
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, aspen, and cottonwood communities by approximately 95 percent since the late 1800s. Native ungulates can also severely reduce or eliminate palatable grasses and forbs from herbaceous riparian communities. By eliminating woody vegetation and security 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 trapping 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 fell 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 those riparian associations (Youngblood et al. 1985, Windell 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 (Pimlott 1965, Bobek 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)

recently reported on the impact of ungulate browsing on the park's willow (*Salix* spp.) communities. Barmore (1981), Houston (1982), Chase (1986), Despain et al. (1986), Chadde (1989), Despain (1989), and Kay (1990) provide additional information or different perspectives on how wildlife has affected Yellowstone's riparian communities.

Similar wildlife/riparian interactions occur in other Western national park, including Rocky Mountain, Olympic, Mount Rainier, Grand Teton, Banff, and Jasper, where ungulates have been allowed to concentrate in wetland areas. Similar conditions also exist in western Wyoming where large populations of elk are maintained by winter feeding (Anderson 1958, Beetle 1979, Strickland 1987, Boyce 1989) and where large numbers of moose winter in riparian areas (Bassett 1951, Rudersdorf 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"¹ the park's northern winter range, including willow communities (Rush 1932, Kittams 1959, Pengelly 1963, Tyers 1981, Kay 1985, 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 assisting but nonessential adjunct to the regulation of ungulate populations. If wolves were present, they would only kill the animals slated 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 retrogressive 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 equilib-

rium, 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.²

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). Any 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 willow communities into short willow types, this would be additional grounds for rejecting "natural regulation."

To evaluate the effects of succession, 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.

Historical Distribution and Abundance. Kay (1990:229) made forty-four repeat photosets of willow communities on Yellowstone's northern range. The earliest sets date from 1871. Some photosets contained four photographs taken in 1893, 1921, 1954, and 1986-1988. In forty-one out of forty-four comparative photosets, tall willow communities totally disappeared. In three other photosets, only 5 to 10 percent of the original tall willows remained (Kay 1990).

In 1871 Captains Barlow and Heap (1872:40) 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 rivulets 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

¹Terms such as *overgrazing*, *range damage*, and *unnatural* elk populations were used in nearly all early governmental reports about the northern range. Since these terms are value laden, they are used throughout this paper only in their historical context.

²See 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; Peek 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 (Peek et al. 1967, Lovaas 1970). Where deep snow to the south or hunters north of the park limit elk use, willows grew taller (Kay 1990).

Kay (1990:236) made four photosets of willow communities on Yellowstone's Gallatin winter range. Three contained four pictures taken in 1924, 1949, 1961, and 1986, while the other included 1937, 1961, and 1989 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 50 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 seral to conifers. In some instances, this is true but not for most willow communities on Yellowstone's

Table 1. Percent willow canopy cover on permanent transects inside and outside Yellowstone exclosures from 1958 to 1988. Adapted from Kay (1990) and Chadde and Kay (1988, 1991).

Exclosure-transect	Mean percent willow canopy cover*				
	Date of first measurement			Date of most recent measurement	
	1958	1962	1963	1986	1988
Mammoth					
Outside	7.5	—	—	—	12.3
Inside	4.5	—	—	—	109.2
Junction Butte					
Outside	—	6.6	—	—	21.0
Inside	—	16.1	—	—	93.2
Lamar-East					
Outside†	6.0	—	—	—	9.7
Inside	8.2	—	—	—	86.5
Lamar-West					
Outside†	—	5.4	—	—	9.7
Inside	—	1.7	—	—	92.0
Slough Creek					
Outside	—	—	20.0	28.0	—
Inside	—	—	46.0	114.0	—
Totals					
Outside		9.1			17.1
Inside		15.3			99.4
p ‡		n.s.			<.01

*All permanent willow belt transects in Yellowstone Park contain some nonwillow communities. Those areas were excluded in the 1986-1988 measurements.

†The Park Service uses the same outside plot for both the Lamar-East and the Lamar-West exclosures.

‡Percentages were arc sine transformed; Student's *t* test.

northern range. Of the forty-eight repeat photosets of willow communities reported by Kay (1990), 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 photosets (10 percent) showed conifer invasion of what were once willow communities (Kay 1990).

Exclosures. Kay (1990:Chapter 6) 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 Leege 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 ($p < .01$; 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 15.3 percent in 1958–1963 to 99.4 percent by 1986–1988 ($p < .01$; 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

Table 2. Average height of all willow species on permanent transects inside and outside Yellowstone exclosures from 1958 to 1988. Adapted from Kay (1990), Chadde and Kay (1988, 1991), and Singer (1987).

Exclosure-transect	Mean height (cm)				
	Date of first measurement			Date of most recent measurement	
	1958	1962	1963	1986	1988
Mammoth					
Outside	28	--	--	--	22
Inside	64	--	--	--	316
Junction Butte					
Outside	--	56	--	--	35
Inside	--	29	--	--	210
Lamar-East					
Outside*	29	--	--	--	45
Inside	27	--	--	--	282
Lamar-West					
Outside*	--	32	--	--	45
Inside	--	28	--	--	287
Slough Creek					
Outside	--	--	80	100	--
Inside	--	--	120	300	--
Totals					
Outside		45			51
Inside		54			279
p†		n.s.			<.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 (1960) and Stevens (1980) noted that willows increased in canopy cover and height inside exclosures where elk were excluded. On elk and moose winter range in Banff National Park, Trottier and Fehr (1982) reported that willows inside an exclosure 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 exclosures, they also photographed the permanent willow-belt transects each time they were sampled. Kay (1990) repeated those photographs in 1986–1988. The resulting multiple-image photosets confirm that willows inside the exclosures have increased in height and canopy cover since they were protected while willow communities outside the exclosures have not increased in height.

ther, only eight male aments were found in an additional 1.13 ha of willow-dominated habitat that was searched adjacent to the four exclosures on Yellowstone's northern range. In contrast *Salix bebbiana*, *S. boothii*, *S. lutea*, and *S. geyeriana* produced an average, respectively, of 1445, 583, 694, and 1346 female aments per m² of canopy cover inside exclosures (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. lutea* and averaged nearly 307,000 (Table 3). By combining the mean sex ratio, species canopy cover, and species seed production values, Kay (1990:185–91) 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

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

Species	Mean number of seed per m ² of female willow canopy cover	
	Outside exclosure	Inside exclosure
<i>Salix bebbiana</i>	0	318,854
<i>Salix boothii</i>	0	233,142
<i>Salix lutea</i>	0	583,876
<i>Salix geyeriana</i>	0	108,972
Totals	0*	306,988*

* $p < .001$, Student's *t* test.

