

Wildlife Encounters by Lewis and Clark: A Spatial Analysis of Interactions between Native Americans and Wildlife

ANDREA S. LALIBERTE AND WILLIAM J. RIPPLE

The Lewis and Clark journals contain some of the earliest and most detailed written descriptions of a large part of the United States before Euro-American settlement. We used the journal entries to assess the influence of humans on wildlife distribution and abundance. Areas with denser human population, such as the Columbia Basin and the Pacific Coast, had lower species diversity and a lower abundance of large mammals. The opposite effect was observed on the Plains. We believe that overhunting before Euro-American contact and the introduction of the horse, which heightened the effects of hunting, may have been major contributors to the historical absence of some species that are present in the archaeological record. The results show considerable human influence on wildlife even under relatively low human population densities. This finding has major implications for conservation biology and ecological restoration, as human influence is often underestimated when considering presettlement conditions.

Keywords: historical ecology, Lewis and Clark, wildlife distribution, buffer zones, predation

Historical reference conditions are often used as a baseline for comparison with current and future natural resource management regimes (Aronson et al. 1995). There may be much debate about which point in time, what area, and what spatial extent should be used as a reference condition (Wagner et al. 2000), but understanding the past is undeniably important to the proper management of present and future ecosystem conditions. First-hand explorer journals offer one way to assess the past. The journals of Lewis and Clark's 1804–1806 expedition provide the earliest and most detailed written descriptions of a large part of the United States before Euro-American settlement, as well as geographic coordinates of daily campsites.

Human influence on North American ecosystems before European settlement has to be considered, because indigenous peoples brought about changes to the environment long before the arrival of the first Europeans. Native people used fire, modified vegetation, and influenced animal populations, with the result that North America was not a pristine wilderness (White and Cronon 1998). It is well known that Lewis and Clark found an abundance of wildlife in the Plains but encountered little game in parts of the Rocky Mountains and the Columbia Basin, where they often had to rely on dogs and horses for sustenance (Cutright 1969, Ronda 1984). On the basis of those observations, we hypothesized that predation attributable to humans was at least in part responsible

for the observed wildlife distribution and abundance. This hypothesis leads to the prediction that wildlife would be more abundant farther from human settlements. In this article, we assess the role of humans and other underlying causes for the observed wildlife distribution and abundance along the Lewis and Clark trail.

Buffer zones and predation

Prey can escape predators in the relative safety of a refugium, where prey populations can increase (Taylor 1984). Applied to human hunters, the theory is that wildlife may be able to escape predation in such an area, where the human population density and predation risk are low. Several examples exist in which wildlife has been observed to be more abundant in so-called buffer zones, areas with low numbers of mammalian or human predators. In a declining population of white-tailed deer, survivors were found almost exclusively

Andrea S. Laliberte (e-mail: alaliber@nmsu.edu) is a rangeland remote sensing scientist for the US Department of Agriculture's Agricultural Research Service at the Jornada Experimental Range, Las Cruces, NM 88003. William J. Ripple (e-mail: Bill.Ripple@orst.edu) is a professor in the Environmental Remote Sensing Applications Laboratory in the Department of Forest Resources, Oregon State University, Corvallis, OR 97331. © 2003 American Institute of Biological Sciences.

along the edges of wolf territories; wolves avoided those zones to reduce encounters with the neighboring packs (Mech 1977). Researchers studying trophic cascades hypothesized that wolves could positively influence plant growth through a predation-risk effect by changing elk movement and browsing patterns (Ripple and Larsen 2000, Ripple et al. 2001).

Similar observations have been made with humans as predators. In a buffer zone between the Chippewa and Sioux Indians in Minnesota, deer were plentiful in the area between the warring tribes; however, once a truce had been established, the buffer ceased to exist. Deer were hunted extensively again, their numbers declined rapidly, and a famine ensued (Hickerson 1965). Another example of an ecological buffer zone is the demilitarized zone that separates North and South Korea. Numerous plant and animal species that were previously considered extirpated, endangered, or threatened thrive in this heavily fortified 4-kilometer (km) by 250-km-long corridor, although they are absent on either side (Kim 1997). Areas between territories of warring native groups, which served as animal preserves, existed on the central plains of North America in the 1820s and 1830s. Different tribes hunted in these areas, but none was strong enough to control them. Therefore, most of those areas were not occupied year-round, and animals sought them out as refuges. With the disappearance of these "neutral zones," the bison decreased in numbers (West 1995).

Disease is another factor in creating ecological buffer zones. Epidemics have often been followed by periods of wildlife abundance, which may have resulted from reduced native human populations. Following the 1837 smallpox epidemic, the trader Pierre Chouteau remarked that bison had never been so abundant, since no Indians were around to kill them (Sundstrom 1997). On 29 August 1806, Captain Clark noted, "I have observed that in the country between the nations which are at war with each other the greatest numbers of wild animals are to be found" (Moulton 1986–1996, vol. 8, p. 328).

The Lewis and Clark expedition

The Lewis and Clark expedition was the brainchild of President Thomas Jefferson. On 20 June 1803, Jefferson gave Captain Lewis specific instructions for the expedition. Its main mission was to find a waterway connecting the Missouri River with the Pacific Ocean: "The object of your mission is to explore the Missouri river, & such principal stream of it, as, by its course and communication with the waters of the Pacific ocean, whether the Columbia, Oregon [sic], Colorado or any other river may offer the most direct & practicable water communication across this continent for the purposes of commerce" (Jackson 1978, p. 61).

However, Jefferson was also interested in "other objects worthy of notice": "You will therefore endeavor to make yourself acquainted, as far as a diligent pursuit of your journey shall admit, with the names of the nations & their numbers;...the soil & face of the country, it's [sic] growth & vegetable productions, the animals of the country generally, & especially those not known in the U.S.; the remains and

accounts of any which may be deemed rare or extinct" (Jackson 1978, p. 63). Other objectives of the expedition included recording geography, mineral productions, and climate. Those specific objectives explain the detailed notes that Lewis and Clark took on their journey, notes that can help to paint a picture of the ecological conditions that existed 200 years ago. For example, Lewis and Clark described 122 vertebrate species previously undescribed by scientists (Cutright 1969).

Meriwether Lewis, William Clark, and the rest of the Corps of Discovery left St. Louis, Missouri, on 20 May 1804. They spent the winter of 1804–1805 at Fort Mandan in North Dakota, then traveled to the Pacific Coast and spent the winter of 1805–1806 at Fort Clatsop in Oregon. They began their return trip in the spring of 1806, arriving in St. Louis on 23 September 1806.

