CHAPTER VI

TALL WILLOW COMMUNITIES

INTRODUCTION

Houston (1982:129) stated that the distribution of willows on the northern range may have declined by roughly 50% since Yellowstone Park was established, and 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 (1976a) 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" paradigm. Because "natural regulation" is an equilibrium model, grazing-induced changes in vegetation stature (height) since Yellowstone Park was created would also indicate that the herbivores have not been in equilibrium with their food resources. Therefore, if ungulate browsing on the northern range has changed what were once tall willow communities into short willow stands, this would be additional grounds for rejecting the "natural regulation" paradigm (see Chapter 1 above).

To evaluate the effects of succession, climate, and ungulate browsing on willow communities, I measured willows inside and outside four exclosures on Yellowstone's northern range (Table 3, Fig. 3, Chapter 2 above). I also used the data collected by Chadde et al. (1988; see Chapter 2 above) to evaluate the trend and status of those willow communities. Chadde et al.'s (1988) classification of willow communities on the northern range is presented in Appendix C.

RESULTS AND DISCUSSION

Measurements Inside-Outside Exclosures

Willows were taller and had greater canopy-coverage inside than outside each exclosure (Tables 29-31). Other less palatable shrubs, such as rose and river birch (Nelson and Leege 1982), exhibited this same pattern. When pooled, these differences were statistically significant across all exclosures (Tables 32 and 33). Outside these exclosures, the mean height of all willow species was 34cm while inside it was 274cm. On average, willows had 10% canopy-coverage outside the exclosures, but 74% canopy-coverage where ungulates were excluded. However, all belt transects contained some non-willow communities (Table 34). When the non-willow portions of the belt transects were excluded, willow canopy-coverage averaged 14% outside the exclosures and 95% inside, also a statistically significant difference (Table 32). Thus, willow canopy closure was nearly complete inside the exclosures.

When my line-intercept, canopy-coverage data were compared with the Park Service's grid measurements, no significant difference existed for the transects outside the exclosures. However, the agency's method significantly underestimated the amount of willow canopy-coverage inside the exclosures (Table 35). I believe my line-intercept data more accurately represent the true conditions within the exclosures because my own aerial photographs show nearly complete willow canopy closure (Kay unpub. photos) .

At another willow exclosure on Slough Creek just north of the park (Table 3, Fig. 3), willows increased in height and canopy-coverage when protected from ungulate browsing (Chadde and Kay 1988) . At the Slough Creek exclosure, winter snow accumulation normally precludes that area's utilization as elk winter range, and winter use is generally limited to moose. Elk occasionally use the Slough Creek area in late fall and early spring or during winters of low snowfall.

Inside three exclosures in the Gallatin River drainage (Table 3,

Table 29. Average canopy-coverage and plant height of woody species inside and outside the Junction Butte exclosure on Yellowstone's northern range. August 1988.

Species	Mean percent canopy-coverage		Mean plant height (cm)	
	Outside	Inside	Outside	Inside
Salix lutea	6.7	22.8*	27.5	167.0*
Salix bebbiana	6.7	55.8*	32.5	272.0*
Salix geyeriana	1.5	2.0	43.5	192.2*
Rosa woodsii	1.0	10.7*	31.0	70.5*
Potentilla fruticosa	14.7	19.5	32.8	57.0*
Ribes spp.	0.3	2.3	38.2	113.0*
Populus tremuloides	1.8	0.0	30.8	----
Total willows	14.7	80.6*		
Total shrubs	32.5	112.8*		

* $p < .01$, t-test; percentages were arcsine transformed.

Table 30. Average canopy-coverage and plant height of woody species inside and outside Lamar-West and Lamar-East exclosures on Yellowstone's northern range, August 1988.

	Mean percent canopy-coverage			Mean plant height (cm)		
Species	Lamar-East Outside	Lamar-East Inside	Lamar-West Inside	Lamar-East Outside	Lamar-East Inside	Lamar-West Inside
Salix bebbiana	3.0	40.3*	40.8*	49.05	357.0*	317.0*
Salix geyeriana	3.7	15.7*	0.0	40.8	330.5*	---
Salix boothii	0.0	4.0	36.2*	---	160.0	257.0
Rosa woodsii	3.2	2.8	0.7	29.0	71.0*	62.0*
Potentilla fruticosa	13.3	3.5	0.3	39.0	43.0	65.0
Ribes spp.	0.5	0.5	0.0	53.5	82.5	---
Populus tremuloides	0.0	3.2	2.8	---	161.0	375.8
Lonicera involucrata	2.0	4.2	0.0	34.0	91.8*	---
Symphoricarpos albus	0.0	0.0	T	---	---	37.5
Total willows	6.7	60.0*	77.0*			
Total shrubs	25.7	74.2*	81.2*			

* *p* < .01, t-test; percentages were arcsine transformed.