Those photographs also demonstrated that willows inside the exclosures 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 exclosures more closely approximate 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 ecologically equivalent to the tall willow communities that once existed on the park's northern range (Despain et al. 1986). To test one aspect of this assumption, Kay (1990) and Kay and Chadde (1992) measured willow seed production inside and outside Yellowstone exclosures. Outside the exclosures, 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 additional 1.13 ha of willow-dominated habitat that was searched adjacent to the four exclosures on Yellowstone's northern range. In contrast *Salix bebbiana*, *S. boothii*, *S. lutea*, and *S. geyeriana* produced an average, respectively, of 1445, 583, 694, and 1346 female aments per m² of canopy cover inside exclosures (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. lutea* and averaged nearly 307,000 (Table 3). By combining the mean sex ratio, species canopy cover, and species seed production values, Kay (1990:185–91) 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 exclosure and zero outside; in the Lamar-East exclosure, 6,961,000 seeds were produced inside and zero outside; the Lamar-West exclosure had 7,016,000 seeds produced inside and zero outside; and in the Mammoth exclosure, 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 no aments were produced on that portion of the plant exposed to browsing (Table 4). Repeated ungulate 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 Chadde 1992), willows protected for three growing seasons increased in

Table 4. Number of aments produced above and below the browse height (2.5 m) on individual willows in Yellowstone National Park near Geode Creek. Adapted from Kay (1990) and Kay and Chadde (1992).

Species-plant	Plant size (m ²) canopy cover	Number of stems above browse height	Number of aments per plant	
			Below browse height	Above browse height
<i>Salix lutea</i>				
A - female	12	5	0	1680
B - female	2	1	0	78
C - female	2	2	0	170
D - male	3	9	0	1140
<i>Salix geyeriana</i>				
E - female	4	2	0	160
F - female	1	3	0	1351
G - female	3	5	0	600
<i>Salix boothii</i>				
H - female	2	2	0	182
Means			0*	670*

* $t = 2.80, p < .02$.

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 disappear. 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 produced by periodic large-scale disturbances such as fire (Despain 1989). Yellowstone's 1988 fires occurred 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; Romme and Despain 1989a, 1989b; 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 (Brichta 1987, Chadde et al. 1988). These areas, normally unfavorable to willow seed germination and seedling 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 seedling establishment of willow (Brinkman 1974). Yet Kay and Chadde (1992) observed few willow seedlings growing in those areas.

The data would suggest that practically no willow seeds were produced on Yellowstone's northern range to colonize 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 1990:202).

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 (Houston 1982, Despain et al. 1986). According to Houston (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 (1990:157) rephotographed that site in 1983, 1986, 1987, and 1988. In addition Chadde et al. (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.

So the area changed from bare gravel to willows to grass in only nine years. Not only is this much faster than normal plant succession but it is also contrary to expected successional directions. By the usual successional sequence in this area, colonizing willows would be replaced by other willow species and perhaps cottonwoods (*Populus* spp.) or eventually Engelmann spruce (*Picea engelmannii*) but not grasses, sedges, or forbs. Some willow communities on the northern range are seral; but on many sites, willows normally form stable or climax communities (Chadde et al. 1988). In nearly all instances, willows are not seral to grasslands unless there has been a change in hydrology (Chadde et al. 1988) that has not occurred at this site along the Gardiner River.³

The decline of willows on the northern range has also been attributed to climatic change, especially to the drought during the 1930s (Houston 1982:129–34). This suggestion, though, is not supported by data from the exclosures, where the climate is the same on both sides of the fence. The microclimate inside the exclosures is certainly different today, but that is an incorporated variable caused by the plants' response to elimination of ungulate browsing and is not the cause of the vegetation's response. Inside a small exclosure near Yellowstone's Tower Junction, willows grew vigorously during and after the 1930's drought while those outside did not (Kay 1990:158). Moreover, it is not climate that prevents the plants from growing to their full biological potential outside the exclosures. Measurements of subsurface water levels throughout the summer inside and outside the exclosures failed to show any less water available to the plants on the outside (Brichta 1987, Chadde et al. 1988).

The climate-change hypothesis also is not supported by photographic evidence and firsthand accounts. Willows started declining before the 1930's drought, and they have continued to decline in recent years. For example, willows in the western portion of Round Valley were severely hedged in 1949 but were still alive. By 1988 a major decline had occurred in those willows even though precipitation had been near normal during the 1949 to 1988 period, and there still are abundant springs and seeps at the site (Kay 1990).

Yellowstone's 2 ha Tower Junction willow exclosure was constructed in 1957; and by the late 1960s, the protected willows had significantly increased in height and canopy cover (Singer 1987). That exclosure was removed in the early 1970s and the protected plants

³During the mid 1970s, a few tall willows were still alive above and below this gravel bar (Kay 1990). Those plants probably produced the seeds that became established on this gravel bar. Since that time, continued ungulate browsing, in combination with insects and pathogens, has eliminated those tall willows (Kay 1990).

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 1930's drought. Climatic variation also appears to be unimportant since that area has abundant subsurface soil moisture (Brichta 1987, Chadde et al. 1988).

In recent years, the mean annual temperature on the northern range at Mammoth increased 0.5 to 1.0°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 (Brichta 1987). Most perennial woody florals have so much biological or vegetational inertia that large-scale climatic changes of long duration are required before major shifts in plant species composition or stature occur (Smith 1965, Cole 1985, Davis and Botkin 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 20 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 lightning-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 (Romme and Knight 1981, Baker 1987).

Finally, there is no evidence to support the idea that burning will cause resprouting willows to grow so fast or to be so chemically defended that they can grow beyond the reach of elk and reform tall 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 browsed 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 [resprouted] 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 1978, willow utilization on the northern range averaged over 91 percent (Houston 1982:149) and has not decreased in recent years (Kay 1990:163). 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 1800s and early 1900s. 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 1920s 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 1968). 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 (1968) 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 wil-

low 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 1988, 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 those 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 zootic climaxes 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 52,000 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 1981, Youngblood et al. 1985, Windell et al. 1986, Baker 1987, Mueggler 1988, Padgett et al. 1989). Heavy livestock grazing has long been recognized as a detriment to reproduction of cottonwoods (Crouch 1979) and aspen (Clary and Medin 1990) situated in riparian zones, but few studies have addressed the impact ungulates may have on cottonwood- or aspen-dominated riparian communities.

Late 1880s 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. 1988, 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 inside/outside park comparisons, repeat photographs, as well as exclosures 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 parsnip (*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 arc sine transformed data) (Kay 1990:75). Cow parsnip 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 parsnip is readily eaten by ungulates, and elk in Yellowstone select cow parsnip even in summer when other forage is abundant. Moreover, cow parsnip is very susceptible to trampling damage. Simulated elk trampling research has shown that tall forbs are the class of plants most severely affected by trampling (Bradley 1982). Since cow parsnip is very sensitive to herbivory (Youngblood and Mueggler 1981:12, Stivers 1988) and there have been substantially fewer elk outside the park (Kay 1985, 1990) where cow parsnip is more abundant, it appears reasonable to attribute the observed differences to elk grazing.

