CHAPTER 16

**Tall-Willow Communities on
Yellowstone's Northern Range:
A Test of the
"Natural-Regulation" Paradigm**

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Prior to 1968, Park Service personnel contended that an "unnaturally" large elk (*Cervus elaphus*) population which had built up in Yellowstone during the late 1800s and early 1900s had severely "damaged" the park's northern winter range, including willow (*Salix* spp.) communities (Skinner 1928; Rush 1932; Grimm 1939; Cahalane 1941, 1943; Kittams 1959; Pengelly 1963; Tyers 1981; Kay 1985, 1990; Chase 1986). Later biologists questioned the reality of any significant population buildup (Houston 1982:11–17) and hypothesized that the northern range population was "naturally regulated," its general level not having changed significantly in the 1800s and early 1900s except for short-term fluctuations associated with variations in winter weather (Cole 1971).

Terms such as *over grazing*, *range damage*, and *unnatural* elk population were used in nearly all early government reports about the northern range. Since these terms are value laden, they are used here only in their historical context.

The "natural-regulation" hypothesis, first announced in 1967 as the "natural-control" management policy, has been difficult to test because there is no single succinct and comprehensive publication of the concept and its assumptions, supporting evidence, and implications. Except for a brief discussion in Houston (1982:67–68), various aspects of the hypothesis have been presented by different authors in overview publications that make general reference to unpublished research reports, but do not explicitly cite scientific data from which generalizations are inferred (see Cole 1971, 1974, 1983; Houston 1976; Despain et al. 1986). Hence any definition of the model's specifications, assumptions, hypotheses, predictions, and a priori criteria for acceptance is subject to interpretation. The account that follows is our understanding of the model based on careful consideration and synthesis of the above publications.

If human influence is removed from the system, elk populations in Yellowstone will "naturally regulate" their numbers through density-dependent reduction in recruitment and survivorship resulting from intraspecific competition for food, primarily winter forage (Cole 1971). There may be some density-independent mortality associated with winter weather of varying severity. Although predation was invoked in the "natural-control" version of the model, under "natural-regulation" predation is considered to be an assisting but nonessential adjunct to the regulation of ungulate populations through density-dependent homeostatic mechanisms (Cole 1971; Houston 1976). If wolves or other predators were present, they would kill only animals slated to die of other causes, and hence would not limit or lower ungulate populations (see Cole 1971).

Although the elk population is essentially food limited, the park biologists reasoned on evolutionary grounds that the ungulates could not have "progressively reduced food sources that limit their own densities" (Cole 1971). Thus ungulate populations and vegetation must have been in rough equilibrium (Despain et al. 1986), and the vegetation conditions prevailing at the time of the park's formation must have reflected that equilibrium. Houston (1982:129) did observe that willows on the northern range may have declined by roughly 50 percent since the park was established, but that was attributed to primary succession, suppression of fire, and climate change, not to ungulate browsing.

In a 1971 American Association for the Advancement of Science symposium on research in national parks, Houston (1976) proposed a set of bases for rejecting the "natural-regulation" hypothesis. One was evidence that ungulates caused retrogressive plant succession. If willow communities had actually declined on the northern range because of ungulate browsing, this would be a basis for rejecting the hypothesis. Because the

"natural-regulation" concept is based on an equilibrium model, grazing-induced changes in vegetation stature (height) would also indicate that the herbivores were not in equilibrium with their food resources.

A second basis for rejection would be competitive exclusion of sympatric herbivores (Houston 1976). According to the "natural-regulation" hypothesis, sympatric herbivores in the park have been over time, and are, in interspecific equilibrium through resource partitioning (Houston 1982:169–178; Despain et al. 1986). Any change in their abundance resulting from ungulate competition would question the existence of a "natural-regulation" equilibrium at the time of park formation.

The preceding is our interpretation of the "natural-regulation" model which was proposed in the early 1970s and is in essence held by park biologists up to the present (see Despain et al. 1986). This chapter examines historical changes in willow communities on the northern range and evaluates the factor or factors responsible for the evident, extensive changes which have occurred in the riparian habitats. It further considers evidence of change in sympatric herbivores and collectively presents this evidence as a test of the "natural-regulation" model based on the criteria for rejection proposed by Houston (1976).

METHODS

Study Area

The study area in this chapter encompasses the northern range of Yellowstone National Park, which is essentially the winter range of the northern elk herd (Despain et al. 1986). Houston (1982) provides a description of its climate, physiography, and vegetation.

In 1957 the Park Service constructed 2.1-ha ungulate-proof exclosures at Mammoth and Lamar-East that enclosed willow communities. Two additional 2.1-ha willow-containing exclosures at Lamar-West and Junction Butte were built in 1962. A fifth willow exclosure was erected at Tower Junction in 1957, but was removed in the early 1970s. Houston (1982:415–420) and Barmore (1981:453–459) provide background information on these exclosures.

Houston (1982) and Despain et al. (1986) should be consulted for Park Service interpretations regarding the northern Yellowstone elk herd. Chase (1986), Kay (1985, 1987, 1990), and Tyers (1981) provide alternative views.

