indicate that aboriginal hunting tended to extirpate or to drive out game animals (e.g., Post 1938:11), and resource depletion around camps and villages has frequently been reported in studies of modern hunter-gatherers (e.g., Smith and Winterhalder 1992). This pattern would be expected if people pursued an optimal-foraging strategy with no effective conservation practices (see below). Tribal territory boundary zones also explain how early explorers could encounter an abundance of game in a few locations and a lack of game elsewhere. Not only were ungulate populations generally low, but these data strongly suggest that aboriginal hunting limited ungulate numbers. The presence of aboriginal buffer zones also indicates that predation by wolves and other carnivores (see below) was not the primary factor limiting precolumbian ungulate populations.

HOW ABORIGINAL HUNTERS LIMITED UNGULATE POPULATIONS

Aboriginal hunters could limit the numbers of ungulates by several means, including cooperative hunting; use of drives, traps, and corrals;

use of dogs; weapons that kill at a distance; long-distance pursuit; use of snowshoes; food storage; and the use of fire.

Although not often explicitly stated, the idea that prehistoric humans lived a brutish existence and spent every waking moment in the quest for food underlies most biologists' out-of-hand dismissal of Native Americans as important ecological factors. Anthropologists, however, abandoned this stereotype of "primitive" people three decades ago with the publication of Lee's (1968) research on the !Kung and the subsequent "Man the Hunter" conference (Lee and DeVore 1968). Lee demonstrated that the !Kung spent relatively little time in the quest for food despite living in one of the most inhospitable environments on Earth. Lee suggested that "primitive" people had more leisure time than the average person living in today's "most advanced" western civilizations. Sahlins (1972) went so far as to call hunter-gatherers "the original affluent society." Although more recent studies have shown that Lee's original estimates for !Kung work effort were too low, the !Kung and other present-day hunter-gatherers still spend relatively little time provisioning themselves, and they certainly do not live a hand-to-mouth existence (e.g., Hawkes 1987; Hawkes and O'Connell 1981; Hawkes et al. 1985).

Numerous ethnohistoric accounts indicate that Native Americans commonly ran down ungulates (e.g., Anell 1969). Carrier (1984) has even suggested that humans evolved as long-distance endurance predators. Wolves and mountain lions, on the other hand, seldom chase ungulates more than 400 to 800 m. Where there is a differential accumulation of snow in western mountains, Native Americans on snowshoes could simply run ungulates uphill into deeper and deeper snow where they were able to kill the floundering animals, including elk, often with no more than handaxes or clubs (e.g., Lewis and Clark 1893:623; Smith 1974:54–55).

In addition, Native Americans used dogs to hunt all species of ungulates. Because of its effectiveness, that practice has been outlawed in all western states since the inception of modern game management. In the Kalahari, one !Kung with trained hunting dogs brought in 75% of the total meat obtained by one camp, while six hunters who lacked dogs accounted for the remaining 25% (Washburn and Lancaster 1968: 294–295). Not only did Native Americans hunt in a truly cooperative manner, they also employed various drives (including fire drives), traps, and corrals to take all species of ungulates (e.g., Anell 1969). Whether they used spears, atlatls, or bows and arrows, aboriginal peoples in North America have always killed at a distance, thereby reducing the risk of physical injury that carnivorous predators face each time they attempt a kill. Powerful sinew-backed horn bows, common to many intermountain tribes, could drive arrows completely through even the largest ungulates (Townsend 1978).

Humans also derive an advantage from the division of labor in hunter-gatherer societies where males hunt and females gather mainly vegetal foods. Male wolves do not kill with tools, butcher, transport, and share with females who have been gathering other foods that are in turned shared with males. Unlike carnivorous predators, humans usually extend considerable care to sick or injured group members. The success of the hunting and gathering way of life lay in adaptability that permitted a single species to occupy most of the Earth with a minimum of biological adaptation to local conditions (Washburn and Lancaster 1968).

Aboriginal peoples' ability to kill ungulates depended not only on their behavior but also on the prey's. For instance, moose that stand and hold their ground when tested by wolves have a higher probability of survival than individuals that attempt to flee (Peterson 1977). This behavioral strategy, evolved through eons of coevolution, may be adaptive when moose encounter wolves, but the same strategy is fatal when moose are hunted by Native Americans who kill at a distance. Aboriginal peoples used dogs to bay moose in order to take full advantage of this situation. This combination of factors made killing moose extremely easy, despite those animals' large size.

Clearly, native peoples possessed the technical skills and physical means to kill any and all ungulate species, often at will. Native Americans armed with no more than spears, for instance, were able to kill even grizzly bears with little difficulty or risk to human life (Birkedal 1993).

THEORETICAL CONSIDERATIONS SUPPORTING ABORIGINAL LIMITATION OF UNGULATE POPULATIONS

There are also several theoretical considerations that support the hypothesis for aboriginal limitation of ungulate populations, including prey switching and the use of nonungulate foods, optimal-foraging theory, age structure of the kills, sex of the kills, synergism between aboriginal and carnivore predation, and the lack of effective aboriginal conservation practices.

Prey Switching

According to predation theory, a single predatory species cannot take a single prey species to extinction because the energy required to locate the last remaining prey is more than the predator would receive from securing those prey items. Bergerud (1983) demonstrated, however, that prey switching by a single predatory species in a relatively simple ecosystem drove one prey species to near extinction, damped the cyclic fluctuations of a second prey species, and limited the population of a third species, an ungulate. The predator maintained a higher population level by feeding on three prey species than by subsisting on only a single prey. In addition, the predator exerted more predatory pressure on all prey species than it could have exerted if only one had been available.