An overview of the study

Others have studied the Lewis and Clark journals with regard to wildlife. Martin and Szuter (1999a) examined Lewis and Clark's wildlife observations on a broad scale, labeling areas where wildlife was abundant and humans were not as "war zones" and areas with abundant humans and less wildlife as "game sinks." Those authors concluded that human predation was responsible for the observed wildlife distribution. Lyman and Wolverton (2002) reexamined the same data and concluded that boundaries between war zones and game sinks were not abrupt, as suggested by Martin and Szuter (1999a), but rather were gradual, and that there was variation within each zone. Lyman and Wolverton attributed the wildlife distribution to a combination of human predation, biogeographic history, habitat differences, and climatic influences.

We examined the role of humans in greater detail and expanded on previous work in several ways. First, from the Lewis and Clark journals (Moulton 1986–1996), we collected the daily information on numbers and species of wildlife killed and wildlife observed and on the location of human settlements. We recorded information about nine mammals that were reported consistently and were also hunted by the expedition's members: (1) white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), (2) elk (*Cervus elaphus*), (3) bison (*Bison bison*), (4) pronghorn antelope (*Antilocapra americana*), (5) bighorn sheep (*Ovis canadensis*), (6) grizzly bear (*Ursus arctos*), (7) black bear (*Ursus americanus*), (8) wolf (*Canis lupus*), and (9) beaver (*Castor canadensis*). White-tailed deer and mule deer were combined, because Lewis and Clark were not always specific about which of these two species they encountered. Second, we determined the degree of human influence by using two variables: distance to the nearest occupied human settlement from each campsite and density of occupied human settlements within a 50-km radius around each campsite. Third, we performed a spatial analysis using geographic information systems (GIS) to link each observation to the coordinates of that day's campsite. Finally, we determined the abundance of wildlife and humans for five major ecoregions:

Parkland, Plains, Rocky Mountains, Columbia Basin, and Cascades/Pacific Coast (Bailey 1994).

Assessing human influence

The study area encompasses the Lewis and Clark trail from St. Louis, Missouri, to the Pacific Coast and back (figure 1). Lewis and Clark's daily observations were linked with the 506 campsites along the trail. A campsite was counted as a human settlement only if Lewis and Clark actually passed through it and if it was inhabited by the native population or by white settlers (in settlements near St. Louis). The expedition members were not counted as settlers, since they represented a constant influence along the trail. References to abandoned villages and settlements at a distance from the trail were not included, because Lewis and Clark did not see those locations. Since we wanted to assess the influence of humans on wildlife that was seen or killed at each campsite for a particular time (1 day's travel), we decided to count settlements only if they were occupied at the time that Lewis and Clark passed through.

For each of the nine species, we recorded whether an animal was present and how many were killed at each campsite. If the party remained at the same campsite for several days, we divided the number of animals killed by the days spent at that site. We also calculated the species richness by adding the number of species seen at each campsite. All observations

were linked to the location of the daily campsites in a spatial database.

We used ArcGIS software (ESRI 1999) to calculate the distance to the nearest occupied settlement from each campsite. Settlement density was assessed by calculating the number of known occupied settlements located along the trail within a 50-km radius of each campsite. We assumed that greater settlement density was associated with higher human population density and greater human influence. The two variables, distance to the nearest settlement and settlement density, were each divided into three categories or classes. For distance categories, we chose 0–1 km, 1.1–50 km, and 50.1–460 km. For the number of settlements within a 50-km radius, we also used three categories: 0, 1–6, and 7–13 settlements. Because there was much variation, combining the data into three classes helped to smooth the data. We chose class boundaries to categorize the degree of human influence. The first boundary was set at 1 km, based on the assumption that the primary activities at a settlement encompassed that distance. A histogram of the distances also showed a natural breakpoint at 1 km. The cutoff point for the second class was based on comments in the journals. For example, while at Fort Mandan, the hunting parties had to travel 48 to 64 km to reach good hunting grounds. Also, the hunters' camp in that area was located 48 km from their home base (Moulton 1986–1996).

To determine abundance for each species, we calculated the percentage of the campsites around which each species was present and grouped those results by the three distance categories and the three settlement density categories. We then calculated the odds ratio for encountering each species in adjoining distance and settlement density categories. The odds ratio, a cross-product ratio calculated from a contingency (2×2) table (Ramsey and Schafer 1997), is the appropriate way of comparing two groups of binary responses from a retrospective study.

Human settlement density

The relationship between wildlife and human settlement is illustrated best with a map. In general, the number of species present was highest in areas with little human settlement, in the west-central Plains (figure 1). Conversely, the fewest species were seen in areas of higher settlement density, such as the Columbia Basin and the Cascades–Pacific

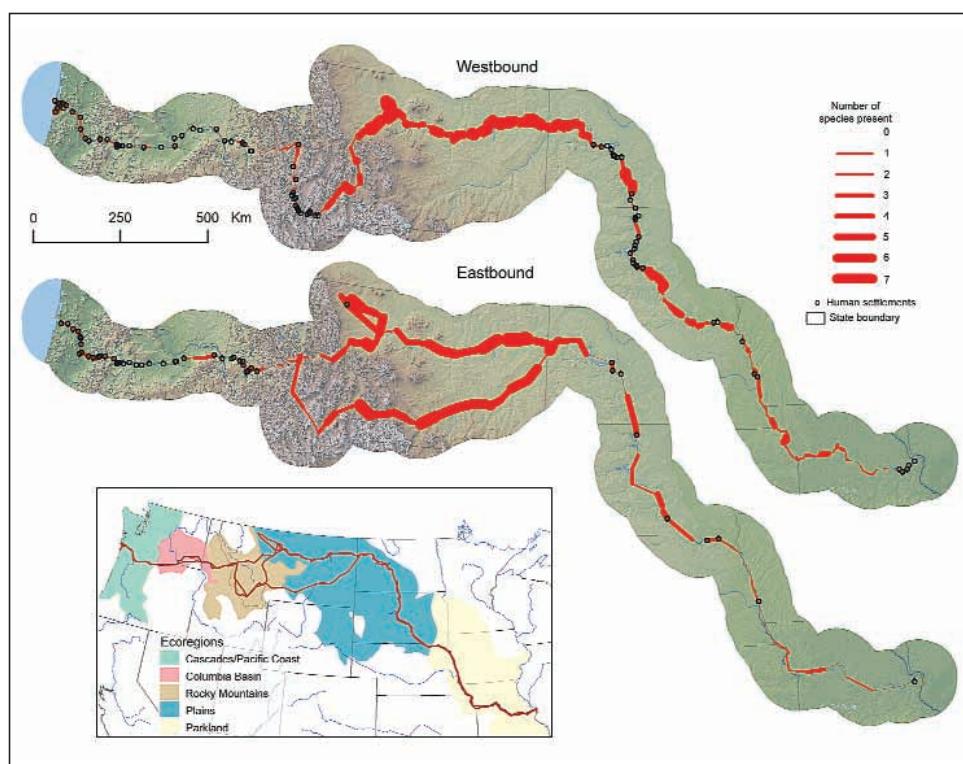


Figure 1. Species richness on the Lewis and Clark trail. Line width indicates the number of species present along the westbound and eastbound trails. Thicker lines indicate more species encountered. Of nine mammals surveyed, a maximum of seven were encountered at selected locations. The overview map illustrates the ecoregions and the Lewis and Clark trail.

