

The Canadian Field-Naturalist

Volume 121, Number 1

January–March 2007

Were Native People Keystone Predators? A Continuous-Time Analysis of Wildlife Observations Made by Lewis and Clark in 1804-1806

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Kay, Charles E. 2007. Were native people keystone predators? A continuous-time analysis of wildlife observations made by Lewis and Clark in 1804-1806. *Canadian Field-Naturalist* 121(1): 1–16.

It has long been claimed that native people were conservationists who had little or no impact on wildlife populations. More recently, though, it has been suggested that native people were keystone predators, who lacked any effective conservation strategies and instead routinely overexploited large mammal populations. To test these hypotheses, I performed a continuous-time analysis of wildlife observations made by Lewis and Clark because their journals are often cited as an example of how western North America teemed with wildlife before that area was despoiled by advancing European civilization. This included Bison, Elk, Mule Deer, Whitetailed Deer, Blacktailed Deer, Moose, Pronghorn Antelope, Bighorn Sheep, Grizzly Bears, Black Bears, and Grey Wolves. I also recorded all occasions on which Lewis and Clark met native peoples. Those data show a strong inverse relationship between native people and wildlife. The only places Lewis and Clark reported an abundance of game were in aboriginal buffer zones between tribes at war, but even there, wildlife populations were predator, not food-limited. Bison, Grizzly Bears, Bighorn Sheep, Mule Deer, and Grey Wolves were seldom seen except in aboriginal buffer zones. Moose were most susceptible to aboriginal hunting followed by Bison and then Elk, while Whitetailed Deer had a more effective escape strategy. If it had not been for aboriginal buffer zones, Lewis and Clark would have found little wildlife anywhere in the West. Moreover, prior to the 1780 smallpox and other earlier epidemics that decimated native populations in advance of European contact, there were more aboriginal people and even less wildlife. The patterns observed by Lewis and Clark are consistent with optimal foraging theory and other evolutionary ecology predictions.

Key Words: Native hunting, aboriginal buffer zones, Lewis and Clark, keystone predation, reference conditions, Elk, Bison, Grizzly Bears, Mule Deer, Whitetailed Deer, western North America.

It has long been postulated that native people were conservationists who had little or no impact on wildlife populations (e.g.; Speck 1913, 1939a, 1939b). Studies of modern hunter-gatherers, however, have found little evidence that native people purposefully employ conservation strategies (Alvard 1993, 1994, 1995, 1998a, 1998b; Hill and Hurtado 1996), while archaeological data suggest that prehistoric people routinely overexploited large-mammal populations (Broughton 1994a, 1994b, 1997; Jones and Hilderbrant 1995; Janetski 1997; Butler 2000; Chatters 2004). Elsewhere, I have proposed that native people were keystone predators, who once structured entire ecosystems (Kay 1994, 1995, 1997a, 1997b, 1998, 2002).

To test these competing hypotheses, I performed a continuous-time analysis of wildlife observations made by Lewis and Clark on their expedition across North America in 1804-1806 because their journals are often cited as an example of how the West teemed with wildlife before that area was despoiled by advancing European civilization (Botkin 1995, 2004; Patten 1998: 70; Wilkinson and Rauber 2002; Nie 2003: 1). Lewis

and Clark were the first Europeans to traverse what eventually became the western United States, and many of the native peoples they met had never before encountered Europeans. In addition, historians universally agree that Lewis and Clark's journals are not only among the earliest, but also the most detailed and accurate, especially regarding natural history observations (Burroughs 1961; Ronda 1984; Botkin 1995, 2004). Thus, the descriptions left by Lewis and Clark are thought by many to represent the "pristine" state of western ecosystems (Craighead 1998: 597; Patten 1998: 70; Wilkinson and Rauber 2002; Botkin 2004). Botkin (1995: 1), for instance, described Lewis and Clark's journey as "the greatest wilderness trip ever recorded."

Methods and Study Area

Recently, Martin and Szuter (1999a, 1999b, 2002, 2004), Lyman and Wolverton (2002), and Laliberte and Ripple (2003) presented contrasting interpretations of western ecosystems based on Lewis and Clark's journals, but those analyses are flawed, in part, because they either did not separate ungulates by species or they did

not correlate wildlife sightings with the abundance of native people on each day of the entire trip. Instead, I developed three measures to quantify the wildlife observations recorded by Lewis and Clark in their original journals, which have recently been re-edited and republished (Moulton 1986, 1987a, 1987b, 1988, 1990, 1991, 1993 – hereafter cited only by volume and page). First, game seen. If Lewis and Clark reported old sign of a species, that was assigned a value of one, fresh sign a two, and if they actually saw the animal, a three. This included Bison (*Bison bison*), Elk (*Cervus elaphus*), Whitetailed Deer (*Odocoileus virginianus*), Mule Deer (*O. hemionus hemionus*), Blacktailed Deer (*O. h. columbianus*), Moose (*Alces alces*), Pronghorn Antelope (*Antilocapra americana*), Bighorn Sheep (*Ovis canadensis*), Grizzly Bears (*Ursus arctos*), Black Bears (*U. americanus*), and Grey Wolves (*Canis lupus*). This was done each day for the entire 863 days of the expedition.

Second, game killed. On each day, Lewis and Clark recorded the exact number of animals that were killed to provision their party. In three instances, though, Lewis and Clark reported that “some” Whitetailed Deer (day 78), Elk (day 365), or Bison (day 413) were killed. In these cases, “some” was recorded as three animals killed. In 12 instances, Lewis and Clark reported that “several” Whitetailed Deer (days 46, 365, 367, 373, 408, and 811), Bison (days 354, 406, 408, and 413), Mule Deer (day 404), or Blacktailed Deer (day 602) were killed. In those cases, “several” was recorded as seven animals killed. Similar to game seen, the number of animals killed was recorded for all species on all days.

Third, herd size. If Lewis and Clark reported sighting large numbers of a particular animal, a value of ten was assigned to that species on that day. A value of ten was also assigned if Lewis and Clark reported killing 10 or more of one species on a single day. I then added game seen, game killed, and herd size values for all species on each day to obtain a daily measure of wildlife abundance. Again, this was done for all 863 days of the expedition.

I also developed a similar convention to quantify the relative abundance of native people that Lewis and Clark encountered each day of their journey. If Lewis and Clark observed old sign, that was assigned a value of one, fresh sign a two, and if Lewis and Clark actually saw native people, a three. If Lewis and Clark met more than ten native people on a given day that was assigned a value of ten. On most days Lewis and Clark traveled together but on a few occasions they took separate routes, most notably on the return trip. In those cases, Lewis’ observations were recorded separately from Clark’s. These conventions produced nearly 40 000 numerical data entries. To facilitate analysis, Lewis and Clark’s route was divided into 55 trip segments (Table 1), for which mean daily abundances of wildlife and mean daily abundances of native people were cal-

culated. It should be noted that Lewis and Clark generally sent their best hunters ahead of the main party so that game would more readily be encountered.

Lewis and Clark left St. Louis, Missouri on 14 May 1804 and proceeded, via watercraft, up the Missouri River through present-day Missouri, Kansas, Nebraska, Iowa, South Dakota, and into North Dakota where they built Fort Mandan in close proximity to the Mandan and Hidatsa villages. Lewis and Clark over-wintered at Fort Mandan, and then ascended the Missouri River into present-day Montana during the spring of 1805. After leaving their larger boats and portaging the Great Falls, Lewis and Clark continued up the Missouri to Three Forks before ascending the Jefferson and Beaverhead Rivers, on whose upper reaches they met the Shoshone. After obtaining horses from the Shoshone, Lewis and Clark cached their canoes where Clark Canyon Reservoir is now situated and traveled over the Continental Divide into Idaho and down the Lemhi and Salmon Rivers. From there, Lewis and Clark ascended the North Fork of the Salmon and crossed Lost Trail Pass, re-entering Montana.

