The Impact of Native Ungulates and Beaver on Riparian Communities in the Intermountain West

Charles E. Kay
Institute of Political Economy
Utah State University
Logan, UT 84322-0725

Abstract

This paper reviews the impact native ungulates, primarily elk and moose, and beaver can have on riparian communities in the Western United States. In Yellowstone National Park and in other areas where ungulates are not managed, repeated browsing has reduced tall willow, alpine, and cottonwood communities by approximately 85 percent since the late 1950s. Native ungulates can also severely reduce or eliminate palatable grasses and forbs from herbaceous riparian communities. By eliminating woody vegetation and water cover and by altering plant-species composition, native ungulates can alter bird, mammal, and aquatic communities. They can even negatively affect endangered species like grizzly bears for which riparian areas provide critical habitat. In many respects, excessive use by native ungulates is similar to overgrazing by domestic livestock.

Beaver is a keystone species that alters the hydrology, energy flow, and nutrient cycling of aquatic systems. Unlike ungulates, which tend to degrade riparian habitats, beaver actually create and maintain riparian areas. Beaver dams not only impound water but they also trap sediments that raise the water table and allow the extension of riparian communities into former upland areas. By tripping silt over thousands of years, beaver have actually created many of the West's fertile valleys. Prior to the arrival of Europeans, Western streams supported large populations of beaver. During one five-day period in 1825, Peter Skene Ogden's fur brigade trapped 511 beaver. Today, state and federal land-management agencies are using beaver to restore damaged riparian areas. Beaver, however, can become a nuisance when they dam irrigation facilities, plug highway culverts, or eat streamside trees valued by landowners.

INTRODUCTION

Most classifications of Intermountain wetland plant communities have failed to address what impact wildlife may have had on the species and structural composition of these riparian associations. (Youngblood et al. 1985, Wendelle et al. 1986, Kovalchik 1987, Hansen et al. 1988, Padgett et al. 1989). While ungulate-induced reductions in tree and shrub canopy cover and growth have been widely reported for various upland plant communities (Pinzolt 1965, Bohak et al. 1979, Stewart et al. 1987, Alverson et al. 1988, Tilghman 1989, Veblen et al. 1989, Brandner et al. 1990), only a few wildlife grazing studies have dealt specifically with riparian communities (Patten 1968).

This paper explores the impact native ungulates, primarily elk (Cervus elaphus) and moose (Alces alces), and beaver (Castor canadensis) have on riparian communities in the Western United States. Emphasis is placed on Yellowstone National Park—not because that area has unique wildlife/riparian relationships but because it is one of the few areas where researchers have concentrated on wildlife/riparian interactions. Chadde et al. (1988) classified wetland plant communities on Yellowstone's northern winter range, while Chadde and Kay (1988, 1991)

Similar wildlife/riparian interactions occur in other Western national parks, including Rocky Mountain, Mount Rainier, Grand Teton, Band, and Jasper, where ungulates have been allowed to concentrate in wetlands areas. Similar conditions also exist in western Wyoming where large populations of elk are maintained by winter feeding (Andersen 1958, Beadle 1975, Strickland 1981, Boyle 1989) and where large numbers of moose winter in riparian areas (Bassett 1954, Rudsodorf 1952, Harry 1957, Houston 1968, Collins 1976).

UNGULATE IMPACTS

WILLOWS

Until 1968 the National Park Service contended that an “unnaturally” large elk population, which had built up in Yellowstone during the late 1800s and early 1900s, had severely “damaged” the park’s northern winter range, including willow communities (Rush 1963, Kittm 1959, Pengelly 1963, Tyers 1981, Kay 1986, Chase 1986). However, agency biologists (Houston 1976, 1982) now believe elk and other animals in Yellowstone are “naturally regulated,” being resource (food) limited.

A complete discussion of how the Park Service developed and formulated its “natural regulation” program is beyond the scope of this paper; but under “natural regulation,” (1) predation is an assiting but nonessential adjunt to the regulation of ungulate populations. If wolves were present, they would only kill the animals slaled to die from other causes, primarily starvation, and, thus, would not lower the ungulate populations; (2) if ungulates and vegetation have coevolved for a long period of time and if they occupy an ecologically complete habitat, the ungulates cannot cause regressive plant succession or range damage. The ungulates and vegetation will reach an equilibrium where continued grazing will not change plant species composition or the physical structure of the plant community; and (3) at equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone this means elk have not caused a decline in the numbers of other ungulates or beaver.

Park Service biologists now believe that elk and other herbivores and vegetation in Yellowstone have been in equilibrium for several thousand years (Despain et al. 1986). Many changes in plant-species composition since the park was created are believed to be due primarily to suppression of lightning fires, normal plant succession, or climatic change, not to ungulate grazing. Houston (1982:129) concluded that “while ungulates and other herbivores affected the rate of primary succession, changes in distribution of willow were mostly climatically determined.” He (1982:131) also suggested that suppression of lightning fires may have adversely affected willows.

Houston (1976) indicated that if willow communities had actually declined on the northern range because of ungulate browsing this would be a basis for rejecting the “natural regulation” hypothesis. Because “natural regulation” is a global equilibrium model, grazing-induced changes in vegetation height or physical structure would also indicate the herbivores are not in equilibrium with their food resources. If ungulate browsing has changed what were once tall white willow communitues into short willow types, this would be additional grounds for rejecting “natural regulation.”

To evaluate the effects of successon, climate, and ungulate browsing on Yellowstone’s willow communities, the following data are presented on the historical distribution and abundance of willows in the park, ungulate-proof willow exclosures, and willow seed production.


In 1871 Captains Barlow and Heep (1872:60) toured Yellowstone Park. On the northern range, they reported “thickets of willows along the river banks.” Norris (1880:613), Yellowstone’s second superintendent, noted that the park was “well supplied with ripules in invariably bordered with willows.” Norris (1880:617) added that there were “innumerable dense thickets of willow” in Yellowstone. Based on an analysis of pollen in the sediments from lakes and

Terms such as overgrazing, range damage, and unnaturally large elk populations were used in nearly all early governmental reports about the northern range. Since these terms are value lades, they are used throughout this paper only in their historical context.

4See Kay 1990, Chapter 1, for a detailed analysis of how “natural regulation” was developed.
ponds on the northern range, Barnosky (1988) reported that willow pollen had declined since the early 1900s. Thus, the available evidence indicates that tall willow communities were once common on the northern range but that they are now virtually absent.

Historically, Yellowstone's Gallatin River drainage has had an elk situation similar to that on the northern range (Packer 1963; Patten 1963, 1969; Streeter 1965; Peck et al. 1967; Lovaas 1970). Patten (1968) reported vegetation along the Gallatin River changed rapidly from an area nearly devoid of willows near the park's boundary to extensive willow thickets a few kilometers upstream in the park. He (p. 1107) noted that "between these areas lies a transition zone of stunted and dead willows." The area with the fewest willows had the largest concentrations of wintering elk (Peck et al. 1967, Lovaas 1970). Where deep snow to the south or hunters north of the park limit elk use, willows grew taller (Kay 1980).