Table 31. Average canopy-coverage and plant height of woody species inside and outside Mammoth exclosure on Yellowstone's northern range, August 1988.

	Mean percent canopy-coverage		Mean plant height (cm)	
Species	Outside	Inside	Outside	Inside
Salix lutea	3.2	0.2	21.5	180.0*
Salix bebbiana	6.8	53.3*	23.8	403.2*
Salix geyeriana	0.0	12.0*	----	328.0
Salix boothii	0.0	13.2*	----	353.8
Betula occidentalis	4.7	5.0	82.5	481.8*
Rosa woodsii	0.8	12.0*	19.8	77.8*
Potentilla fruticosa	0.7	0.0	45.5	----
Total willows	10.0	78.7*		
Total shrubs	16.2	95.7*		

* $p < .01$, t-test; percentages were arcsine transformed.

Table 32. Average willow canopy-coverage inside and outside Yellowstone exclosures. Entire belt transects compared with only the portion of those transects which contain willow communities, August 1988.

	Mean percent willow canopy-coverage	
Exclosure	Entire belt transect	Willow type only
Mammoth		
Outside	10.0	12.3
Inside	78.5	109.2
Junction Butte		
Outside	14.7	21.0
Inside	80.7	93.2
Lamar - East		
Outside	6.7	9.7
Inside	60.0	86.5
Lamar - West		
Inside	77.0	92.0
Totals		
Outside	10.5	14.3
Inside	74.0	95.2
*t**	8.83	4.74
p	< .01	< .01

*Percentages were arcsine transformed.

Table 33. Average height all willow species and rose inside and outside Yellowstone exclosures.

	Mean Height (cm)	
Exclosure	All willow species	Rosa woodsii
Mammoth		
Outside	22	20
Inside	316	78
Junction Butte		
Outside	35	31
Inside	210	70
Lamar - East		
Outside	45	29
Inside	282	71
Lamar - West		
Inside	287	62
Totals		
Outside	34	27
Inside	274	70
t	7.67	9.62
p	< .01	< .01

Table 34. Community types found on permanent willow belt transects inside and outside exclosures on Yellowstone's northern range. Types follow Chadde et al. (1988).

Exclosure - willow belt	Year established	Association or Community Type with Transect Percentage
Junction Butte-IN	1962	*Salix geyeriana*/*Carex rostrata* (87%) *Potentilla fruticosa*/*Deschampsia cespitosa* (13%)
Junction Butte-OUT	1962	*Salix geyeriana*/*Deschampsia cespitosa* (80%) *Populus tremuloides*/*Poa pratensis* (20%)
Lamar East-IN	1957	*Salix geyeriana*/*Carex rostrata* (65%) *Phleum pratense* (29%) *Populus tremuloides*/*Phleum pratense* (6%)
Lamar East-OUT	1957	*Salix geyeriana*/*Poa pratensis* (70%) *Potentilla fruticosa*/*Poa pratensis* (30%)
Lamar West-IN	1962	*Salix geyeriana*/*Carex rostrata* (85%) *Carex rostrata* (15%)
Mammoth-IN	1957	*Salix geyeriana*/*Carex rostrata* (69%) *Juncus balticus* (16%) *Carex nebraskensis* (15%)
Mammoth-OUT	1957	*Salix bebbiana*/*Agrostis stolonifera* (80%) *Poa pratensis* (20%)

Table 35. Percent willow canopy-coverage inside and outside exclosures on Yellowstone's northern range, 1958 - 1988. Park Service 1958-1986 data from Singer (1987).