Next, Lewis and Clark traveled down the Bitterroot Valley to Lolo Creek, which they traced to its source. Lewis and Clark then followed the high ridges north of Idaho’s Lochsa River and eventually descended to the lower Lochsa, where the explorers met the Nez Perce. At this point, Lewis and Clark left their horses and proceeded via canoe down the Clearwater, Snake, and Columbia Rivers through present-day Oregon and Washington state. Finally, Lewis and Clark built Fort Clatsop and overwintered on the south bank of the Columbia near the Pacific Ocean.

During the spring of 1806, Lewis and Clark retraced their route, with minor variations, until the expedition reached present-day Lolo, Montana, where the party divided. Lewis ascended the Blackfoot River, crossed the Continental Divide, and proceeded to the Great Falls on the Missouri River, where the party split a second time. Lewis left most of his men to repair the boats cached in 1805, while he and three companions traveled by horseback to Cutbank Creek, where they met the Blackfeet. After the only fatal encounter with native people on the entire trip, Lewis retreated to the Missouri, where he rejoined the rest of his men and together they floated down that river until reunited with Clark below the Yellowstone in present-day North Dakota.

Clark, on the other hand, left Lolo, Montana, and ascended the Bitterroot River to Chief Joseph Pass, where he entered the Big Hole. From there, Clark crossed to the Beaverhead and reloaded the canoes cached in 1805. Clark’s party then proceeded by land and water to Three Forks, where the group split a second time. Clark sent some of his men and the canoes down the Missouri to meet Lewis at Great Falls, while he traveled overland via Bozeman Pass to the Yellowstone. At this point, Clark fashioned canoes and floated down the Yellowstone and Missouri Rivers until reunited with

TABLE 1. Trip segments and itinerary of Lewis and Clark 1804-1806.

Trip segment	Segment length (days)	Description	Dates
1	30	St. Louis to Grand River, Missouri	5/14-6/12/1804
2	50	Grand River to Council Bluffs, Nebraska	6/13-8/1/1804
3	20	Council Bluffs to Big Sioux River, Nebraska	8/2-8/21/1804
4	4	Big Sioux River to above Vermillion River, Nebraska	8/22-8/25/1804
5	8	Above Vermillion River	8/26-9/2/1804
6	22	Above Vermillion River to Bad River, South Dakota	9/3-9/24/1804
7	22	Bad River to below the Cannonball River, North Dakota	9/25-10/16/1804
8	7	Cannonball River to Mandan Villages, North Dakota	10/17-10/23/1804
9	9	Mandan Villages, North Dakota	10/24-11/1/1804
10	156	Fort Mandan, North Dakota	11/2/1804-4/6/1805
11	6	Fort Mandan to Little Missouri River, North Dakota	4/7-4/12/1805
12	13	Little Missouri River to Yellowstone River, North Dakota	4/13-4/25/1805
13	12	Yellowstone River to Milk River, Montana	4/26-5/7/1805
14	12	Milk River to Musselshell River, Montana	5/8-5/19/1805
15	14	Musselshell River to Marias River, Montana	5/20-6/2/1805
16	13	Marias River to Great Falls, Montana	6/3-6/15/1805
17	29	Great Falls portage	6/16-7/14/1805
18	10	Great Falls to Three Forks, Montana	7/15-7/24/1805
19	13	Three Forks to Big Hole River, Montana	7/25-8/6/1805
20	6	Big Hole River to meeting Shoshone in Idaho – Lewis' account	8/7-8/12/1805
21	14	Present Clark Canyon Reservoir across divide to Lemhi River, Idaho – Lewis' account	8/13-8/26/1805
22	16	Above Three Forks to present Clark Canyon Reservoir, Montana – Clark's account	8/1-8/16/1805
23	12	Clark Canyon Reservoir to Lemhi River to Salmon River and return to Lemhi – Clark's account	8/17-8/28/1805
24	13	Lemhi River, Idaho, to present Lolo, Montana	8/29-9/10/1805
25	9	Lolo, Montana, over Lolo Trail to lower Lochsa River, Idaho	9/11-9/19/1805
26	17	Lower Lochsa River – canoe camp	9/20-10/6/1805
27	18	Canoe Camp to the Dalles, Washington	10/7-10/24/1805
28	9	Cascade Mountains and portage, Washington	10/25-11/2/1805
29	22	Cascade Mountains to the mouth of Columbia River on the north bank, Washington	11/3-11/25/1805
30	11	Crossed to south bank of the Columbia River, Oregon	11/26-12/6/1805
31	106	Ft. Clatsop, Oregon	12/7-3/22/1806
32	15	Ft. Clatsop to the Cascade Mountains, Washington	3/23-4/6/1806
33	12	Cascade Mountains to the Dalles, Washington	4/7-4/18/1806
34	25	The Dalles to Camp Chopunnish, Idaho	4/19-5/13/1806
35	27	Camp Chopunnish, Idaho	5/14-6/9/1806
36	15	Attempted crossing of mountains	6/10-6/24/1806
37	5	Crossed mountains on Lolo Trail	6/25-6/29/1806
38	3	Present Lolo, Montana – here Lewis and Clark separated	6/30-7/2/1806
39	5	Lewis – up Blackfoot River and across Continental Divide, Montana	7/3-7/7/1806
40	14	Lewis – Divide to Great Falls (split party) Lewis to Cutbank Creek, Montana	7/8-7/21/1806
41	6	Lewis – Upper Cutbank Creek, met Piegan, fled back to Missouri River	7/22-7/27/1806
42	11	Lewis – Marias River down Missouri to Yellowstone River, North Dakota	7/28-8/7/1806
43	4	Lewis – Down Missouri until reunited with Clark	8/8-8/11/1806
44	10	Clark – Lolo, Montana, up Bitterroot into Big Hole Valley then to present Clark Canyon Reservoir and down to Three Forks where the party again split	7/3-7/12/1806
45	3	Clark – Three Forks to Bozeman Pass and on to the Yellowstone River, Montana	7/13-7/15/1806
46	18	Clark – Down Yellowstone River to Missouri River, North Dakota	7/16-8/2/1806
47	9	Clark – Down Missouri River until reunited with Lewis, North Dakota	8/3-8/11/1806
48	6	Little Missouri River to Mandan Villages to Ft. Mandan, North Dakota	8/12-8/17/1806
49	3	Heart River to Cannonball River, North Dakota	8/18-8/20/1806
50	2	Aricara villages, South Dakota	8/21-8/22/1806
51	7	Moreau River to White River, South Dakota	8/23-8/29/1806
52	5	White River to Vermillion River, Nebraska	8/30-9/3/1806
53	5	Big Sioux River to Council Bluffs, Nebraska	9/4-9/8/1806
54	9	Platte River to Grand River, Missouri	9/9-9/17/1806
55	6	Grand River to St. Louis, Missouri	9/18-9/23/1806

Lewis. Lewis and Clark then descended to St. Louis (2: 64; 3: 6; 4: 6; 5: 6, 110, 176; 6: 6, 80; 7: 6; 8: 8-9, 49, 84).

Results

Lewis and Clark's observations show an inverse relationship between wildlife and native people (Figure 1). Wildlife was abundant only where native people were absent, and if it had not been for the presence of aboriginal buffer zones between tribes at war (Hickerson 1965; Steffian 1991; Martin and Szuter 1999a, 1999b, 2002, 2004; Farr 2001; Laliberte and Ripple 2003), there would have been little wildlife anywhere in the West.

Yankton Sioux buffer zone

As Lewis and Clark ascended the Missouri River, they met the Omahas and Ottos on day 97 and the Yankton Sioux on day 108 (Figure 2). These two groups were at war (2: 488), and wildlife was abundant only in the buffer zone between the tribes. Bison, in particular, were found only in the center of the buffer zone.