Prey switching by wolves between age classes of prey, between ungulate species, and even to smaller mammals, like beaver, has been widely reported. Messier (1985) and Messier and Crete (1985) suggest that prey switching to nonungulate foods enabled wolves in Ontario to subsist despite low moose densities. In fact, the wolf populations that they studied would not have been able to survive without nonungulate alternative foods. Voigt et al. (1976) also reported that alternative prey permitted wolves to maintain relatively stable, high-density populations, while Fuller and Keith (1980) found that garbage dumps enabled wolves to achieve higher densities than was otherwise possible.

Unlike purely carnivorous predators, humans can switch from large game to small mammals, fish, insects, or vegetal foods, and ultimately to agriculture. Contrary to the notion that Native American diets were primarily meat (McCabe and McCabe 1984:28), anthropologists have long noted that aboriginal peoples should more appropriately be called gatherer-hunters. Except for Arctic Eskimos and perhaps Plains tribes after the introduction of the horse, vegetal foods and fish comprised 80% to 90% of historical and prehistoric diets, especially in the Intermountain West. Native Americans preferred meat when it was available, however (Webster 1983:44); vegetal foods ranked a poor second despite their high nutritional value (e.g., Gould 1982:77). Moreover, all cultures accorded hunting more prestige and status than they did gathering (Hawkes 1990, 1991, 1992, 1993).

By prey switching to a diet of largely fish or vegetal foods, Native American populations could have continued to grow despite the increasing scarcity of their preferred ungulate foods and diminishing returns of the hunt. In the eastern United States, Webster (1979) reports that the Huron hunted white-tailed deer despite a "considerable energetic loss." Although diminishing returns act as a homeostatic mechanism to control populations of some predators, little such control has operated in the case of humans (Cohen 1977:187). Unlike wolves, humans could severely limit or exterminate ungulates without causing a major decline in their own population because people could rely on vegetal resources or fish. Prey switching and food storage make humans perhaps the most starvation tolerant of all predators, and the more starvation tolerant a predator is, the greater the impact it can have on its preferred prey. Optimal-foraging theory supports similar conclusions.

Optimal-Foraging Theory

Optimal-foraging theory represents an attempt to develop a set of models general enough to apply to a broad range of species yet rigorous and precise enough to explain details of individual behavior. The theory assumes foraging behavior evolved by natural selection to respond to changing conditions in ways that maximize each forager's individual survival and reproductive success. Optimal-foraging theory attempts to specify a general set of decision rules for predators based on cost-benefit considerations which are in turn deducible from first principles of adaptation via natural selection (Stephens and Krebs 1986). Originally developed by biologists to study nonhuman animals, optimal-foraging models have been employed by anthropologists to examine human foraging. They have been used with success to study a number of hunter-gatherer societies, and to improve our understanding of the archaeological record (e.g., Simms 1984).

Recent optimal-foraging research on modern hunter-gatherers has, in general, concluded that (1) men usually hunt while women mostly gather, and only men hunt ungulates; (2) most food selection follows the prey-choice instead of the patch-choice model; (3) ungulates or other large mammals are the highest ranked resources; (4) meat and fats have three to four times more value per calorie than plant foods; (5) hides give ungulates added value; and (6) better hunters have higher reproductive success (e.g., Alvard 1993a, 1993b; Smith 1983, 1991; Smith and Winterhalder 1992; Winterhalder 1987). So not only do ungulates have higher-ranked, energy-based handling efficiencies than most other diet items (i.e., ungulate hunting yields more calories per unit time than the procurement of other foods), they are also valued for their high fat content, hides, and for other social considerations. These additional currencies, and any reproductive advantages that superior hunters may enjoy, have the effect of increasing ungulate handling efficiencies. This makes ungulates even more profitable to pursue and puts additional harvest pressure on them even at low population densities.

According to optimal-foraging theory, ungulates will be taken whenever they are encountered, and a diet of low-ranked items, such as vegetal foods or fish, means that high-ranked items are rare or absent. Recall that aboriginal diets throughout the Intermountain West were high in vegetal foods, small mammals, and fish, all low-ranked items, and low in high-ranked ungulates. This implies that, historically and prehistorically, all ungulate populations were low. Optimal-foraging theory also predicts that high-ranked items are the most susceptible to overexploitation. These factors suggest that in precolumbian times Native Americans were probably overexploiting elk and other ungulates.

At winter densities of 20 to 40 elk per square kilometer, which are now common in Yellowstone Park, optimal-foraging models would predict aboriginal diets should be nearly 100% elk. But archaeologically, that did not happen. This can only mean that few elk were actually available to prehistoric hunters, and that today's ungulate population densities do not represent precolumbian conditions. This is true not only in Yellowstone, but throughout the Intermountain West.

Age Structure of Aboriginal Kills

Archaeologists (e.g., Lyman 1987) have used the shape of mortality profiles to establish whether those ungulates were killed all at once or over a period of time. This catastrophic versus attritional mortality dichotomy, however, is based on the assumptions that the populations from which those samples were drawn had stable age structures and that all age classes were randomly distributed through the populations (Voorhies 1969). Unfortunately, this assumption is not valid because wild ungulate populations rarely exhibit stable age structures (Eberhardt 1987:117) and because most ungulates segregate by sex or age (e.g., Clutton-Brock et al. 1985).[7] Although mortality profiles do not indicate how animals were killed, they do provide an estimation of predator effectiveness and relative ungulate mortality rates. A population subjected to increasing predation will be dominated by younger animals.