Coast region. Even within the Plains, areas with human settlements were typically associated with fewer species. The results showed the same pattern for the mean number of animals killed per day.

One exception to this pattern was observed in parts of the Rocky Mountains along the Lolo Trail, where Lewis and Clark found very little game and no settlements. Two possible explanations for the lack of game may be the higher elevation (1600 meters at Lolo Pass) and the time of year. In 1805, Lewis and Clark passed through this area in the middle of September, with cold and snow hampering their progress. The following year, they covered the same area during the middle and end of June and had to turn back once because of snow. We assume, therefore, that some wildlife species avoided those high-elevation areas during that time because of inclement weather.

Human population density is reflected in the distribution of campsites in the various distance and settlement density categories (figure 2). The highest settlement density was encountered in the Columbia Basin and Cascades–Pacific Coast regions, while the Plains and Parkland regions had the lowest settlement density. The high settlement density in the Columbia Basin may have been a result of the presence of salmon. The Rocky Mountains were in an intermediate position, with fewer settlements in the eastern mountains and more settlements in the west. The farthest distance to the nearest settlement was 33 km for the Columbia Basin and 11 km for the Cascades–Pacific Coast. In contrast, 70 percent of the camps in the Plains were located between 50 and 460 km away from the nearest settlement (figure 2).

Wildlife abundance in relation to human settlements

Mammals generally became abundant with increasing distance from the nearest settlement and with decreasing settlement density. This trend was more pronounced for relatively common species such as deer, elk, bison, antelope, and beaver. For species that were less common, such as bighorn sheep, grizzly bear, and black bear, the trend was less pronounced. (figure 3). Nevertheless, the odds of encountering animals were always higher with increasing distance from humans and with lower settlement density. The exceptions to this pattern resulted from low sample size, which was reflected in larger confidence intervals (table 1). The trend for the mean number of animals killed per day was identical to the trend for the presence of animals at a campsite (figure 4). Our results did not show strong differentiations between beaver, a relatively sedentary species, and other mammals with greater seasonal movement. In fact, the odds ratios for beaver were similar to those of pronghorn and elk.

Deer, black bear, beaver, and humans were found in all five ecoregions. Bison, elk, grizzly bear, and

wolves were predominantly found in the Plains, while no elk, antelope, bison, bighorn sheep, or wolves were encountered in the Columbia Basin. In ecoregions with higher proportions of humans, fewer animal species were observed (figure 5).

Our results are consistent with the prediction that wildlife would be more abundant farther from human settlements. The results are more pronounced for species with a larger sample size, that is, species that were more abundant and that provided a source of food for the expedition members, such as deer, elk, bison, antelope, and beaver. The pattern for animal sightings was nearly identical with the pattern for kills. We did not expect to see such a strong relationship between the animal sighting data and the kill data, because the expedition members killed only what was needed for food or clothing (with the exception of some grizzly bears, which were killed in self-defense). These data suggest that proximity to humans had an effect on the expedition hunters' ability to find and kill animals, indicating that human influence was a factor responsible for the wildlife distribution and abundance.

The relationship between humans and wildlife was also reflected in the need to kill and consume horses and dogs in areas with a higher human population and lack of game. A total of 11 horses were killed for food in the Rocky Mountains and in the eastern portion of the Columbia Basin. The Lewis and Clark party also consumed 195 dogs, all in the Columbia Basin and the Cascades–Pacific Coast, the regions

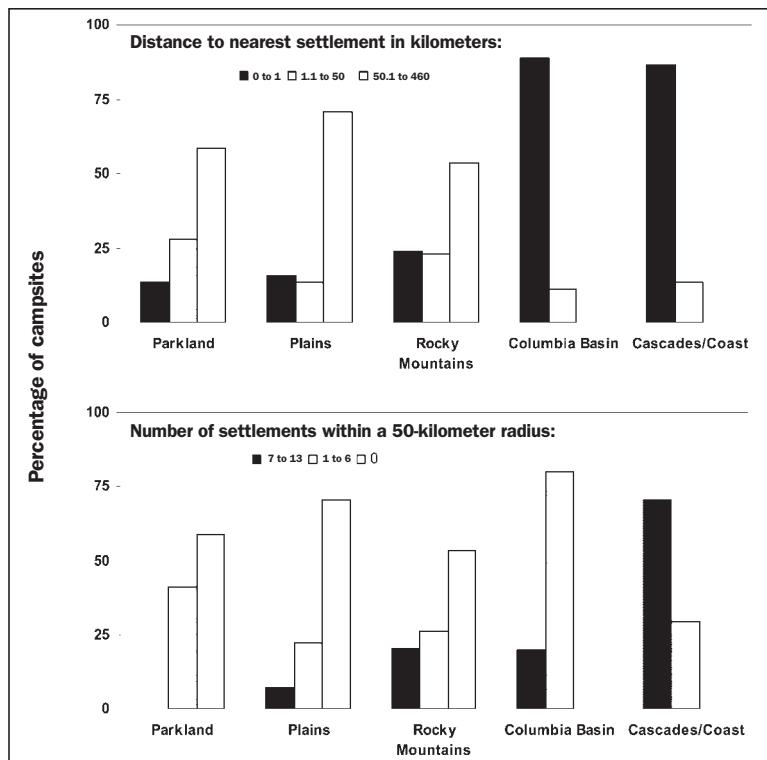


Figure 2. Percentage of campsites in each ecoregion for two variables: (top) percentage of campsites in three distance classes and (bottom) percentage of campsites in three settlement density classes. Dark bars indicate more human influence.