Kay (1990:290) made four photo sets of willow communities on Yellowstone's Gallatin winter range. These contained four pictures taken in 1924, 1949, 1961, and 1986, while the other included 1937, 1961, and 1986 photos. Tall willows declined markedly along this section of the Gallatin River and lower Daly Creek between 1924 and 1961. Since the 1970s, the Montana Department of Fish, Wildlife, and Parks has made a concerted effort to control this elk herd when it migrates from Yellowstone Park. By instituting late-season hunts, the department reduced the Gallatin elk population by at least 56 percent in recent years (Kay 1990). In apparent response to this decline in elk numbers, photos repeated in 1986 and 1989 show that willows have increased in height and canopy cover since the 1960s, but they still show more signs of browsing than willows did in 1924 (Kay 1990).

Houston (1982:276–77) suggested that willows were serial to conifers. In some instances, this is true but not for most willow communities on Yellowstone's


<table>
<thead>
<tr>
<th>Tract</th>
<th>Date of first measurement</th>
<th>Date of most recent measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mannoh Outside</td>
<td>7.5</td>
<td>4.5</td>
</tr>
<tr>
<td>Inside</td>
<td>6.6</td>
<td>16.1</td>
</tr>
<tr>
<td>Juntion Butte Outside</td>
<td>6.0</td>
<td>8.2</td>
</tr>
<tr>
<td>Inside</td>
<td>5.4</td>
<td>9.2</td>
</tr>
<tr>
<td>Lumar-East Outside</td>
<td>20.0</td>
<td>11.4</td>
</tr>
<tr>
<td>Inside</td>
<td>40.8</td>
<td>28.0</td>
</tr>
<tr>
<td>Totals Outside</td>
<td>9.1</td>
<td>15.3</td>
</tr>
<tr>
<td>Inside</td>
<td>14.0</td>
<td>14.0</td>
</tr>
</tbody>
</table>

*p = n.s. < .01

*All permanent willow belt transects in Yellowstone Park contain some nonwillow communities. These areas were excluded in the 1986–1988 measurements.
The Park Service uses the same outside plot for both the Lumar-East and the Lumar-West enclosures.
Percentages were arcsine transformed; Student's t test.
northern range. Of the forty-eight, repeat photo sets of willow communities reported by Kay (1980), only two showed complete replacement by conifers. In three others, approximately 20 to 60 percent of the willow communities in the original photos were replaced by conifers. So only five of forty-eight photo sets (10 percent) showed conifer invasion of what were once willow communities (Kaye 1980).

Exclusions. Kay (1980: Chapter 8 and Chadde and Kay 1988, 1991) reported on willow communities inside and outside five ungulate-proof grazing exclosures on Yellowstone's northern range. Willows were taller and had greater canopy cover inside than outside each exclosure (Tables 1–2). Other less palatable shrubs, such as rose (Rosa woodsii) and river birch (Betula occidentalis) (Nelson and Leech 1982), exhibited the same pattern (Kay 1990). When pooled, these differences were statistically significant across all exclosures (Tables 1–2). Outside these exclosures, the mean height of all willow species was 51 cm while inside it was 279 cm. On average, willows had 17 percent canopy cover outside the exclosures but 99 percent canopy cover where ungulates were excluded. Thus, willow canopy closure was nearly complete inside the exclosures.

In addition, willows inside the exclosures increased significantly in height and canopy cover over time while those outside did not (Tables 1–2). Mean willow height outside the exclosures when they were first established (1958–1963) was 45 cm and only 51 cm when they were recently measured (1986–1988) (n.s.; Student's t test). Inside the exclosures, willows had a mean height of 54 cm in 1958–1963 and 279 cm in 1986–1988 (p < 0.01; Student's t test). At the date of first measurement (1958–1963), willows outside the exclosures had a mean canopy cover of 9.1 percent, which increased to 17.1 percent by 1986–1988; but that difference was not statistically significant. Inside the exclosures, willow canopy cover increased from 13.3 percent in 1958–1963 to 99.4 percent by 1986–1988 (p < 0.01; Student's t test on arc sine transformed percentages).

Inside three exclosures in the Gallatin River drainage, willows attained heights of 3 to 4 m with near-complete canopy closure while unprotected plants were all less than 1 m tall (Kay 1990:150). In Rocky

| Mean height (cm) |
| Date of final measurement 1958 1962 1963 | Date of most recent measurement 1986 1988 |
| Exclusion-site |  |
| Mammoth |  |
| Outside | 28 | 28 | 28 | 22 |  |
| Inside | 44 | 44 | 44 | 316 |  |
| Junction Butte |  |
| Outside | 56 | 56 | 56 | 35 |  |
| Inside | 29 | 29 | 29 | 219 |  |
| Lamar East |  |
| Outside | 29 | 29 | 29 | 45 |  |
| Inside | 27 | 27 | 27 | 282 |  |
| Lamar-West |  |
| Outside | 32 | 32 | 32 | 45 |  |
| Inside | 24 | 24 | 24 | 287 |  |
| Shoshone Creek |  |
| Outside | 80 | 80 | 80 | 200 |  |
| Inside | 120 | 120 | 120 |  |

| Totals | 45 | 45 | 51 | 51 |
| Inside | 54 | 54 | 279 | 279 |

*p < 0.01

* The Park Service uses the same outside plot for both the Lamar-East and the Lamar-West exclosures. Student's t test.
Mountain National Park, Gysel (1990) and Stevens (1980) noted that willows increased in canopy cover and height inside enclosures where elk were exclud-
ed. On elk and moose winter range in Banff National Park, Trottier and Fehr (1992) reported that willows inside an enclosure were significantly taller than those exposed to ungulate browsing.

In addition to the measurements of plant height and cover that the Park Service made over the years at Yellowstone's willow enclosures, they also photographed the permanent willow-belt transects each time they were sampled. Kay (1990) repeated those photographs in 1996–1998. The resulting multiple-image photosets confirm that willows inside the enclosures have increased in height and canopy cover since they were protected while willow communities outside the enclosures have not increased in height.

Table 3. Mean number of seeds produced by willows inside and outside Yellowstone enclosures. Adapted from Kay (1990) and Kay and Chadsde (1992).

<table>
<thead>
<tr>
<th>Species</th>
<th>Outside enclosure</th>
<th>Inside enclosure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salix bebbiana</td>
<td>0</td>
<td>318,854</td>
</tr>
<tr>
<td>Salix boothii</td>
<td>0</td>
<td>233,142</td>
</tr>
<tr>
<td>Salix utahae</td>
<td>0</td>
<td>583,976</td>
</tr>
<tr>
<td>Salix geyeriana</td>
<td>0</td>
<td>168,972</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>0</strong></td>
<td><strong>360,888</strong></td>
</tr>
</tbody>
</table>

*α < 0.01, Student's t-test.