Sioux-Mandan buffer zone

Lewis and Clark met the Teton Sioux on day 135, the Arikaras on day 148, and the Mandan-Hidatsa on day 164. Wildlife was not abundant in the area between the Teton Sioux and the Arikaras, but was abundant between the Arikaras and the Mandan-Hidatsa (Figure 3). This was because the Teton Sioux and Arikaras were allied against the Mandan-Hidatsa (3: 156, 161, 195-196, 207, 226, 233-234, 243-244, 251, 272-273, 295-297, 304-305; Porsche and Loendorf 1987; Bouchet-Bert 1999). That is, peace had a negative impact on wildlife populations while war had a beneficial effect, similar to conditions Hickerson (1965) reported in the upper Mississippi Valley (Farr 2001).

Missouri-Yellowstone buffer zone

In 1804-1806 all of Montana between the Missouri and Yellowstone Rivers was a six-sided buffer zone between warring tribes (4: 21-22, 67, 108-109, 159-160, 216, 222, 354, 379, 401, 426, 437; 5: 8-9, 45, 68-71, 77-80, 85, 87-91, 96-97, 102-106, 123-124, 178, 197, 259, 318; 7: 242, 250; 8: 88, 93-94, 104, 113, 123, 143, 182, 195, 278, 321, 323). The north was controlled by the Blackfeet Confederation, which consisted of five tribes (Ewers 1958), while on the west were the Flathead, Salish, Kootenay, and their allies. The Shoshone occupied the southwest (Trenholm and Carley 1964), the Crow the south-central, and the Sioux, Cheyenne, and their allies the southeast. To the east were the Mandan, Hidatsa, and their allies (Ahler et al. 1991). Within this large buffer zone (Martin and Szuter 1999a, 2002, 2004; Farr 2001), wildlife was relatively more abundant (Figures 4-7) because the warring factions did not hunt along the Yellowstone and Missouri as frequently as they did more secure environments closer to each tribe's core area. As noted by Lewis and Clark, tribes did venture into the buffer zone,

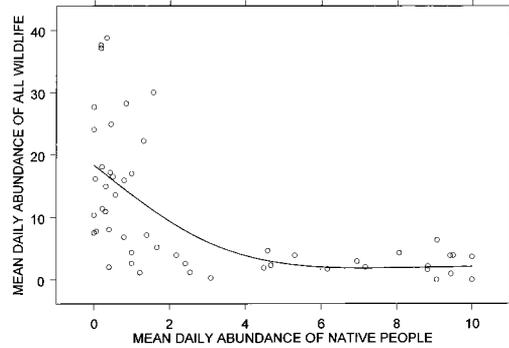


FIGURE 1. Relationship between the abundance of native people and the abundance of wildlife as observed by Lewis and Clark in 1804-1806. Plotted are the mean daily abundance of all wildlife species and the mean daily abundance of native people by trip segments – segments 1, 2, 54, and 55 were excluded because those areas were near European settlements. Line fitted using a smoothing spline with cross validation (Mathsoft 1997: 158-167). X and Y axes are offset. Note that there are no data points in the upper right as might be expected if cultural beliefs fostered conservation. Clearly, it made little difference what native people believed, or said they believed. Instead, aboriginal hunting followed predictions derived from optimal foraging theory and other evolutionary ecology models.

but only in force due to fear of attack. So the Missouri-Yellowstone buffer zone was not un hunted (4: 232), instead the area was just hunted less frequently (Farr 2001), which apparently was sufficient to permit greater numbers of wildlife.

Deer

Lewis and Clark killed more Whitetailed Deer than all other large mammals combined. By comparison, Mule Deer were rare and were found only in tribal boundary zones, while blacktails were restricted to the Cascade Mountains west to the Pacific (6: 328, 331, 403-404). Even along the lower Columbia, though, Lewis and Clark encountered more whitetails than blacktails. This was because whitetails had a more effective escape strategy than the other deer (Geist 1998; Whittaker and Lindzey 2001; Lingle 2002; Robinson et al. 2002) and thus were less affected by native hunting. Even where native people were abundant, some whitetails were usually able to survive (Figure 8a) because, when discovered, whitetails quickly fled into riparian thickets from which they could not easily be dislodged (5: 87; 6: 403). Lewis and Clark noted that Mule Deer and Elk when chased fled into the open (4: 136-137; 6: 403), making those species easier to hunt.

Elk

Lewis and Clark reported that Elk were easier to kill than Whitetailed Deer (6: 85, 242), which is reflected in the fact that native hunters had a greater impact on

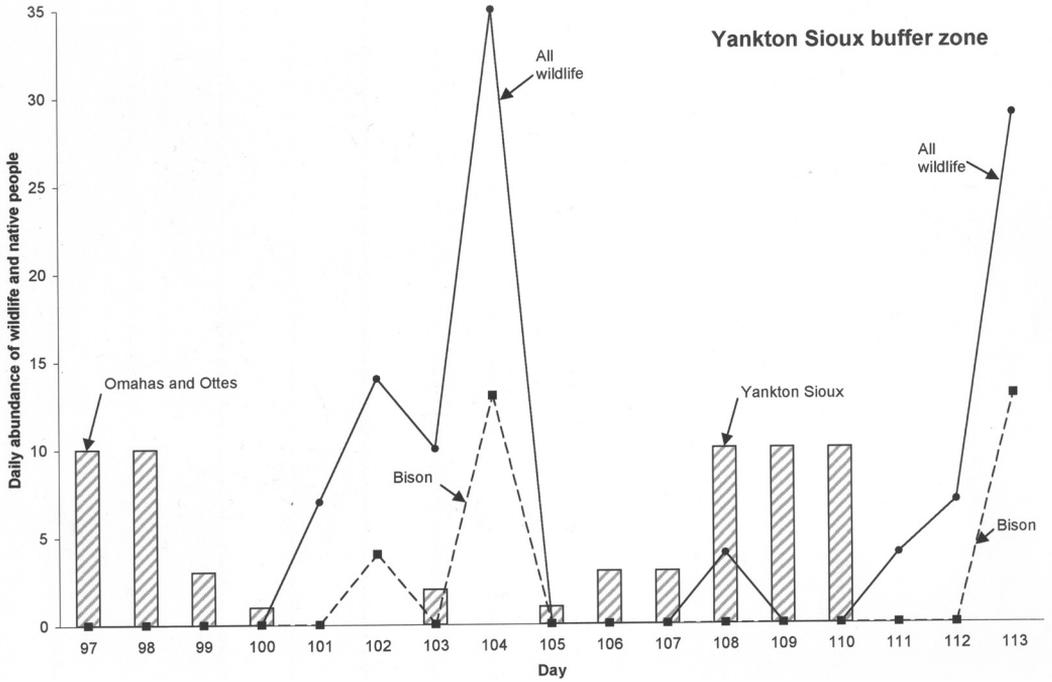


FIGURE 2. Yankton Sioux buffer zone along the Missouri River as reported by Lewis and Clark in 1804. Wildlife was abundant only in the zone between warring tribes.