Repeat Photography

Archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State Univer-

sity, the Museum of the Rockies, the University of Wyoming, the Colorado Historical Society, the Library of Congress, the National Archives, and the U.S. Geological Survey's Denver Photographic Library were searched for historical photos of willow communities on the northern range. Nearly fifty thousand images taken in the park were reviewed. However, only a small number were taken on the northern range and fewer still contained views of willow communities. Other historical photographs were obtained from Warren (1926) and Jonas (1955). Seton (1909) provided several drawings of willow communities and beaver dams near Tower Junction in 1897.

The locations in these historical pictures were rephotographed during 1986–1989 to form sets of comparative photos, a process called repeat photography (Rogers, Malde, and Turner 1984). The photosets were visually evaluated to determine changes in the abundance and distribution of tall-willow communities (G. Rogers, personal communication 1987). Houston (1982) and Gruell (1980a, 1980b) also used comparative photography to study vegetation changes in the Greater Yellowstone Ecosystem.

Field Measurements

Willow communities and their environments were sampled and classified as part of a recent study of wetlands on the northern range (Chadde, Hansen, and Pfister 1988). Sample plots were located within relatively homogeneous stands of willows, based on species composition and dominance within the stand. The canopy-coverage (Daubenmire 1959) and height of all species occurring with 50-m^2 sample plots were estimated.

Soils were sampled and described using standard pedon description methods and terms (Soil Survey Staff 1975; Brichta 1987). Soils associated with willow communities were described to the family level. Water levels associated with representative willow stands were monitored from May to September of 1986 and 1987 using 1-m-long PVC tubes and a portable ceramic-tipped tensiometer. Other soil-water characteristics (conductivity, pH, dissolved-oxygen content) and physical features (elevation, aspect, topographic position) were recorded for each willow plot.

To develop a classification, sample plots were grouped into sets based on floristic similarities in both overstory and undergrowth layers (Chadde, Hansen, and Pfister 1988). Information on soil and site characteristics allowed the placement of community groupings along environmental and successional gradients. Associations or stable communities in equilibrium with environmental conditions were defined, as were seral community types. Grazing relationships for each community were inferred from field observations of browsing levels and from previously published studies on palatability and browsing response.

When the exclosures were constructed, the Park Service established one permanent willow belt transect inside and another outside each exclosure except at Lamar-West (Barmore 1981:453–459; Houston 1982:415–420; Singer 1987). At Lamar-West, a willow transect was established inside the exclosure but not outside. Instead, the agency used the Lamar-East outside willow belt as a control for both the Lamar-East and Lamar-West exclosures. Thus seven permanent willow belt transects are associated with these exclosures, three outside and four inside. The belt transects at Mammoth, Lamar-East, and Lamar-West are all 1.5 × 30.5 m (5 × 100 ft.). Those at Junction Butte are 1.5 × 22.9 m (5 × 75 ft.).

Data on willow canopy-coverage, plant height, and number of individual plants have been collected by the Park Service at intervals since the exclosures were constructed (Singer 1987). They plotted each willow clump within the transect on graph paper and then determined canopy-coverage by using a grid method. However, these belt transects have inherent inadequacies limiting their usefulness in long-term willow trend studies. First, the single canopy-coverage value inside and outside each exclosure precludes statistical testing of mean differences. Second, the plotting technique is subject to a wide degree of observer variability and error. Third, each belt transect includes significant portions of nonwillow communities. Fourth, rare species and other undergrowth shrubs are underestimated or not recorded. Park Service counts of individual willow plants have also been highly variable.

For this study, a series of line intercepts (Hanley 1978) within the existing belt transects were established so that willow canopy-coverage within and outside each exclosure could be compared statistically. Each belt transect was subdivided into six 30.5-m line intercepts, except at Junction Butte, where there were six 22.9-m line intercepts. The length of each line intercepted by various willow species, as well as other shrub species, was recorded to the nearest centimeter. The maximum height of each plant was recorded. These transects were sampled in August 1988.

According to Hurlbert (1984), comparison inside and outside of a single exclosure represents pseudo-replication. However, the transects and the individual plants are not homogeneous and some measure of variance is necessary to evaluate the adequacy of sampling procedures. Statistical tests on data collected inside and outside one exclosure indicate only that the vegetation is different at that site. Statistical tests using each exclosure as a sample point are true replicates, and those results are more conclusive. Our statistical results should be viewed with these concepts in mind.

RESULTS

Historical Perspective

Forty-four repeat photosets were made of willow communities on Yellowstone's northern range. The earliest date from 1871. Some photosets contain four photographs, taken in 1893, 1921, 1954, and 1986–1988. Several contain three photos, taken in 1921, 1954, and 1986–1988. Forty-one out of forty-four comparative photosets show that tall willow communities have totally disappeared (figures 16.1–16.3). In the three other photosets, visual estimates indicate that only 5–10 percent of the original tall willows remain.

In 1871 Captains John W. Barlow and David P. Heap (1872:40) toured Yellowstone Park. On the northern range, they reported "thickets of willows along the river banks." Philetus W. Norris (1880:613), Yellowstone's second superintendent, noted that the park was "well supplied with rivulets invariably bordered with willows" (emphasis added). Norris (1880:617) further stated that there were "innumerable dense thickets of willow" in Yellowstone. Based on an analysis of pollen in the sediments from lakes and ponds on the northern range, Barnosky (1988) reported that willow pollen had declined since the early 1900s. All available evidence indicates that tall-willow communities were once common on the northern range but are now almost completely absent.