Those photographs also demonstrated that willows inside the enclosures now have the same height and physical structure that willows on the northern range had in the 1870s to 1890s (Kay 1990:150). So the conditions inside these enclosures were closely approximated the level of ungulate use that existed when Yellowstone Park was established in 1872 than conditions in the park today.

Seed Production. The Park Service believes that Yellowstone’s present short-statured willows are ecolo-
logically equivalent to the tall willow communities that once existed on the park’s northern range (Depain et al. 1986). To test one aspect of this assumption, Kay (1990) and Kay and Chadsde (1992) measured willow seed production inside and outside Yellowstone enclosures. Outside the enclosures, no aments (male or female flowering parts) were present on any of the permanent willow-belt transects. Fur-
ther, only eight male aments were found in an addi-
tional 1.13 ha of willow-dominated habitat that was searched adjacent to the four enclosures on Yellowstone’s northern range. In contrast Salix bebbiana, S. boothii, S. utahae, and S. geyeriana pro-
duced an average, respectively, of 1445, 583, 694, and 1346 female aments per m² of canopy cover inside enclosures (Kay 1990:Chapter 7).

The number of seeds per m² of female willow canopy cover ranged from a low of around 109,000 for S. geyeriana to over 583,000 for S. utahae and averaged nearly 307,000 (Table 3). By combining the mean sex ratio, species canopy cover, and species seed produc-
tion values, Kay (1990:85–91) estimated the total number of seeds produced inside and outside willow-
belt transects. Approximately 5,857,000 seeds were produced on the willow transect inside the Junction

Butte enclosure and zero outside; in the Lamar-East enclosure, 6,161,000 seeds were produced inside and zero outside; the Lamar-West enclosure had 7,016,000 seeds produced inside and zero outside; and in the Mammoth enclosure, 3,177,000 seeds were produced inside and zero outside.

Kay (1990:191) reported that individual plants with a few stems beyond the reach of ungulates on Yellowstone’s northern range showed an identical pattern. Willow stems above the browse height (2.5 m) produced an abundance of male or female aments while aments on that portion of the plant exposed to browsing (Table 4). Repeated ungul-
ate browsing has virtually eliminated willow seed production on the northern range and other winter ranges within the Greater Yellowstone Ecosystem.

In a related study (Kay and Chadsde 1992), willows protected for three growing seasons increased in
Table 4. Number of shoots produced above and below the browse height (2.5 m) on individual willows in Yellowstone National Park near Cody Creek. Adapted from Kay (1990) and Kay and Chadde (1992).

<table>
<thead>
<tr>
<th>Species-plant</th>
<th>Plant size (m²) canopy cover</th>
<th>Number of shoots above browse height</th>
<th>Number of shoots per plant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Below browse height</td>
<td>Above browse height</td>
</tr>
<tr>
<td>Salix intera</td>
<td>A - female</td>
<td>12</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>B - female</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>C - female</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>D - male</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>Salix geyeriana</td>
<td>E - female</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>F - female</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>G - female</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Salix bochtii</td>
<td>H - female</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Means</td>
<td>0*</td>
<td>676*</td>
</tr>
</tbody>
</table>

*r = 2.80, p < 0.01.

height but produced less than two male or female
aments per m². It apparently takes several years for
willows to reach their full reproductive potential once
they are no longer subjected to ungulate browsing.

As a consequence, once the existing willows die of
old age, disease, insects, or other causes they cannot be
replaced by new plants produced from local seed.
Under these conditions, willows will eventually dis
appear. Willows commonly colonize new habitats by
producing vast numbers of wind-dispersed seeds.
Yet during a three-year study to classify wetland
communities on the northern range, Chadde et al.
(1988) observed few willow seedlings on newly created
gravel bars and mud flats, which normally provide
ideal seed beds.

Without abundant seed crops, willows also cannot
take advantage of recruitment opportunities pro
duced by periodic large-scale disturbances such as
fire (Despain 1989). Yellowstone's 1988 fires oc
urred under extreme burning conditions during an
extended drought and are thought to be an event that
occurs only every 100 to 300 years (Davis and Mutch
1989, Remme and Despain 1989a, 1996a; Schullery
1989a, 1989b). Hence, those fires were able to burn
a limited number of normally wet riparian zones
(Knight and Wallace 1989), many of which had thick
sedge (Carex spp.) mats and accumulations of organic
matter (Brichits 1987, Chadde et al. 1988). These
areas, normally unfavorable to willow seed germina
tion and seeding establishment, "were burned down
to mineral soil, killing rhizomes and root systems"
(Knight and Wallace 1989:704). This burning creat
ed bare mineral soil and ash substrates that had
abundant soil moisture (especially after snowmelt in
1989), ideal conditions for germination and seeding
establishment of willow (Brichits 1987). Yet Kay
and Chadde (1990) observed few willow seedlings
growing in those areas.

The data would suggest that practically no willow
seeds were produced on Yellowstone's northern range
and colonized this newly created habitat. Reduction in
seed production decreases the probability of plants
colonizing new sites (Allison 1987). The virtual
elimination of willow seed production by ungulates
also suggests that herbivores and vegetation are not
in equilibrium as proposed by the Park Service's
"natural regulation" paradigm (Kay 1990:222).

Why Have Willows Declined? The Park Service
has postulated that the observed decline in
Yellowstone's tall willow communities is due to (1)
normal plant succession, (2) climatic change, and (3)
fire suppression but not to ungulate browsing (Ho
(1982:129-34), the willow decline may also have been
due in part to the lack of new substrate for willows
to colonize. He presented a 1974 photo of a newly
formed gravel bar in the Gardiner River and a 1978
retake that showed willows had colonized that area.
Kay (1990:137) rephotographed that site in 1983,
(1988) established plots at that site as part of their
riparian classification study. By 1983 willows were
almost entirely absent from that gravel bar and had
been replaced by grasses and other herbaceous plants.
exposed to ungulates. By the late 1970s and early 1980s, those willows were extensively hedged and were either dead or reverting to lower-statured plants (Kay 1990). Those changes certainly cannot be attributed to the 1930s drought. Climatic variation also appears to be unimportant since that area has abundant subsurface soil moisture (Bricha 1987, Chadde et al. 1988).

In recent years, the mean annual temperature on the northern range at Mammoth increased 0.5°C while the mean annual precipitation declined 1 to 2 cm (Houston 1982:101-7). No study, however, has demonstrated that a climatic shift of that magnitude will have a long-term impact on tall willows, especially since nearly all willow communities are subirrigated (Bricha 1987). Most perennial woody floras have so much biological or vegetative inertia that large-scale climatic changes of long duration are required before major shifts in plant species composition or stature occur (Smith 1965, Cole 1965, Davis and Bockin 1985, Davis 1986, Neilson 1986).

It has also been suggested that willow communities need to burn at frequent intervals if they are to persist on the northern range (Houston 1982) or if willows are to grow beyond the reach of browsing ungulates. Houston (1973, 1982:107) calculated mean intervals of 50 to 25 years between fires on the northern range during the 300 to 400 years before Yellowstone Park was established; and the government began to suppress fires. Despite a policy that has been in effect since the early 1970s to let many lightening-caused fires burn, 1988 was the first year fire burned more than a small area on the northern range.