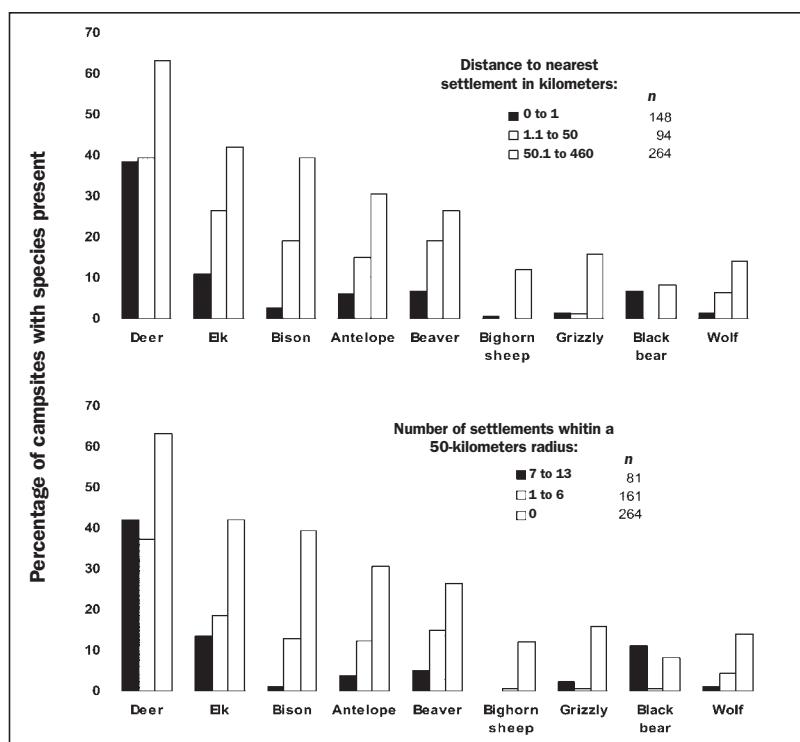


Figure 3. Species abundance along the Lewis and Clark trail: (top) abundance in three distance classes and (bottom) abundance in three settlement density classes. Abundance is the percentage of campsites with the species present. Dark bars indicate more human influence.

with the densest human population. Although it is possible that dogs were purchased to rely less on hunting and to save time, the strong relationship between numbers of wild animals killed and numbers seen suggests that, given the small numbers of animals sighted in these regions, the purchase of dogs was at least partly necessary because of a lack of game.

An exception to the general trend in the relationship between humans and wildlife was found in the Cascades–Pacific Coast ecoregion, where more elk were killed in areas of greater settlement density. This could be traced to one campsite at Fort Clatsop in Oregon. This location had 12 settlements within a 50-km radius, and elk were the main food source for the expedition's members. While the expedition camped at Fort Clatsop, elk were reported to be numerous on several occasions; however, there were also several reports of game being scarce, of the corps living on spoiled elk meat, and of the hunters being away from camp for several days without killing anything. With regard to large game, the hunters killed 116 elk and 14 deer between 1 December 1805 and 20 March 1806. Considering Lewis's statement on 13 July 1805 that they required either four deer, one elk and one deer, or one bison to "supply us

Table 1. Ratios and confidence intervals (in parentheses) for comparing the odds of encountering species in adjoining distance and settlement density classes.

	Odds ratios and confidence intervals (in parentheses) ^a					
	Comparison of distance classes			Comparison of settlement density classes		
	1 to 2	2 to 3	1 to 3	1 to 2	2 to 3	1 to 3
Deer	1.0 (0.6–1.8)	2.7 (1.6–4.3)	2.8 (1.8–4.2)	3.0 (1.9–4.4)	0.8 (0.5–1.4)	2.4 (1.4–4.0)
Elk	3.0 (1.5–6.0)	2.0 (1.2–3.4)	6.0 (3.4–10.6)	3.2 (2.0–5.1)	1.5 (0.7–3.1)	4.6 (2.3–9.1)
Bison	8.5 (2.8–26.0)	2.7 (1.6–4.9)	23.4 (8.4–65.1)	4.3 (2.6–7.3)	12.0 ^b (1.6–90.9)	52.0 ^b (7.1–379.5)
Pronghorn	2.7 (1.1–6.5)	2.5 (1.4–4.7)	6.8 (3.3–14.1)	3.1 (1.8–5.3)	3.7 ^b (1.1–12.8)	11.5 ^b (3.5–37.5)
Bighorn sheep	—	—	20.3 ^b (2.7–150.0)	22.1 ^b (3.0–163.2)	—	—
Grizzly bear	0.8 ^b (0.1–8.8)	17.6 ^b (2.4–129.7)	13.8 ^b (3.3–57.9)	30.3 ^b (4.1–222.2)	0.3 ^b (0.1–2.8)	7.5 ^b (1.8–31.6)
Black bear	—	—	1.3 (0.6–2.7)	14.6 ^b (1.9–109.0)	0.1 ^b (0.0–0.4)	0.7 (0.3–1.7)
Wolf	5 ^b (1.0–25.2)	2.4 (1.0–5.9)	11.9 ^b (2.8–50.1)	3.6 (1.6–8.3)	3.6 ^b (0.4–30.1)	13.0 ^b (1.8–96.6)
Beaver	3.3 (1.4–7.4)	1.5 (0.9–2.7)	5.0 (2.5–10.0)	2.1 (1.2–3.4)	3.4 (1.1–10.1)	7.0 (2.5–19.7)

Note: Breakdown of distance and settlement density classes are followed by sample size (out of a total of 506 campsites). Distance class (distance from nearest settlement): class 1, 0 to 1 kilometer (km) (148 campsites); class 2, 1.1 to 50 km (94 campsites); class 3, 50.1 to 460 km (264 campsites). Settlement density class (number of lodges within a 50 km radius from the campsite): class 1, 0 lodges (264 campsites); class 2, 1 to 6 lodges (161 campsites); class 3, 7 to 13 lodges (81 campsites). Blank cells indicate no observations in a class.

a. If the odds ratio was two, for example, then the odds of encountering a species in the second distance class or category were twice the odds of encountering that species in the first distance category.

b. Cell values in a 2 × 2 table were less than 5.

plentifully 24 hours" (Moulton 1986–1996), the amount of game killed at Fort Clatsop was not extraordinary and was comparable to game killed at Fort Mandan in North Dakota and Camp Chopunnish in Idaho, two other sites where the corps remained for extended periods.

Lewis reported that the natives of this area appeared to subsist mostly on fish and roots, and less on "the flesh of the Elk when they happen to be fortunate enough to procure it which is but seldom" (Moulton 1986–1996). Lewis and Clark observed the natives driving elk into pits and using dogs to hunt them; however, the dense forests and marshes of the area acted as refugia, enabling the elk to escape their pursuers. The expedition members were probably somewhat more successful hunters than the local inhabitants, for several reasons: They had reliable firearms and sufficient ammunition; they had a hunting party devoted strictly to that purpose; and they preferred meat to any other food, making hunting a priority.

Animal behavior described by Lewis and Clark

Lewis and Clark's descriptions of animal behavior also indicate whether animals had been hunted by humans extensively or had encountered few humans before. Areas with reports of "wild" or "shy" animals were located in the eastern Columbia Basin; in the Cascades region, near Portland, Oregon; in the central Rocky Mountains; and near Fort Mandan—all locations close to human settlement. Areas where wildlife was described as "gentle" were located on the Plains, in central South Dakota, and in eastern Montana.