	Percent willow canopy-coverage							
	Park Service measurements						This study	
Exclosure-Transect	1958	1962	1965	1974	1981	1986	Entire transects 1988	Willow type only 1988
Junction Butte								
Outside	---	6.6	6.9	10.6	11.2	13.2	14.7	21.0
Inside	---	16.1	13.2	25.8	33.0	49.1	80.7	93.2
Lamar-East								
Outside	6.0	5.4	6.5	9.5	9.3	9.0	6.7	9.7
Inside	8.2	14.2	23.3	28.4	18.9	37.2	60.0	86.5
Lamar-West								
Inside	---	1.7	5.6	16.6	18.7	43.1	77.0	92.0
Mammoth								
Outside	7.5	8.6	6.2	9.3	8.8	12.9	10.0	12.3
Inside	4.5	10.3	25.2	31.2	26.9	31.2	78.5	109.2
Totals								
Outside						11.7	10.5*	
Inside						40.2	74.0**	

* ns.
** p < .01

Fig. 3), willows attained heights of 3-4m with near-complete canopy closure while unprotected plants were all <1m tall (Kay unpub. photos). In Rocky Mountain National Park, Gysel (1960) and Stevens (1980) noted that willows increased in canopy-coverage 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.

Repeat Photographs of Exclosures

In addition to the measurements of plant height and cover which the Park Service has made over the years, they also photographed the willow belt transects each time they were sampled. I repeated those photographs in 1986-88. The resulting multiple-image photosets confirm that willows inside the exclosures have increased in height and canopy-coverage since they were protected while willow communities outside the exclosures have not (Figs. 10-12).

These comparative photos were also used to evaluate changes in willow communities observed in other repeat photosets (see Chapter 8 below) because visual estimates from the exclosure photographs could be compared with actual plant measurements. This served to calibrate the visual estimation technique used in this study (see Chapters 2 and 8 herein). It also demonstrated that willows inside the exclosures now have the same stature that willows on the northern range had in the 1870s-1890s (see Chapter 8 below). Thus, the conditions inside the exclosures more closely approximate the level of ungulate use which existed when Yellowstone was created than conditions in the park today.

WHY HAVE WILLOWS DECLINED?

The observed decline (see Chapter 8 below) in tall willow communities has been postulated to be due to (1) normal plant

Fig. 10. Willow belt transect (1.5x22.9m) outside Junction Butte exclosure in 1965 and 1988. Two steel posts mark the east end of the belt transect. Camera position is between the two steel posts on the transect's west boundary. NPS photo 65-521, 9/29/65. Charles Kay photo 3,041-21, 8/16/88. Haze in retake is from the 1988 forest fires.

1965

1988

Fig. 11. Willow belt transect (1.5x22.9m) inside Junction Butte exclosure in 1965 and 1986. Exclosure was constructed in 1962. Exclosure fence is in top of 1965 photo. Two steel posts mark the west end of the belt transect in 1965 photo. The camera position for the 1965 photo was between the two steel posts on the transect's east boundary. The camera position for the 1986 retake was moved approximately 5m to the east and shows the transect's east marker posts not visible in the 1965 photo. NPS photo 65-520, 9/29/65. Charles Kay photo 58,982-25, 7/25/86.

1965

1986

Fig. 12. Willows inside and outside the Junction Butte exclosure in 1962 and 1988. Exclosure was constructed in 1962 and the fence is approximately 2.5m tall. The outside willow belt transect is in the left center of the photos while the inside willow belt transect is on the right center. All belt transect posts are visible in the 1962 photo. Trees visible inside the exclosure in 1988 are aspen. Aspen is present inside and outside the exclosure in both pictures. The two small fenced areas to the left of the exclosure fence visible in the 1988 retake are mini-exclosures built by Chadde et al. (1988) to monitor willow growth (see Chapters 2 and 7 herein). Haze in 1988 photo is from forest fires. NPS photo 62-553, 1962. Charles Kay photo 3,041-23, 8/16/88.

1962

1988

succession, (2) climatic change, (3) fire suppression, or (4) ungulate browsing (Houston 1982, Despain et al. 1986). According to Houston (1982:129-134), 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 which showed willows had colonized that area.

I rephotographed that site in 1983, 1986, 1987, and 1988 (Kay unpub. data). Chadde et al. (1988) also 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. Thus, this area changed from bare gravel to willows to grass in only 9 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, colonizing willows would have been replaced by other willow species and perhaps cottonwoods (<u>Populus</u> spp.) or eventually Englemann spruce, 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) which has not occurred at this site along the Gardiner River.

As mentioned above, previous studies recorded the number of individual willow plants on the belt transects inside and outside the exclosures. Those data (Houston 1982:419, Singer 1987) generally show more "plants" outside the exclosures than inside and have been used to infer the relative ecological health of these communities, independent of plant height or canopy-coverage (Houston 1982:99). Despain et al. (1986) implied that since there were more willow "plants" outside the exclosures than within, outside willow communities were in better condition than willows inside exclosures.

