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Viewpoint: Ungulate herbivory, willows, and political ecology in Yellowstone

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Abstract

Contentions that willows (*Salix* spp.) on Yellowstone National Park's northern range have declined because of climatic change, fire suppression, reduced chemical defenses, or other natural factors are not supported by available data. Instead, willows have declined due to repeated browsing by an unnaturally large elk population. By established standards Yellowstone contains some of the worst overgrazed willow communities in the entire West, but that was not true in earlier times. Prior to park establishment, predation by Native Americans kept elk and other ungulate numbers low which, in turn, prevented herbivores from impacting Yellowstone's plant communities, as those animals do today. Finally, the condition of willows in the park is also a test of Yellowstone's "natural regulation" program, and that paradigm must also be rejected.

Key Words: elk, Yellowstone National Park, beaver, natural regulation, park management, Native Americans, aboriginal overkill.

Singer et al. (1994) presented a discussion of ungulate herbivory and willows (*Salix* spp.) on Yellowstone's northern range, but they failed to put their work in proper historical and ecological perspective. Therefore, we first present a short history of wildlife management in Yellowstone followed by a discussion of willow ecology in that park.

History of Wildlife Management

After Yellowstone was designated as the world's first national park in 1872, a succession of civilian (1872–1886), military (1886–1916), and National Park Service (1916 –present) administrators concluded that there were not enough game animals so they fed wintering elk (*Cervus elaphus*) and other ungulates, and they killed predatory animals such as wolves (*Canis lupus*) and mountain lions (*Felis concolor*). During the 1920s, however, concerns grew that too many elk were overgrazing the park's northern winter range, so the agency began trapping and transplanting elk to areas outside the park. Because trapping alone did not reduce the herd to the range's estimated carrying capacity, rangers began shooting elk in the park to prevent resource damage. This program was called direct reduction, and by 1967 the Park Service had killed over 13,500 elk from Yellowstone's northern herd (Houston 1982).

This upset many people who exerted political pressure to stop the Park Service from shooting elk in the park. After a U.S. Senate (1967) Subcommittee hearing at which the chairman threatened to terminate park funding, the Park Service agreed to abandon its direction reduction program—although the agency still contended that Yellowstone was seriously overgrazed. By 1968, the Park Service had switched to a management program called "natural control" which was changed to "natural regulation" in the early 1970s. These changes occurred without public review (Chase 1986, Wagner et al. 1995). The Park Service originally based "natural regulation" on a presumed "balance-of-nature," but more recently the agency has cited Caughley's (1976) plant-herbivore model to support its "natural regulation" paradigm (Kay 1990). Under "natural regulation," the Park Service completely revised its interpretation of elk in Yellowstone.

Until 1968, Park Service officials contended that an unnaturally large elk population, which had built up in Yellowstone during the late 1800s and early 1900s, had severely damaged the park's northern winter range, including willow communities (Tyers 1981). However, agency biologists now hypothesize that elk and other ungulates in Yellowstone are "naturally regulated," being resource (food) limited, and that the condition of the ecosystem today is much like it was at park formation (Houston 1982, Despain et al. 1986). Elk influences on Yellowstone's vegetation are now thought to be "natural" and to represent the "pristine" condition of the park. According to the Park Service, Yellowstone is not now, nor has it ever been overgrazed, and all previous studies to that effect are wrong (Houston 1982).

First, under "natural regulation," predation is an assisting but non-essential adjunct to the regulation of ungulate populations. If wolves are present, they take only the ungulates slated to die from other causes, such as starvation, and hence predation will not lower ungulate numbers. In the current debate over reintroducing wolves to Yellowstone, the Park Service has adamantly denied that wolves are needed to control the park's elk herds (Boyce 1992). Second, if ungulates and vegetation have co-evolved for a long period of time and if they occupy an ecologically complete habitat, the ungulates cannot cause retrogressive plant succession or range damage. The ungulates and vegetation will reach an equilibrium, termed ecological carrying capacity,

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where continued grazing will not change plant species composition or the physical appearance of plant communities. According to the Park Service, thousands of elk starving to death during winter is natural. Third, at equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone, this means that competition by elk has not reduced the numbers of other ungulates or beaver (*Castor canadensis*) since park formation.

The Park Service's "natural regulation experiment" (cf. Despain et al. 1986) is predicated on the assumption that large numbers of elk (12,000–15,000) wintered on Yellowstone's northern range for the last several thousand years. Park Service biologists hypothesize that elk, vegetation, and other herbivores in Yellowstone have been in equilibrium for that period of time (Houston 1982, Despain et al. 1986). The agency now believes that any changes in plant communities, including willows, since the park was established are due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. If Yellowstone's willows have declined due to ungulate browsing, then "natural regulation" would have to be rejected (Houston 1976). Moreover, since "natural regulation" is an equilibrium model, grazing-induced changes in vegetation stature (height) since Yellowstone Park was created would also indicate that the ungulates and their food resources are not in equilibrium (Houston 1976). Therefore, if ungulate browsing has changed what were once tall-willow communities into short-statured plants, this would be additional grounds for rejecting "natural regulation."