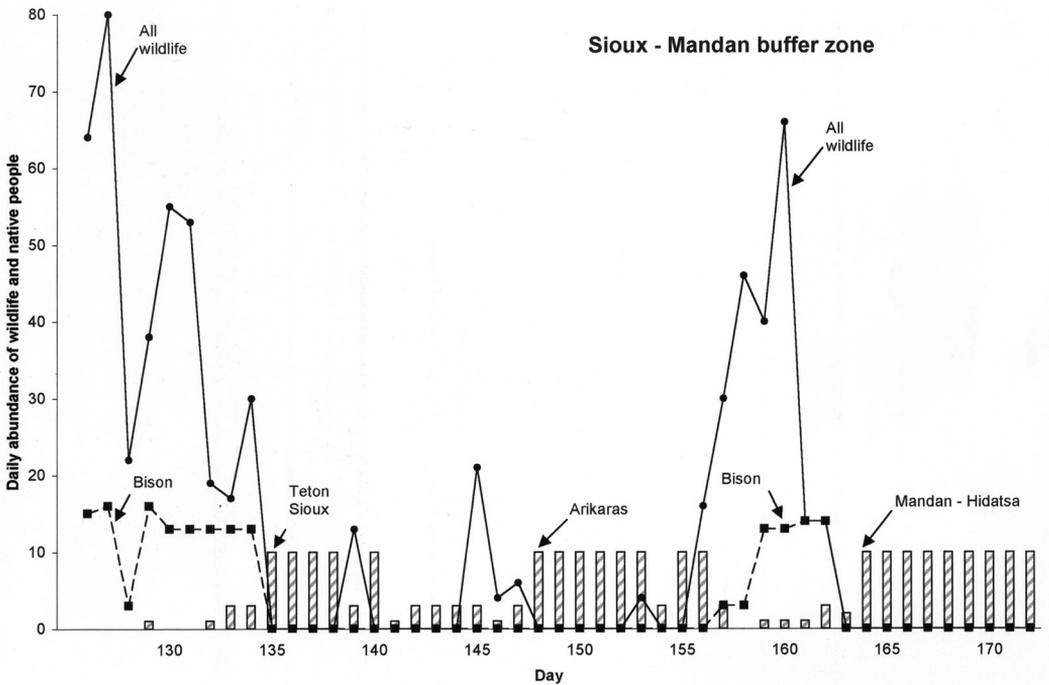


FIGURE 3. Sioux-Mandan buffer zone along the Missouri River as reported by Lewis and Clark in 1804. The Teton Sioux were allied with the Arikaras against the Mandan-Hidatsa and wildlife was abundant only in the zone between warring factions. There was little wildlife and no Bison in the area between the allied tribes.

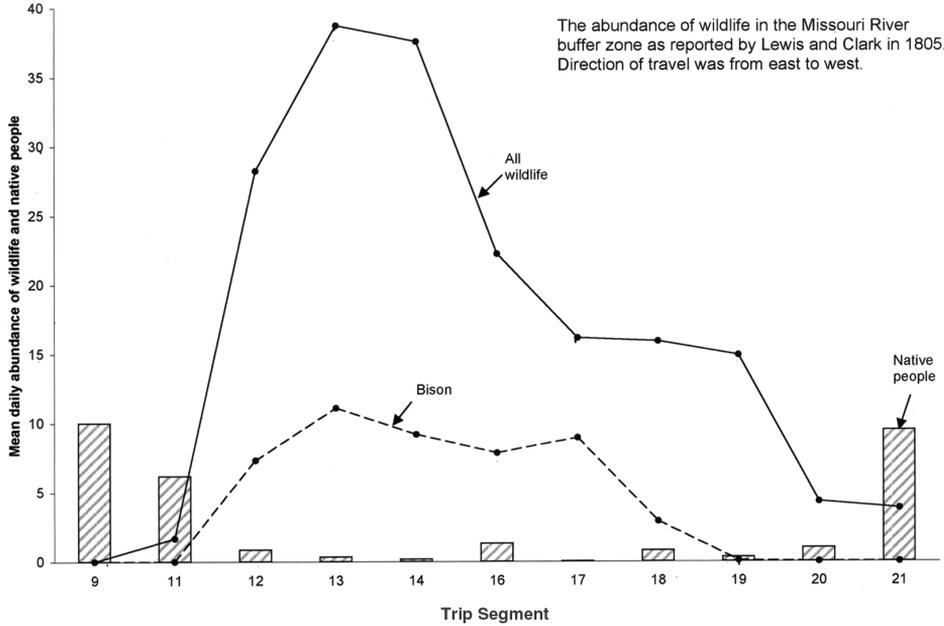


FIGURE 4. The mean daily abundance of wildlife and native people along the Missouri River buffer zone as reported by Lewis and Clark in 1805. On their trip across this section of Montana, Lewis and Clark did not see a single native person from the time they left the Mandan (trip segments 9 and 11) until they met the Shoshone along the Montana-Idaho border (trip segment 21). Bison were observed only where native people were absent.

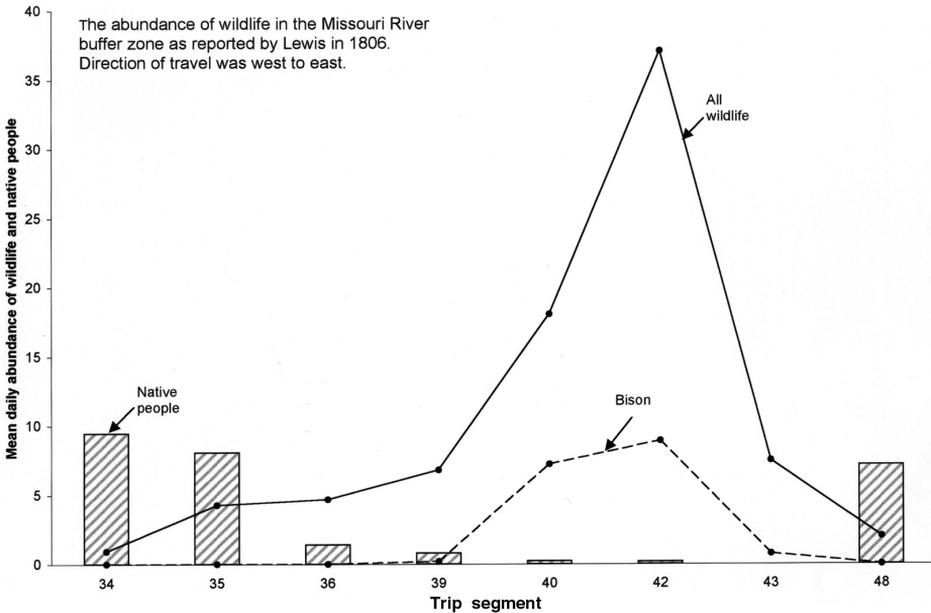


FIGURE 5. The mean daily abundance of wildlife and native people along the Missouri River buffer zone as reported by Lewis and Clark in 1806. Trip segment 34 included tribes in central Washington, while Lewis and Clark spent trip segment 35 with the Nez Perce. Lewis and Clark then crossed the Bitterroot Mountains (trip segment 36) and separated at Lolo, Montana. By trip segment 40, Clark was back at Great Falls on the Missouri River, which he descended to the Mandan villages (trip segment 48). As on the upstream journey (Figure 4), Clark did not see a single native person on this section of the Missouri and wildlife was abundant only where native people were absent. Bison, in particular, occurred only in the center of the buffer zone.

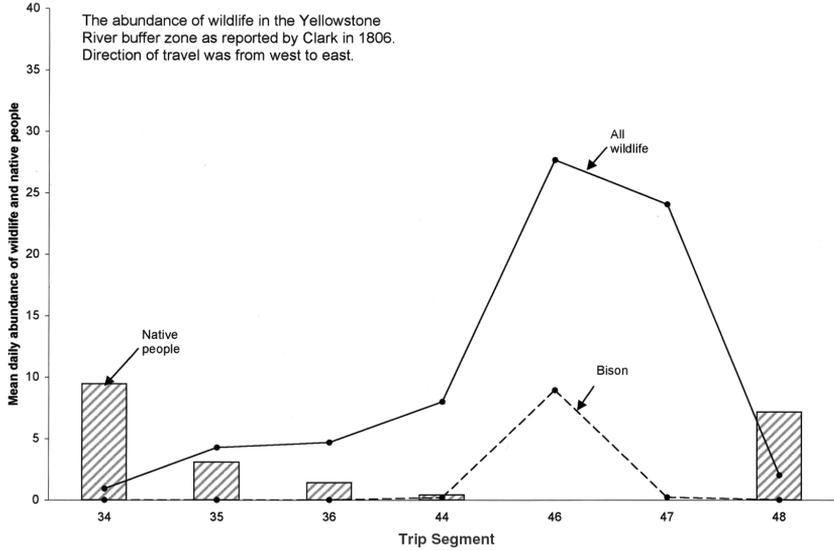


FIGURE 6. The mean daily abundance of wildlife and native people along the Yellowstone River buffer zone as reported by Clark in 1806. Trip segments 34, 35, and 36 are the same as those in Figure 5. After Lewis and Clark separated, Clark returned to Three Forks by trip segment 44 and was on the Yellowstone River by trip segment 46. Although the Crow stole all of Clark’s horses on the Yellowstone, he did not actually see a single native person on his return trip across Montana until he neared the Mandan villages (trip segment 48). The only place wildlife was abundant was along the Yellowstone River and Bison were only seen in the center of that buffer zone.