Ecological studies (e.g., Carbyn et al. 1993) have shown that wolves and mountain lions usually kill a disproportionate number of young-of-the-year and old ungulates (Figure 1a). Carnivores also tend to prey on sick, malnourished, or otherwise debilitated animals. Temple (1987:669) notes that "The degree to which substandard individuals of a particular prey species are taken disproportionately by a predator seems to be a direct function of how difficult it normally is for the predator to capture and kill individuals of that species." The more difficult it is for a predator to capture a particular prey, the more that predator will take substandard individuals and young. If two or more predators are preying upon the same species, the least efficient predator will tend to kill fewer prime-age animals (Okarma 1984).

While wolves and other carnivores kill primarily young-of-the-year and old animals, Native Americans killed mostly prime-age ungulates. For instance, Frison (1971) excavated a pre-horse Shoshone antelope (*Antilocapra americana*) processing site in Wyoming's upper Green River Basin. Of 79 antelope at the Eden-Farson site whose ages could be determined, 80% were less than 2.3 years old and none were older than 6.3 years (Nimmo 1971). During 1985, the Wyoming Game and Fish Depart-

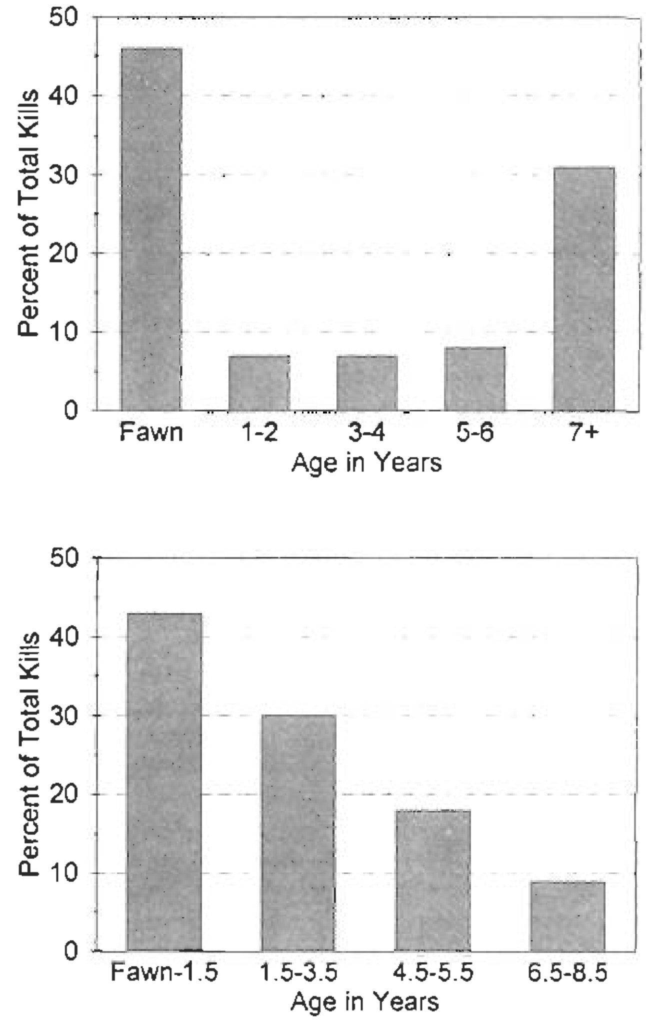

Figure 1. Age structure of ungulates killed by wolves and Native Americans. *(a)* Age structure of white-tailed deer killed by wolves in Minnesota (Fritts and Mech 1981). Wolves and other North American carnivores generally take a disproportionate number of very young and very old animals. *(b)* Age structure of mule deer unearthed from the (4200 BP) Dead Indian Creek archaeological site in northwest Wyoming east of Yellowstone Park (Simpson 1984). Unlike carnivores, Native Americans killed a predominance of prime-age ungulates—an indication that Native Americans were more efficient predators. This also indicates that aboriginal peoples had a greater impact on prey population dynamics than carnivores, especially given the fact that natives killed mostly females (see text).

ment live-trapped 333 antelope in that same area (Roper 1986). Those antelope included fewer fawns and more old individuals than the aboriginally hunted animals. That is to say, the antelope killed by Native Americans had a younger age structure than today's herd, which is heavily harvested by modern hunters. The 4,200-year-old Dead Indian Creek site is located in Wyoming's Sunlight Basin near the northeast boundary of Yellowstone Park (Frison and Walker 1984). Mule deer dominate the ungulate faunal remains from that site (Table 1). Forty-three percent of the aged deer ($n = 60$) were less than 1.5 years old, 73% were under 3.5 years, and 92% were less than 5.5 years old (Figure 1b).

Since ungulates recovered from intermountain archaeological sites usually exhibit mortality profiles dominated by prime-age animals, this suggests that, in general, Native Americans were more efficient ungulate predators than wolves or other carnivores. Killing mostly prime age animals, however, runs contrary to any maximum sustained yield strategy (Hastings 1983, 1984; Michod 1979) and indicates that Native Americans could have had a major impact on precolumbian ungulate populations. This is even more true when one considers the sex of ungulates killed by Native Americans.

Sex of Aboriginal Kills

Demographic studies (e.g., Nelson and Peek 1982) have shown that ungulate populations are most sensitive to adult female mortality. To maximize sustainable harvest, few prime-age females should be killed (e.g., Short 1979). If too many adult females are killed, the population will fall, often precipitously. Ecological studies have found that wolves and mountain lions kill a disproportionate number of males. Some authors claim that Native Americans also spared females so there would be no diminution in the supply of game animals (Heizer 1955:4–5; Roberts 1932:290). This contention, however, is not supported by historical accounts, studies of modern hunter-gatherers, or archaeological data (e.g., Alvard 1993a; Teit 1928:243; Wright and Miller 1976:301). Instead, Native Americans preferred to kill females because those animals were fatter and had better hides than males.