Outside the exclosures, Park Service biologists counted a few stems less than 1m tall as an individual plant as they did another small group of similar-sized stems a short distance from the first "individual." However, unless the roots are excavated or genetic tests performed, it is impossible to determine whether nearby stems are really part of the same plant or different individuals. Some willow clumps may have been broken into "separate plants" by repeated browsing. Moreover, Park Service investigators contend that a plant with a few short stems outside an exclosure is ecologically equivalent to a plant inside the exclosure which has several hundred stems each 3m tall. In my opinion, the enumeration of supposed individual willow plants inside and outside exclosures is not an appropriate measure upon which to base ecological interpretations unless size-class data are also considered and individual plants positively identified.

The decline of willows on the northern range has also been attributed to climatic change, especially to the drought during the 1930s (Houston 1982:129-134). This suggestion is not supported by data from the exclosures, since 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, not the cause of the vegetation's response (see Chapter 4 above). Inside a small exclosure near Tower Junction, willows grew vigorously during and after the 1930s drought while those outside did not (see *NPS* photos *15078-4, 1936; 51-21,* 1951). Moreover, it is not climate which 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 first-hand accounts. Willows started declining before the 1930s 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 that community (Fig. 13) even though precipitation had been near normal during the 1949-1988 period (Houston 1982:104, Kay unpub. data), and there still are abundant springs and seeps at the site.

Yellowstone's Tower Junction willow exclosure (Table 3, Fig. 3) was constructed in 1957, and by the late 1960s, the protected willows had significantly increased in height and canopy-coverage (Singer 1987, Kay unpub. photos). That exclosure was removed in the early 1970s and the protected plants exposed to ungulates. By the late 1970s and early 1980s those willows were extensively hedged and were reverting to lower-statured plants (Kay unpub. photos). Those changes certainly cannot be attributed to the 1930s drought. Climatic variation appears to be unimportant since this area has abundant subsurface soil moisture (Brichta 1987, Chadde et al. 1988).

As previously noted, the mean annual temperature on the northern range at Mammoth increased 0.5-1.0°C while the mean annual precipitation declined 1-2cm (Houston 1982:101-107). However, to the best of my knowledge, no one has demonstrated that a climatic shift of that size will have a long-term impact on tall willows, especially since nearly all willow communities are subirrigated (Brichta 1987). Most perennial woody floras 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, see also Chapter 4 above).

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

Fig. 13. Heavily browsed willows along the west edge of Round Prairie, near Pebble Creek, Yellowstone National Park in 1949 and that same area in 1988. Note the nearly complete decline of willows which occurred over the last 39 years. Numerous springs and seeps still are found in this area which suggests that climatic change or lack of water is not primarily responsible for the observed change in plant communities. NPS photo 49-331; Charles Kay photo 2,976-19A, 6/21/88.

1949

1988

ungulates. Houston (1973, 1982:107) calculated mean intervals of 20-25 years between fires on the northern range during the 300-400 years before Yellowstone Park was established and the government began to suppress fires. Despite a policy which has been in effect since the early 1970s to let many lightning-caused fires burn, 1988 was the first year fires 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. Riparian areas and willows are generally too wet to burn (Romme and Knight 1981, Baker 1987).

Furthermore, cottonwoods (Populus trichocarpa and P. angustifolia) have also declined and failed to regenerate successfully on the northern range (Chadde et al. 1988). These species are extremely susceptible to fire and are easily killed by even a light burn. Frequent fires certainly would not enhance cottonwood regeneration in the park.