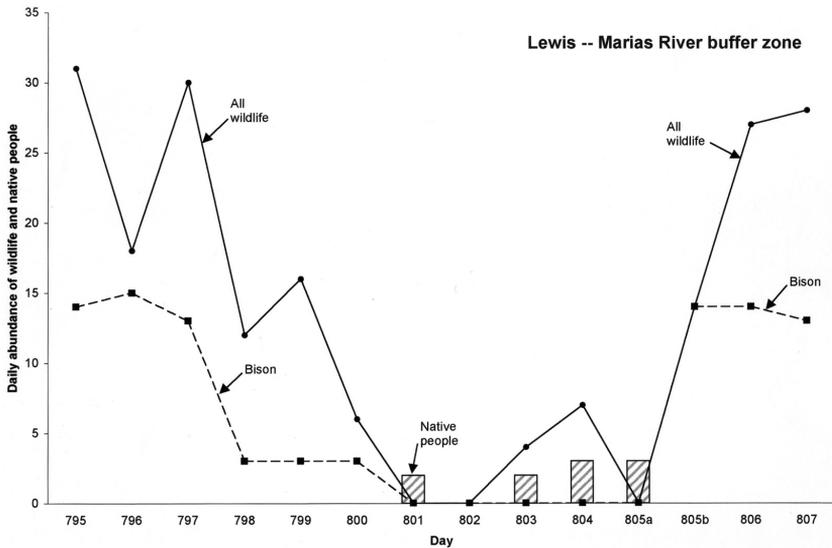


FIGURE 7. Marias River buffer zone. After returning to Great Falls, Lewis ascended the Marias River and Cutbank Creek in what is now the Blackfoot Indian Reservation. As Lewis traveled from the Missouri, wildlife became less and less abundant, while Bison disappeared. Wildlife was reported on days 803 and 804 only because Lewis sent his hunters downstream 30-40 km to kill Whitetailed Deer for food. On day 804 Lewis met seven Blackfeet who told him their village was less than one-half day’s travel. Lewis camped with this small group of Blackfeet and next morning (day 805a) awoke to find the Blackfeet attempting to steal his guns and horses. An altercation followed and at least one Blackfoot was killed, the only native person killed by Lewis and Clark on their entire journey. Fearing retaliation and annihilation, Lewis fled back to the Missouri, and by his own account, traveled more than 160 km by nightfall (day 805b). Thus within one day’s hard travel, Lewis went from an area with no game and native people to an area with abundant game and no natives. Bison were found only where native people were absent (8: 112-140).

the abundance of Elk (Figure 8b) than they did deer (Figure 8a). Lewis and Clark did kill a number of Elk at Fort Clatsop, but only because they purposefully built the fort where Elk were relatively more common and native people infrequent (6: 92-93, 95-96, 105, 108, 112). That is, Lewis and Clark constructed Fort Clatsop in an intervillage buffer zone to take advantage of the more abundant Elk. Nevertheless, Lewis and Clark observed that most of the Elk they killed during the winter of 1805-1806 had old arrow wounds (6: 208, 210), indicative of intense native hunting. "Many of the Elk we have killed since we have been here, have been wounded with these arrows, the short piece with the barb remaining in the animal and grown up in the flesh" (6: 208). Lewis and Clark also described how native people used pit traps to kill Elk. "Then pits are employed in taking the Elk, and of course are large and deep, some of them a cube of 12 or 14 feet. These are usually placed by the side of a large fallen tree, which as well as the pit [lie] across the [trails] frequented by the Elk. [The] pits are disguised with the slender boughs of trees and moss; the unwary Elk in passing the tree precipitates himself into the pit which is sufficiently deep to prevent his escape" (6: 208). Thus, even in thick coastal forests, Elk were intensely hunted by native people.

Pronghorn Antelope

Native hunting had an even greater impact on the abundance of Pronghorn Antelope (Figure 8c). Despite their great speed, pronghorns were relatively easy for native people to kill (3: 176; Frison 1991).

Bison

Native hunting controlled the distribution and number of Bison on the northern Great Plains (Figure 8d). The only places Lewis and Clark saw Bison, and especially in large numbers, were in the center of aboriginal buffer zones between warring tribes. This is similar to what West (1995) documented on the central Great Plains – if it had not been for warring tribes and buffer zones, there would have been few Bison anywhere in North America (Kay 2002).

Bighorn Sheep

Native hunting had an even greater effect on Bighorn Sheep (Figure 8e). Lewis and Clark reported an abundance of bighorns only in the center of buffer zones far removed from native people.

Grizzly Bears

Native hunters also controlled the distribution and abundance of Grizzly Bears (Figure 8f). This is similar to what Birkedal (1993) reported in Alaska. Aside from a few grizzlies killed in the rugged Idaho mountains, Lewis and Clark only observed grizzlies in aboriginal buffer zones.

Black Bears

Based on Lewis and Clark's observations and kill rates, Black Bears were less common than grizzlies, even in forested areas.

Moose

Despite spending substantial amounts of time in what is currently prime Moose habitat, Lewis and Clark recorded Moose only once (6: 313; 7: 326; 8: 95) and that was in the center of the buffer zone between the Blackfeet and the Flathead-Salish. As explained elsewhere, native hunting controlled the distribution and abundance of Moose throughout western North America (Kay 1997b). Contrary to what is generally believed, Moose are more abundant in western North America today (Stevens 1971; Pierce and Peek 1984) than they were in Lewis and Clark's time, or any other point in the past (Kay 1997b).

Grey Wolves

Lewis and Clark observed a direct relationship between the abundance of game and the abundance of wolves. Wolves were common only where game was relatively abundant (4: 85). Thus, wolves were largely restricted to the same aboriginal buffer zones as were Bison, Elk, and other ungulates.

Dogs and horses

I also recorded the number of dogs (*Canis familiaris*) Lewis and Clark purchased when game was in short supply, and the number of horses (*Equus caballus*) the explorers killed for food. Lewis and Clark killed nine horses and bought (ate) 210 dogs, primarily in the Columbia Basin, where native people were particularly abundant and wildlife was virtually non-existent (7: 49, 92). Lewis and Clark also bought large quantities of other foodstuffs from various native peoples, especially corn from the Mandan-Hidatsa and salmon from tribes throughout the Columbia Basin.