All aboriginal people have a preference for animal fats over nearly all other foods (e.g., Speth 1987; Speth and Spielmann 1983). The consumption of animals fats may even have been a physiological necessity for many Native Americans (e.g., Speth 1989, 1991; Spielmann 1989). This demand for fats would have caused native hunters to kill a disproportionate number of females because, for most of the year, female ungulates have greater stores of fat than males, especially during fall

and early winter (e.g., Anderson et al. 1972; Flook 1970). Moreover, prime-age ungulates have larger fat deposits than young animals (Johns et al. 1984).

Nelson (1973:98, 1983:165), Binford (1978:40), Speth (1983), and others have reported that hunters tend to take the age and sex classes of ungulates that have the greatest fat levels during any particular hunt. Nelson (1983:165) notes that "skilled hunters can pick out the best animals [moose] at a glance by their dark color, the curve of their back and their general fullness." In addition, females were generally preferred because they have better hides than males. They lack thick dermal shields, which makes their hides easier to tan, and females are seldom scarred from intraspecific fighting (Geist 1986; Post 1938:19).

In summary, wolves and mountain lions kill primarily those age and sex classes that have the lowest relative reproductive value; namely young-of-the-year, the old, the unfit, and males, whereas Native Americans focused their efforts on animals with the greatest reproductive value, such as prime-age individuals and females. For a given number of ungulates harvested, Native Americans had a greater impact on prey populations than if carnivorous predators had killed an identical number of animals. It is doubtful that the Native Americans' propensity for harvesting prime-age animals and females would ever have led to an offtake approaching maximum sustained yield (e.g., Hastings 1983, 1984).

Carnivore Predation

Recent research in Alaska and Canada indicates that wolves and other carnivores, more often than not, limit ungulate populations (e.g., Carbyn et al. 1993; Gasaway et al. 1992; Messier 1991, 1994; Seip 1991, 1992). These studies can be summarized as follows. (1) In many situations, wolves and other predators limit ungulate populations below the level set by food resources; that is, ungulates are not resource limited or "naturally regulated," and any compensatory response of the ungulate population to predators is not enough to offset predation losses. (2) Human and carnivore predation on ungulate populations are additive, not compensatory. (3) If grizzly or black bears (*Ursus americanus*) are present, they often prey heavily on newborn and, to a lesser degree, adult ungulates. Wolf and bear predation are additive, not compensatory, and together can have a major impact on ungulate numbers. (4) If ungulate populations have been reduced by severe weather, human overexploitation, or other causes, wolves and other predators can drive ungulate numbers even lower and maintain them at that level. This condition is commonly called a predator pit, and there is no field evidence that ungulates can escape from a predator pit even if hunting is banned, unless wolves and other predators are reduced. As Alaska biologists have noted, "prey [ungulate] populations can reach extremely low densities under natural conditions, contrary to the 'balance of nature' concept" (Gasaway et al. 1983:6). Throughout much of Alaska and Canada, ungulate populations are now being kept at low levels by the combined actions of carnivorous predators even in areas where they are not hunted.

Wolves and other carnivores limit ungulate numbers by reducing recruitment and increasing adult mortality, not by killing off all the game, instances of surplus killing notwithstanding. In any given year, a number of adults die from natural causes, disease, or predation. When expressed as a percentage, this is termed the adult mortality rate. In that same year, a number of calves or fawns are born, but those young also face disease, accidents, and predation, and only a few survive their first year of life to join the adult population. This is called the recruitment rate. For a stable population, recruitment, and especially female recruitment, must balance adult mortality. If recruitment is less, the population declines, and if it is greater, numbers increase (Bergerud 1990, 1992).

As indicated above, wolves and other carnivores prey most heavily on young-of-the-year, which lowers the recruitment rate of the prey populations. Predators also kill a few prime-age adults (Figure 1a). By increasing adult female mortality and at the same time lowering recruitment, carnivores can cause ungulate populations to decline. Stabilizing recruitment for caribou is about 15 female yearlings per 100 cows. Caribou herds with few predators have recruitment rates of 20 to 40 female yearlings per 100 cows, which allow those populations to increase, whereas caribou herds subject to heavy predation have recruitment rates of 10 or less. So predation causes ungulate populations to gradually decline over time—wolves do not normally wipe out game herds in a single year or two.

This slow decline is what happened in Alaska and Canada. During the 1950s and 1960s, when wolf control was widespread and effective, game herds grew and the north country became known as a hunter's paradise. Government wolf control ended by 1970, and predator populations began to expand, but it took ten or more years before significant declines were seen in game herds. In Wood Buffalo National Park, for instance, there were approximately 12,000 bison when wolf control was terminated, but today there are fewer than 3,500 and the population is still falling. Wolf predation of calves has been identified as the primary factor responsible for that decline, since the bison are not hunted (Carbyn et al. 1993).

Across Canada and Alaska, moose and caribou populations not subject to heavy predation have densities ten times greater than populations where carnivore numbers are high (e.g., Gasaway et al. 1992; Messier 1994). The presence of large numbers of carnivores reduces the numbers of ungulates available for human hunters by up to 90% or more. As in the case of Wood Buffalo National Park, wolves alone can completely eliminate any "surplus" ungulates that would otherwise be available for human consumption.[6] Moreover, if carnivore predators can limit ungulate numbers, and if they are less efficient predators than Native Americans, as I have argued, then it is easy to see how aboriginal peoples could have had a major impact on precolumbian ungulate populations.