Four additional photosets were made of willow communities on Yellowstone's Gallatin winter range. Three contained four pictures, taken in 1924, 1949, 1961, and 1986, and the other photoset included 1937, 1961, and 1989 photos. Historically, the Gallatin has had an elk situation similar to that on the northern range (Packer 1963; Patten 1963, 1969; Streeter 1965; Peek, Lovaas, and Rouse 1967; Lovaas 1970). Patten (1968) reported that the 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 noted, "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, Lovaas, and Rouse 1967; Lovaas 1970). Where deep snow to the south or hunters north of the park limit elk use, tall willows occur.

Based on visual evaluation of the photographic evidence, tall willows decreased almost completely 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 concentrated effort to reduce this elk herd when it migrates from Yellowstone Park. By instituting

Figure 16.1 a. Tall-willow communities in Yancey's Hole on Yellowstone's northern range. 1893 photo by F. Jay Haynes (H-3080) viewed east. Photo courtesy Haynes Foundation Collection, Montana Historical Society, Helena.

b. That same area in 1988. Note the disappearance of tall-willow communities, less than one hundred years later. Other photos of this area show that the tall willows had been heavily browsed and were declining by 1921. Tall willows were absent in 1954 photos. Photo by Charles E. Kay (no. 3051-12 and 3051-13), August 20.

Figure 16.2 a. Close-up of a tall-willow community in Yancy's Hole on Yellowstone's northern range. 1915 photo by Bailey (1930:57) viewed north. Note the dead willow in the right foreground and the hedged appearance of other willows due to "winter browsing by elk." Bailey (1930:55–57) stated that in the early 1910s, "willows of many species are an abundant source of food supply along the streams and meadows. They are often trimmed to mere stumps during winter and in some places they are actually killed out by close browsing." From Vernon Bailey, *Animal Life of Yellowstone National Park* (1930); courtesy of Charles C. Thomas, Publisher, Springfield, Ill.

late-season hunts, the department has reduced the Gallatin elk population by at least 50 percent in recent years (L. Ellig, pers. comm. 1988). In apparent response to this decline in elk numbers, willows have increased in height and canopy-coverage, as shown in repeat photos from 1986 and 1989 (Kay 1990).

Willow Communities on the Northern Range

Willow communities on the northern range occur in a wide range of environments, elevations, and topographical settings. Brichta (1987) identified four general settings that support willow communities: (1) adjacent to stream and river channels, and on floodplains; (2) in overflow channels, in depressions and around kettle lakes formed by blocks of glacial ice; (3) adjacent to springs and seeps on foothill slopes; and (4) in abandoned beaver channels and ponds.
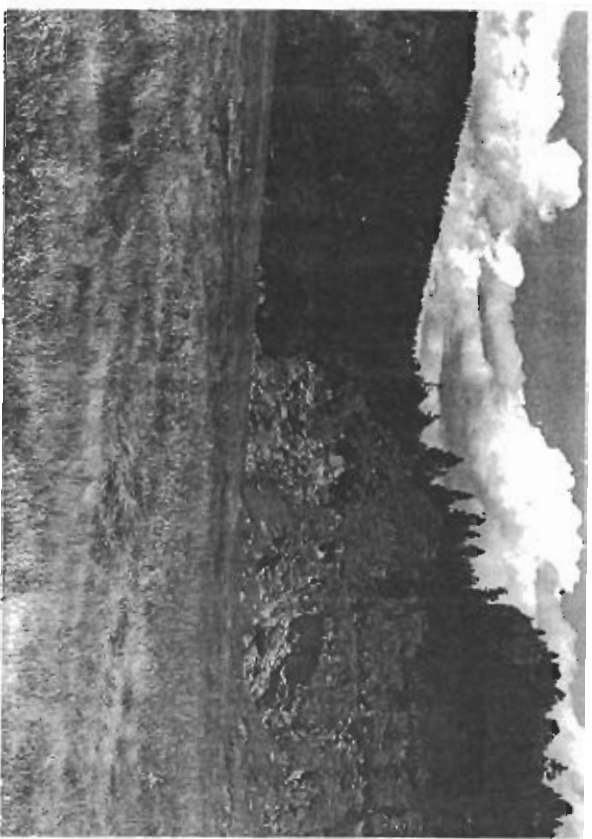
b. That same area in 1987; note the disappearance of tall willows since the 1915 photograph. Photo by Charles E. Kay (no. 2895-25), August 11.

Eight unique willow associations and community types were identified on the northern range (Chadde, Hansen, and Pfister 1988), ranging from low-willow carrs (shrub-dominated wetlands on wet organic soils) to tall-willow types on seasonally dry mineral soils:

1. *Salix candida/Carex rostrata* association. These are infrequent at higher elevations of the northern range. They are restricted to anchored organic mats along pond and lake margins. In addition to *Salix candida* and *Carex rostrata*, *Carex aquatilis* and *Calamagrostis canadensis* may also be present. The low stature of *Salix candida* (maximum height of about 1 m) and its higher-elevation location preclude much ungulate winter use of this species. However, utilization during snow-free periods and the inability of this species to produce vigorous basal sprouts following repeated browsing may result in a conversion to dominance by *Carex rostrata*.