Despite what were considered the worst burning conditions in the park's history, riparian communities were not overly susceptible to the 1988 fires. Some willow communities did burn, but the fires commonly skipped over others because riparian areas and willows are generally too wet to burn (Ronne and Knight 1981, Baker 1987).

Finally, there is no evidence to support the idea that burning will cause reseeding of willows to grow so fast as to be so chemically defended that they can grow beyond the reach of elk and other willow communities as has been postulated by park personnel (Kay 1990). Observations of experimental willow burns conducted by the Park Service on the northern range indicate that elk browse all of the new sprouts and none were able to grow taller than 1 m except where physical barriers prevented elk use (Kay 1990:162). Stein and Price (1990:336) reported that in an experimental situation "elk fed primarily on [reseeded] willows that had been burned" as compared to unburned plants. Suter (1990:340) clipped winter dormant willows to simulate ungulate browsing and then measured proanthocyanidic tannins in twigs that grew the following year. She found that
“after two repeated clipping treatments in successive years, tannin levels decreased at all clipping intensities.” She noted that “at extreme clipping levels plant reserves [were] not large enough to meet the demands of both a compensatory growth response and increased tannin production.” Suter (1990) concluded that “a rapid growth response was an ineffective deterrent to future browsing.”

Based on this evidence, Kay (1990) and Chadde and Kay (1991) concluded that frequent, repeated ungulate browsing was primarily responsible for the decline of tall willow communities on the northern range. Browsing by elk and moose presently prevents the willows that do exist on the northern range from expressing their full biological height and canopy cover. From 1970 through 1976, willow utilization on the northern range averaged over 91 percent (Houston 1982:149) and has not decreased in recent years (Kay 1994:143). Likewise, Barmore (1981:358) concluded that willows had declined on the northern range due to repeated ungulate browsing, not to climatic change.

During the late 1950s and early 1960s when the Park Service believed that an “unnaturally” high population of elk was causing “range damage” in Yellowstone, the herd was reduced by trapping, transplanting, and killing elk (Kay 1990:Chapter 1). Barmore (1981:357) noted that “by the late 1960s, the growth form and condition of Salix spp. on most of the winter range began to more closely resemble the less heavily browsed conditions of the late 1950s and early 1960s. This change was associated with major reduction of the northern Yellowstone elk herd suggesting that the decline in the distribution and condition of Salix spp. from the 1950s to the early 1960s was at least partly due to heavy browsing by elk.”

On the Gallatin River, willows declined only where wintering elk concentrated (Patten 1965). The willows upstream and downstream from the main elk wintering area have not declined and commonly exceed 3 m in height. Climatic or hydrologic conditions could not be primarily responsible for the decline near the park boundary since all sections of the river were subjected to the same physical factors. Patten (1965) found that willows farthest from the river had the highest grazing-induced mortality rates. He concluded that plants subjected to physiological stress were less able to withstand grazing pressure. It was ungulate browsing, though, that actually caused most of the mortality and reduction in plant growth form. Neilson (1986), who worked on a similar climatic-change versus grazing problem, concluded that the vegetation would have persisted despite drought, but the additional stress of grazing completely altered the flora.

Repeated ungulate browsing can change tall willow communities into grazing-maintained short willow types and can also eliminate willows entirely. Unrestricted browsing by large populations of wild ungulates has the same impact commonly associated with “excessive” livestock grazing in riparian zones (Knopf and Cannon 1982, Cannon and Knopf 1984, General Accounting Office 1986, Schulz and Leininger 1990). After examining riparian communities in Yellowstone National Park, Dr. William Platts, U.S. Forest Service (USFS) riparian researcher and past president of the American Fisheries Society, stated that Yellowstone contained some of the worst overgrazed riparian areas that he had ever witnessed. He added that if this had occurred on Bureau of Land Management (BLM) or USFS-administered lands with domestic livestock these agencies would have revoked the grazing permits.

Elk have also altered riparian communities in several other Western national parks including Rocky Mountain in Colorado (Stevens 1980, Braun et al. 1991) and Olympic in Washington (Houston et al. 1990). As in Yellowstone, the National Park Service contends that those altered areas are zoetic climates that are “natural” and that they are not a sign of overgrazing. Based on an extensive analysis of historical journals and archaeological faunal remains, however, Kay (1990) demonstrated that large populations of elk did not exist anywhere in the intermountain West over the last 8,000 or so years. Instead, today’s herds are a recent phenomenon associated with park management. Of more than 50,000 ungulate bones identified at more than 500 intermountain archaeological sites, only 3 percent were elk and only one moose bone was unearthed (Kay 1990).

Aspen and Cottonwoods

Various species of cottonwood (Populus spp.) and aspen (Populus tremuloides) commonly grow in riparian settings throughout the Intermountain West (Youngblood and Mueggler 1961, Youngblood et al. 1985, Windell et al. 1986, Baker 1987, Mueggler 1986, Padgett et al. 1989). Heavy livestock grazing has long been recognized as a detriment to reproduction of cottonwoods (Crouch 1979) and aspen (Clary and Modin 1990) situated in riparian zones, but few studies have addressed the impact ungulates may have on cottonwood- or aspen-dominated riparian communities.

Late 1950s photos of Slough Creek and the Lamar River on Yellowstone’s northern range show dense cottonwood and aspen riparian forests (Kay unpub. photos). Photos of those same areas taken during 1986–1988 show that the riparian gallery forest trees have declined approximately 90 percent since the park was established (Kay unpub. photos).

The few large cottonwoods (Populus trichocarpa and P. angustifolia) remaining along waterways in
Yellowstone Park produce abundant seeds, some of which establish on gravel bars along rivers and streams. Virtually none of those plants, however, has been successfully recruited into their sexually reproducing populations over the last eighty or so years because repeated ungulate browsing has prevented the young cottonwoods from growing taller than 1 m (Chadde et al. 1985, Kay unpub. photos). As the older trees die from various causes, they are not replaced by new trees grown from seed; and under present conditions, ungulate browsing will eventually eliminate cottonwoods from the park.

Kay (1985, 1990) conducted a detailed analysis of aspen communities on Yellowstone's northern range and throughout the Greater Yellowstone ecosystem including riparian aspen types. He utilized insider outside park comparisons, repeat photographs, as well as conclusions in his study of aspen ecology. He concluded that, as with willows, ungulate browsing—not normal plant succession, climatic change, or fire suppression—was primarily responsible for the decline of aspen throughout the Yellowstone area. He noted that under the present levels of ungulate browsing once the remaining older aspen trees die communities with an aspen-tree overstory will be eliminated from the park and much of the Yellowstone ecosystem because repeated ungulate browsing has suppressed aspen regeneration for the last eighty or so years. Except where elk and other ungulates are physically excluded, repeated browsing prevents aspen suckers from growing taller than 1 m, including aspen growing in riparian zones (Kay 1990).