Finally, there is no evidence to support the idea that burning will cause resprouting willows to grow so fast or 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 (D. Despain, pers. commun. 1988). 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 1m except where physical barriers prevented elk use (Kay unpub. photos). Stein and Price (1990) reported that in an experimental situation, "elk fed primarily on [resprouted] willows that had been burned" as compared to unburned plants. Suter (1990) clipped winter dormant willows to simulate ungulate browsing and then measured proanthocyanidid tannins in twigs which grew the following year. She found that "After 2 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 the available evidence, I conclude that frequent, repeated ungulate browsing is primarily responsible for the decline of tall willow communities on the northern range. Browsing by elk and moose presently prevents the willows which do exist on the northern range from expressing their full biological height and canopy-coverage. From 1970 through 1978, willow utilization on the northern range averaged over 91% (Houston 1982:149) and has not decreased in recent years (S. Chadde, pers. commun. 1989; F. Singer, pers. commun. 1989). Likewise, Barmore (1981:358) concluded that willows had declined on the northern range due to repeated ungulate browsing, not 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, they reduced the herd by trapping, transplanting, and killing elk (see Chapter 1 above). 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 have declined only where wintering elk concentrated most heavily (Patten 1968). The willows upstream and downstream from the main elk wintering area have not declined and commonly exceed 3m in height. Thus, 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. However, it was ungulate browsing which actually caused most of the mortality and reduction in plant growth form. Neilson (1986), who worked on a similar climatic change _vs_. grazing problem, concluded that the vegetation would have persisted despite drought, but the additional stress of grazing completely altered the flora.

Houston (1982:131) argued that ungulates were not primarily responsible for the decline of willows on the northern range because willows had also declined outside Yellowstone, as well as on the park's summer range. 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 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% of the streams and their associated riparian areas had been severely altered by livestock grazing (Shute 1981). Furthermore, moose and elk also feed upon willows on the park's summer range (McMillan 1950, 1953) and until exclosures 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%." He (1980:139) reported that on the park's summer range "53% 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% on three of the four transects, with an overall decline from 20%

cover to 9%. Salix planifolia declined from 37% to 29% cover" (Stevens 1980:135). These reductions occurred in only 8 years as the elk herd built up in that park (Stevens 1980:136).

ASSOCIATED ECOSYSTEM EFFECTS

Effects on Beaver Populations

The decline of tall willow and aspen communities on the northern range has had a negative impact on animals which are usually associated with that habitat, such as beaver. Houston (1982:182-183) implied that beaver were not widespread in Yellowstone until around 1900 and suggested "ephemeral colonies may be characteristic of most of the park." However, in 1835, 1836, and 1837 Osborne Russell (1965) trapped beaver in Yellowstone Park where he found a great many on the northern range. For instance, he and his companions trapped beaver from August 3rd to August 20th, 1835 on the upper Gardiner River. In 1836, Russell and his party spent several days trapping beaver on the streams which flow into Lamar Valley. The next year he and his associates spent nearly 3 weeks trapping beaver on Slough and Hellroaring Creeks.

Norris (1880b: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 abundant near Tower Junction on the northern range in 1897. Skinner (1927:176) noted that "beaver have always been quite common in Yellowstone National Park, and although fluctuations are noticed at times, the actual number present remains about the same throughout a course of years." Skinner added that "beaver occur in practically every stream and pond (where there is suitable food) in the park." He estimated there were "about 10,000" beaver in the park during the early 1900s.

Bailey (1930:112-114) 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." Thus, 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 the northern range around Tower Junction (Fig. 14). He estimated a population of 236 beaver and reported extensive beaver dams (Table 36). Jonas (1955) repeated Warren's study in the early 1950s and found no beaver nor any recent beaver activity (Table 36). 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." In 1986-88, I repeated Warren's and Jonas' surveys and found no beaver nor any indication of major beaver activity which might have taken place since the 1950s (Table 36, Figs. 15-17).

Beaver need tall willows or aspen as food and dam-building materials. Aspen and willows cut by beaver normally resprout (Warren 1926, Kindschy 1989) and in turn provide additional beaver food. However, once the mature aspen trees or tall willows are cut, 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

Fig. 14. Location of Warren's (1926) beaver colonies on the Yellowstone's northern range near Tower Junction. 1) Yellowstone Bridge, 2) Petrified Tree Road, 3) South Fork of Elk Creek, 4) Elk Creek Bench, 5) North Fork of Elk Creek, 6) Crescent Hill, 7) Tower Creek, 8) Carnelian Creek, 9) Lost Creek, 10) Lost Lake, 11) Natural Ponds, and 12) Yellowstone River.