2. *Salix wolfii/Carex aquatilis* association. These common low-willow communities are found at mid-to-high elevations, where they occupy extensive areas of valley bottoms and basins. Soils are typically wet with organic surface horizons. Major species include *Salix wolfii*, *Salix planifolia*, *Potentilla fruticosa*, *Carex aquatilis*, *Carex rostrata*, and *Deschampsia cespitosa*. Ungulate use of these willows is typically heavy, with

willows maintained at heights of 60 cm or less. A conversion to sedge-dominated communities is likely as willow clumps die and are not replaced.

3. *Salix wolfii/Deschampsia cespitosa* association. This low-willow association is a minor type of stream-side terraces and seeps. It typically occupies drier environments than the *Salix wolfii/Carex aquatilis* association. Major shrubs include *Salix wolfii, Salix planifolia,* and *Potentilla fruticosa.* Important herbaceous plants include *Deschampsia cespitosa, Juncus balticus,* and *Poa pratensis.* Ungulates frequently graze these communities and browse on the short-statured willows.

4. *Salix lutea/Carex rostrata* association. These minor tall-willow communities are found on slopes adjacent to springs and seeps. Soils are wet and range from organic to mineral. *Salix lutea* and *Salix pseudomonticola* are often codominant. Other tall willows, such as *Salix bebbiana* and *S. geyeriana,* are common. Undergrowths are dominated by *Carex rostrata, C. aquatilis,* and *Poa palustris.* These communities could potentially form dense thickets 3–4 m tall. Current levels of ungulate browsing typically limit heights to 1 m or less. Canopy-coverages are also greatly reduced by repeated browsing.

5. *Salix geyeriana/Carex rostrata* association. These widely distributed communities are found on fine-textured mineral soils of alluvial terraces, broad valley bottoms, and adjacent to former beaver ponds. Common tall-willow species include *Salix geyeriana, S. bebbiana, S. drummondiana,* and *S. planifolia.* Herbaceous species include *Carex rostrata, Calamagrostis canadensis,* and *Poa palustris.* Elk and moose use is high and results in willows of low stature and reduced canopy cover.

6. *Salix geyeriana/Deschampsia cespitosa* association. These common tall-willow communities occur on loamy soils adjacent to seeps and streams. *Salix geyeriana, S. boothii,* and *S. bebbiana* are the dominant willows. *Deschampsia cespitosa, Juncus balticus,* and *Poa pratensis* are common herbaceous species. These communities are potentially highly productive of both browse and forage. However, ungulate browsing maintains willows at heights of 1 m or less versus potential heights of 3–4 m.

7. *Salix bebbiana/Agrostis stolonifera* community type. This tall-willow community type occupies small areas adjacent to seeps and streams. Soils are mineral but may have surface organic matter accumulations. *Salix bebbiana, Rosa woodsii,* and *Betula occidentalis* are common. The introduced species *Agrostis stolonifera, Poa palustris, P. pratensis,* and *Phleum pratense* typically dominate undergrowths and probably are the result of repeated grazing. Browsing has produced open, short-statured stands, in contrast to potential growth of 3–4 m.
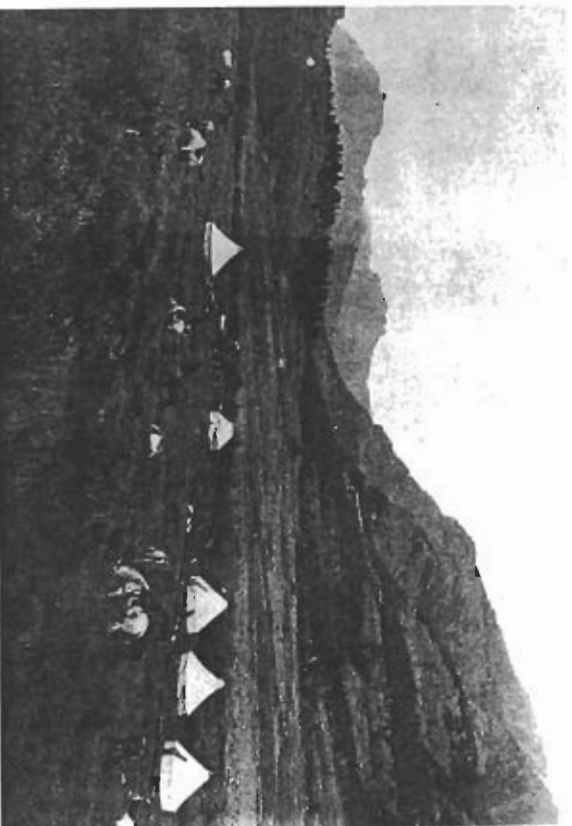
Figure 16.3 a. A tall-willow community in the lower Soda Butte Valley on Yellowstone's northern range. Photo taken in 1896 or 1897 by A. E. Bradley; viewed northeast. Photo courtesy A. E. Bradley Collection (72-158), Mansfield Library, University of Montana, Missoula.

b. That same area in 1988; note the disappearance of tall willows since the earlier photograph. Photo by Charles E. Kay (no. 2976-15A), June 21.