**Herbaceous Riparian Communities**

Tiedemann and Berndt (1972), Hanley and Taber (1980), Bradley (1982), and Edgerton (1987) concluded that grazing and trampling by elk on upland sites limited shrubs and tall forbs while favoring grasses, sedges, and low-growing forbs. Since elk and other ungulates have a preference for mesic habitats, it appears reasonable to assume that ungulates would have a similar impact on riparian understory plants and herbaceous riparian communities, though few researchers have specifically investigated this subject.

As part of his aspen ecology study, Kay (1990) measured understory species composition in aspen stands on Yellowstone's northern range. He compared understory species composition in the park with that of aspen stands immediately outside the park in Eagle Creek where fewer elk winter. He reported that the understories of aspen stands in the park were dominated by plants resistant to grazing or ones that are less palatable, while understories in Eagle Creek were dominated by shrubs and tall forbs sensitive to grazing and trampling. For example, cow parsley (Heracleum lanatum) had an average canopy cover of 12.3 percent in Eagle Creek aspen communities and only 0.5 percent in park stands (p < .001, t-test on arcsine transformed data) (Kay 1990:75). Cow parsley had a constancy (the percentage of total measured stands containing the species) of 73 percent in Eagle Creek and 24 percent in the park. Cow parsley is readily eaten by ungulates, and elk in Yellowstone select cow parsley even in summer when other forage is abundant. Moreover, cow parsley is very susceptible to trampling damage. Simulated elk trampling research has shown that tall forbes are the class of plants most severely affected by trampling (Bradley 1982). Since cow parsley is very sensitive to herbivory (Youngblood and Muggel 1981:12, Stivers 1988) and there have been substantially fewer elk outside the park (Kay 1965, 1990) where cow parsley is more abundant, it appears reasonable to attribute the observed differences to elk grazing.

Although commonly found in riparian areas throughout the West, cow parsley is rarely found in wetland plant communities on Yellowstone's northern range (Chadde et al. 1986). In the park's riparian zones, cow parsley is often found growing only where it is physically protected from ungulate browsing. For instance, cow parsley has been observed growing inside clumps of dying willows where dead branches apparently act as nurse plants to protect the umbel from elk (Kay unpub. photos). Most aspen communities in the park have understoreys dominated by non-native grasses such as timothy (Phleum pratense) or Kentucky bluegrass (Poa pratensis). On average, timothy had a canopy cover of 33.4 percent in park aspen stands but only 2.6 percent in Eagle Creek (p < .001, t-test on arcsine transformed data) (Kay 1990:75). Houston (1982:415) indicated that timothy dominated "about seventeen percent" of the aspen stands he measured in the park but provided no other data. In the park, Kay (1990:75-76) reported that timothy had average canopy covers of 42.4 percent and 36.5 percent respectively with constancies of 88 percent and 77 percent in his North and South Lamar study areas. Timothy is resistant to grazing and tends to increase with grazing pressure or disturbance (Chadde et al. 1988). Elsewhere, aspen and riparian communities dominated by non-native grasses have been classified as grazing climax (Youngblood et al. 1985, Muggel 1986, Padgett et al. 1989).

Chadde et al. (1985) and Chadde (1989) reported a similar pattern in riparian communities throughout the northern range. Undergrowth tended to be dominated by grasses while palatable shrubs and tall forbs were rare. This trend is also clearly evident at the Lower Beaver Meadows exclusion in Rocky Mountain National Park. There, a herbaceous riparian
community inside the enclosure is dominated by cow parsnip, white angelica (Angelica arguta), and tall blue bells (Mertensia spp.), while grasses and sedges predominate on the outside (Kay unpub. photos).

In Isle Royale National Park, Michigan, by treading cow completely altered the species composition, and understorey structure of the forests (Hansen et al. 1973, Krefting 1974, Janke 1976, Snyder and Janke 1976, Ristenhoover and Masses 1987, Moen et al. 1990) and is even eliminating balsams fir (Abies balsamea) from most of the inland (Brandner 1986, Brandner et al. 1990). In addition, Aho and Jordan (1979) and Jordan (1987) noted that grazing by moose had a marked negative impact on aquatic plants (Nuphar variegatum, Nymphicola odorata, and Potamogeton spp.) over the entire island, while Fraser and Hristienko (1983) reported that moose had eliminated much of the aquatic vegetation in Sibley Provincial Park, Ontario.

HIDING OR SECURITY COVER

Hiding or security cover, another measure of vegetation height and plant density or spacing, is important to many wildlife species. For instance, grizzly bears (Ursus arctos) seldom use a food source far from cover (Kay 1989). Lebl et al. (1997) demonstrated that hiding cover for mule deer (Odocoileus hemionus) favors in willow, aspen, and herbaceous riparian habitats was significantly reduced with heavy livestock use.

Kay (1999) measured security cover in willow and aspen habitats inside and outside Yellowstone Park enclosures, as well as along Montana's East Front. He noted that the security cover offered by willows on Yellowstone's northern range was only 11 percent while it was 100 percent inside willow enclosures and in East Front willow communities. He also reported a similar trend in aspen types. Kay (1999) concluded that grizzly bears in Yellowstone seldom use low-elevation riparian and aspen communities in the park, in part because repeated ungulate browsing has drastically reduced the security-cover value of those habitats. Where security-cover values are high, such as along the East Front, grizzlies show a decided preference for low-elevation willow and aspen communities (Aune et al. 1986, Aune and Bramm 1997, Aune and Kasworm 1989).

SUMMER RANGE

Houston (1982:131) argued that ungulates were not primarily responsible for the decline of willows in Yellowstone because willows had also declined outside the park as well as on Yellowstone's summer ranges. Willows have in fact declined throughout the West since European settlement; but that has been primarily due to agricultural practices such as irrigation and livestock grazing, not to climatic change (Meehan and Platts 1978, Dobyns 1981, Myers 1981, Marcussen 1983, Platts et al. 1983, General Accounting Office 1986). A recent study of 262 miles of streams in southwest Wyoming found that since the 1850s 83 percent of the streams and their associated riparian areas had been severely altered by livestock grazing (Shute 1981). Furthermore, moose and elk feed upon willows on Yellowstone's summer ranges (McMillan 1950, 1953); and until enclosures are built in those areas, there is no way to determine what impact summer ungulate utilization is having on those communities.

In Western Canada, Morgantini and Hudson (1989) reported that elk shifted their diet to willows on summer ranges. In Rocky Mountain National Park, Stevens (1980:14) concluded that "willow forms a major part of the summer diet for elk, about 21 percent." He (1980:130) reported that on the park's summer range "55 percent of the elk were observed on willow types." Moreover, he found that elk grazing caused willows to decline on the park's summer range. "Salix brachycarpa decreased an average of 55 percent on three of the four transects, with an overall decline from 20 percent cover to 9 percent. Salix planifolia declined from 37 percent to 29 percent cover" (Stevens 1980:135). These reductions occurred in only eight years as the elk herd built up in that park (Stevens 1980:130). Reporting on a continuation of that study, Braum et al. (1993) noted that from 1971 to 1989 willow canopy cover on permanent plots in Rocky Mountain National Park's alpine zone decreased from 49 percent to 36 percent while willow canopy cover on subalpine plots declined from 57 percent to 27 percent due to reported elk browsing.