Although commonly found in riparian areas throughout the West, cow parsnip is rarely found in wetland plant communities on Yellowstone's northern range (Chadde et al. 1988). In the park's riparian zones, cow parsnip is often found growing only where it is physically protected from ungulate browsing. For instance, cow parsnip 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 understories 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 arc sine 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 disclimaxes (Youngblood et al. 1985, Mueggler 1988, Padgett et al. 1989.)

Chadde et al. (1988) and Chadde (1989) reported a similar pattern in riparian communities throughout the northern range. Undergrowths 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 exclosure 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, browsing by moose completely altered the species composition and understory structure of the forests (Hansen et al. 1973, Krefling 1974, Janke 1976, Snyder and Janke 1976, Risenhoover and Maass 1987, Moen et al. 1990) and is even eliminating balsam fir (*Abies balsamea*) from most of the island (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*, *Nymphaea 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). Loft et al. (1987) demonstrated that hiding cover for mule deer (*Odocoileus hemionus*) fawns in willow, aspen, and herbaceous riparian habitats was significantly reduced with heavy livestock use.

Kay (1989) 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 (1989) 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 Brannon 1987, 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 dewatering, channelization, and livestock grazing, not to climatic change (Meehan and Platts 1978, Dobyns 1981, Myers 1981, Marcuson 1983, Platts et al. 1983, General Accounting Office 1988). 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 (1980:139) reported that on the park's summer range "53 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 1980:136). Reporting on a continuation of that study, Braun et al. (1991) 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 (1982) reported that summering elk had severe impacts on wetland 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; Edge et al. 1987, 1988).

A large segment of the southern Yellowstone or Jackson Hole elk herd once summered in Wyoming's Teton Wilderness, including Big Game Ridge (Anderson 1958, Houston 1982, Boyce 1989). Croft and Ellison (1960) 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), Gruell (1973), and Boyce (1989) questioned 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 1880s 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. Range 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 (1984), 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 fell streamside cottonwoods and aspen, which humans find aesthetically pleasing and which enhance property values (Hall 1960, Beier and Barrett 1987, Platts and Onishuk 1988). However, because beaver-felled aspen, cottonwoods, and willows usually resprout or reseed into an area (Hall 1960; Kindschy 1985, 1989; Masslich et al. 1988; Beier and Barrett 1989), it is not as if beaver eliminated those 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, 1983a, 1983b), 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 Currant 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 Melillo 1984; Parker et al. 1985; Naiman 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 1980, Apple 1983). In addition beaver dams regulate stream flow by storing water, reducing peak or flood flow, and augmenting low flows during summer (Smith 1983b). During dry periods, 30 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 (1982, 1983) reported that a typical creek without beaver furnishes 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 time and reduced shading, fisheries production is enhanced in these beaver-dominated aquatic systems (Gard 1961). Beaver ponds also produce an abundance of aquatic insects (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 1980).

YELLOWSTONE'S BEAVER

Houston (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 (1965) 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 (1965:27) 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 Hellroaring Creeks.

Norris (1880:613) 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 (1909) found beaver abun-

dant 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 (1935:72) 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 siltation of beaver ponds were caused by "overgrazing." From 1986 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; Kindschy 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 (McMillan 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 McCabe 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 (Dobyns 1981).

HISTORICAL ABUNDANCE

While it is common knowledge that large numbers of beaver were trapped in the West during the 1800s (Chittenden 1986), 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 (1950) 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, 68 on the third, 67 on the fourth, and 23 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 600 beaver in the same area, though some of that system has been flooded by Pineview Reservoir (Don Paul, pers. comm. 1991).

Ogden (1972) 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 6 they left the Humboldt at its junction with the Little Humboldt River. During that time, Ogden reported that his men trapped 519 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 (1972:194) 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 (1972:144) 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 (1972:149) 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 (Walt 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 1986). In his chronicle of the human-induced destruction of riparian zones in New Mexico and Arizona, Dobyns (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 downcut from three 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 keyed 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 Manuel 1968, Ross et al. 1970, Page et al. 1978, Crouch 1982, Mosconi and Hutto 1982, Casey and Hein 1983, Platts et al. 1983, Taylor 1986, Loft et al. 1987, Tucker 1987, Brooks and Healy 1988, Finch 1988, Knopf et al. 1988, Medin and Clary 1989, Putman 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 1989) and white-tailed deer (*Odocoileus virginianus*) (Kay 1990). 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 1990:178). 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 flood 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 on 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 Rob and Bessie Welder 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 Mueggler, Dr. William Platts, and Dr. Phil Urness for reviewing this manuscript and for offering constructive suggestions.

REFERENCES

- Aho, R. W., and P. A. Jordan. 1979. Production of aquatic macrophytes and its utilization by moose on Isle Royale National Park. Pages 341-48 in R. M. Linn, ed. Proceedings of the first conference on scientific research in the national parks. Vol. I. November 9-12, 1976. New Orleans, La. U.S. Department of the Interior, National Park Service Transactions and Proceedings Series No. 5.
- Allison, T. D. 1987. The reproductive biology of Canada yew (*Taxus canadensis*) and its modification by herbivory: Implications for wind pollination. Ph.D. dissertation, University of Minnesota, Minneapolis.
- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests to deer: Edge effects in northern Wisconsin. *Conservation Biology* 2:348-58.
- Anderson, C. C. 1958. The elk of Jackson Hole: A review of Jackson Hole elk studies. Wyoming Game and Fish Commission Bulletin 10, Cheyenne.
- Apple, L. L. 1983. The use of beavers in riparian/aquatic habitat restoration in a cold desert gully-cut stream system: A case history. *American Fisheries Society* 18:29-35.
- Aune, K., and B. Brannon. 1987. East Front grizzly studies. Montana Department of Fish, Wildlife, and Parks, Helena.
- Aune, K., M. Madel, and C. Hunt. 1986. Rocky Mountain Front grizzly bear monitoring and investigation. Montana Department of Fish, Wildlife, and Parks, Helena.
- Aune, K., and W. Kasworm. 1989. Final report, East Front grizzly studies. Montana Department of Fish, Wildlife, and Parks, Helena.
- Bailey, V. 1930. Animal life of Yellowstone National Park. Charles C. Thomas, Springfield, Ill; Baltimore, Md.
- Baker, W. L. 1987. Recent changes in the riparian vegetation of the montane and subalpine zones of western Colorado, U.S.A. Ph.D. dissertation, University of Wisconsin, Madison.
- Balda, R. P. 1975. Vegetation structure and breeding bird diversity. Pages 59-80 in D. R. Smith, tech. coord. Proceedings of the symposium on management of forest and range habitats for nongame birds. May 6-9, 1975. Tucson, Ariz. U.S. Department of Agriculture, Forest Service General Technical Report WO-1.
- Barlow, J. W., and D. P. Heap. 1872. Report of a reconnaissance of the basin of the upper Yellowstone in 1871. U. S. 42d Congress, 2d Session, Senate Executive Document No. 66.
- Barmore, W. J. 1981. Population characteristics, distribution, and habitat relationships of six ungulate species on winter range in Yellowstone National Park. Unpublished report on file, Research Office, Yellowstone National Park, Wyo.
- Barnosky, C. W. 1988. The relationship of climate to sedimentation rates in lakes and ponds. Page 4 in F. Singer, ed. First annual meeting of research and monitoring on Yellowstone's northern range. U. S. Department of the Interior, National Park Service, Yellowstone National Park, Wyo.