8. *Salix exigua/Agrostis stolonifera* community type. This tall-willow community type is typically restricted to low-elevation stream banks and cobble bars, often below high-water levels. *Rosa woodsii* is common. Other tall-growing willows may be present, indicating successional trends toward other willow types. Heavy browsing, however, often reduces or eliminates stands of this community type, leading to replacement by such herbaceous species as *Agrostis stolonifera* and *Poa palustris*.

In general, all willow stands are affected by ungulate browsing, higher-elevation stands being less affected than lower-elevation stands because of greater snow depths. Repeated browsing has resulted in sharp reductions in willow heights and canopy-coverage when contrasted with potential community structure.

Willow Exclosures

Willows inside exclosures are taller and have greater canopy-coverage than those outside (tables 16.1–16.3). Other less palatable shrubs, such as rose (*Rosa woodsii*) and river birch (*Betula occidentalis*) (Nelson and Leege 1982), exhibit this same pattern. When pooled, these differences are statistically significant across all exclosures (tables 16.4 and 16.5). Outside these exclosures, the mean height of all willow species was 34 cm whereas inside it was 274 cm. On average, willows had 10 percent canopy-coverage outside the exclosures, but 74 percent canopy-coverage where ungulates are excluded. However, all belt transects contained some nonwillow communities (table 16.6). When the nonwillow portions of the belt transects were excluded, willow canopy-coverage averaged 14 percent outside the exclosures and 95 percent inside, also a statistically significant difference (table 16.4). Thus willow canopy closure was nearly complete inside the exclosures.

When our 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 16.7). We believe our line-intercept data more accurately represent the true conditions within the exclosures because aerial photos (Kay 1990) show nearly complete willow canopy closure.

At another willow exclosure on Slough Creek just north of the park, Chadde and Kay (1988) reported that willows increased in height and canopy-coverage when protected from ungulate browsing. At the Slough Creek exclosure, snow accumulation normally precludes that area's utilization as elk winter range, and winter use is generally limited to moose (*Alces*

Table 16.1 Average canopy-cover and plant height of woody species inside and outside the Junction Butte exclosure on Yellowstone's northern range, August 1988

Species	Canopy-Coverage (%)		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	—	30.8	—
Total willows	14.7	80.6*		
Total shrubs	32.5	112.8*		

*p < .01.

Table 16.2 Average canopy-coverage and plant height of woody species inside and outside the Lamar-West and Lamar-East exclosures on Yellowstone's northern range, August 1988

Species	Canopy-Coverage (%)				Plant Height (cm)			
	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*		49.5	357.0*	317.0*	
Salix geyeriana	3.7	15.7*	—		40.8	330.5*	—	
Salix boothii	—	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	—		53.5	82.5	—	
Populus tremuloides	—	3.2	2.8		—	161.0	375.8	
Lonicera involucrata	2.0	4.2	—		34.0	91.8*	—	
Symphoricarpos albus	—	—	T		—	—	37.5	
Total willows	6.7	60.0*	77.0*					
Total shrubs	25.7	74.2*	81.2*					

*p < .01.

Table 16.3 Average canopy-coverage and plant height of woody species inside and outside the Mammoth exclosure on Yellowstone's northern range, August 1988

Species	Canopy-Coverage (%)		Plant Height (cm)	
	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	—	12.0*	—	328.0
Salix boothii	—	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	—	45.5	—
Total willows	10.0	78.7*		
Total shrubs	16.2	95.7*		

*$p < .01$.

alces). 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 willows attained heights of 3–4 m with near-complete canopy closure, whereas unprotected plants were all less than 1 m tall (Kay 1990). In Rocky Mountain National Park, Gysel (1960) and Stevens (1980) noted that willows increased in canopy-coverage and height inside exclosures that excluded elk. On elk and moose winter range in Canada's 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 has made over the years, they also photographed the willow belt transects each time they were sampled. Those photographs were repeated by Kay (1990) in 1987–1988. The resulting multiple-image photosets confirm that willows inside the exclosures have increased in height and canopy-coverage since they were protected, whereas willow communities outside the exclosures have not.

These comparative photos were also used to evaluate changes in willow communities observed in other repeat photosets because visual estimates from the exclosure photographs could be compared with actual plant measurements. This served to refine or calibrate the visual estimation technique used in this study. It also demonstrated that willows inside the exclosures

Table 16.4 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

Exclosure	Willow Canopy-Coverage (%)	
	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
Total		
Outside	10.5	14.3
Inside	74.0	95.2
t	9.20	10.77
p	< .01	< .01

now have the same stature as willows on the northern range did between 1870 and 1900. Thus the conditions inside the exclosures more closely approximate the level of ungulate use which existed when Yellowstone was created than do conditions in the park today.

WILLOW TRENDS

The observed decline in tall-willow communities has been attributed to (1) normal plant succession, (2) climatic change, (3) fire suppression, and (4) ungulate browsing (Houston 1982; Despain et al. 1986). According to Houston (1982:129–134), the willow decline may have been due in part to the lack of new substrates for willows to colonize. He presented a 1974 photo of a newly formed gravel bar in the Gardner River and a 1978 retake, which showed that willows had colonized that area.