Bradley (1992) reported that browsing elk had severe impacts on willow communities in the subalpine zone of Washington's Mount Rainier National Park. He reported that a combination of elk grazing and trampling caused extensive soil erosion that eventually destroyed many riparian zones in elk summering areas. As noted previously, this is not surprising since nearly all habitat-use studies have shown that summering elk have a decided preference for mesic areas (Skovlin 1982, Edje et al. 1987, 1998).

A large segment of the southern Yellowstone or Jackson Hole elk herd once summered in Wyoming's Teton Wilderness, including Big Game Ridge (Anderson 1995, Houston 1992, Boyce 1999). Coft and Ellison (1980) reported that grazing and trampling by large numbers of elk on Big Game Ridge caused extensive soil erosion that was so severe that huge boulder-choked mudflows descended several miles down from the ridge and completely buried miles of riparian habitat. This destruction could not be blamed on domestic livestock, as they had never been allowed
in that area (Croft and Ellison 1960).

Cole (1969), Grulich (1971), and Boyce (1986) question this interpretation. They believe that the situation on Big Game Ridge is "natural" and claim that large herds of elk have summered there for the last several thousand years. They insist that excessive soil erosion began when the area was burned during the 1890s and then subjected to extensive pocket-gopher-induced (Thomomys spp.) soil disturbance. Croft (1974) and Beetle (1974) criticized this reinterpretation.

This area was once part of the Teton State Game Preserve, and hunting was not permitted from 1905 to 1942. During the thirty-eight years when hunting was not allowed, large numbers of elk summered on Big Game Ridge. Damage damage on Big Game Ridge was first reported in 1951, and by 1960 massive soil erosion had occurred (Croft and Ellison 1960). As more and more hunters used the area, though, fewer and fewer elk summered on Big Game Ridge. Today relatively few elk summer there, and mudflows have not occurred since the late 1960s despite a continued abundance of pocket-gopher activity.

Moreover, Kay (1990) reported that despite extensive archaeological surveys and excavations not a single elk bone has been unearthed from any of the several hundred known archaeological sites in Jackson Hole. Wright (1894), who made an extensive study of aboriginal subsistence patterns in northwestern Wyoming, concluded that native peoples who inhabited Jackson Hole for the last 10,000 or so years subsisted mainly on vegetal foods and that there was no evidence that large herds of elk or other ungulates summered or wintered in that area until after European influences. It appears that the soil erosion, which completely buried miles of riparian habitat at some distance from Big Game Ridge, was not natural but occurred when elk concentrated in an area closed to hunting.

BEAVER IMPACTS

NEGATIVE IMPACTS

Unlike ungulates, which tend to negatively affect or eliminate riparian habitats, beaver actually create and maintain riparian areas. Many people, though, harbor negative attitudes toward beaver because they often interfere with human activities. For instance, beaver are held in low regard by many Western agricultural interests because they frequently dam irrigation ditches, highway culverts, and other facilities (Grasse and Putnam 1955). Land owners often consider beaver a nuisance because they fill streamside cottonwoods and aspen, which humans find aesthetically pleasing and which enhance property values (Hall 1960, Beier and Barrett 1967, Platts and Onishuk 1985). However, because beaver-felled aspen, cottonwoods, and willows usually resprout or reseed into an area (Hall 1960; Kindchay 1985, 1989; Mannlisch et al. 1988; Beier and Barrett 1989), it is not as if beaver eliminated these species.

POSITIVE IMPACTS

During the 1930s, the Soil Conservation Service (SCS) enlisted beaver as an ally in its water-conservation program (Scheffer 1938). The SCS transplanted beaver to unoccupied areas because beaver dams "served ... to stabilize the flow of the streams by reducing the force of the water and the crest of floods" (Scheffer 1938). The SCS even went so far as to parachute beaver into remote areas. The animals were housed in wooden cages and simply ate their way free after they landed.

Because their research demonstrated that beaver create and maintain riparian areas that are critical to other wildlife (Munther 1982, 1983; Smith 1980, 1985a, 1985b), both the BLM and the Forest Service have recently transplanted beaver to restore livestock-damaged riparian areas. The Forest Service used beaver to improve wetlands in Montana and Oregon (Johnson 1984, Bergstrom 1985, Kay 1988), while the BLM established two beaver-transplant demonstration projects on livestock-degraded streams in southwestern Wyoming. BLM’s projects on Sage and Current Creeks were extremely successful and have been widely reported in the popular press (Michelmore 1984, Skinner 1986, Kay 1988).

Other researchers have demonstrated that beaver is a keystone species that completely alters the hydrology, energy flow, and nutrient cycling of aquatic systems (Naiman and Meiblo 1984; Parker et al. 1985; Naughton et al. 1986, 1988; Platts and Onishuk 1988; Johnston and Naiman 1990; Smith et al. 1991). Beaver dams impound water and trap sediments that raise the water table, increase the wetted perimeter, and allow the extension of riparian communities into former upland sites (Smith 1986; Apple 1983). In addition, beaver dams regulate streamflow by storing water, reducing peak or flood flow, and augmenting low flows during summer (Smith 1983b). During dry periods, 50 to 60 percent of the water in a stream system can be held in beaver ponds (Smith 1983a). By trapping silt over thousands of years, beaver dams created many of the West’s fertile valley bottoms (Ives 1942, Apple 1983). Munther (1992, 1993) reported that a typical creek without beaver furnishings only about two to four acres of riparian habitat per stream mile in the northern Rockies; but with beaver activity, that area can be expanded to twenty-four
acres per mile.

Gebhardt et al. (1989:57) noted that frequent flood events appear to have little hydrological effect on beaver-dominated streams. They added that "larger, less frequent flood events may not cause more than some localized [stream] degradation." They concluded that "this lack of system degradation is probably attributable to the continuous presence of the beaver providing a consistent, rapid, and adaptable stream control." They also observed that "loss of beaver without adequate vegetation reestablishment prior to a flood occurrence can result in a very primitive, degraded [stream] channel."

In many Western cold-water streams, beaver ponds enhance fisheries production (Grasse and Putnam 1955). In those systems, low water temperatures usually inhibit fish growth; but because water temperatures are elevated in beaver ponds due to longer retention times and reduced shading, fisheries production is enhanced in these beaver-dominated aquatic systems (Gard 1961). Beaver ponds also produce an abundance of aquatic insect (Hodkinson 1975; Naiman et al. 1984, 1986), which are readily consumed by fish thereby increasing fisheries production. In warmer water systems, though, beaver ponds and beaver removal of streamside shade trees can increase water temperatures to such an extent that trout can be negatively affected or eliminated (Grasse and Putnam 1955, Churchill 1960).