- Bassett, N. R. 1951. Winter browse utilization and activities of moose on the Snake and Buffalo River bottoms of Jackson Hole, Wyoming. M.S. Thesis, Utah State University, Logan.
- Beetle, A. A. 1974. Letter to Charles T. Costen, Forest Supervisor, Bridger-Teton National Forest, Jackson, Wyo.
- Beetle, A. A. 1979. Jackson Hole elk herd: A summary after 25 years of study. Pages 259-62 in M. S. Boyce and L. D. Hayden-Wing, eds. North American elk, ecology, behavior and management. University of Wyoming, Laramie.
- Beier, P., and R. H. Barrett. 1987. Beaver habitat use and impact in Truckee River Basin, California. *Journal of Wildlife Management* 51(4): 794-99.
- Beier, P., and R. H. Barrett. 1989. Beaver distribution in the Truckee River Basin, California. *California Fish & Game* 75(4): 233-38.
- Bergerud, A. T., and F. Manuel. 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. *Journal of Wildlife Management* 32(4): 729-46.
- Bergstrom, D. 1985. Beavers: Biologists "rediscover" a natural resource. *Forestry Research West* (October): 1-5.
- Bobek, B., K. Perzanowski, J. Siwanowicz, and J. Zielinski. 1979. Deer pressure on forage in a deciduous forest. *Oikos* 32:373-80.
- Boyce, M. S. 1989. The Jackson elk herd: Intensive wildlife management in North America. Cambridge University Press, Cambridge; New York.
- Bradley, W. P. 1982. History, ecology, and management of an introduced wapiti population in Mount Rainier National Park, Washington. Ph.D. dissertation, University of Washington, Seattle.
- Brandner, T. A. 1986. Density dependent effects of moose herbivory on balsam fir in Isle Royale National Park, Michigan. M.S. Thesis, Michigan Technological University, Houghton.
- Brandner, T. A., R. O. Peterson, and K. L. Risenhoover. 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. *Ecology* 71(1): 155-64.
- Braun, C. E., D. R. Stevens, K. M. Giesen, and C. P. Melcher. 1991. Elk, white-tailed ptarmigan and willow relationships: A management dilemma in Rocky Mountain National Park. Pages 74-85 in R. E. McCabe, ed. Transactions of the fifty-sixth North American wildlife and natural resources conference. March 17-22, 1991. Edmonton, Alberta. Wildlife Management Institute, Washington, D. C.
- Brichta, P. H. 1987. Environmental relationships among wetland community types of the northern range, Yellowstone National Park. M.S. Thesis, University of Montana, Missoula.
- Brinkman, K. A. 1974. *Salix l.*—willow. Pages 746-50 in Seeds of woody plants in the United States. U.S. Department of Agriculture, Forest Service Agriculture Handbook No. 450.
- Brooks, R. T., and W. M. Healy. 1988. Response of small mammal communities to silvicultural treatments in eastern hardwood forests of West Virginia and Massachusetts. Pages 313-18 in R. C. Szaro, K. E. Severson, and D. R. Patton, tech. coords. Management of amphibians, reptiles, and small mammals in North America: Proceedings of the symposium. July 19-21, 1988. Flagstaff, Ariz. U.S. Department of Agriculture, Forest Service General Technical Report RM-166.
- Cannon, R. W., and F. L. Knopf. 1984. Species composition of a willow community relative to seasonal grazing histories in Colorado. *Southwestern Naturalist* 29(2): 234-37.
- Casey, D., and D. Hein. 1983. Effects of heavy browsing on a bird community in deciduous forest. *Journal of Wildlife Management* 47(3): 829-36.
- Chadde, S. 1989. Willows and wildlife of the northern range, Yellowstone National Park. Pages 168-69 in R. E. Gresswell, B. A. Barton, and J. L. Kershner, eds. Practical approaches to riparian resource management: An educational workshop. May 8-11, 1989. Billings, Mont. U. S. Department of the Interior, Bureau of Land Management BLM-MT-PT-89-001-4351.
- Chadde, S. W., and C. E. Kay. 1988. Willows and moose: A study of grazing pressure, Slough Creek enclosure, Montana, 1961-1986. Montana Forest and Conservation Experiment Station Research Note 24, University of Montana, Missoula.
- Chadde, S. W., and C. E. Kay. 1991. Tall-willow communities on Yellowstone's northern range: A test of the "natural regulation" paradigm. Pages 231-62 in R. B. Keiter and M. S. Boyce, eds. The greater Yellowstone ecosystem: Redefining America's wilderness heritage. Yale University Press, New Haven, Conn.
- Chadde, S. W., P. L. Hansen, and R. D. Pfister. 1988. Wetland plant communities of the northern range, Yellowstone National Park. School of Forestry, University of Montana, Missoula.
- Chase, A. 1986. Playing God in Yellowstone: The destruction of America's first national park. Atlantic Monthly Press, Boston, Mass.
- Chittenden, H. M. [1935] 1986. The American fur trade of the far West. Reprint. University of Nebraska Press, Lincoln. 2 vols.