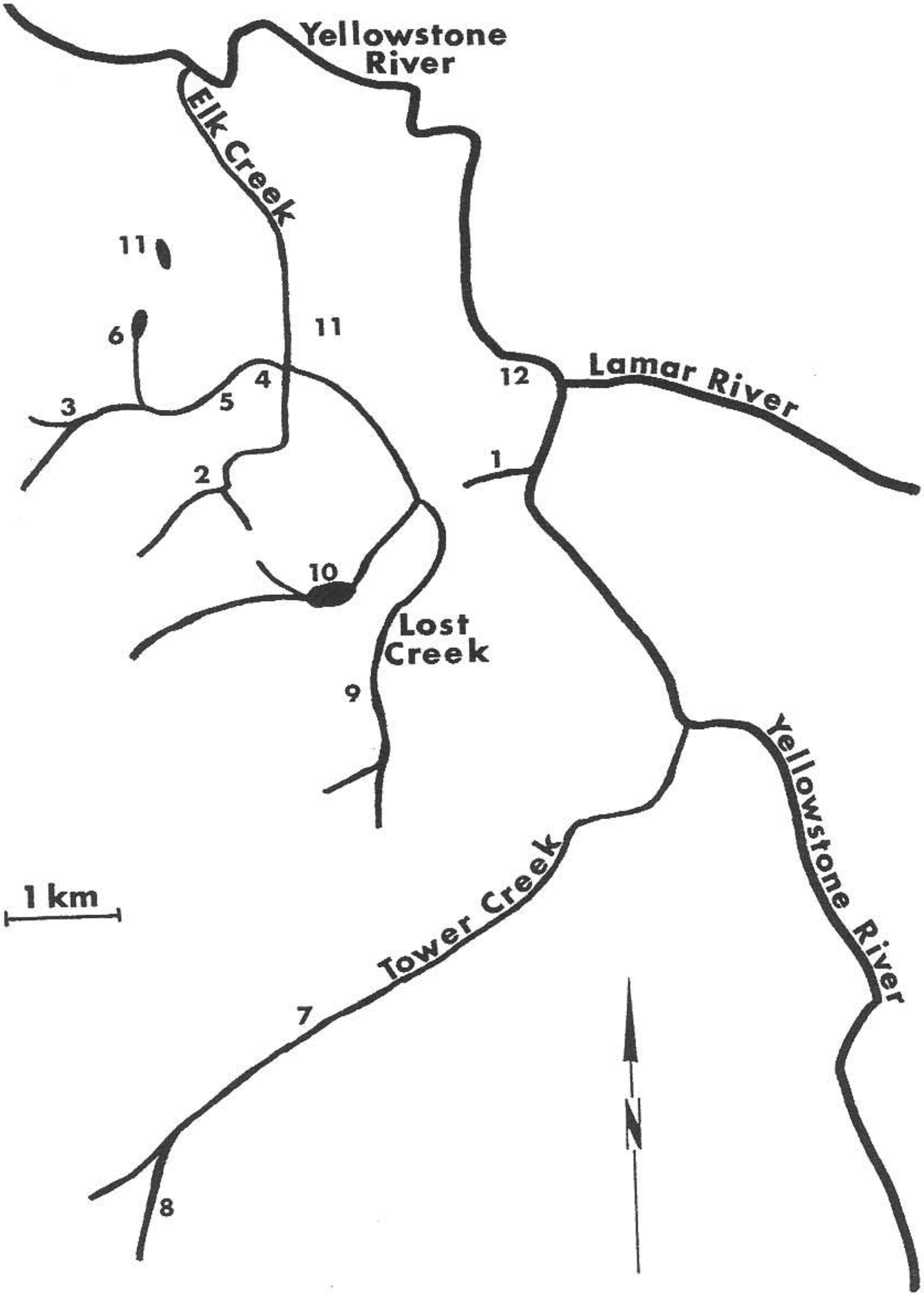

Yellowstone River
Elk Creek
11
11
6
3
5
4
12
Lamar River
1
2
10
Lost Creek
9
Yellowstone River
Tower Creek
1 km
7
N
8

Table 36. Number of beaver on Yellowstone's northern range near Tower Junction 1923-1988.

	Number of beaver by years		
Location	1921-23*	1953-54**	1986-88
1. Yellowstone bridge colony	11	zero	zero
2. Petrified tree road colony	20	zero	zero
3. South Fork of Elk Creek	8	zero	zero
4. Elk Creek bench colony	8	zero	zero
5. North Fork of Elk Creek	40	zero	zero
6. Crescent Hill ponds	16	zero	zero
7. Tower Creek	50	zero	zero
8. Carmelian Creek	25	zero	zero
9. Lost Creek	25	zero	zero
10. Lost Lake	8	zero	zero
11. Natural ponds	20	zero	zero
12. Along Yellowstone River	5	zero	zero
Total	236	zero	zero

* From Warren (1926).