Table 16.5 Average height of all willow species and rose inside and outside Yellowstone exclosures

Exclosure	Average Height (cm)	
	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
Total		
Outside	34	27
Inside	274	70
t	7.67	9.62
p	< .01	< .01

Kay (1990) rephotographed that site in 1983, 1986, 1987, and 1988. Chadde, Hansen, and Pfister (1988) also established plots at that site as part of their riparian classification study. By 1983, willows were almost entirely absent from the 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 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, colonizing willows would have been 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, Hansen, and Pfister 1988). In nearly all instances, willows are not seral to grasslands unless there has been a change in hydrology (Chadde, Hansen, and Pfister 1988). That has not occurred at this site along the Gardner River.

Houston (1982:276–277) also suggested that willows were seral to conifers. In some instances this is true, but not for most willow commu-

Table 16.6 Associations and community types found on permanent willow belt transects inside and outside exclosures on Yellowstone's northern range

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-West–In	1962	Salix geyeriana/Carex rostrata (85)
		Carex rostrata (15)
Lamar-East–Out	1957	Salix geyeriana/Poa pratensis (70)
		Potentilla fruticosa/Poa pratensis (30)
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)

Note: Types follow Chadde et al. 1988.

nities. Of the forty-eight repeat photosets of willow communities made for this study, only two show complete replacement by conifers (mainly Engelmann spruce). In three others, approximately 20 to 60 percent of the willow communities in the original photos have now been replaced by conifers. Thus only five of forty-eight photosets (10 percent) show conifer invasion of what were once willow communities. If beaver had not been virtually eliminated from the northern range due to interspecific competition with elk (see discussion below), they might have flooded several of these sites and thereby prevented conifer establishment.

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).

Outside the exclosures, a few stems shorter than 1 m were counted as an individual plant as were another small group of similar-sized stems a short distance from the first "individual." However, unless the roots are exca-

Table 16.7 Willow canopy-coverage inside and outside exclosures on Yellowstone's northern range, 1958–1988

Exclosure-Transect	Willow Canopy-Coverage (%)							
	Park Service Measurements						This Study	
	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
Total								
Outside							11.7	10.5*
Inside							40.2	74.0**

*$t = 0.45$, ns.

**$t = 6.77$, $p < .01$.

Source: National Park Service data, 1958–1986, from Singer (1987).

vated or genetic tests performed, it is impossible to determine whether neighboring 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 outside an exclosure with a few short stems is equivalent to a plant inside the exclosure with several hundred 3-m-tall stems. In our opinion, the enumeration of supposed individual willow plants inside and outside exclosures is not an appropriate measure upon which to base ecological interpretations.

The decline of willows on the northern range has also been attributed to climatic change, especially 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. Inside a small exclosure near Tower Junction, willows grew vigorously during and after the 1930s drought whereas those outside did not (see NPS photos 15078-4, 1935;51–21, 1951). Moreover, it is not climate that prevents the plants from growing to their full biological potential outside the exclosures. Measurements of subsurface water levels inside and outside throughout the summer failed to show any less water available to the plants on the outside (Brichta 1987; Chadde, Hansen, and Pfister 1988).

The climate-change hypothesis is also not supported by photographic evidence or firsthand accounts. Willows started declining before the 1930s drought (figure 16.2; Kay 1990), and they have continued to decline in recent years. Willows in the western portion of Round Valley, for example, were severely hedged in 1949 but still alive. By 1988, a major decline had occurred in that community (figure 16.4) even though precipitation had been near normal during the 1949–1988 period (Houston 1982:104). Further, there still are abundant springs and seeps at the site (Kay, 1990).

Yellowstone's Tower Junction willow exclosure was constructed in 1957, and by the late 1960s the protected willows had significantly increased in height and canopy-coverage (Singer 1987; Kay 1990). 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 1990). These changes certainly cannot be attributed to the 1930s drought. In addition, recent climatic variation appears to be unimportant since this area has abundant subsurface soil moisture (Brichta 1987; Chadde, Hansen, and Pfister 1988).

Houston (1982:101–107) noted that since the late 1890s the mean annual temperature on the northern range at Mammoth had increased 0.5–1.0°C, whereas the mean annual precipitation had declined 1–2 cm. However, to the best of our knowledge, no one has demonstrated that a climatic shift of that size will have any 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 (Cole 1985; 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
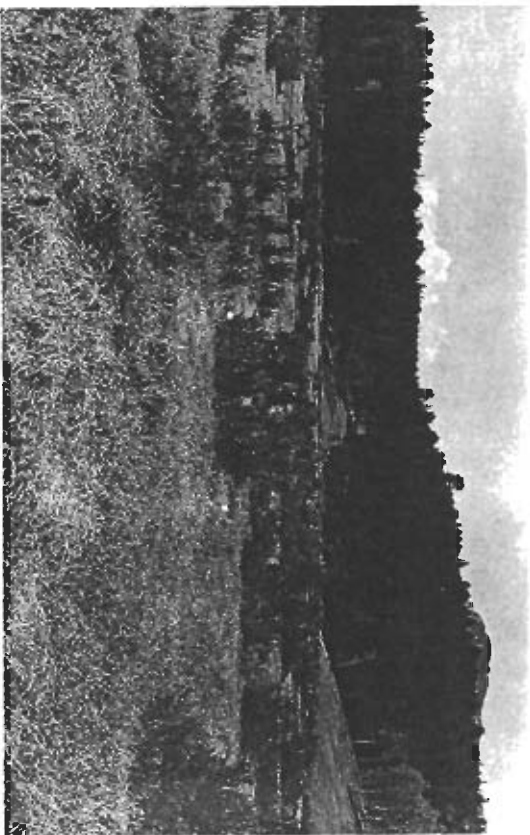
Figure 16.4 a. Heavily browsed willows along the west edge of Round Prairie, Pebble Creek Valley, Yellowstone National Park, in 1949. National Park Service photo no. 49-331.