- Churchill, J. E. 1980. Beaver are killing our trout streams! *Trout* 21(4): 22-25.
- Clary, W. P., and D. E. Medin. 1990. Differences in vegetation biomass and structure due to cattle grazing in a northern Nevada riparian ecosystem. U.S. Department of Agriculture, Forest Service Research Paper INT-427.
- Cole, G. F. 1969. The elk of Grand Teton and southern Yellowstone National Parks. U.S. Department of the Interior, National Park Service Research Report GRTE-N-1. Reissued (1978) by Office of Natural Science Studies, National Park Service.
- Cole, K. 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. *American Naturalist* 125(2): 289-303.
- Collins, T. C. 1976. Population characteristics and habitat relationships of beavers, *Castor canadensis*, in north-west Wyoming. Ph.D. dissertation, University of Wyoming, Laramie.
- Cox, J. R., H. L. Morton, T. N. Johnsen, Jr., G. L. Jordan, S. C. Martin, and L. C. Fierro. 1982. Vegetation restoration in the Chihuahuan and Sonoran deserts of North America. U.S. Department of Agriculture, Agricultural Research Service, Agricultural Reviews and Manuals ARM-W-28.
- Croft, A. R. 1974. A critique of "An ecological evaluation of Big Game Ridge." Unpublished report.
- Croft, A. R., and L. Ellison. 1960. Watershed and range conditions on Big Game Ridge and vicinity, Teton National Forest, Wyoming. U.S. Department of Agriculture, Forest Service, Ogden, Utah.
- Crouch, G. L. 1979. Long-term changes in cottonwoods on a grazed and an ungrazed plains bottomland in northeastern Colorado. U.S. Department of Agriculture, Forest Service Research Note RM-370.
- Crouch, G. L. 1982. Wildlife on ungrazed and grazed bottomlands on the South Platte River, northeastern Colorado. Pages 186-97 in J. M. Peek and P. D. Dalke, eds. Wildlife-livestock relationships symposium: Proceedings 10. April 20-22, 1981. Coeur d'Alene, Idaho. University of Idaho, Forest, Wildlife and Range Experiment Station, Moscow.
- Davis, K. M., and R. W. Mutch. 1989. The fires of the Greater Yellowstone Area: The saga of a long hot summer. *Western Wildlands* 15(2): 2-9.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. Pages 269-84 in J. M. Diamond and T. J. Case, eds. *Community ecology*. Harper & Row, New York.
- Davis, M. B., and D. B. Botkin. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. *Quaternary Research* 23:327-40.
- Despain, D. G. 1989. Interpretation of exclosures in riparian vegetation. Page 188 in R. E. Gresswell, B. A. Barton, and J. L. Kershner, eds. *Practical approaches to riparian resource management: An educational workshop*. May 8-11, 1989. Billings, Mont. U.S. Department of the Interior, Bureau of Land Management BLM-MT-PT-89-001-4351.
- Despain, D. G., D. Houston, M. Meagher, and P. Schullery. 1986. *Wildlife in transition: Man and nature on Yellowstone's northern range*. Roberts Rinehart, Boulder, Colo.
- Dieter, C. D. 1987. Habitat use by beaver along the Big Sioux River. M.S. Thesis, South Dakota State University, Brookings.
- Dieter, C. D., and T. R. McCabe. 1989a. Notes and discussion: Factors influencing beaver lodge-site selection on a prairie river. *American Midland Naturalist* 122(2): 408-11.
- Dieter, C. D., and T. R. McCabe. 1989b. Habitat use by beaver along the Big Sioux River in eastern South Dakota. Pages 135-40 in R. E. Gresswell, B. A. Barton, and J. L. Kershner, eds. *Practical approaches to riparian resource management: An educational workshop*. May 8-11, 1989. Billings, Mont. Department of the Interior, Bureau of Land Management BLM-MT-PT-89-001-4351.
- Dobyns, H. F. 1981. *From fire to flood: Historic human destruction of Sonoran desert riverine oases*. Ballena Press, Socorro, N. Mex.
- Edge, W. D., C. L. Marcum, S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: A multivariate approach. *Journal of Wildlife Management* 51(4): 844-51.
- Edge, W. D., C. L. Marcum, S. L. Olson-Edge. 1988. Summer forage and feeding site selection by elk. *Journal of Wildlife Management* 52(4): 573-77.
- Edgerton, P. J. 1987. Influence of ungulates on the development of the shrub understory of an upper slope mixed conifer forest. Pages 162-67 in F. D. Provenza, J. T. Flinders, and E. D. McArthur, ed. *Proceedings: Symposium on plant-herbivore interactions*. August 7-9, 1985. Snowbird, Utah. U.S. Department of Agriculture, Forest Service General Technical Report INT-222.
- Finch, D. M. 1988. Bird-habitat relationships in subalpine riparian shrublands of the central Rocky Mountains. Pages 162-72 in C. A. Troendle, ed. *Management of subalpine forests: Building on 50 years of research: Proceedings of a technical conference*. July 6-9, 1987.

- Silver Creek, Colo. U. S. Department of Agriculture, Forest Service General Technical Report RM-149.
- Flook, D. R. 1964. Range relationships of some ungulates native to Banff and Jasper National Parks, Alberta. Pages 119-28 in D. J. Crisp, ed. *Grazing in terrestrial and marine environments: A symposium of the British Ecological Society, Bangor, 11-14 April 1962*. Blackwell Scientific Publications, Oxford.
- Fraser, D., and H. Hristienko. 1983. Effects of moose, *Alces alces*, on aquatic vegetation in Sibley Provincial Park, Ontario. *Canadian Field-Naturalist* 97:57-61.
- Gard, R. 1961. Effects of beaver on trout in Sagehen Creek, California. *Journal of Wildlife Management* 25(3): 221-42.
- Gebhardt, K. A., C. Bohn, S. Jensen, and W. S. Platts. 1989. Use of hydrology in riparian classification. Pages 53-59 in R. E. Gresswell, B. A. Barton, J. L. Kershner, eds. *Practical approaches to riparian resource management: An educational workshop*. May 8-11, 1989. Billings, Mont. U. S. Department of the Interior, Bureau of Land Management BLM-MT-PT-89-001-4351.
- General Accounting Office. 1988. Public rangelands: Some riparian areas restored but widespread improvement will be slow. GAO RCED-88-105, Washington, D. C.
- Grasse, J. E., and E. F. Putnam. 1955. *Beaver management and ecology in Wyoming*. 2d ed. Wyoming Game and Fish Commission Bulletin No. 6, Cheyenne.
- Gruell, G. E. 1973. *An ecological evaluation of Big Game Ridge*. U.S. Department of Agriculture, Forest Service Intermountain Region.
- Gysel, L. W. 1960. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. *Journal of Forestry* 58(9): 696-703.
- Hall, J. G. 1960. Willow and aspen in the ecology of beaver on Sagehen Creek, California. *Ecology* 41(3): 484-94.
- Hanley, T. A., and R. D. Taber. 1980. Selective plant species inhibition by elk and deer in three conifer communities in western Washington. *Forest Science* 26(1): 97-107.
- Hansen, H. L., L. W. Krefting, and V. Kurmis. 1973. *The forest of Isle Royale in relation to fire history and wildlife*. University of Minnesota, Agricultural Experiment Station Technical Bulletin 294, St. Paul, Minn.
- Hansen, P. L., S. W. Chadde, and R. P. Pfister. 1988. *Riparian dominance types of Montana*. Montana Forest and Conservation Experiment Station Miscellaneous Publication 49.
- Harry, G. B. 1957. Winter food habits of moose in Jackson Hole, Wyoming. *Journal of Wildlife Management* 21:53-57.
- Hodkinson, I. D. 1975. A community analysis of the benthic insect fauna of an abandoned beaver pond. *Journal of Animal Ecology* 44(2): 533-52.
- Houston, D. B. 1968. *The Shiras moose in Jackson Hole, Wyoming*. Grand Teton Natural History Association Technical Bulletin 1, Wyo.
- Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* 54(5): 1111-17.
- Houston, D. B. 1976. Research on ungulates in northern Yellowstone National Park. Pages 11-27 in *Research in the parks: Transactions of the national park centennial symposium*. December 28-29, 1971. U. S. Department of the Interior, National Park Service Symposium Series No. 1.
- Houston, D. B. 1982. *The northern Yellowstone elk: Ecology and management*. Macmillan, New York.
- Houston, D. B., E. G. Schreiner, B. B. Moorhead, and K. A. Krueger. 1990. Elk in Olympic National Park: Will they persist over time? *Natural Areas Journal* 10(1): 6-11.
- Hubert, W. A., R. P. Lanka, T. A. Wesche, and F. Stabler. 1985. Grazing management influences on two brook trout streams in Wyoming. Pages 290-94 in R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, eds. *Riparian ecosystems and their management: Reconciling conflicting uses*. U.S. Department of Agriculture, Forest Service General Technical Report RM-120.
- Ives, R. L. 1942. The beaver-meadow complex. *Journal of Geomorphology* 5:191-203.
- Janke, R. A. 1976. Moose-boreal forest ecology in Isle Royale National Park. Pages 70-90 in J. A. Hancock and W. E. Mercer, eds. *Proceedings of the 12th North American moose conference and workshop*. March 23-26, 1976. St. John's, Newfoundland. North American Moose Conference and Workshop.
- Johnson, D. R., and D. H. Chance. 1974. Presettlement overharvest of upper Columbia River beaver populations. *Canadian Journal of Zoology* 52:1519-21.
- Johnson, P. 1984. The dam builder is at it again! *National Wildlife* (June-July): 9-15.
- Johnston, C. A., and R. J. Naiman. 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. *Landscape Ecology* 4(1): 5-19.
- Jonas, R. J. 1955. A population and ecological study of the