Predator-prey models have also been developed in which carnivore and human predation act in concert on ungulate populations (Haber 1977; Walters et al. 1981). Computer simulations with these models have shown that small amounts of human predation added to wolf-bear-ungulate systems can cause the virtual collapse of both ungulate and wolf populations, even if humans are limited to killing only males (Figure 2). That is to say, the combined action of hunting and carnivore predation on a common ungulate prey is additive and synergistic, not compensatory. So if Native American hunters even slightly lowered ungulate numbers, carnivores alone could continue to drive prey numbers lower, and keep those herds from recovering. Carnivore predation not only greatly complicates any harvest system, maximum sustained yield or otherwise, it also probably precluded Native Americans from developing specific practices to conserve ungulates.

Aboriginal Conservation

The American natives' role in nature has often been viewed as that of conservationists who were too wise and knowledgeable to overexploit their environment (McCabe and McCabe 1984:57). This belief, which can be traced to Rousseau's concept of the "noble savage," has a long history in the popular press (Speck 1913, 1939a, 1939b; Roberts 1932). The environmental movement in the late 1960s and early 1970s further romanticized the image of hunter-gatherers as original conservationists (Steinhart 1984). The idea that aboriginal peoples did not damage their resource base, which has been implicitly assumed by most anthropological theory since the beginning of that discipline (Heizer 1955), is still popular in some circles (Feit 1987, and others). I, however, have been unable to find any evidence that Native Americans effectively conserved ungulates.

Early writers claimed that defended exclusive use areas were com-

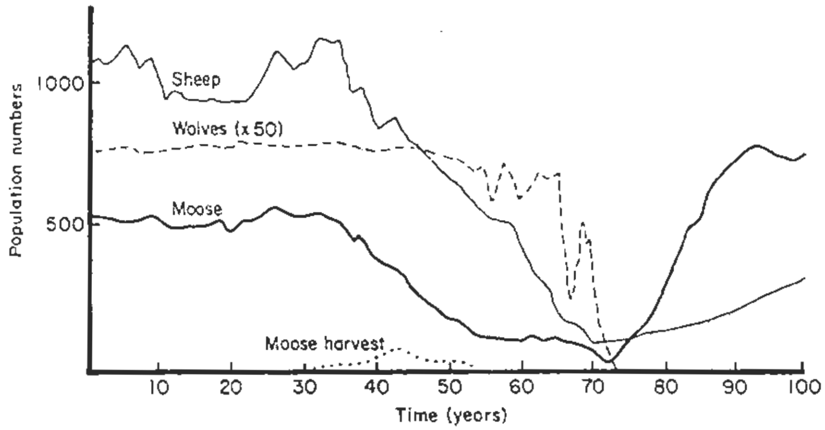

Figure 2. Model of Alaskan wolf-ungulate interactions simulated under circumstances in which human harvest of moose triggered a catastrophic decline in both predator and prey. Without hunting, numbers of wolves, moose, and Dall sheep *(Ovis dalli)* are low but relatively stable. The addition of a small human harvest of moose, however, destabilizes the entire system. Even after hunting is halted, wolves continue to drive the moose population downward. The wolves then switch to Dall sheep and drive their numbers down as well. In this simulation, wolves go extinct before they can kill the few remaining ungulates, allowing prey populations to recover. This would not be the case, though, if humans continued to prey on the ungulates. Grizzly bear predation on newborn moose calves, and to a lesser extent on adults, is also important in this system, but that factor was not modeled separately. Instead, grizzly predation was included in calculation of moose survival rates internal to the model. Adapted from Haber (1977) and Walters et al. (1981).

mon, if not universal, among Native Americans (Heizer 1955:5). Although the origin of hunting territories has a long history of controversy, today most anthropologists hold the view that they were not aboriginal, but developed with the fur trade (e.g., Albers and Kay 1987; Bishop 1970). Even if we ignore the available evidence and grant that Native Americans were able to exclude other humans from their personal hunting territories, the problem is that they still never had exclusive use of the ungulates in those or any other areas. Carnivores were free to prey on any and all unguiates. This would have lowered territorial benefits and made exclusive use areas uneconomical to defend (Dyson-Hudson and Smith 1978). So it is likely that carnivore predation precluded the formation of hunting territories specifically designed to conserve ungulate numbers.

Early writers also claimed that each native hunter "can tell at any time the number of animals which he can dispose of each year in his district without damaging his supply" (McLeod 1936:565). More recently, some anthropologists have asserted that native peoples harvested ungulates under principles similar to sustained yield management (Feit 1987; Nelson 1982), but Native American preference for prime-age females runs counter to any maximum sustained yield or conservation strategy.

Others have contended that Native Americans' religious belief systems prevented those peoples from overutilizing their resources (e.g., Speck 1939b; Nelson 1983). Native Americans tended to view wildlife as their spiritual kin and believed that success in the hunt was obtained by following prescribed rituals and atonement after the kill (e.g., Bettinger and Baumhoff 1982:503; Feit 1987). A scarcity of animals or hunting failures were not viewed as biological or ecological phenomena, but rather as a spiritual consequence of social events or circumstances. If a Native American could not find any game, it was not because he had overharvested the resource, but because he had done something to displease the gods. Since Native Americans saw no connection between their hunting and game numbers, their system of religious beliefs actually fostered the overexploitation of ungulate populations. Religious respect for animals does not equal conservation.