1982) or grow beyond the reach of browsing ungulates. Based on a sample of fire-scarred trees, Houston (1973, 1982:107) calculated mean intervals of twenty to twenty-five years between fires on the northern range during the three to four centuries before Yellowstone Park was established and the agency began to suppress fires. Although a policy to let many lightning-caused fires burn has been in effect since the early 1970s, 1988 was the first year fires burned more than a small area on the northern range.

In spite of 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 frequently skipped over them (Kay and Chadde, personal observation). Riparian areas and willows are generally too wet to burn. Furthermore, cottonwoods (*Populus trichocarpa* and *P. angustifolia*) have also declined and failed to regenerate successfully on the northern range (Chadde, Hansen, and Pfister 1988). These species are extremely susceptible to fire and are easily killed by even a light burn. Frequent fires certainly would not enhance cotton-wood regeneration in the park. Finally, there is no evidence to support the idea, postulated by park personnel (D. Despain, pers. comm. 1988), that burning will cause resprouting willows to grow so fast or become so chemically defended that they can grow beyond the reach of elk and reform

b. That same area in 1988. Note the near-complete decline of willows that has occurred in the past four decades. Numerous springs and seeps still can be found in this area, which suggests that climatic change or lack of water is not primarily responsible for the observed change in plant communities. In all probability, the willows were killed by repeated ungulate browsing. Photo by Charles E. Kay (no. 2976-19A), June 21.

tall-willow communities. Observations of experimental willow burns conducted by the Park Service on the northern range indicate that elk browsed all of the new sprouts; none were able to grow taller than 1 m except where physical barriers prevented elk use (Kay 1990).

Based on a process of elimination and the data we have presented, we 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 percent (Houston 1982:149) and has not decreased in recent years (Chadde unpubl. data; F. Singer, pers. comm. 1989). Barmore (1981:358) likewise 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 in the park. Barmore (1981:357) noted, "By the late 1960's, 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 1800's and early 1900's. 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 1920's to the early 1960's 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 3 m. 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. Neilson (1986), who worked on a similar climatic change versus grazing problem, concluded that the vegetation would have persisted despite drought had the additional stress of grazing not 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 such agricultural practices as irrigation, dewatering, channelization, and livestock grazing, not climatic change (Meehan and Platts 1978; Dobyns 1981; Myers 1981; Marcuson 1983; Platts et al. 1983; U.S. General Accounting Office 1988). A recent study of 262 miles of streams in southwestern 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 also feed upon willows on the park's summer range (McMillan 1950, 1953). Until exclosures are built there, the impact of summer ungulate utilization on those communities cannot be determined.

Morgantini and Hudson (1989) reported that elk in western Canada shifted their diet to willows on summer ranges. In Rocky Mountain National Park, according to Stevens (1980:145), "willow forms a major part of the summer diet for elk, about 21%." Stevens (1980:139) also 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 declines occurred in only eight years as the elk herd built up in the park (Stevens 1980:136).

IMPACT ON OTHER SPECIES

Beaver. The decline of tall-willow communities on the northern range has in all probability 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 suggests that "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 3 to 20, 1835, on the upper Gardner 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 three weeks trapping beaver on Slough and Hellroaring creeks.

Norris (1880:613) reported that beaver were 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, "beaver occur in practically every stream and pond (where there is suitable food) in the park." He estimated that there were "about 10,000" beaver in the park.

Bailey (1930:112–114) observed, "beavers are found along almost every stream in Yellowstone Park." He also noted that "the extensive herds of elk" on the northern range kept down the growth of the beavers' food supply, young aspen and willows. Wright and Thompson (1935:72) concluded that beaver in Yellowstone were "endangered through the destruction of aspen and willow on their overbrowsed elk winter ranges." Thus, the available evidence strongly suggests that beaver were common in the Yellowstone area and on the northern range from before park establishment
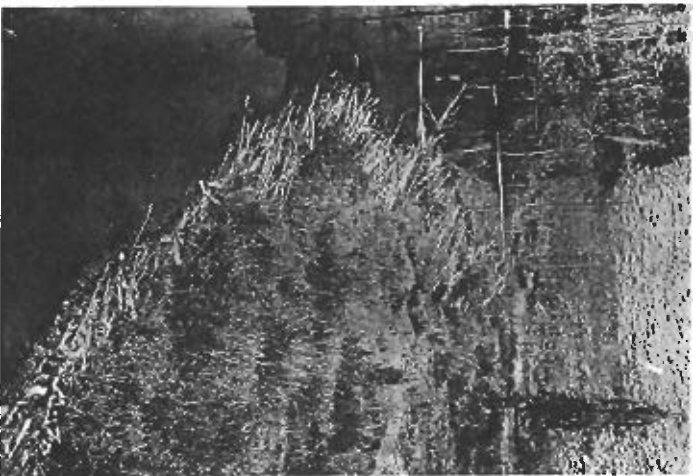
Figure 16.5 a. Beaver dam on the north fork of Elk Creek on Yellowstone's northern range near Tower Junction in 1921. Note aspen in upper left and willows to the right of the dam. Photo by Edward Warren (1926:84) courtesy College of Environmental Science and Forestry, State University of New York, Syracuse. Photo no. 5145, August 10.