** From Jonas (1955).

Fig. 15. Repeat photoset of a beaver dam on the North Fork of Elk Creek on Yellowstone's northern range near Tower Junction. (a) In this 1921 photo, note aspen in the upper left and willows to the right of the dam. Photo by Edward Warren (1926:84) courtesy SUNY College of Environmental Science and Forestry, Syracuse, NY. Photo No. 5145, 8/10/21. (b) The same area in 1954. Note the decline of aspen and willows while the stream has downcut approximately 2m through the old beaver dam. Photo courtesy Robert Jonas (1955:37), 6/12/54. (c) The same area in 1986. Note the continued absence of aspen and willows, as well as, the browse line on the conifers mainly Englemann spruce. Most of the area in the original photo has reverted to a dry grassland type. The stream has continued to downcut and is severely eroding its banks off the photo to the right. Charles Kay photo No. 3,081-33, 7/15/86.

a.

b.

c.

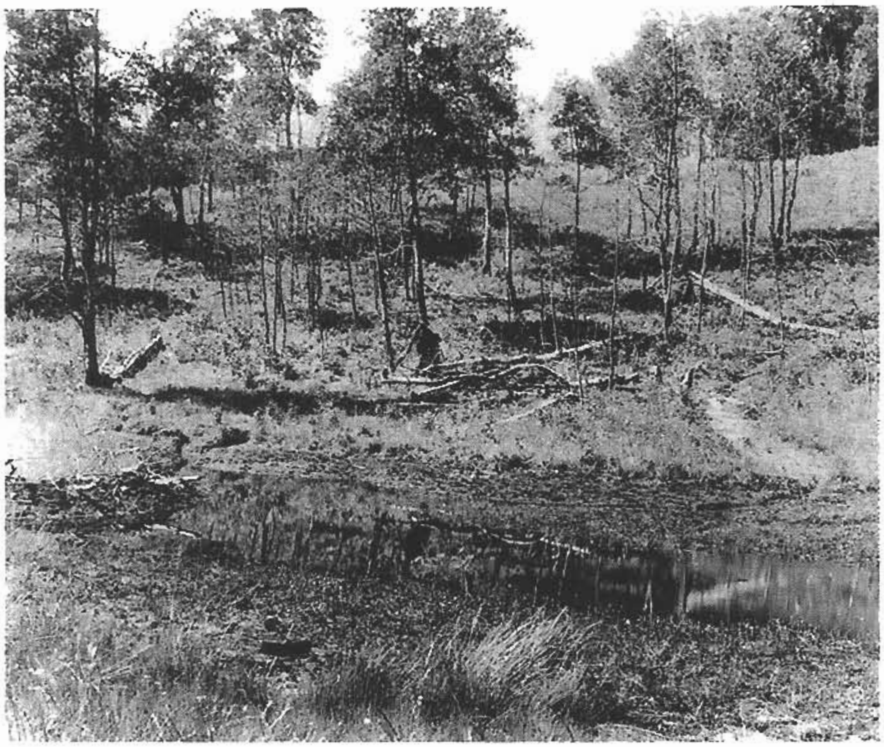
Fig. 16. Repeat photoset of beaver dams below Crescent Hill on Yellowstone's northern range west of Tower Junction. (a) In this 1921 photo, note aspen in the left center and around the beaver ponds. Aspen shows evidence of high-lining and bark wounding by elk. Photo by Edward Warren (1926:95) courtesy SUNY College of Environmental Science and Forestry, Syracuse, NY. Photo No. 5070, 7/22/21. (b) The same area in 1953; camera point has been moved forward. Note the near total decline of aspen. The dead standing tree on the left, as well as the fallen trees (left and center) are all aspen. Note the old beaver dam in right center, large boulder on the left, and high-lined conifers. Photo courtesy Robert Jonas (1955:41), 7/29/53. (c) The same area in 1986; note large boulder in the lower left. All traces of aspen have been eliminated and the conifers are high-lined. Original beaver dam is still visible in lower right. Photo by Charles Kay, No. 58,989-27, 7/17/86.

a.

b.

c.