Discussion

Optimal-foraging theory

According to optimal-foraging theory, high-ranked diet items are more susceptible to overexploitation than lower-ranked items (Smith 1983; Stephens and Krebs 1986; Smith and Winterhalder 1992; Butler 2000). Theoretical considerations and studies of modern hunter-gatherers both indicate that large mammals are the highest-ranked diet items, and that, in general, the larger the animal, the higher its rank (Smith and Winterhalder 1992; Hill and Hurtado 1996). Moreover, if risk to the hunter or travel distances are great, only the highest-ranked diet items should be pursued (Smith and Winterhalder 1992). Thus, optimal-foraging theory would predict that when native people entered aboriginal buffer zones, they should have concentrated their hunting on the larger species, such as Bison and Elk, causing those species to decline accordingly. This would also imply that native people lacked any effective conservation strategy regarding these prey items. This pattern was, in fact, observed by Lewis and Clark as they left various native peoples and entered buffer zones, first Whitetailed Deer increased, then Elk and then Bison. Conversely, as Lewis and Clark exited a buffer zone, Bison disappeared first, followed by Elk, while

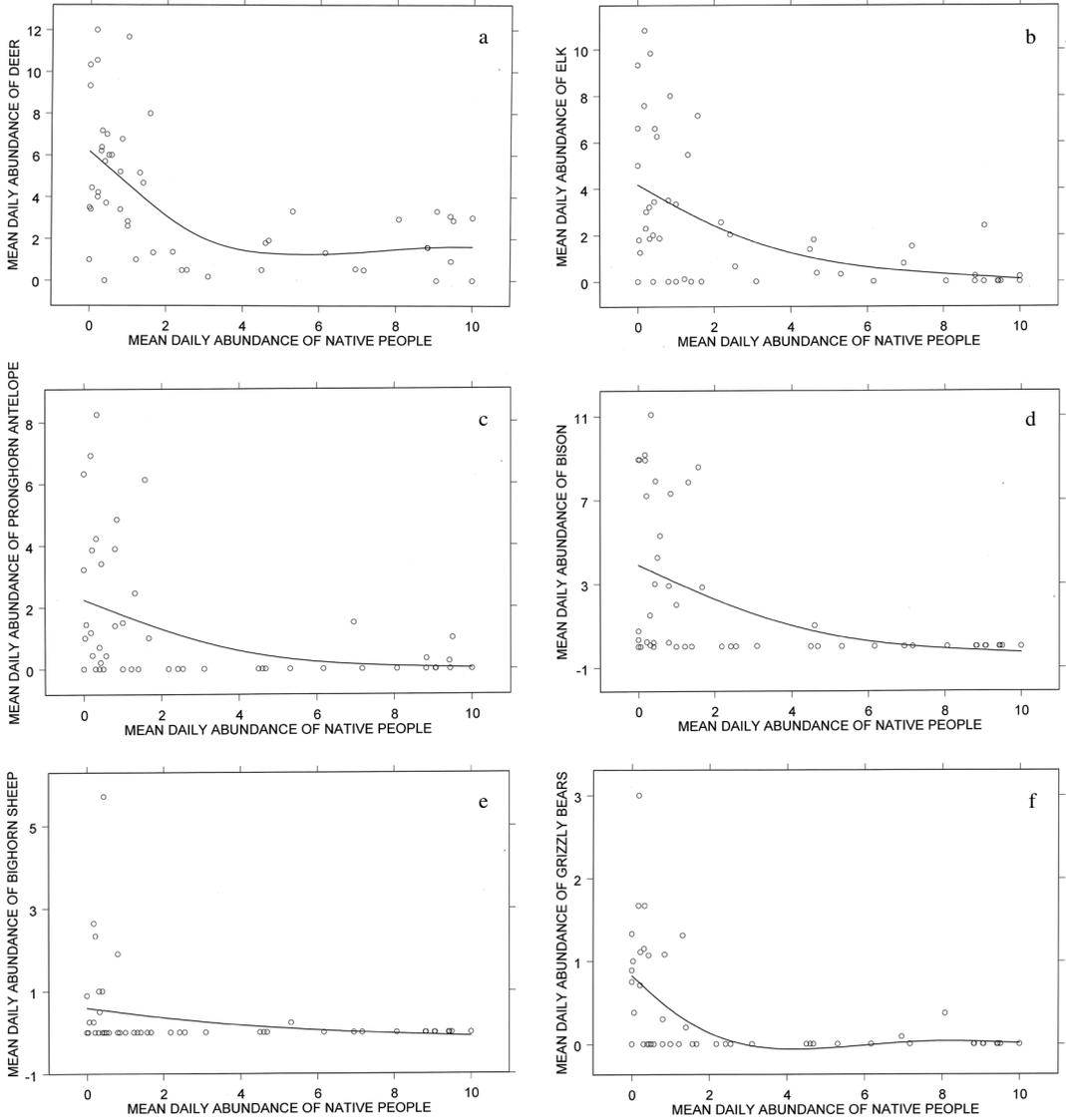


FIGURE 8. Relationship between the abundance of native people and the abundance of various wildlife species as observed by Lewis and Clark in 1804-1806. Plotted are the mean daily abundance of species and the mean daily abundance of native people by trip segments – segments 1, 2, 54, and 55 were excluded because those areas were near European settlements. Lines fitted using a smoothing spline with cross validation (Mathsoft 1997: 158-167). X and Y axes are offset. (a) Whitetailed Deer, (b) Elk, (c) Pronghorn Antelope, (d) Bison, (e) Bighorn Sheep, and (f) Grizzly Bears.

some Whitetailed Deer were usually able to escape native hunters (Figure 9). Furthermore, Lewis and Clark noted that native hunters preferred to kill female ungulates (3: 61, 270) due to that sex's higher fat content. Now, killing females runs counter to any conservation strategy (Kay 1994, 1997b, 1998; Kay and Simmons 2002).

Alvard (1998b, 2002) recently reviewed the conditions under which evolution by natural selection might favor resource conservation by humans. In short, con-

servation will be favored by evolution only if the resource is economical to defend. For instance, if 1000 kcal are spent defending a resource, but less than 1000 kcal are derived from that resource, evolution will not favor conservation. For a variety of reasons, including competition from carnivore predators, large mammals were seldom, if ever, economical to defend (Kay 1994, 1998, 2002). Instead the logical, rational thing to do was to kill-out the large mammals as quickly as possible and then move on to other resources,

which is exactly what aboriginal people did (Kay 1998, 2002). Counter-intuitively, once that was accomplished, native populations actually increased because people were forced to consume lower-ranked, but more abundant diet items (Hawkes 1991, 1992, 1993). There is also an evolved discount rate that acts to negate a wide range of possible conservation practices (Rogers 1991, 1994).

Predator-limited

Even within buffer zones, though, wildlife was not as abundant as one might think, because the animals were predator, not food, limited (Kay 1998, 2002). Food-limited ungulates invariably destroy berry-producing shrubs and woody riparian vegetation due to repeated browsing, and once willows (*Salix* spp.), cottonwoods (*Populus* spp.), and aspen (*Populus tremuloides*) decline, so do associated species like Beaver (*Castor canadensis*) (4: 189-190), which are dependent upon those plants for food (Kay 1998 and references therein; Nietvelt 2001). Lewis and Clark, however, reported that riparian thickets were common in buffer zones, as were Beaver and berry-producing shrubs (e.g.: 4: 70, 145-146, 189-190, 247, 278, 332, 374, 391-392, 399, 414, 419, 428, 435, 451; 5: 14, 42, 46, 59). In addition, Lewis and Clark noted that Whitetailed Deer often had twin fawns or triplets, and that even lactating deer were fat (4: 165), which would not have been physiologically possible if ungulate populations had been food-limited. Thus, carnivore predation and occasional hunting by native people (4: 232) kept buffer zone ungulate populations well below what the habitat could otherwise support (White et al. 1998; Kay 2002).