Jacobs (1971:237) and others have asserted that, "Native peoples lived according to what the conservationist Aldo Leopold has called a land ethic." Despite the widespread acceptance of the assumption that environmental attitudes predicate a society's actual environmental impacts, scholars have demonstrated the inadequacy of that paradigm (J. Kay 1985a, 1985b; Kay and Brown 1985; Tuan 1968, 1970). That is to say, there is no correlation between how a people say they are managing their resources and how they actually treat their environment. Belief systems are only a small part of the factors that influence how a people interact with their environment. There is no evidence that belief systems in and of themselves foster the actual implementation of conservation practices.

In summary, Native Americans had no practices that were specifically designed to conserve ungulates.[4] All native hunters are essentially opportunistic and tend to take high-ranking ungulates regardless of the size of the prey populations or the likelihood of their becoming extinct. Native Americans had no concept of maximum sustained yield and did not manage ungulate populations to produce the greatest offtake. Human predation and predation by carnivores are additive and work in concert to reduce ungulate numbers. Moreover, competition from carnivores tended to negate any possible conservation practices.

ABORIGINAL POPULATIONS AND THE WILDERNESS MYTH

The idea that human populations purposefully limit their numbers so they will not overuse their resources has a long history in anthropology (Bates and Lees 1979). Some have claimed that the mere existence of human populations living in long-term relationships with ungulate species would seem, a priori, to argue for the existence of effective aboriginal management systems to prevent irrevocable depletion or extirpation of those resources (Freeman 1985). Coupled with this concept is the notion of limited needs. Hunter-gatherers, who were thought to need little, limited what they took from available resources (Hawkes et al. 1985).

Questions regarding aboriginal numbers are important since they indicate how often resource patches or hunting areas would have been revisited, as well as the total pressure exerted on the resource base. The idea that humans self-regulated their numbers relies on a group-selection argument. Since in practice groups do not go extinct often enough for group selection to be an important evolutionary force, individual selection will always be more powerful (Heinen and Low 1992). The long intervals between births in some hunter-gatherer societies, though, have been cited as practices that balance human population with resources. Blurton-Jones (1986, 1987b), however, has demonstrated that birth intervals are limited by biological considerations, not by social constraints. Hawkes et al. (1985) and Hawkes (1987) have found the concept of limited needs inaccurate; foragers respond instead to biological considerations, not to preordained social restraints. Blurton-Jones (1987a) suggests that low work rates may also be due to sharing or tolerated-theft considerations, not to measures that conserve resources. Hawkes (1990, 1991, 1992, 1993) postulates that male reproductive strategies designed to maximize individual fitness may effectively limit human population growth.

Writers have long recognized that Native Americans lacked immunological resistance to epidemic and endemic European diseases and that many epidemics reduced aboriginal numbers by 50% to 90% at each passing (e.g., Cook and Lovell 1992; Stearn and Stearn 1945). Only recently, however, has it been realized that many epidemics swept in advance of even the earliest explorers. Dobyns (1983) postulated that Native American populations were severely reduced 100 to 200 years before the first European chroniclers. Ramenofsky (1987), who tested Dobyns's hypothesis against the archaeological record, found that the tribes along the middle Missouri River were decimated by European

disease ca. AD 1600, two hundred years before the arrival of Lewis and Clark. Campbell (1990) tested Dobyns's hypothesis against the archaeological record of the Columbia Plateau and concluded that European disease decimated those aboriginal populations ca. AD 1550. Taking this factor into consideration, several authors have recently revised aboriginal population estimates for North America upwards by as much as tenfold, to 100 million or more. These new figures suggest that precolumbian Native American populations were of sufficient size to make overexploitation of ungulates highly probable. Besides, as explained above (see Figure 2), human predation does not have to be particularly intense to trigger a collapse of ungulate numbers.

North America was not a "wilderness" waiting to be "discovered" but instead was home to tens of millions of aboriginal peoples before European-introduced diseases decimated their numbers. Prior to European arrival, most of this continent was owned, used, and modified by native peoples (e.g., Denevan 1992; Gomez-Pompa and Kaus 1992; Simms 1992). The idea that North America was a "wilderness" untouched by the hand of man prior to 1492 is a myth, a myth created, in part, to justify appropriation of aboriginal lands and the genocide that befell native peoples (Bowden 1992).

TESTING THE ABORIGINAL OVERKILL HYPOTHESIS

As discussed, my aboriginal overkill hypothesis developed from research in the Yellowstone ecosystem. To evaluate that paradigm's wider applicability, I tested it on several longstanding ecological problems in western North America. These included (1) why large herds of bison and other ungulates were absent from the Columbian Basin at historical contact and in precolumbian times; (2) the biogeography of moose in western North America—why moose were exceedingly rare or absent from the northern Rockies, most of British Columbia, and much of Alaska historically and prehistorically—areas that today support several hundred thousand moose; (3) the Kaibab deer incident in northern Arizona—what kept deer numbers low historically and prehistorically and why the population irrupted and severely overgrazed the range ca. 1920; and (4) why mule deer were rare in the Great Basin historically and in precolumbian times, only to irrupt in the early 1900s.

In each of these cases, I reviewed the various hypotheses that have been proposed to explain the observed variation in ungulate abundance. In all instances, I found that the available data do not support other interpretations but do support the aboriginal overkill model. (Papers on each of these subjects are in preparation.) Thus, aboriginal overkill appears to be a robust hypothesis that applies not only to elk but also to moose, bison, mule deer, and other ungulates throughout the Intermountain West, and I suspect that it applies to other areas of the Americas as well.[10] Birkedal (1993), for instance, suggested that aboriginal hunting even limited grizzly bear populations.