Political Ecology

Singer et al. (1994) indicated that there was concern over the condition and trend of willows on Yellowstone's northern range, but they failed to capture the intensity of the debate or the ecological, political, and legal importance of the issue. Even as the Park Service was formulating its "natural regulation" paradigm, one Yellowstone biologist warned that the agency had no data to support "natural regulation" (Barmore 1968). Later, Chase (1986) concluded that "natural regulation" was a scientific fraud and that the Park Service had routinely fabricated "data" to support its politically motivated management. More recently, 2 Park Service research biologists accused their agency of "inventing" ecological data to support management decisions and of only funding studies that would not "prove park policy wrong" (Clifford 1993, Mattson and Craighead 1994, Wagner et al. 1995).

The Park Service has denied all these accusations, but the agency has not been receptive to independent review of its "natural regulation" program. In the early 1990s, the Society for Range Management, the Ecological Society of America, the American Fisheries Society, and the Wildlife Society asked the Park Service for approval to conduct an independent review of the Yellowstone situation, but they failed to obtain permission. More recently, a group of preeminent ecologists informed the Secretary of Interior that they would be willing to serve, without pay, on a panel to review the entire Yellowstone matter, but the Secretary declined (Kay in press a). An independent commission, originally empaneled by the Wildlife Society to review wildlife management in the entire National Park System, recently concluded that there was no scientific data to support "natural regulation" in Yellowstone or in any other U.S. National Park (Wagner et al. 1995).

Establishing whether ungulates in Yellowstone are "naturally regulated" is important because it is relevant to that park's management direction, and to similar management schemes in other national parks in the U.S. and around the world (Kay and White 1995). In a broader context, it tests an ecological model which attempts to explain how ungulate populations interact with their plant resources (Kay 1990). Establishing the validity of Singer et al.'s (1994) work is important for similar reasons. If sustained, Singer et al.'s (1994) hypothesis would also absolve the Park Service of responsibility in Yellowstone; i.e., current conditions are within the range of historical variability. Singer et al. (1994), however, misrepresented earlier work in Yellowstone (Chadde and Kay 1988, 1991; Chadde et al. 1988; Chadde 1989; Kay 1990; Kay and Chadde 1992; Kay and Wagner 1994), and their analysis is not supported by the available data.

Chemical Defense

Given the conditions on Yellowstone's northern range, we fail to see the relevance of Singer et al.'s (1994) work on willow chemical defenses. Studies throughout western North America have demonstrated that willows are among the most palatable and most preferred browse species for elk and other ungulates (Nelson and Leege 1982). Since the early 1900's, though, elk have routinely consumed more chemically defended species in Yellowstone (Rush 1932, Tyers 1981). Elk and other ungulates in the park are forced by starvation (1,000–5,000 elk deaths annually; Lemke 1989) to consume normally unpalatable species, such as spruce (*Picea* spp.) and other conifers. In fact, one of the conspicuous characteristics of today's northern range, and indeed other parts of the park as well, is the browsing highline on conifers (Kay and Wagner 1994).

Now if wintering elk are compelled to eat spruce, which is one of the most chemically defended plants on Yellowstone's northern range, it is highly unlikely that a few milligrams change in tannin content between unbrowsed and browsed willows, as reported by Singer et al. (1994), has any bearing on whether or not elk will consume the "more chemically defended" willows. Singer et al.'s (1994) conclusion that "changes in chemical production" have in any way contributed to the decline of willows in the park is untenable given the other more chemically defended species that elk routinely consume in Yellowstone.

Willow Height Classes

Singer et al. (1994) divided willows that they measured "into 3 categories ... (1) height suppressed = nearly all plants were ≤ 80 cm, (2) intermediate = plants were 81-120 cm tall, and (3) tall willows = most plants were 121+ cm." Others who have worked in Yellowstone, however, have defined tall willows as only those plants beyond the reach of browsing elk; i.e. plants ≥ 2 m tall (Chadde and Kay 1988, 1991; Chadde et al. 1988, Chadde 1989; Kay 1990; Kay and Chadde 1992). Based on 44 repeat photosets of willow communities on Yellowstone's northern range dating to 1871, tall-willow communities have declined by approximately 95% since the park was established (Figure 1) (Kay 1990, Chadde and Kay 1991). The only tall willows that exist on the northern range today are (1) inside ungulate-proof exclosures, (2) a few "mushroom" plants that have somehow been able to withstand repeated browsing (Kay and Chadde 1992), (3) or those protected by deep snow which limits ungulate use. Tall willows, as defined by Singer et al. (1994), are certainly not comparable to the park's original tall-willow communities.