In eastern Montana, Lewis wrote, "The whole face of the country was covered with herds of buffalo, elk & antelopes; deer are also abundant, but keep themselves more concealed in the woodland. The buffalo, elk and antelope are so gentle that we pass near them while feeding, without appearing to excite any alarm among them, and when we attract their attention, they frequently approach us more nearly to discover what we are, and in some instances pursue us a considerable distance apparently with that view" (Moulton 1986–1996, vol. 4, p. 67). Clark added that "antelope are curious and will approach any thing which appears in motion near them" (Moulton 1986–1996). When the first European hunters arrived in this area, it was common practice to attract antelope by waving a flag or creating other movements; however, Theodore Roosevelt reported that in the 1880s few places existed where the antelope were still tame enough for this stratagem to work (Roosevelt et al. 1903). With increasing human population, the animals displayed predator-avoidance behavior. Other authors have shown that prey unfamiliar with predators for 50 to 130 years were highly vulnerable but

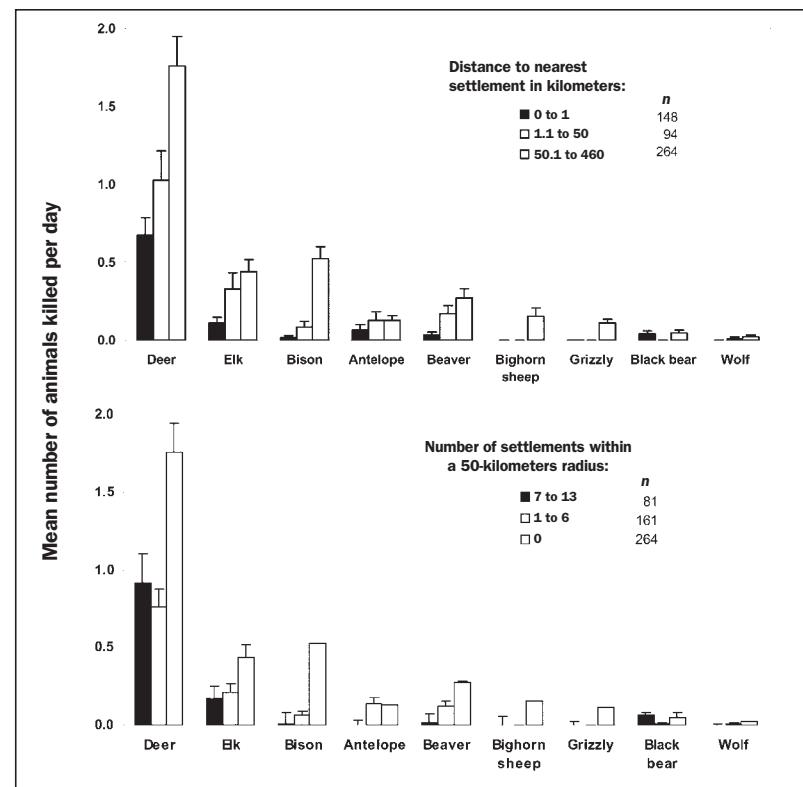


Figure 4. Mean number of animals killed per day: (top) animals killed in three distance classes and (bottom) animals killed in three settlement density classes. Relatively few bighorn sheep, grizzly bears, black bears, and wolves were killed, resulting in fewer than three classes with observations for those species. Lines over bars indicate standard error; dark bars indicate more human influence.

were also capable of learning how to avoid predators within a single generation (Berger et al. 2001).

Grizzly bear density

Two hundred years ago, grizzlies, wolves, and elk were found predominantly on the Plains, the predators following the abundant prey animals living in this ecoregion. Lewis also reported differences in behavior displayed by grizzly bears in different areas. On the Plains, he observed that grizzlies "feed principally on flesh, like the wolf," while he noticed that the grizzlies encountered at Camp Chopunnish in Idaho were "not as ferocious as those on the plains." Lewis believed that this was due to lack of game and to the fact that the animals were living mostly on roots and berries (Moulton 1986–1996, vol. 7, p. 261).

Since encounters with grizzlies were a dramatic event for the corps and were documented in detail, we were able to estimate the historical grizzly density. Our estimate was based on the method used by Botkin (1995), who assumed that the expedition was able to see an average distance of 1 mile (about 1.6 km) on the Plains. Botkin used earlier editions of the Lewis and Clark journals and arrived at a count of 37 grizzlies on the westbound journey. He estimated the grizzly

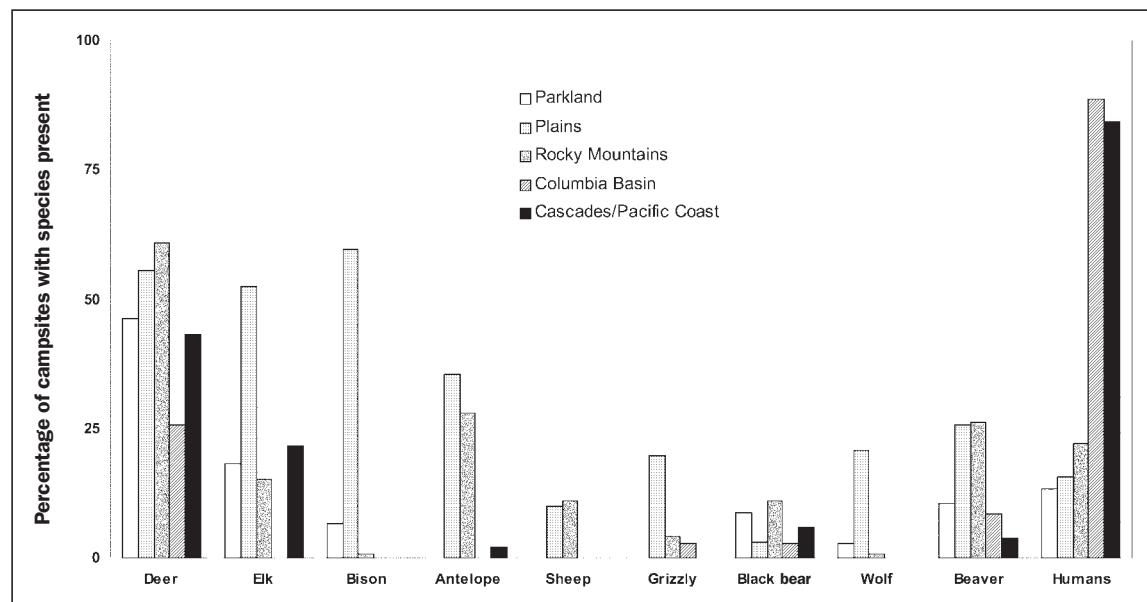


Figure 5. Species distribution and abundance, by ecoregion.

density at 3.7 bears per 100 square miles (1.4 bears per 100 square km) by dividing the total number of grizzlies encountered by the distance traveled and multiplying by 1 mile. Using grizzly observations for the westbound and eastbound journeys, we determined that the expedition killed 43 grizzlies. In addition, Lewis and Clark reported 42 grizzlies seen, as well as two instances where they reported "many" and four instances where they reported "some" grizzlies. By counting "some" and "many" as 2 grizzlies each, we estimated that at least 97 grizzly bears were encountered.