- beaver (*Castor canadensis*) of Yellowstone National Park. M. S. Thesis, University of Idaho, Moscow.
- Jonas, R. J. 1956. Northern Yellowstone's changing water conditions and their effect upon beaver. *Yellowstone Nature Notes* 30(1): 6-9.
- Jonas, R. J. 1959. Beaver. *Naturalist* 10(2): 60-61.
- Jordan, P. A. 1987. Aquatic foraging and the sodium ecology of moose: A review. *Swedish Wildlife Research Supplement* 1(1): 119-37.
- Kay, C. E. 1985. Aspen reproduction in the Yellowstone Park-Jackson Hole area and its relationship to the natural regulation of ungulates. Pages 131-60 in G. W. Workman, ed. *Western elk management: A symposium*. Utah State University, Logan.
- Kay, C. E. 1988. Leave it to beaver-stream rehab specialists. *Montana Magazine* No. 89:15-16.
- Kay, C. E. 1989. Why Yellowstone's grizzly bears are declining: An alternative hypothesis. Paper presented at Examining the Greater Yellowstone ecosystem: A symposium on land and resource management. April 13-15, 1989. University of Wyoming, Laramie.
- Kay, C. E. 1990. Yellowstone's northern elk herd: A critical evaluation of the "natural regulation" paradigm. Ph.D. dissertation, Utah State University, Logan.
- Kay, C. E., and S. W. Chadde. 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. Pages 92-99 in W. P. Clary, E. D. McArthur, D. Bedunah, and C. L. Wambolt, eds. *Proceedings—symposium on ecology and management of riparian shrub communities*. May 29-31, 1991. Sun Valley, Idaho. U. S. Department of Agriculture, Forest Service General Technical Report INT-289, Ogden, Utah.
- Kindschy, R. R. 1985. Response of red willow to beaver use in southeastern Oregon. *Journal of Wildlife Management* 49(1): 26-28.
- Kindschy, R. R. 1989. Regrowth of willow following simulated beaver cutting. *Wildlife Society Bulletin* 17(3): 290-94.
- Kittams, W. H. 1959. Future of the Yellowstone wapiti. *Naturalist* 10(2): 30-39.
- Knight, D. H., and L. L. Wallace. 1989. The Yellowstone fires: Issues in landscape ecology. *BioScience* 39:700-706.
- Knopf, F. L., and R. W. Cannon. 1982. Structural resilience of a willow riparian community to changes in grazing practices. Pages 198-207 in J. M. Peek and P. D. Dalke, eds. *Wildlife-livestock relationships symposium: Proceedings* 10. April 20-22, 1981. Coeur d'Alene, Idaho. University of Idaho, Forest, Wildlife and Range Experiment Station, Moscow.
- Knopf, F. L., J. A. Sedgwick, and R. W. Cannon. 1988. Guild structure of a riparian avifauna relative to seasonal cattle grazing. *Journal of Wildlife Management* 52(2): 280-90.
- Kovalchik, B. L. 1987. Riparian zone associations: Deschutes, Ochoco, Fremont, and Winema National Forests. U. S. Department of Agriculture, Forest Service R6-Ecol-TP-279-87.
- Krefting, L. W. 1974. The ecology of the Isle Royale moose: With special reference to the habitat. University of Minnesota, Agricultural Experiment Station Technical Bulletin 297, St. Paul, Minn.
- Loft, E. R., J. W. Menke, J. G. Kie, and R. C. Bertram. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. *Journal of Wildlife Management* 51(3): 655-64.
- Lovaas, A. L. 1970. People and the Gallatin elk herd. Montana Fish and Game Department, Helena.
- McMillan, J. F. 1950. Summer food habits of moose (*Alces americana shirasi* Nelson) and effects of various factors on food supply in Yellowstone Park. Ph.D. dissertation, University of Michigan, Ann Arbor.
- McMillan, J. F. 1953. Some feeding habits of moose in Yellowstone National Park. *Ecology* 34:102-10.
- Marcuson, P. E. 1983. Overgrazed streambanks depress fishery production in Rock Creek, Montana. Pages 143-57 in J. W. Menke, ed. *Proceedings of the workshop on livestock and wildlife-fisheries relationships in the Great Basin*. May 3-5, 1977. Sparks, Nev. University of California, Berkeley, Special Publication 3301.
- Masslich, W. J., J. D. Brotherson, and R. G. Cates. 1988. Relationship of aspen (*Populus tremuloides*) to foraging patterns of beaver (*Castor canadensis*) in the Strawberry Valley of central Utah. *Great Basin Naturalist* 48(2): 250-62.
- Medin, D. E., and W. P. Clary. 1989. Small mammal populations in a grazed and ungrazed riparian habitat in Nevada. U. S. Department of Agriculture, Forest Service Research Paper INT-413.
- Meehan, W. R., and W. S. Platts. 1978. Livestock grazing and the aquatic environment. *Journal of Soil and Water Conservation* 33(6): 274-78.
- Michelmores, P. 1984. The amazing beavers of Currant Creek. *Readers Digest* (April): 109-13.
- Moen, R. A., J. Pastor, and Y. Cohen. 1990. Seasonal patterns of browsing by moose (*Alces alces*) in Isle