Estimate of pre-Columbian wildlife populations

A number of investigators have cited Lewis and Clark's descriptions of abundant wildlife without realizing that those accounts only apply to the center of buffer zones (Craighead 1998; Wilkinson and Rauber 2002). Botkin (1995: 49-86; 2004: 141-147), for instance, used Lewis and Clark's observations of grizzlies along the Missouri and Yellowstone Rivers to estimate the number of bears in the western United States prior to European contact, and arrived at a figure of 56 000, which others increased to 100 000 for the entire continent (e.g.: Flores 1998: 61). Although Botkin (1995: 165-169) acknowledged that native people could be important ecological factors, he failed to realize that native hunting controlled the distribution and numbers of grizzlies throughout North America (Figure 8f; Birkedal 1993). During pre-Columbian times, there may have been no more than 4000-5000 grizzlies in all of North America because the bears were simply large packages of fat meat that native hunters killed at will (Hallowell 1926: 31-37; Birkedal 1993). Similarly, there never were 60 million Bison on the Great Plains (Seton 1929; Roe 1951), as is commonly believed (Shaw 1995; Geist 1996; Kay 2002).

Canadian buffer zones

Aboriginal buffer zones also occurred throughout western Canada. Palliser, for instance, reported that "As a general rule the more dangerous the country [due to Indian attack] the greater the probability of finding [an] abundance of game, showing in more ways than one the truth of the old sportsman's adage the more danger the more sport. This part of the country is so evidently the line of direction [demarcation] between the three hostile tribes, that none of them dare venture into it for hunting, except when driven to desperation by hunger, they endeavor to snatch their game from between the jaws of Scylla and Charybdis. Much therefore as I enjoyed [this] locality for a hunting camp, seeing buffalo on all sides, elk feeding in the distance, and fresh deer tracks in every direction... Boucharville [Palliser's companion] did not relish it at all, and began already to calculate how soon we were to go away" (Palliser 1969: 266-267). "The abundance of game here [and not anywhere else] is accounted for by its being the neutral ground of the Crees, Assineboines, and Blackfeet; none of these tribes are in the habit of resorting to its neighborhood except in war parties.... We are now in the heart of the buffalo country. This region may be called a buffalo preserve, being the battle-ground between the Crees and the Blackfeet..." (Spry 1968: 146). Like Lewis and Clark, Palliser observed grizzlies primarily in aboriginal buffer zones.

Alexander Henry the Younger, describing conditions on the Red River, also noted that grizzlies were found almost exclusively in aboriginal buffer zones – "they [grizzlies] are – very numerous, and seldom are molested by the hunters [Indians], it being the Frontier of the Sioux [sic] and their enemy where none can hunt in safety. Here they [the bears] breed and multiply in the greatest security" (Gough 1988: 72). While Henry Hind (1971: 28-29) reported the presence of five aboriginal buffer zones on the northern Great Plains – four in Canada and one in the United States. "The following are celebrated 'war-paths,' where hunting is generally disallowed although game from that circumstance is usually more abundant. 1. 'The War-path River' and war road of the Lac la Pluie, Ojibways and the Sioux, from Rainy River to Red Lake River, thence across the prairies in the Valley of Red Lake River to Miniwahan or Devil's Lake, in Dakotah [sic] Territory. 2. 'War-path River,' from the southwest corners of Lake of the Woods to Roseau River, thence to the prairies west of Red River – same tribes. 3. 'War-path River', from Lake Winnipeg to the Little Sashatchewan [sic], thence to the prairies south of Manitobah [sic] Lake – the old war-path of the Swampy Crees, the Assinaiboines and Sioux, also of the Swampy Crees and the Lake Winnipeg Ojibways. 4. The 'war-road' near the Elbow of the South Branch of the Sashatchewan [River], on the flanks of the Grand Coteau, of the Blackfeet and Plain Crees. 5. The 'war-road' of the Sioux, Blackfeet and

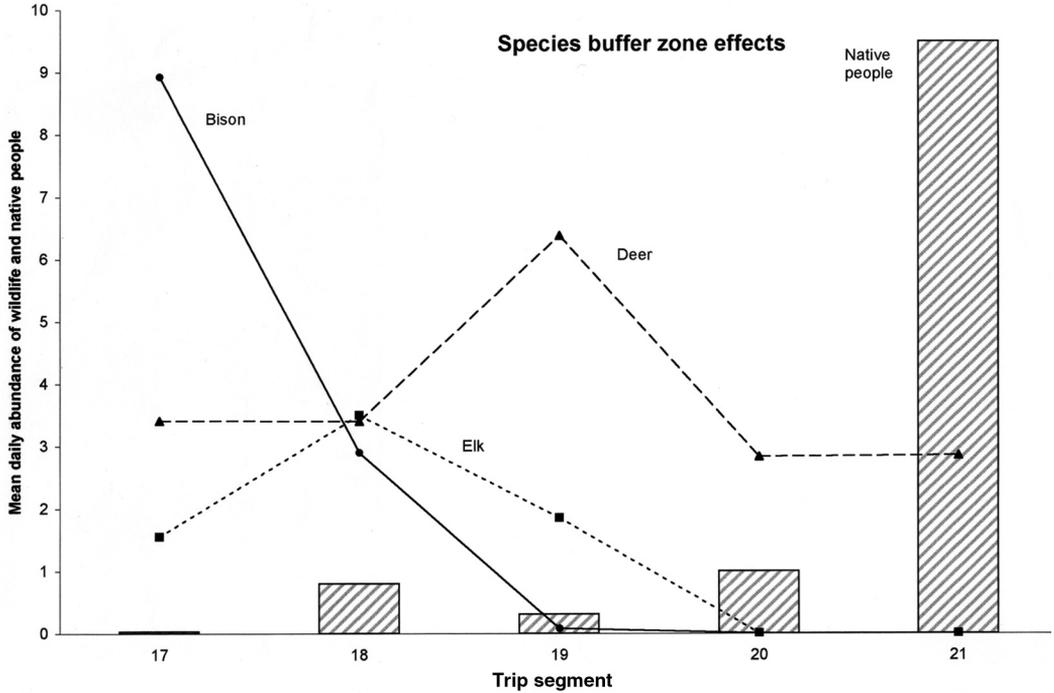


FIGURE 9. The effect of native hunting on Bison, Elk, and Whitetailed Deer. As Lewis and Clark ascended the Missouri River from Great Falls (trip segment 17) and finally met the Shoshone (trip segment 21), wildlife became less and less abundant. First, Bison disappeared, and then Elk, until only a few Whitetailed Deer remained. This is the pattern that would be expected if native hunters foraged optimally without regard to conservation.

Crows, in the Valley of the Yellowstone [River]”. In addition, both Alexander Mackenzie and Samuel Black noted the presence of an aboriginal buffer zone along the lower Peace River in northern British Columbia (Rich 1955: 112; Lamb 1970: 279, 288-289, 404-407). Similarly, Alexander Mackenzie reported a major Indian-Inuit buffer zone in the far north on his 1789 trip to the Arctic Ocean (Lamb 1970: 181-233) as did Franklin (1969) in 1821-1822.

As in the United States, most observations of wildlife in western Canada recorded by early European explorers, including virtually all sightings of Grizzly Bears, occurred in aboriginal buffer zones. Heretofore these buffer zone observations have been interpreted to mean that all of western Canada once teemed with game, which is simply not true. Instead, many areas of western Canada were almost devoid of wildlife due to intense native hunting (Kay et al. 2000).