YELLOWSTONE'S BEAVER

Houghton (1982:182-83) implied that beaver were not widespread in Yellowstone until around 1900 and suggested that "ephemeral colonies may be characteristic of most of the park." In 1835, 1836, and 1837, however, Osborne Russell (1865) found large numbers of beaver on Yellowstone's northern range. For instance, he and his companions trapped beaver on the upper Gardiner River from August 3 to August 20, 1835. That same year, Russell (1865:27) met some Shoshone Indians in Yellowstone's Lamar Valley who told him that "there had been a great many beaver on the branches of this stream [Lamar River] but they [Indians] had killed nearly all of them for food." Yet in 1836, Russell and his party spent several days trapping beaver on streams flowing into Lamar Valley, which would suggest the Shoshone had actually left a fair number of beaver. The next year, Russell and his associates spent nearly three weeks trapping beaver on Slough and Bellowing Creeks.

Norris (1860:613) reported beaver to be common in the park during the 1870s and 1880s. He stated that trappers took "hundreds, if not thousands" of beaver skins from the park each year during his tenure as superintendent. Seton (1869) found beaver abundant near Tower Junction on the northern range in 1897. Skinner (1927:176) noted that "beaver have always been quite common in Yellowstone National Park, and although fluctuations are noticed at times, the actual number present remains about the same throughout a course of years." Skinner added that "beaver occur in practically every stream and pond [where there is suitable food] in the park." He estimated there were "about 10,000" beaver in the park during the early 1900s.

Bailey (1930:112–14) observed that "beavers are found along almost every stream in Yellowstone Park." He also noted that "the extensive herds of elk on the northern range keep down the growth of the beavers' food supply, young aspen, and willows. Wright and Thompson (1933:72) concluded that in Yellowstone beaver were "endangered through the destruction of aspen and willow on the overbrowsed elk winter ranges." The available evidence indicates that beaver were common in the Yellowstone area and on the northern range from before park establishment in 1872 through the early 1900s. Warren (1926:183) suggested that beaver had increased during the early 1900s, but he attributed it to "the protection from molestation by trappers" and the "killing of predatory animals" by the Park Service.

In the early 1920s, Warren (1926) conducted a detailed beaver study on a small portion of the northern range near Tower Junction. He reported extensive beaver dams and estimated a population of 236 beaver. Jonas (1955) repeated Warren's study in the early 1950s and found no beaver nor any recent beaver activity. Jonas (1955, 1956, 1959) attributed the decline in beaver to three factors: (1) lack of preferred food plants, (2) poor water conditions, and (3) the rapid silting in of beaver ponds. He (1955) concluded that the beavers' "unfortunate food situation ... was a result more from the overpopulation of elk than from any other single cause." He also noted that the poor water conditions and the silting of beaver ponds were caused by "overgrazing." From 1956 to 1988, Kay (1990:166) repeated Warren's and Jonas' surveys and found no beaver nor any indication of major beaver activity that might have taken place since the 1950s. Although a few beaver still persist in parts of Yellowstone, for all practical purposes that species is ecologically absent from the northern range.

Beaver need tall willows or aspen as food and dam-building materials. Aspen and willows cut by beaver normally resprout (Warren 1926; Kowlesley 1985, 1989) and in turn provide additional beaver food. Once the mature aspen trees or tall willows are cut, however, the new suckers are entirely within reach of browsing elk (McMilan 1950). By preventing aspen and willows from growing into sizeable plants, elk and moose eliminate beaver foods. Flook (1964)
reported that high elk numbers negatively affected beaver through interspecific competition for willows and aspen in Banff and Jasper National Parks. Bergerud and Manuel (1968) and Collins (1976) noted that high moose densities had a similar negative effect on beaver in Newfoundland and in Jackson Hole. Heavy grazing by domestic livestock not only reduces woody vegetation but also negatively affects beaver populations (Platts et al. 1983, Smith and Flake 1983, Dieter 1987, Dieter and McBride 1989a, 1989b).

According to the Park Service’s ‘natural regulation’ hypothesis, competitive exclusion of sympatric herbivores will not occur. Elk and moose, however, have acted to competitively exclude beaver from the northern range. Moreover, in the absence of beaver, several streams on the northern range have downcut 1-2 m (Chadde and Kay 1991), undoubtedly lowering the water table and reducing the wetted perimeter. The virtual elimination of beaver has probably had a greater long-term adverse effect on water resources available to willow communities than any drought or hypothesized climatic change. In all probability, many riparian communities on the northern range have become drier over the years due to the competitive exclusion of beaver by elk. This result would also be true throughout the Intermountain West where human settlement and trapping have eliminated or severely reduced the number of beaver that occupied those systems prior to European influence (Dobyrs 1981).

Historical Abundance

While it is common knowledge that large numbers of beaver were trapped in the West during the 1800s (Chittenden 1968), ecologists have not used available historical source materials to obtain estimates of beaver abundance prior to European disturbance. Peter Skene Ogden’s (1950, 1961, 1972) journals written in the 1820s provide a vivid firsthand account of how abundant beaver were throughout the Intermountain West before the fur trade.

Members of Ogden’s (1850) party were the first whites to trap the streams in what has become known as Ogden Valley or Ogden’s Hole. The Ogden River drains a relatively small area east of Utah’s Wasatch Mountains and flows west into the Great Salt Lake. Ogden’s fur brigade first entered the valley in May of 1825. On that day, they caught 244 beaver and added 109 more on the second day, 66 on the third, 67 on the fourth, and 83 on the fifth. A total of 511 beaver were trapped in five days. Today the Utah Division of Wildlife Resources estimates that there are probably only 300 to 400 beaver in the same area, though some of that system has been flooded by Pineview Reservoir (Don Paul, pers. comm. 1991).

Ogden (1872) and his fur brigade were also the first whites to trap Nevada’s Humboldt River. Ogden’s trappers first struck the Humboldt near present day Winnemucca on November 9, 1828, and traveled upstream until they left the Humboldt east of Elko on December 16. During that period, Ogden reported that his men took 627 beaver. On May 10, 1829, Ogden’s party again struck the Humboldt east of Winnemucca and trapped its way downstream to Humboldt Sink before returning upriver to where on June 8 they left the Humboldt at its junction with the Little Humboldt River. During that time, Ogden reported that his men trapped 918 beaver. Earlier in that same year, April 8 to 15, 1829, Ogden and his fur brigade caught seventy-eight beaver on the upper reaches of the Humboldt between present day Carlin and Elko. Thus, by actual count of Ogden’s daily journal entries, his party trapped 1,224 beaver on the Humboldt during 1828-1829.

The actual number of beaver they took, however, was probably somewhat greater because by comparing the brigade’s total take with Ogden’s daily entries, it can be determined that he apparently failed to record all the beaver his people caught each day. Also, along the entire Humboldt, Ogden encountered large numbers of Native Americans who constantly harassed his fur brigade. The Indians repeatedly stole the traps his men had set and presumably the beaver they held. Ogden (1872:144) finally abandoned the Humboldt in June of 1829 because he only had fifty traps left, and it was no longer profitable to continue the hunt.