Fig. 17. Repeat photoset of a beaver dam below Crescent Hill on Yellowstone's northern range west of Tower Junction. (a) In this 1921 photo the crest of the beaver dam runs from lower right to left center. Note beaver trails and cutting in the aspen stand behind the pond. Also note the large boulder on the hillside. Photo by Edward Warren (1926:96) courtesy SUNY College of Environmental Science and Forestry, Syracuse, NY. Photo No. 5,069, 7/22/21. (b) The same area in 1986, note large boulder on hillside. Aspen has been completely eliminated and conifers have all been high-lined by elk. Photo by Charles Kay, No. 58,989-33, 7/17//86.



a.

b.

numbers negatively impacted beaver through interspecific competition for willows and aspen in Banff and Jasper National Parks. Bergerud and Manuel (1968) noted that high moose densities had a similar negative effect on beaver in Newfoundland. Heavy grazing by domestic livestock not only reduced woody vegetation but also negatively impacted beaver populations (Smith and Flake 1983, Dieter 1987, Dieter and McCabe 1989). Though a few beaver still persist in Yellowstone, for all practical purposes, that species is ecologically absent from the northern range.

Recent studies by Bureau of Land Management and Forest Service researchers have shown that beaver create and maintain riparian areas which are critical to other wildlife. In fact, both agencies have transplanted beaver to restore livestock-damaged riparian areas (Munther 1981, 1983; Smith 1980, 1983a, 1983b). Moreover, other researchers have demonstrated that beaver is a keystone species which completely alters the hydrology, energy flow, and nutrient cycling of aquatic systems (Parker et al. 1985, Naiman et al. 1986, Platts and Onishuk 1988).

Beaver dams impound water and trap sediments which raise the water table, increase the wetted perimeter, and allow the extension of riparian communities into what were once 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, 30-60% 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 floors (Apple 1983).

Munther (1981, 1983) reported that a typical creek without beaver furnishes only about 2-4 acres of riparian habitat per stream mile in the northern Rockies. With beaver activity, that area can be expanded to 24 acres per mile (Munther 1981, 1983). Hence, the elimination of beaver over most of the northern range may well have significantly altered the ecology of areas that formerly supported the species.

According to the "natural regulation" hypothesis, competitive exclusion of sympatric herbivores will not occur. However, elk and moose have acted to competitively exclude beaver from the northern range. Moreover, in the absence of beaver, several streams on the northern range have downcut 1-2m (Fig. 15, Kay unpub. photos). This has undoubtedly lowered the water table and reduced 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. Thus, 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.

Effects on Other Species

A small population of white-tailed deer inhabited Yellowstone's north range during the late 1800s and early 1900s (Skinner 1929). That population declined during the 1920s and was essentially extinct by 1930 (Houston 1982:182). Those whitetails were associated with thickets of riparian vegetation (Skinner 1929:102) as is the case throughout their range north of the park today. In recent years, whitetail populations have increased outside the park and a few have been observed in Yellowstone (Singer 1989, Kay unpub. photos). However, whitetails have not become reestablished in the park. In my opinion, the absence of tall willow communities and other tall deciduous shrub habitats (see Chapter 7 below) on the northern range due to repeated browsing makes it highly unlikely that whitetails will regain a permanent foothold in the park.

Based on other studies (Page et al. 1978, Casey and Hein 1983, Marcuson 1983, Platts et al. 1983, Taylor 1986, Loft et al. 1987, Knopf et al. 1988, Medin and Clary 1989, Putman et al. 1989), the decline of tall willow communities on Yellowstone's northern range may also have adversely affected birds, small mammals, and even grizzly bears (Kay

1989). Elimination of beaver and willow bank cover probably has also caused decreases in the distribution and numbers of native trout species (W. Platts, pers. commun. 1989). Thus, entire plant and animal communities, not just tall willows, have been altered by ungulate use in the park. Clearly, the physical stature of the vegetation is important in determining the composition of animal communities which use that habitat. The grazing-induced short willow communities which presently exist in the park are not ecologically equivalent to the tall willow communities that once occupied those same areas.

CONCLUSIONS

1. Willows protected from ungulates exhibit significantly greater height growth and canopy-coverage than unprotected plants and in physical stature resemble the willows which existed in the park during the late 1800s (see Chapter 8 below).

2. The decline (see Chapter 8 below) and current suppression of tall willows over the entire northern range is due primarily to frequent, repeated ungulate browsing, not climatic change, plant succession, or suppression of lightning fires.

3. Ungulate browsing has not only changed the stature and abundance of tall willows on the park's northern range, but has also impacted animals commonly associated with those riparian habitats.

4. Ungulate browsing has acted to competitively exclude beaver from nearly all the northern range.

5. The virtual elimination of beaver may have had a negative effect on the extent of willow communities by lowering water tables and reducing stream flows.