ARCHAEOLOGICAL DATA REVISITED

If my hypothesis is correct and if Dobyns's disease paradigm is true, the first wave of European diseases decimated Native American populations about 500 years ago, which in turn resulted in less hunting pressure and in greater numbers of ungulates, especially those most susceptible to overexploitation. These changes should then have been reflected by an increase in those species' relative abundances in human diets. As predicted, this pattern is observed in the archaeological record. Elk, in any number, first appeared in the intermountain archaeological record only 500 years ago (Frison 1991), and published reports indicate an identical pattern of mule deer abundance in Great Basin archaeological sites (Kay 1990). In Alaska and the western subarctic, moose bones do not appear in any numbers at archaeological sites until the past 500 years (Yesner 1989).

Similarly, if my aboriginal overkill hypothesis is correct, then archaeological sites used by aboriginal peoples who exploited or lived in cultural boundary zones should contain a higher proportion of elk remains than sites situated within the main cultural areas. And if Dobyns's disease hypothesis is correct, the proportion of elk should increase in those sites after ca. AD 1500. Such a pattern is observed, for instance, in the Nicola Valley of south-central British Columbia. "The Nicola Valley (and Canadian Okanogon) lack, to a great extent, the anadromous fish resources of the Thompson and Fraser Rivers to the west and north, and the American Okanogon to the south. This lack, combined with local topography, made [the Nicola] a valley region of comparatively low population density with social ties to the more resourceful region to the west and part of a prehistoric 'buffer zone' serving to maintain the Northern Plateau–Southern Plateau [cultural] boundary" (Wyatt 1972: abstract). At historical contact, an Athabaskan isolate, the Nicola, were surrounded by more numerous and powerful Interior Salish–speaking groups (Wyatt 1972:7).

Wyatt (1972) excavated eleven archaeological sites in the Nicola Valley. Of the ungulate faunal remains recovered and dated between 2200 and 500 BP, elk represented 44%. Archaeological sites located in areas to the north and west (e.g., Langemann 1987; Rousseau and Richards 1988) and south (e.g., Campbell 1985) contain, on average, less than 5% elk. After ca. 500 BP, the proportion of elk in Nicola Valley sites increased to 70% of recovered ungulate remains (Wyatt 1972). So, spacial and temporal patterns of archaeologically recovered ungulate faunal remains support both the aboriginal overkill hypothesis and Dobyns's disease paradigm. There are, however, exceptions to aboriginal overkill.

EXCEPTIONS TO ABORIGINAL OVERKILL

According to predator-prey theory, prey populations will increase if they have a refugium where they are safe from predation (e.g., Taylor 1984). So, ungulates that could avoid aboriginal hunters should have been more abundant. Moreover, refugia do not have to be complete to be effective. Partial refugia will also enable prey populations to survive.

Unlike in other areas of the West, archaeological sites on the Washington, Oregon, and British Columbia coasts usually contain elk remains. Of the ungulate bones unearthed at those sites, elk constitute about 50% (Kay 1990). Thick coastal forests provided some refuge for elk because the plant communities were usually too wet to burn. Native peoples could not employ fire to open up the country and make hunting easier to the same extent that they did in other ecosystems (Lewis 1973, 1977; Lewis and Ferguson 1988). Because coastal regions receive little snowfall, aboriginal hunters also could not kill animals by chasing them into deep snow as natives commonly did elsewhere.

Early explorers reported that elk were also common in California's Central Valley along the Sacramento and San Joaquin rivers (McCullough 1971). When disturbed, however, those animals would flee into swamps where they could not be hunted. This behavior was observed by John Work (1945:62), who led a Hudson's Bay Company fur brigade through California in 1831–1832.

> The people are rather short of food and no more can be got, the hunters are not able to kill the elk. There are a good many along the marshy borders of the lake but they seldom venture out on the hard ground and when any of them happen to be found out, they fly immediately in among the water and bulrushes where they cannot be pursued.

Work noted, however, that when floodwaters forced elk from the swamps, they were easily killed by native peoples, who often simply ran the animals down and killed them with knives or spears. Without refuge provided by the tule swamps, large herds of elk would not have survived in California's Central Valley.

Herds of bison on the Great Plains and caribou in the Arctic had no physical refugia; instead they had refugia in time. By undertaking extensive migrations, bison and caribou were able to outdistance most of their human and carnivorous predators. Wolves with young, for instance, simply could not keep pace with or even follow the migrating herds (Bergerud 1990, 1992). The same was true of humans who had to transport children, as well as their possessions. Caribou that migrate long distances today have densities ten times greater than nonmigratory populations (Seip 1991).

Research in Africa's Serengeti has shown that resident ungulates are limited by predators while migratory animals are not and that Serengeti ungulates migrate primarily to avoid predation, not to secure food (Crete and Huot 1993:2295; Fryxell et al. 1988). I suggest that this was also the case in North America, and that bison and caribou would have been much less abundant if they had not migrated long distances. Migration not only took bison and caribou beyond the reach of most humans, but the Great Plains and the Arctic tundra provided few alternative foods that could sustain aboriginal populations when ungulates migrated. As noted above, tribal boundary or buffer zones also provided refugia for ungulate populations. Without refugia, few ungulates would have been able to withstand the onslaught of human predators.