The average height of willows on the park's northern range is primarily related to average snow depth. In fact, Singer et al.'s (1994) own data show that willow height is correlated with altitude, and hence snow depth, as snow depth increases with increasing elevation on the northern range (Houston 1982).

Marginal Sites

At several points in their paper, Singer et al. (1994) indicated that willows on "marginal" sites may have declined more than plants on other sites. Repeat photographs (Kay 1990, Chadde and Kay 1991), however, show that tall willows on stream banks, along pond margins, and near springs, have declined just as much as other willows (Figs. 1 and 2). This and other data suggest that climatic variation has not been an important factor in the decline of willows on the park's northern range.

Beaver

Singer et al. (1994) noted that the loss of beaver has contributed to the decline of willows in the park, and we concur (Kay 1990, Chadde and Kay 1991). This, though, raises the question of why beaver have declined? Beaver are now ecologically extinct (Estes et al. 1989) on the northern range because repeated ungulate browsing has destroyed the tall-willow and aspen (*Populus tremuloides* Michx.) communities that beaver need for food and dam building materials (Kay 1990, 1994b; Chadde and Kay 1991). Thus, the loss of beaver is due to a long history of excessive grazing, not other factors. Outside the park where the climate is similar but where there are fewer elk, beaver are still common (Kay 1994b, 1994c). In the absence of beaver, park streams have downcut and lowered water tables drying out what were once riparian communities and further reducing the suitability of the northern range as willow or beaver habitat.

Rosgen (1993) reported 100 times more bank erosion on Yellowstone's denuded streams than on the same willow-lined streams outside the park. Rosgen concluded that many of the hydrological changes seen in the park's streams were elk-induced, and were not related to climatic variation or other factors.

Willow Biomass

Singer et al. (1994) measured yearly biomass production on willows inside and outside long-term ungulate-proof exclosures on Yellowstone's northern range, and found that willows protected for 31 years "still produced only 35% the aboveground biomass ... that tall willows did [on outside plots]." They implied that their tall repeatedly browsed, willows were healthier than protected plants.

From an evolutionary perspective, though, ungulate-stimulated vegetative growth is of little value if reproductive output is impaired. Kay and Chadde (1992) measured seed production inside and outside exclosures on Yellowstone's northern range and found that protected willows produced an average of over 306,000 seeds per m^2 of female canopy cover, while plants outside produced none; a difference that is both statistically and ecologically significant (Fig. 2). Without abundant seed crops, willows cannot take advantage of recruitment opportunities produced by periodic large-scale disturbances such as fire.

Fig. 1. A repeat photoset taken in Yellowstone National Park showing the dramatic impact that native ungulates have had on willow communities. (a) Willows in this 1915 photograph already show the effects of repeated ungulate browsing. Note the dead willow in the right foreground and the hedged appearance of other willows due to browsing by elk. Bailey (1930:55-57), who took this photograph, noted that in the early 1910s, "willows of many species are an abundant source of food supply along [Yellowstone's] streams and meadows. [However] they are often trimmed to mere stumps during winter and in some places they are actually killed out by close browsing." Photo courtesy of the National Archives (RR 22-WB, Box 34, 16,009). (b) That same area in 1987; note the disappearance of tall willows since the 1915 photograph. Yancy's Creek now hidden by grass in the foreground has downcut, but still flows year round which suggests that climatic variation has not caused the observed decline of willows. Lost Creek, which flows at the base of the cliff, has downcut 2 m since the earlier photograph, but is still a perennial stream. Photo by Charles E. Kay, No. 2895-25.