Ogden (1872:144) also complained that the Indians, by using his stolen traps and other means, such as firing beaver lodges, destroyed many beaver before his men arrived at new sections of the river. At one point, Ogden (1872:149) wrote, “I have already observed the Indians in this river (Humboldt) destroy a great number of beaver, and I am correct in saying so for scarcely one have I seen but his shoes are made of beaver skin, and when I consider how numerous they (Indians) are the number of beaver destroyed must be great.” Due to protection in the early 1900s, some transplanting, the Humboldt’s relatively remote location, and today’s low fur prices, the Nevada Department of Wildlife estimates that river still supports 80 percent of the beaver it held in Ogden’s time (Wall Manderville, pers. comm., 1991). From Ogden’s journals, as well as from accounts left by other fur trappers, it is apparent that most hydrologic systems in the Intermountain West developed with large numbers of beaver. Equally clear, early fur trappers decimated or exterminated beaver populations over most of the West (Johnson and Chance 1974, Chittenden 1980). In his chronicle of the human-induced destruction of riparian zones in New Mexico and Arizona, Dobyrs (1981) attributed
those areas' initial decline to the extermination of beaver by the fur trade. Cox et al. (1982) reported that when beaver were trapped out of one Arizona stream, within five years the channel downstream from these to twenty feet, which, in turn, led to a reduction of streamside riparian vegetation. Since it is clear that systems with beaver behave differently than those without beaver, the historical reduction or elimination of beaver from many intermountain streams no doubt altered the ecology and hydrology of the associated riparian systems.

**ECOSYSTEM EFFECTS**

While this paper has focused primarily on the impact of ungulates and beaver on riparian vegetation, it should not be forgotten that many different species of insects, birds, and mammals are key to riparian habitats. Since the physical stature or structure of the vegetation is important in determining the composition of animal communities (Balda 1975), any alterations in those plant communities—such as the previously documented reduction or elimination of tall willows, cottonwoods, and aspen—would have serious consequences for other species. Based on other studies (Bergerud and Maclay 1988, Ross et al. 1970, Page et al. 1978, Crouch 1982, Mosconi and Hutte 1982, Casey and Hein 1983, Platta et al. 1983, Taylor 1986, Loft et al. 1987, Tucker 1987, Brooks and Healy 1988, Finch 1988, Knapf et al. 1988, Medlin and Clay 1989, Putnam et al. 1989), the decline or elimination of tall, woody riparian vegetation may have completely altered bird and small-mammal communities, as well as negatively affected larger animals such as grizzly bears (Kay 1999) and white-tailed deer (Odocoileus virginianus) (Kay 1999). In Rocky Mountain National Park, Braun et al. (1991) suggested that, by reducing the disturbance and abundance of willows, elk were having a negative effect on white-tailed ptarmigan (Lagopus leucurus) populations.

Ungulate-induced elimination of beaver and willow bank cover may also have caused decreases in the distribution and numbers of native trout species (Marcuson 1983, Hubert et al. 1985, Kay 1990:179). Entire plant and animal communities, not just riparian vegetation, have most likely been altered by ungulate use in Yellowstone National Park and other areas. The grazing-induced short-willow communities that presently exist in various national parks are not ecologically equivalent to the tall-willow communities that once occupied those same areas (Chadde and Kay 1991). Pastor et al. (1987, 1988) went so far as to conclude that by changing plant communities moose on Isle Royale altered soil microbes and even soil development.

**CONCLUSIONS**

1. Concentrations of native ungulates tend to eliminate woody riparian vegetation such as willows, cottonwoods, and aspen.
2. Willows protected from native ungulates exhibit significantly greater height growth and canopy cover than unprotected plants and in physical stature resemble the willows that existed during the late 1800s.
3. Browsing by native ungulates can reduce or eliminate willow seed production. This lack of seed production can prevent willows from colonizing new habitats that become available following floods or fire.
4. Grazing and trampling by native ungulates tend to reduce tall forb and shrub components of riparian systems while increasing the proportion of grasses and sedges in herbaceous communities.
5. Repeated use by native ungulates reduces the hiding or security-cover value of riparian habitats.
6. While alteration of riparian communities has been most frequently documented in wintering areas, native ungulates can also have severe negative effects on riparian habitats on higher-elevation summer ranges.
7. Browsing by native ungulates not only changes the stature and abundance of tall willows and other riparian vegetation but also affects animals commonly associated with riparian habitats.
8. Browsing by native ungulates acts to competitively exclude beaver from riparian habitats.
9. Prior to European influences, beaver were generally much more common and abundant throughout the Intermountain West than they are today.
10. Beaver is a keystone species that completely...
alters the hydrology, energy flow, and nutrient cycling of aquatic and riparian systems. Systems with beaver are completely different from systems without beaver.

11. Beaver dams impound water and trap sediments that raise the water table, increase the wetted perimeter, and allow the extension of riparian communities into former upland sites.

12. Beaver create and maintain riparian areas that are critical to a host of other wildlife species. By trapping silt over thousands of years, beaver dams created many of the West’s fertile valley floors.

13. Beaver can be used to restore riparian systems that have been damaged by native ungulate or livestock grazing, but it may be necessary to exclude ungulates from the area so that the woody plants can recover and provide food and dam-building materials for the beaver.

14. The elimination of beaver has a negative effect on the extent of willow and other riparian communities by lowering water tables and reducing stream flows.

ACKNOWLEDGMENTS

My Yellowstone research was funded by the Roh and Basie Weider Wildlife Foundation, Sinton, Texas, and this paper is Contribution No. 373. Steve Chadde helped measure willow communities and willow seed production in Yellowstone Park. I thank Steve Chadde, Dr. Walter Musgiller, Dr. William Platt, and Dr. Phil Urenna for reviewing this manuscript and for offering constructive suggestions.

REFERENCES


General Accounting Office. 1968. Public rangelands: Some riparian areas restored but widespread improvement will be slow. GAO RCED-88-105. Washington, D.C.


Jones, R. J. 1955. A population and ecological study of the
beaver (Castor canadensis) of Yellowstone National Park, M. S. Thesis, University of Idaho, Moscow.


Native peoples had always placed goods in the graves of their departed, and this practice escalated with the arrival of European goods. Archaeologists have found enormous caches of European trade goods in the graves of Indians on the East Coast. Native weapons changed dramatically as well, creating an arms race among the peoples living in European colonization zones. Indians refashioned European brassware into arrow points and turned axes used for chopping wood into weapons. With their loss came the loss of beaver ponds, which had served as habitats for fish as well as water sources for deer, moose, and other animals. Furthermore, Europeans introduced pigs, which they allowed to forage in forests and other wildlands. The natives died by the thousands, inundating whole tribes! The second major occurrence was the Europeans killing off the game and chopping down the forests. Then, the foreigners proceeded to kill the natives and drive them from their ancestral homelands. The Spaniards even sought to rid the natives of their customs and languages, requiring them to adopt the Roman Catholic religion. They stole their riches, desecrated their buildings, and reduced once powerful nations to slaves and servants. The most devastating impact was the introduction of