IMPLICATIONS OF ABORIGINAL OVERKILL

My ideas regarding predation by Native Americans have significant implications for conservation biology, management of natural areas, wilderness management, national park management, range management, and wildlife biology, as well as anthropology-archaeology, since those disciplines seldom consider the impact prehistoric human populations had on their resource base or how aboriginal activities may have structured entire ecosystems. For instance, most national parks, wilderness areas, and natural areas are supposedly managed to represent the conditions that existed in precolumbian times (i.e., so-called natural or pristine conditions). But what is natural? If Native Americans limited ungulate numbers, which in turn determined the structure of entire plant and animal communities, that is a completely different situation than letting resource-limited ungulates do the same (Wagner and Kay 1993). A "hands-off" or "natural regulation" approach by modern land managers will not duplicate the ecological conditions under which those communities developed. If aboriginal predation and burning created those communities, then the only way to maintain what we call "natural areas" today is to duplicate aboriginal influences and processes.

Systems with native peoples are entirely different from those without aboriginal populations (e.g., Western and Gichohi 1993). In fact, the modern concept of wilderness, as areas without human influence, is a myth. As Gomez-Pompa and Kaus (1992) have pointed out, the only "wilderness" is in the mind of Europeans. Setting aside an area as wilderness today will not preserve some remnant of the past but instead create conditions that have not existed for the past 10,000 years. Here in North America, for instance, we view the Amazon as a wilderness to be saved and protected, but to indigenous peoples it is a home—a home they have modified to suit human needs (e.g., Balée 1989).

Likewise, anthropologists have formulated many of their ideas of prehistoric human ecology around the assumption that aboriginal peoples did not overuse their resources and harvested ungulate populations at maximum sustained yield. The data I have collected, though, show that not only did Native Americans have no effective practices to conserve ungulates, but the manner in which those peoples harvested ungulates was, in most instances, the exact opposite of any predicted conservation strategy. For humans, conservation is seldom an evolutionarily stable strategy (e.g., Butzer 1992; Denevan 1992; Diamond 1988, 1992; Heinen and Low 1992). I have also been unable to find any evidence that Native Americans' system of religious beliefs prevented aboriginal peoples from overutilizing ungulate populations. There is little correlation between how a people say they are managing their resources and what they actually do. Instead of being "noble savages" who were too wise to overexploit their resources, Native Americans acted in ways that maximized their individual fitness regardless of their impacts on the environment. Native Americans were the ultimate keystone species that once structured entire ecosystems (Mills et al. 1993). What I am proposing is a major paradigm shift of how ecosystems and aboriginal peoples should be viewed.

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The author received his Ph.D. in wildlife ecology from Utah State University in 1990 and is a Natural Resource Policy Associate with the Institute of Political Economy at Utah State University. He is presently working for Parks Canada on an assessment of the long-term ecosystem states and processes in the central Canadian Rockies. A book on the Yellowstone ecosystem is in press and another book on aboriginal overkill is forthcoming.

NOTES

1. This paper is based on a presentation given at the 92nd annual meeting of the American Anthropological Association held at Washington, D.C. in November 1993. A forthcoming book will include additional data, as well as several thousand citations. This paper contains only an outline of my aboriginal overkill hypothesis, not the full weight of available evidence. Space also precluded developing many topics in detail.

2. Human subsistence studies invariably make this same assumption: that is, carnivore predators had little or no impact on the number of ungulates available to aboriginal people. This assumption, though, is incorrect (as shown in this paper).

3. Kay (1990) contains MNI and NISP data for ungulates unearthed at nearly 300 individual archaeological sites in Wyoming, Montana, Utah, Washington, Oregon, Nevada, and Idaho. I have also completed an analysis of ungulate faunal remains recovered from archaeological sites in the southern Canadian Rockies, and those data exhibit a similar pattern (Kay et al. 1994). Archaeologically, elk were rare where they are now common.

4. Yellowstone was not "officially" discovered by Europeans until 1869 and was one of the last regions to be explored in the western United States (Haines 1977). Moreover, Yellowstone was not on established travel routes and therefore was subject to less direct European disturbance than other areas. The Mountain Shoshone, who inhabited Yellowstone at historical contact, lacked both horses and firearms. So, native participation in the fur trade cannot be blamed for the absence of game in Yellowstone ca. 1800, as was true in some areas.

5. Although my research has been limited to western North America, I suspect aboriginal overkill may be a universal attribute of hunter-gatherer societies, except where prey (ungulates) have refugia (discussed in the section on "Exceptions").

6. These data will be presented in forthcoming publications.

7. To exhibit a stable age distribution, a population must have a constant birth rate, constant age-specific death rates, and a constant size—the population can neither increase or decrease. These conditions rarely, if ever, occur in the wild, and there is no evidence that all three occur simultaneously in any free-ranging ungulate population not subject to human exploitation (e.g., Hamlin and Mackie 1989).

8. Aside from Mithen (1986, 1987, 1989, 1990), I am not aware of any anthropologist or archaeologist who has seriously considered the role that carnivores played in limiting prehistoric ungulate populations, which, in turn, constrained human subsistence patterns. Invariably, human subsistence studies assume that carnivore predation was unimportant and that humans harvested populations at maximum sustained yield based on modern food-limited ungulate population densities (e.g., Osborn 1993). Since both these assumptions are incorrect, published human subsistence strategies must be viewed with caution.

9. The formation of aboriginal buffer zones with their higher ungulate densities, as previously discussed, was an artifact of group or tribal interactions, not the outcome of practices designed to conserve ungulates. Thus, aboriginal buffer zones cannot be considered a conservation practice per se (Alvard 1993a, 1993b) even though they may have permitted localized ungulate populations to prosper.

10. The exact impact of native hunting varied, depending on the abundance of alternative human foods, the behavior of the specific ungulates, the techniques used to hunt those ungulates, and whether or not the ungulates had refugia where they could escape predation, among other factors.

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