- Royale National Park, Michigan, USA. Ecological Society of America Bulletin 71(2): 259.
- Morgantini, L. E., and R. J. Hudson. 1989. Nutritional significance of wapiti (*Cervus elaphus*) migrations to alpine ranges in western Alberta, Canada. Arctic and Alpine Research 21(3): 288-95.
- Mosconi, S. L., and R. L. Hutto. 1982. The effects of grazing on land birds of a western Montana riparian habitat. Pages 221-33 in J. M. Peek and P. D. Dalke, eds. Wildlife-livestock relationships symposium: Proceedings 10. April 20-22, 1981. Coeur d'Alene, Idaho. University of Idaho, Forest, Wildlife and Range Experiment Station, Moscow.
- Mueggler, W. F. 1988. Aspen community types of the intermountain region. U. S. Department of Agriculture, Forest Service General Technical Report INT-250.
- Munther, G. L. 1982. Beaver management in grazed riparian ecosystems. Pages 234-41 in J. M. Peek and P. D. Dalke, eds. Wildlife-livestock relationships symposium: Proceedings 10. April 20-22, 1981. Coeur d'Alene, Idaho. University of Idaho, Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow.
- Munther, G. L. 1983. Integration of beaver into forest management. Paper presented at Colorado/Wyoming Chapter of American Fisheries Society, Laramie, Wyo.
- Myers, L. H. 1981. Grazing on stream riparian habitats in southwestern Montana. Paper presented at Society for Range Management meeting, Tulsa, Okla. Paper on file, BLM office, Dillon, Mont.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38(11): 753-62.
- Naiman, R. J., D. M. McDowell, and B. S. Farr. 1984. The influence of beaver (*Castor canadensis*) on the production dynamics of aquatic insects. Verhandlungen Internationale Vereinigung Limnologie 22:1801-10.
- Naiman, R. J., and J. M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia 62:150-55.
- Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67(5): 1254-69.
- Neilson, R. P. 1986. High-resolution climatic analysis and southwest biogeography. Science 232:27-34.
- Nelson, J. R., and T. A. Leege. 1982. Nutritional requirements and food habits. Pages 323-67 in J. W. Thomas and D. E. Towell, eds. Elk of North America: Ecology and management. Stackpole Books, Harrisburg, Pa.
- Norris, P. W. 1880. Annual report of the superintendent of the Yellowstone National Park. Pages 573-631 in Annual report of the Secretary of the Interior for the year ended June 30, 1880.
- Ogden, P. S. 1950. Peter Skene Ogden's Snake country journals, 1824-25 and 1825-26. E. E. Rich and A. M. Johnson, eds. Hudson's Bay Record Society Publication 13, London.
- Ogden, P. S. 1961. Peter Skene Ogden's Snake country journal, 1826-27. K. G. Davies and A. M. Johnson, eds. Hudson's Bay Record Society Publication 23, London.
- Ogden, P. S. 1971. Peter Skene Ogden's Snake country journals, 1827-28 and 1828-29. G. Williams, ed. Hudson's Bay Record Society Publication 28, London.
- Packer, P. E. 1963. Soil stability requirements for the Gallatin elk winter range. Journal of Wildlife Management 27(3): 401-10.
- Padgett, W. G., A. P. Youngblood, and A. H. Winward. 1989. Riparian community type classification of Utah and southeastern Idaho. U. S. Department of Agriculture Forest Service R4-Ecol-89-01.
- Page, J. L., N. Dodd, T. O. Osborne, and J. A. Carson. 1978. The influence of livestock grazing on non-game wildlife. Cal-Neva Wildlife 1978:159-73.
- Parker, M., F. J. Wood, Jr., B. H. Smith, and R. G. Elder. 1985. Erosional downcutting in lower order riparian ecosystems: Have historical changes been caused by removal of beaver? Pages 35-38 in R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre, eds. Riparian ecosystems and their management: Reconciling conflicting uses. U. S. Department of Agriculture, Forest Service General Technical Report RM-120.
- Pastor, J., R. J. Naiman, and B. Dewey. 1987. A hypothesis of the effects of moose and beaver foraging on soil carbon and nitrogen cycles, Isle Royale. Alces 23:107-24.
- Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. BioScience 38(11): 770-77.
- Patten, D. T. 1963. Vegetational pattern in relation to environments in the Madison Range, Montana. Ecological Monographs 33(4): 375-406.
- Patten, D. T. 1968. Dynamics of the shrub continuum along the Gallatin River in Yellowstone National Park. Ecology 49(6): 1107-12.
- Patten, D. T. 1969. Succession from sagebrush to mixed conifer forest in the northern Rocky Mountains. American Midland Naturalist 82(1): 229-40.
- Peek, J. M., A. L. Lovaas, and R. A. Rouse. 1967. Popula-

- tion changes within the Gallatin elk herd, 1932–65. *Journal of Wildlife Management* 31(2): 304–16.
- Pengelly, W. L. 1963. Thunder on the Yellowstone. *Naturalist* 14(2): 18–25.
- Pimlott, D. H. 1965. Influence of deer and moose on boreal forest vegetation in two areas of eastern Canada. *International Congress of Game Biologists* 6:105–16.
- Platts, W. S., and M. Onishuk. 1988. "Good" beavers, "bad" beavers. *Idaho Wildlife* 41(2): 23–27.
- Platts, W. S., R. L. Nelson, O. Casey, and V. Crispin. 1983. Riparian-stream habitat conditions on Tabor Creek, Nevada, under grazed and ungrazed conditions. Pages 162–74 in *Proceedings of the Western association of fish and wildlife agencies*. July 10–14, 1983. Teton Village, Wyo. Western Association of Fish and Wildlife Agencies.
- Putman, R. J., P. J. Edwards, J. C. E. Mann, R. C. How, and S. D. Hill. 1989. Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. *Biological Conservation* 47:13–32.
- Risenhoover, K. L., and S. A. Maass. 1987. The influence of moose on the composition and structure of Isle Royale forests. *Canadian Journal of Forest Research* 17(5): 357–64.
- Romme, W. H., and D. G. Despain. 1989a. Historical perspective on the Yellowstone fires of 1988. *BioScience* 39:695–99.
- Romme, W. H., and D. G. Despain. 1989b. The Yellowstone fires. *Scientific American* 261(5)(November): 37–46.
- Romme, W. H., and D. H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62(2): 319–26.
- Ross, B. A., J. R. Bray, and W. H. Marshall. 1970. Effects of long-term deer exclusion on *Pinus resinosa* forest in north-central Minnesota. *Ecology* 51(6): 1088–93.
- Rudersdorf, W. J. 1952. The coaction of beaver and moose on a joint food supply in the Buffalo River Meadows and surrounding area in Jackson Hole, Wyoming. M.S. Thesis, Utah State University, Logan.
- Rush, W. M. 1932. Northern Yellowstone elk study. Montana Fish and Game Commission, Helena.
- Russell, O. 1965. Journal of a trapper. A. L. Haines, ed. University of Nebraska Press, Lincoln.
- Scheffer, P. M. 1938. The beaver as an upstream engineer. *Soil Conservation* 3(7): 178–81.
- Schullery, P. 1989a. Yellowstone fires: A preliminary report. *Northwest Science* 63(1): 44–54.
- Schullery, P. 1989b. The fires and fire policy. *BioScience* 39:686–94.
- Schulz, T. T., and W. C. Leininger. 1990. Differences in riparian vegetation structure between grazed areas and exclosures. *Journal of Range Management* 43(4): 295–99.
- Seton, E. T. 1909. Life-histories of northern animals: An account of the mammals of Manitoba. Vol. I. Charles Schribner's Sons, New York.
- Shute, D. A. 1981. Decline of riparian communities in a portion of southwestern Wyoming. Unpublished report on file, U. S. Department of the Interior, Bureau of Land Management, Rock Springs, Wyo.
- Singer, F. J. 1987. Range impacts of the northern Yellowstone elk 20 years after cessation of controls. Unpublished report, Research Office, Yellowstone National Park, Wyo.
- Skinner, M. P. 1927. The predatory and fur-bearing animals of the Yellowstone National Park. *Roosevelt Wild Life Bulletin* 4(2): 163–281.
- Skinner, S. 1986. BLM beavers. *Wyoming Wildlife* 50(7)(July): 10–15.
- Skovlin, J. M. 1982. Habitat requirements and evaluations. Pages 369–413 in J. W. Thomas and D. E. Toweill, eds. *Elk of North America: Ecology and management*. Stackpole Books, Harrisburg, Pa.
- Smith, A. G. 1965. Problems of inertia and threshold related to postglacial habitat changes. *Proceedings of the Royal Society of London, Series B*, 161:331–42.
- Smith, B. H. 1980. Not all beaver are bad; or, an ecosystem approach to stream habitat management, with possible software applications. Pages 32–36 in R. Whaley, ed. *Proceedings of the 15th annual meeting: Colorado/Wyoming Chapter, American Fisheries Society*. Wyoming Game and Fish, Casper.
- Smith, B. H. 1983a. Riparian willow management: Its problems and potentials, within the scope of multiple use on public lands. Pages 15–20 in *Ninth Wyoming Shrub Ecology Workshop*. June 5–6, 1980. Lander, Wyo.
- Smith, B. H. 1983b. Restoration of riparian habitats within the BLM-Rock Springs District. Paper presented at *Wildlife habitat rehabilitation and reclamation symposium*. January 10–11, 1983. Salt Lake City, Utah.
- Smith, M. E., C. T. Driscoll, B. J. Wyskowski, C. M. Brooks, and C. C. Cosentini. 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology* 69:55–61.