Using our numbers of grizzly encounters, we arrived at a grizzly density of 3.1 animals per 100 square km. For comparison, current grizzly density in the greater Yellowstone ecosystem is estimated at 1.1 animals per 100 square km (CERI 2002). Although these are only rough estimates, we concluded that historical grizzly density was considerably higher than the current density. It is possible that increased human population numbers have driven most of the different species that Lewis and Clark found in the Plains to higher elevations in the Rocky Mountains.

Lack of species in the Columbia Basin

Although it seems apparent that humans had a strong influence over wildlife distribution and abundance along the Lewis and Clark trail, the question remains whether humans were actually responsible for the apparent lack of some species in certain ecoregions. Although no antelope were reported seen or killed in the Columbia Basin, Lewis wrote while at Fort Clatsop that "the antelope is found in the great Plains of the Columbia" but is "by no means as plenty on this side of the Rocky Mountains as on the other" (Moulton 1986–1996, vol. 6, p. 336). One has to consider the possibility that the habitat in the Columbia Basin—although it included an abundance

of fish, which attracted humans—was not conducive to supporting large numbers of mammals. If this is true, then the apparent relationship between humans and mammals could be spurious.

For that reason, we examined the archaeological record. Archaeological digs in the Columbia Basin have unearthed remains of elk, antelope, bison, and bighorn sheep (Lyman 1992, Dixon and Lyman 1996). Between 500 BC and AD 1500, small herds of bison were relatively common in eastern Washington. Between AD 1500 and 1800, bison populations decreased considerably, although there is uncertainty associated with this time period because of a smaller sample size. Like the bison, pronghorn became locally extinct between AD 1500 and 1800 (Schroedl 1973). Elk were also present in the Columbia Basin during the last 5000 years, and they appear to have been more widespread in that area before the 19th century; however, detailed changes in distribution and abundance are not available because of a lack of dated archaeological data and an uneven distribution of archaeological sites (Dixon and Lyman 1996). Using archaeological data to estimate historical human and animal populations can have its drawbacks. A lack of such data may mean either that humans or animals were not present or simply that data have not been unearthed yet. A good summary of the use of archaeological data in investigating human–animal interactions can be found in Grayson (2001).

Climatic changes may have been one reason for the decreasing numbers of some wildlife species (Lyman 1992, Lyman and Wolverton 2002), but a lack of detailed local climatic data (Butler 2000) prevents us from drawing more definite conclusions. It is possible that human hunting influenced wildlife numbers, especially if wild animals were not very abundant in this region. Some authors have attributed the low numbers of game in the Columbia Basin to

aboriginal overkill, implying that humans limited the numbers and distribution of wildlife and may even have been responsible for local extinction of some species (Kay 1994, 1995, Martin and Szuter 1999b). We agree with those authors to the extent that human hunting may have been at least one factor in the continuing decline and eventual local extinction of species such as elk and bison, if the local populations of these species were already low or in decline.

Optimal foraging theory and prey switching

When a predator relies on only one prey species, it cannot force its prey to very low population levels or to extinction, because the predator's population will also be reduced as food supplies decline (Truett 1996). Following this reasoning, the native human population could not overhunt the bison to extinction in the Plains, since that species was their main prey. However, if an alternate prey or food source is available, a predator can maintain itself at relatively high densities. This can lead to a rapid decline or even extinction of some prey species. Such prey switching has been observed with moose, caribou, and wolves, when moose became alternate prey by moving into an area. The result of this in-migration is an increase in wolf numbers and a rapid decline in caribou (Bergerud and Elliot 1986).

Prey switching by humans has been observed in the archaeological record. As human populations increased, the proportion of larger species to smaller species decreased (Redford 1992, Truett 1996). By extending the optimal foraging theory to humans, it has been shown that low-ranked resources such as plants and fish are usually consumed to a greater extent when high-ranked resources are rare or non-existent (Grayson 2001). If ungulate numbers in fact decreased because of overhunting in prehistoric times, humans could prey-switch to salmon, allowing ungulates to maintain or even increase their population numbers, while still hunting the now-scarce prey. Once diseases began to reduce the human population in the Columbia Basin during the end of the 18th century, higher-ranked species were able to rebound. A similar subsistence change has in fact been observed in the lower Columbia River region (Butler 2000).

Human population size

It is also possible that humans have influenced wildlife for a much longer time than we previously believed. Kay (1994) argued that the reason large mammals appear in such small numbers in archaeological sites could be that higher-ranked food items are seldom part of a diet if those species are being overexploited. This led him to the conclusion that, except for refugia, most ungulate species were quite rare for the past 10,000 years in the intermountain West. On the basis of what we know about predator-prey cycles, it is reasonable to assume that prey populations may have increased as the human population decreased because of diseases.

From the 1500s through the early 1900s, human population size in North America dropped steadily (Ubelaker 1992). The most recent human population estimates at precontact

time range from just under 2 million (Ubelaker 1992) to 3.8 million (Denevan 1992, McCann 1999). The decrease in population within 100 years after the arrival of Columbus may have been as high as 90 percent (McCann 1999), while population levels in 1800 have been estimated at about 1 million people (Denevan 1992).

The explorer La Verendrye estimated the Mandan Indian population in 1738 at approximately 15,000 to 20,000 people. A smallpox epidemic occurred between 1781 and 1782 and reduced the Mandan to around 1800 people in the period 1804–1805, as reported by Lewis and Clark. Another smallpox wave in 1837 killed between 10,000 and 25,000 members of the Arikara, Minnetare, Assiniboin, Crow, and Blackfeet tribes (Jensen 1972). Boyd (1999) estimated the precontact population of the Columbia Basin at around 87,000, although he conceded that "the number may be much higher." In the Columbia Basin and Pacific Coast, the first smallpox epidemics occurred in 1770, with later outbreaks in 1801 and 1824, followed by measles or fever. From 1805 to 1855, the decrease in population in the lower Columbia Basin has been estimated at 90 percent (Boyd 1999). As shown in figure 6, the Native American population was estimated at nearly 200,000 in the Great Plains culture area and 80,000 in the Plateau culture area before contact with white explorers; by 1900 it had declined to less than 63,000 and 19,000, respectively (Ubelaker 1988). The Great Plains culture area stretches from the Mississippi River to the Rocky Mountains and from the southern parts of Manitoba, Saskatchewan, and Alberta to southern Texas. The Plateau culture area includes eastern Washington, northeastern and central Oregon, southeastern British Columbia, northern Idaho, western Montana, and portions of northern California.

The sudden decrease of the human population caused by smallpox and other introduced diseases may have allowed wildlife numbers to increase, especially in areas that were left with low numbers of people, such as the Plains. However, we need more reliable archaeological data to establish a solid link between human and animal populations and further investigate this hypothesis.