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 around Tower Junction on the northern range. He reported 232 beaver and extensive beaver dams. Jonas (1955) repeated Warren's study in the early 1950s and found no beaver or recent dams. Jonas (1955, 1956, 1959, pers. comm. 1987) 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. Jonas concluded that the beavers' "unfortunate food situation . . . was a result more from the overpopulation of elk than from any other single cause." He also concluded that the poor water conditions and the siltation of beaver ponds were caused by overgrazing. In 1986, Kay (1987, 1990) repeated Warren's and Jonas's surveys. He found no beaver and no indication of beaver activity since the 1950s (figure 16.5).
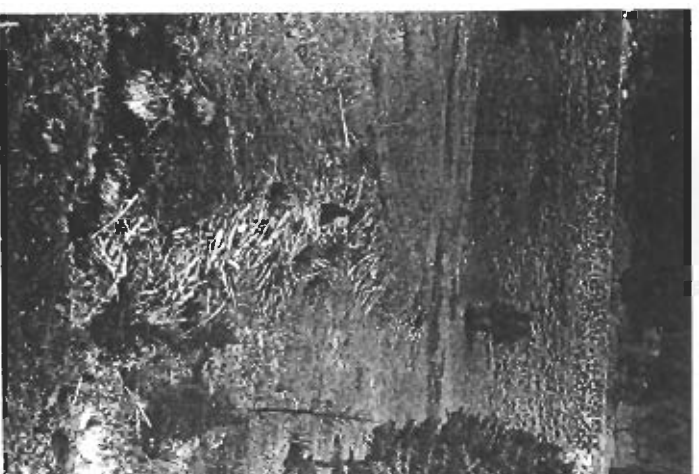
b. That same area in 1954. Note the decline of aspen and willows. The stream has downcut approximately 2 m through the old beaver dam. Photo courtesy Robert Jonas (1955:37), June 12.

Beaver need tall willows or aspen—which have also declined in the park (Kay 1985, 1987, 1990)—as food and dam-building materials. Aspen and willows cut by beaver normally resprout (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 sizable plants, elk and moose eliminate beaver foods, and thus beaver. 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) noted that high moose densities had a similar negative effect on beaver in Newfoundland. In South Dakota, 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 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

c. That same area in 1986. Note the continued absence of aspen and willows as well as the browse line on the conifers. 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. Photo by Charles E. Kay (no. 3081-33), July 15.

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 that completely alters the hydrology, energy flow, and nutrient cycling of aquatic systems (Parker et al. 1985; Naiman, Melillo, and Hobbie 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 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 floors (Apple 1983).

Munther (1981, 1983) reported that a typical creek without beaver furnishes only about one to two hectares of riparian habitat per stream kilometer on the northern Rockies. With beaver activity, that area can be expanded to ten hectares per kilometer (Munther 1981, 1983). Hence, the elimination of beaver over most of the northern range may 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. Since elk and moose have apparently acted to competitively exclude beaver, this is another basis for rejecting the "natural-regulation" paradigm. Moreover, in the absence of beaver, several streams on the northern range have downcut 1–2 m (figure 16.5; Kay 1990), lowering the water table and reducing the wetted perimeter. In our opinion, the virtual elimination of beaver has 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.

White-tailed Deer. A small population of white-tailed deer (*Odocoileus virginianus*) inhabited Yellowstone's northern 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). These whitetails were associated with thickets of riparian vegetation (Skinner 1929:102), as is the case throughout their range north of the park. In recent years whitetail populations have increased outside the park, and a few have been observed in Yellowstone (Singer 1989). However, whitetails have not become reestablished in the park. In our opinion, the absence of tall-willow communities and other tall deciduous shrub habitats on the northern range due to repeated browsing makes it highly unlikely that whitetails will regain a permanent foothold in the park.

Other Species. Judging from other studies (Page et al. 1978; Casey and Hein 1983; Marcuson 1983; Platts et al. 1983; Taylor 1986; Knopf, Sedgwick, and Cannon 1988; Putman et al. 1989), the decline of tall-willow communities on Yellowstone's northern range may also adversely affect birds, small mammals, and even grizzly bears (*Ursus arctos*) (Kay 1990). The elimination of beaver and willow bank cover probably has also caused decreases in the distribution and numbers of native trout species (W. Platts, pers. comm. 1989). Entire plant and animal communities, not just tall willows, may 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 ecologi-

cally equivalent to the tall-willow communities that once occupied those same areas.

Our findings appear to reject the criteria proposed by Houston (1976) for evaluating the "natural-regulation" hypothesis.

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