- Smith, R. L., and L. D. Flake. 1983. The effects of grazing on forest regeneration along a prairie river. *Prairie Naturalist* 15:41-44.
- Snyder, J. D., and R. A. Janke. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. *American Midland Naturalist* 95(1): 79-92.
- Stein, S. J., and P. W. Price. 1990. The effect of fire on stimulating willow regrowth and subsequent herbivore attack. *Ecological Society of America Bulletin* 71(2): 336.
- Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park: A 10-year study. Rocky Mountain National Park ROMO-N-13.
- Stewart, G. H., J. A. Wardle, and L. E. Burrows. 1987. Forest understorey changes after reduction in deer numbers, northern Fiordland, New Zealand. *New Zealand Journal of Ecology* 10:35-42.
- Stivers, T. S. 1988. Effects of livestock grazing on grizzly bear habitat along the east front of the Rocky Mountains, Montana. M. S. Thesis, Montana State University, Bozeman.
- Streeter, R. G. 1965. Environmental factors affecting vegetational patterns in the Daly Basin of northwestern Yellowstone National Park, Montana. M. S. Thesis, Virginia Polytechnic Institute, Blackburg.
- Strickland, D. 1987. Wapiti welfare: Elk feedgrounds. *Wyoming Wildlife* 51(2)(February): 28-31.
- Suter, S. M. 1990. Chemical and morphological response of willow in Alaska to simulated moose browsing. *Ecological Society of America Bulletin* 71(2): 340.
- Taylor, D. M. 1986. Effects of cattle grazing on passerine birds nesting in riparian habitat. *Journal of Range Management* 39(3): 254-58.
- Tiedemann, A. R., and H. W. Berndt. 1972. Vegetation and soils of a 30-year deer and elk enclosure in central Washington. *Northwest Science* 46(1): 59-66.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53(3): 524-32.
- Trottier, G. C., and A. Fehr. 1982. Re-evaluation of four range enclosures in Banff National Park, 1981. Canadian Wildlife Service, Edmonton, Alberta.
- Tucker, T. L. 1987. Cattle grazing affects nongame wildlife populations and fish habitat in a montane riparian area. M. S. Thesis, Colorado State University, Fort Collins.
- Tyers, D. B. 1981. The condition of the northern winter range in Yellowstone National Park: A discussion of the controversy. M.S. Thesis, Montana State University, Bozeman.
- Veblen, T. T., M. Mermoz, C. Martin, and E. Ramilo. 1989. Effects of exotic deer on forest regeneration and composition in northern Patagonia. *Journal of Applied Ecology* 26:711-24.
- Warren, E. R. 1926. A study of the beaver in the Yancey region of Yellowstone National Park. *Roosevelt Wild Life Annals* 1:1-191.
- Windell, J. T., B. E. Willard, D. J. Cooper, S. Q. Foster, C. F. Knud-Hansen, L. P. Rink, and G. N. Kiladis. 1986. An ecological characterization of Rocky Mountain montane and subalpine wetlands. U. S. Department of the Interior, Fish and Wildlife Service Biological Report 86(11).
- Wright, G. A. 1984. People of the high country: Jackson Hole before the settlers. Peter Lang, New York.
- Wright, G. M., and B. H. Thompson. 1935. Fauna of the national parks of the United States. U. S. Department of the Interior, National Park Service Fauna Series No. 2.
- Youngblood, A. P., and W. F. Mueggler. 1981. Aspen community types on the Bridger-Teton National Forest in western Wyoming. U. S. Department of Agriculture, Forest Service Research Paper INT-272.
- Youngblood, A. P., W. G. Padgett, and A. H. Winward. 1985. Riparian community type classification of eastern Idaho-western Wyoming. U. S. Department of Agriculture, Forest Service R4-Ecol-85-01.

Native shrubs and trees for riparian areas in the intermountain west. Derek Tilley, PMC Agronomist, NRCS, Aberdeen, Idaho Dan Ogle, Plant Materials Specialist, NRCS, Boise, Idaho (Ret.) Loren St. John, PMC Team Leader, NRCS, Aberdeen, Idaho J. Chris Hoag, NRCS, Aberdeen, Idaho (Ret.) Joe Scianna, PMC Manager, NRCS, Bridger, Montana. A healthy riparian community. Photo by Derek Tilley.Â Uses Ethnobotanic: Native Americans reportedly pounded the wood of thin leaf alder into a powder to produce a red dye. Wildlife: Cottontail rabbits, muskrats, moose, elk, deer, and snowshoe hares eat the leaves and twigs. Numerous bird species forage on alder seeds, buds, and catkins. Beaver eat the bark and build dams with the stems.