The influence of the horse

Competition from horses (*Equus caballus*) may have been another factor in historical wildlife distribution and abundance. In archaeological studies in the Columbia Basin, horse bones have been found alongside bison bones (Osborne 1953), indicating that bison were hunted in the Columbia Basin at the same time that horses were present, that is, some time after about 1720 (Haines 1938). We hypothesize that the introduction of the horse eventually led to the extinction of the bison in the Columbia Basin in two ways: First, the horse acted as a direct foraging competitor to the bison, and second, it improved the hunting efficiency of the Native Americans. Christman (1971) has also suggested that the extinction of the bison coincided with the time of horse acquisition.

Horse and bison diets have considerable overlap (Salter 1978, Chapman and Feldhamer 1982, Flores 1991, Crane et

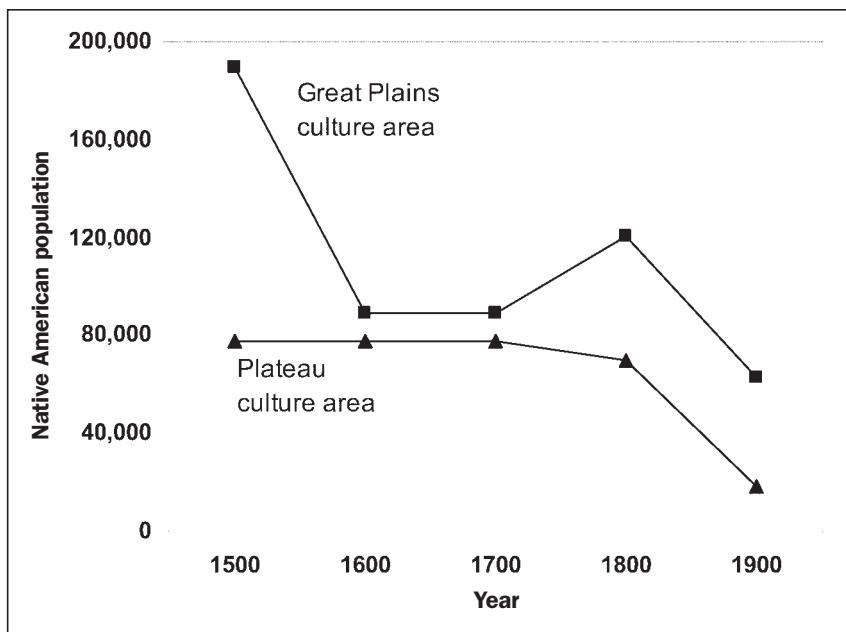


Figure 6. Native American population estimates for people inhabiting the Great Plains and Plateau culture areas from 1500 to 1900 (Ubelaker 1988). The Great Plains culture area stretches from the Mississippi River to the Rocky Mountains and from the southern parts of Manitoba, Saskatchewan, and Alberta to southern Texas. The Plateau culture area includes eastern Washington, northeastern and central Oregon, southeastern British Columbia, northern Idaho, western Montana, and portions of northern California.

al. 1997), and competition for forage may have been high as horse numbers increased over time. Bison have been described as a “weed species” on the Plains, occupying a niche left by Pleistocene extinctions of mammals (Flores 1991). We would argue that horses acted in a similar way in the Columbia Basin. Once introduced, they could increase, especially since few predators were present. Many Columbia Basin tribes were rich in horses, and the Nez Percé were well-known horse breeders and owned large numbers of horses (Haines 1955). Sergeant Gass commented on 25 April 1806 that the Walla Walla tribe had “a great many horses,” and on 9 May 1806 he stated, “Between the great falls of the Columbia and this place [Camp Chopunnish in Idaho], we saw more horses, than I ever before saw in the same space of country” (Moulton 1986–1996, vol. 10, p. 221). Estimates of the number of horses per person for the Nez Percé, Cayuse, Walla Walla, and Umatilla tribes have been estimated to range from 4.3 to 11.7 (data from 1874). Many tribes, however, acquired their maximum number of horses between 1800 and 1825 (Ewers 1955).

Aside from the numerous native-owned horses, Lewis and Clark mentioned wild horses (Moulton 1986–1996). Although there are no numbers for wild horses in the Columbia Basin for that time, it has been estimated that there were about 2 million feral horses between south Texas and the Arkansas River in the mid-19th century (Flores 1991). We assume that horse numbers increased in a similar

fashion in the Columbia Basin and that the horses competed for forage with native wildlife.

Conclusion

It is likely that human influence was a factor in the distribution and abundance of wildlife observed in Lewis and Clark’s time. However, the lack of some species in certain ecoregions is not as easily explained. The current lack of detailed local climatic data and the incomplete archaeological record do not allow us to determine whether climate change or human hunting alone was responsible for the observed lack of some species in the Columbia Basin. We believe, however, that overhunting by humans and the introduction of the horse may have been contributing factors. If relatively low population densities, such as those existing 200 years ago, could affect wildlife distribution and abundance, we hypothesize that the denser population before Euro-American contact had an even greater effect on wildlife.

We hope that this insight into human–wildlife interactions offers a better understanding of the historical reference condition, with major implications for conservation biology and ecological restoration. It underlines the point that researchers need to carefully consider the time, location, and spatial extent of the chosen reference condition and familiarize themselves with the degree of human influence. We also encourage a greater collaboration among ecologists, historians, archaeologists, and anthropologists to broaden cross-disciplinary understanding of the interactions between people and ecosystems.

al. 1997), and competition for forage may have been high as horse numbers increased over time. Bison have been described as a “weed species” on the Plains, occupying a niche left by Pleistocene extinctions of mammals (Flores 1991). We would argue that horses acted in a similar way in the Columbia Basin. Once introduced, they could increase, especially since few predators were present. Many Columbia Basin tribes were rich in horses, and the Nez Percé were well-known horse breeders and owned large numbers of horses (Haines 1955). Sergeant Gass commented on 25 April 1806 that the Walla Walla tribe had “a great many horses,” and on 9 May 1806 he stated, “Between the great falls of the Columbia and this place [Camp Chopunnish in Idaho], we saw more horses, than I ever before saw in the same space of country” (Moulton 1986–1996, vol. 10, p. 221). Estimates of the number of horses per person for the Nez Percé, Cayuse, Walla Walla, and Umatilla tribes have been estimated to range from 4.3 to 11.7 (data from 1874). Many tribes, however, acquired their maximum number of horses between 1800 and 1825 (Ewers 1955).

Acknowledgments

This study was conducted at the College of Forestry, Oregon State University, and funded in part by the college’s Richardson Family Fellowship. We thank Robert Beschta, R. Lee Lyman, Paul S. Martin, and Christian E. Torgersen for reviewing an earlier draft of this article.