Prey behavior

Lewis and Clark also reported a direct relationship between prey behavior and native hunting. In the center of buffer zones, where native people hunted only infrequently, game was relatively tame and could easily be approached (e.g., 4: 67, 108). Elsewhere, however, game was exceedingly wary. “The country about the mouth of this river [Little Missouri] had been recently hunted by the Minetares, and the little game

which they had not killed and frightened away, was so extremely [sic] shy that ... [our] hunters could not get in shoot [range] of them” (4: 26). “The Borders of the river [Missouri] has so much hunted by those Indians ... [that] the game is scarce [sic] and veery [sic] wild” (4: 39). This also applied to Grizzly Bears and other animals. “[The bears] appear more shy here [near the Shoshone] than on the Missouri below the mountains” (4: 426). “These animals [sic] [beaver] in consequence of not being hunted [in a buffer zone] are extremely gentle, where they are hunted [though] they [the beaver] never leave their lodges in the day” (4: 100). Similarly, in 1819 Long observed that Bison fled in panic at the mere scent of humans. “The wind happening to blow fresh from the south, the scent of our party was borne directly [to the Bison], and we could distinctly note every step of [our scent’s] progress through a distance of eight or ten miles, by the consternation and terror it excited among the buffaloes. The moment the tainted gale infected their atmosphere, [the Bison] ran with as much violence as if pursued by a party of mounted hunters” (Thwaites 1905: 255-256) – not unexpectedly, these observations were made in an aboriginal buffer zone along the Platte River in eastern Colorado (West 1995). This is identical to what Diamond (1984) reported in New Guinea, where even low-intensity aboriginal hunting completely altered the be-

havior of prey species, as well as significantly reducing prey number (Kay 2002).

Habitat

Over the years, I have retraced most of Lewis and Clark's route across North Dakota, Montana, Idaho, Washington, and Oregon, and there are no habitat features that could explain the distribution and abundances of the various species observed by the explorers. Lewis and Clark, for instance, did not find any "buffalo" in the large, treeless valleys of southwest Montana. This they attributed to the fact that Bison had been driven-out and/or killed-out by Shoshone hunters, not habitat characteristics (8: 182). At another point in their journey, Lewis and Clark commented on how they could see no difference between the country west of the mountains and the plains along the Missouri, except that wildlife was common only on the latter. "I see very little difference between the apparent face of the country here [eastern Washington and western Idaho] and that of the plains of the Missouri only that these [the Columbia Basin grasslands] are not enlivened by the vast herds of buffaloe [sic] Elk [etc] which ornament the other" (7: 196). Bighorn Sheep are certainly restricted to areas with precipitous escape terrain, but Lewis and Clark found bighorns common only in the center of aboriginal buffer zones. Other suitable habitat was unoccupied because those areas were more frequently used by native people.

Moreover, there is no evidence to support the assertion by Mack and Thompson (1982) or Lyman and Wolverton (2002) that Bison and other ungulates were rare in the Columbia Basin because those grasslands were nutritionally deficient. First as Daubenmire (1985) and others have noted, the Columbia Basin supported an open range livestock industry for nearly 40 years during the late 1800s (Olyphant 1968; Galbraith and Anderson 1971). Since cattle are less efficient herbivores than Bison, there is no physiological reason Columbia Basin grasslands could have supported large numbers of free-ranging cattle and not Bison (Van Vuren 1987; Urness 1989). In addition, a modern Elk herd on Columbia grasslands not only grew at near the maximum rate of increase for that species, but produced huge record-book antlers, as well – all indicative of excellent nutritional conditions (McCorquodale et al. 1988, 1989; McCorquodale 1991, 1993). Free-ranging Bison on other intermountain ranges have also shown high rates of increase (Van Vuren and Bray 1986; Keiter 1997; Bjornlie and Garrott 2001). There is also no evidence to support the notion that historically Columbia Basin Bison populations were kept at low levels by severe winter weather, as proposed by Daubenmire (1985). After all, Bison thrive in Yellowstone National Park (Keiter 1997; Bjornlie and Garrott 2001) and Wood Buffalo National Park (Carbyn et al. 1998) where winter climates are much more severe than in the Columbia Basin (Urness 1989). Instead, Bison and other ungulates were rare or absent from

most of the Columbia Basin because large runs of salmon, and other alternative resources, supported high numbers of native people (Hunn and French 1981), who took their preferred ungulate prey to low levels or local extinction (Kay 1994, 1998, 2002; Chatters 2004).

Native populations and European diseases

It has long been known that native people in the Americas had no immunological resistance to European diseases, but only recently has it been learned that those diseases had a significant impact on native people prior to direct European contact (Dobyns 1983), or how this, in turn, caused abnormal increases in wildlife populations (Neumann 1985; Preston 1996, 1997, 2002; Kay 1998, 2002; Kay and Simmons 2002). European diseases, for instance, preceded Lewis and Clark. The smallpox epidemic of 1780 was especially devastating (Boyd 1985; Trimble 1985), and its aftermath was noted by Lewis and Clark (2: 478-482; 3: 285, 295, 311-312; 6: 81-82, 285, 308). In 1804-1806, Lewis and Clark found four Mandan villages along the middle Missouri but observed that there had been 12 prior to the 1780 epidemic. Similarly, Arikaras villages were reduced from 32 to 2 (Ahler et al. 1991: 57). Thus, if Lewis and Clark had journeyed west in 1775 instead of 1804-1806, they would have met more native people and correspondingly there would have been even less wildlife (Geist 1998: 4-5; Kay 1998, 2002). Furthermore, European diseases may have decimated native populations throughout western North America as early as 1550-1600 (Ramenofsky 1987; Campbell 1990; Kornfeld 1994: 198; Preston 1996, 1997, 2002), which suggests that pre-Columbian wildlife populations were likely much lower than even what Lewis and Clark experienced. Butler (2000), who studied resource depression in the Columbia Basin, reported that high-ranked diet items, such as ungulates, increased only after epidemic diseases decimated native populations ca. 1550. Similarly, Chatters (2004: 72-73) reported that Bison numbers increased only when native populations declined.

Conclusions

Contrary to prevailing paradigms (Lyman and Wolverton 2002; Moore 2002; Wilkinson and Rauber 2002), native people controlled the distribution, abundance, and behavior of wildlife, and large mammals were common only in boundary or buffer zones between warring tribes (Martin and Szuter 1999a, 1999b, 2002, 2004; Farr 2001). It is also clear that Lewis and Clark recognized this phenomenon, for Clark (8: 328) "observed that in the country between the [Indian] nations which are at war with each other the greatest numbers of wild animals are to be found." This pattern can only be explained if native hunters pursued an optimal-foraging strategy and did not employ any effective conservation measures (Alvard 1998b, 2002). Only twice did Lewis and Clark report high wildlife values and encounter

large numbers of native people on the same day. In both cases, native hunters were killing as many animals as possible (3: 176, 253-255). Moreover, Lewis and Clark were only able to complete their journey because of the food, horses, and above all else, knowledge that they received from native people. There were no unnamed streams, there were no unnamed mountains, and there was no wilderness (Kay and Simmons 2002). As noted by Lewis and Clark, the West was even more densely populated prior to the smallpox pandemic that decimated native people in 1780.

These data have important implications for anthropology and archaeology, as well as other disciplines. Most anthropological subsistence models, for instance, incorporate the view that native people harvested ungulates at or near sustained yield levels, yet these and other data do not support that assumption (Kay and Simmons 2002). Similarly, cultural or religious beliefs are often invoked to explain how aboriginal peoples interacted with their environment (Krech 1999), yet irrespective of what the 40 or so native groups encountered by Lewis and Clark believed, or said they believed, the ecological patterns were identical, at least regarding large mammals (see Figure 1). This is similar to what Jerozolimski and Peres (2003) reported for modern subsistence hunters in South America, where neither ethnicity nor culture slowed the depletion of game stocks. Finally, these data support the hypothesis that native people were keystone predators, who once structured entire ecosystems (Kay 1998, 2002; Kay and Simmons 2002); i.e., ecologists need to abandon the myth of once abundant wildlife and instead recognize that un hunted ungulate populations are outside the range of historical variability.

Acknowledgments

This research was supported by a grant from Utah State University and a book contract from Oxford University Press. Susan Durham conducted the smoothing-spline analyses. Fred Wagner, William Preston, Paul Martin, Cliff White, Valerius Geist, Richard Keigley, and Randy Simmons reviewed earlier drafts of this manuscript, as did three anonymous reviewers.

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Received 4 July 2005

Accepted 27 June 2007