References cited

- Aronson J, Dhillon S, Le Floc'h E. 1995. On the need to select an ecosystem of reference, however imperfect: A reply to Pickett and Parker. *Restoration Ecology* 3: 1–3.
- Bailey RG. 1994. Description of the Ecoregions of the United States. Washington (DC): US Department of Agriculture Forest Service. Miscellaneous Publication no. 1391.
- Berger J, Swenson JE, Persson I. 2001. Recolonizing carnivores and naive prey: Conservation lessons from Pleistocene extinctions. *Science* 291: 1036–1039.
- Bergerud AT, Elliot JP. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64: 1515–1529.
- Botkin DB. 1995. *Our Natural History: The Lessons of Lewis and Clark*. New York: Berkley Publishing Group.

Boyd RT. 1999. *The Coming of the Spirit of Pestilence*. Seattle: University of Washington Press.

Butler VL. 2000. Resource depression on the Northwest Coast of North America. *Antiquity* 74: 649–661.

[CERI] Craighead Environmental Research Institute. 2002. North American grizzly population sizes. (1 September 2003; www.grizzlybear.org/grizpop.htm)

Chapman JA, Feldhamer GA. 1982. *Wild Mammals of North America: Biology, Management, and Economics*. Baltimore: Johns Hopkins University Press.

Christman GM. 1971. The mountain bison. *American West* 8: 44–47.

Crane KK, Smith MA, Reynolds D. 1997. Habitat selection patterns of feral horses in southcentral Wyoming. *Journal of Range Management* 50: 374–380.

Cutright PR. 1969. *Lewis and Clark: Pioneering Naturalists*. Lincoln: University of Nebraska Press.

Denevan WM. 1992. The pristine myth: The landscape of the Americas in 1492. *Annals of the Association of American Geographers* 82: 369–385.

Dixon SL, Lyman RL. 1996. On the Holocene history of elk (*Cervus elaphus*) in eastern Washington. *Northwest Science* 70: 262–273.

[ESRI] Environmental Systems Research Institute. 1999. ArcGIS Version 8.1. Redlands (CA): ESRI.

Ewers JC. 1955. The Horse in Blackfoot Indian Culture. Washington (DC): Bureau of American Ethnology. Bulletin no. 159.

Flores D. 1991. Bison ecology and bison diplomacy: The southern Plains from 1800 to 1850. *Journal of American History* 78: 465–485.

Grayson DK. 2001. The archaeological record of human impacts on animal populations. *Journal of World Prehistory* 15: 1–68.

Haines F. 1938. The northward spread of horses among the Plains Indians. *American Anthropologist* 40: 429–437.

—. 1955. *The Nez Percés: Tribesmen of the Columbia Plateau*. Norman: University of Oklahoma Press.

Hickerson H. 1965. The Virginia deer and intertribal buffer zones in the upper Mississippi Valley. Pages 43–66 in Leeds A, Vayda AP, eds. *Man, Culture, and Animals: The Role of Animals in Human Ecological Adjustments*. Washington (DC): American Association for the Advancement of Science. Publication 78.

Jackson D. 1978. Letters of the Lewis and Clark Expedition with Related Documents, Vol. 1. 2nd ed. Urbana: University of Illinois Press.

Jensen M. 1972. The Mandan tragedy. *Indian Historian* 5: 18–22.

Kay CE. 1994. Aboriginal overkill: The role of Native Americans in structuring western ecosystems. *Human Nature* 5: 359–398.

—. 1995. Aboriginal overkill and native burning: Implications for modern ecosystem management. *Western Journal of Applied Forestry* 10: 121–126.

Kim KC. 1997. Preserving biodiversity in Korea's demilitarized zone. *Science* 278: 242–243.

Lyman RL. 1992. Influences of mid-Holocene altithermal climates on mammalian faunas and human subsistence in eastern Washington. *Journal of Ethnobiology* 12: 37–62.

Lyman RL, Wolverton S. 2002. The late prehistoric–early historic game sink in the northwestern United States. *Conservation Biology* 16: 73–85.

Martin PS, Szuter CR. 1999a. War zones and game sinks in Lewis and Clark's West. *Conservation Biology* 13: 36–45.

—. 1999b. Megafauna of the Columbia Basin, 1800–1840: Lewis and Clark in a game sink. Pages 188–204 in Goble DD, Hirt PW, eds. *Northwest Lands, Northwest Peoples*. Seattle: University of Washington Press.

McCann JM. 1999. Before 1492, the making of the pre-Columbian landscape, Part I: The environment. *Ecological Restoration* 17: 15–30.

Mech LD. 1977. Wolf-pack buffer zones as prey reservoirs. *Science* 198: 320–321.

Moulton GE, ed. 1986–1996. *The Journals of the Lewis and Clark Expedition*, by Lewis M, Clark W, Vols. 2–10. Lincoln: University of Nebraska Press.

Osborne D. 1953. Archaeological occurrences of pronghorn antelope, bison and horse in the Columbia Plateau. *Scientific Monthly* 77: 260–269.

Ramsey FL, Schafer DW. 1997. *The Statistical Sleuth*. Belmont (CA): Wadsworth.

Redford KH. 1992. The empty forest. *BioScience* 42: 412–422.

Ripple WJ, Larsen EJ. 2000. Historic aspen recruitment, elk and wolves in Northern Yellowstone National Park, USA. *Biological Conservation* 95: 361–370.

Ripple WJ, Larsen EJ, Renkin RA, Smith DW. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102: 227–234.

Ronda JP. 1984. *Lewis and Clark among the Indians*. Lincoln: University of Nebraska Press.

Roosevelt T, Van Dyke TS, Elliot DG, Stone AJ. 1903. *The Deer Family*. New York: MacMillan.

Salter RE. 1978. Ecology of feral horses in western Alberta. Master's thesis. University of Alberta, Edmonton, Canada.

Schroedl GF. 1973. The Archaeological Occurrence of Bison in the Southern Plateau. Pullman: Washington State University, Laboratory of Anthropology. Reports of Investigations no. 51.

Sundstrom L. 1997. Smallpox used them up: References to epidemic disease in northern plains winter counts, 1714–1920. *Ethnohistory* 44: 305–343.

Taylor RJ. 1984. *Predation*. New York: Chapman and Hall.

Truett J. 1996. Bison and elk in the American Southwest: In search of the pristine. *Environmental Management* 20: 195–206.

Ubelaker DH. 1988. North American Indian population size, A.D. 1500 to 1985. *American Journal of Physical Anthropology* 77: 289–294.

—. 1992. Patterns of demographic change in the Americas. *Human Biology* 64: 361–379.

Wagner MR, Block WM, Geils BW, Wegner KF. 2000. Restoration ecology: A new forest management paradigm, or another merit badge for foresters? *Journal of Forestry* 22–27.

West E. 1995. *The Way to the West*. Albuquerque: University of New Mexico Press.

White R, Cronon W. 1998. Ecological change and Indian–White relations. Pages 417–429 in Washburn WE, ed. *Handbook of North American Indians*, Vol. 4. Washington (DC): Smithsonian Institution.