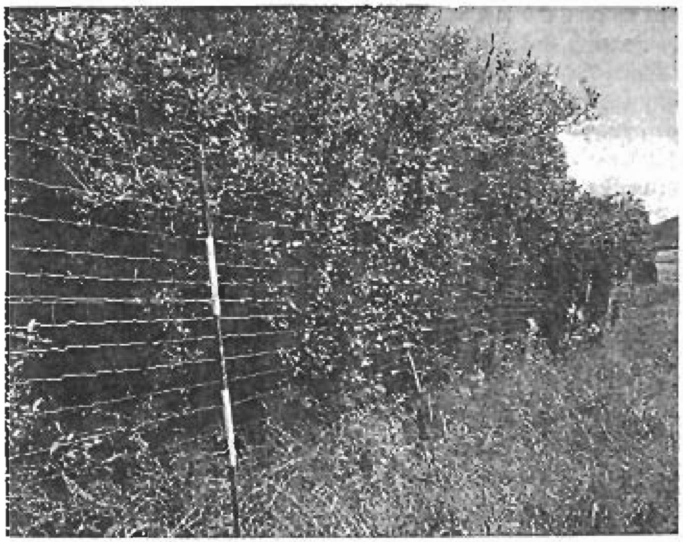

Fig. 2. Fenceline contrast of willows inside and outside the Lamar-West exclosure on Yellowstone Park's northern range. The exclosure was constructed in 1962 and this photograph was taken 25 years later in 1987. Willows inside the exclosure averaged 287 cm tall while those outside averaged only 45 cm. Willows inside averaged 92% canopy coverage while those outside averaged only 10%. Female willows inside produced an average of 416,654 seeds per m^2 of canopy cover while those outside produced none (Kay 1990, Chadde and Kay 1991, Kay and Chadde 1992). According to Singer et al. (1994:435), willows inside Yellowstone's exclosures produced only one-third the biomass of "tall" repeatedly browsed willows "suggesting suppressed willows grow on sites with lower growth potential." In other words, the site seen in this photograph is, according to Singer et al. (1994), "marginal" for willows. In addition, the Park Service contends that there are more individual willow plants per unit area outside this exclosure than inside (Despain 1989). Survey pole (2 m) for scale. Photo by Charles E. Kay.

Yellowstone's 1988 wildfires created ideal conditions for willow seed germination and seedling establishment. Yet, few willow seedlings were observed because practically no seeds were available to colonize this newly created habitat (Kay and Chadde 1992).

Even if willows somehow become established, they rarely can withstand the grazing pressure that occurs in Yellowstone. Houston (1982:129–134) presented a 1974 photo of a newly formed gravel bar along the Gardiner River on Yellowstone's northern range and a 1978 retake that showed willows had colonized the area. At the time, there was a tall-willow (> 2 m) community immediately upstream which most likely produced the seeds that settled on the gravel bar—those tall willows have since died out.

Kay (1990) rephotographed this gravel bar in 1983, 1986, 1987, and 1988, and Chadde et al. (1988) established plots at that site as part of their northern range riparian classification study. By 1983, willows were largely absent from the gravel bar and had been replaced by grasses and other herbaceous plants, probably because of repeated ungulate browsing, as the stream hydrology had not changed (Chadde et al. 1988). This area changed from bare gravel to willows to grass in only 9 years. This is much faster than normal plant succession, and is contrary to expected successional directións. 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 engelmanni* Parry), but not grasses, sedges, or forbs (Chadde and Kay 1991).

Fire

Singer et al. (1994) hypothesized that, "Fire suppression this century on Yellowstone's northern range might have contributed to willow declines," as have Park Service biologists (Houston 1982, Despain et al. 1986). That supposition, though, is not supported by available data. After Yellowstone's 1988 wildfires, Kay (unpub. data) established permanent photopoints in burned willow communities. Many plants produced leader growth in excess of 1 m by the end of 1989, but those willows were browsed to within cms of the ground during the following, and each subsequent winter (Fig. 3). Moreover, burning plus repeated browsing led to the death of several plants. This is not surprising because elk seem to prefer burned willow regrowth over unburned plants (Stein et al. 1992). Furthermore, if fire suppression adversely affects willow communities, the effect should have been expressed inside as well as outside exclosures, which it was not.

Climatic Change

Singer et al. (1994) also attributed the decline of willows on Yellowstone's northern range to climatic change, namely a drying trend. That supposition, though, is not sustained. First, newly enclosed willows flourished during the 1930s drought (Kay 1990), and it is not climate that prevents willows from reaching their biological potential outside exclosures today—mean height outside 34 cm vs. 274 cm inside; mean canopy cover 14% outside vs. 95% inside (Fig. 2) (Chadde and Kay 1991:245–246)

The climate-change hypothesis is also not supported by photographic evidence or firsthand accounts. Willows started declining before the 1930s drought (Fig. 1) and have continued to decline in recent years (Kay 1990). Willows in the western portion of Round Valley, for example, were severely hedged in 1949 but remained alive. By 1988, a major decline had occurred in that community although precipitation had been near normal during the 1949–1980 period (Houston 1982:104), and there were still abundant springs at the site (Chadde and Kay 1991).

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 (Kay 1990). That exclosure was removed in the early 1970s and the protected plants subjected to ungulate browsing. By the late 1970s and early 1980s, those willows were extensively hedged and were reverting to lower-statured plants (Kay 1990). These changes cannot be attributed to the 1930s drought, and recent climatic variation also appears to be unimportant as this site has abundant subsurface soil moisture (Brichta 1987). This area was burned by Yellowstone's 1988 wildfires, but willows have continued to decline (Fig. 3).

Singer et al. (1994) implied that there was no control for Yellowstone, but areas outside the park with similar soils and vegetation can be used to interpret what is happening in Yellowstone, especially with relation to climatic variation. If willows were succumbing to a drying climate, then it is logical to expect that willow communities adjacent to the park would also be

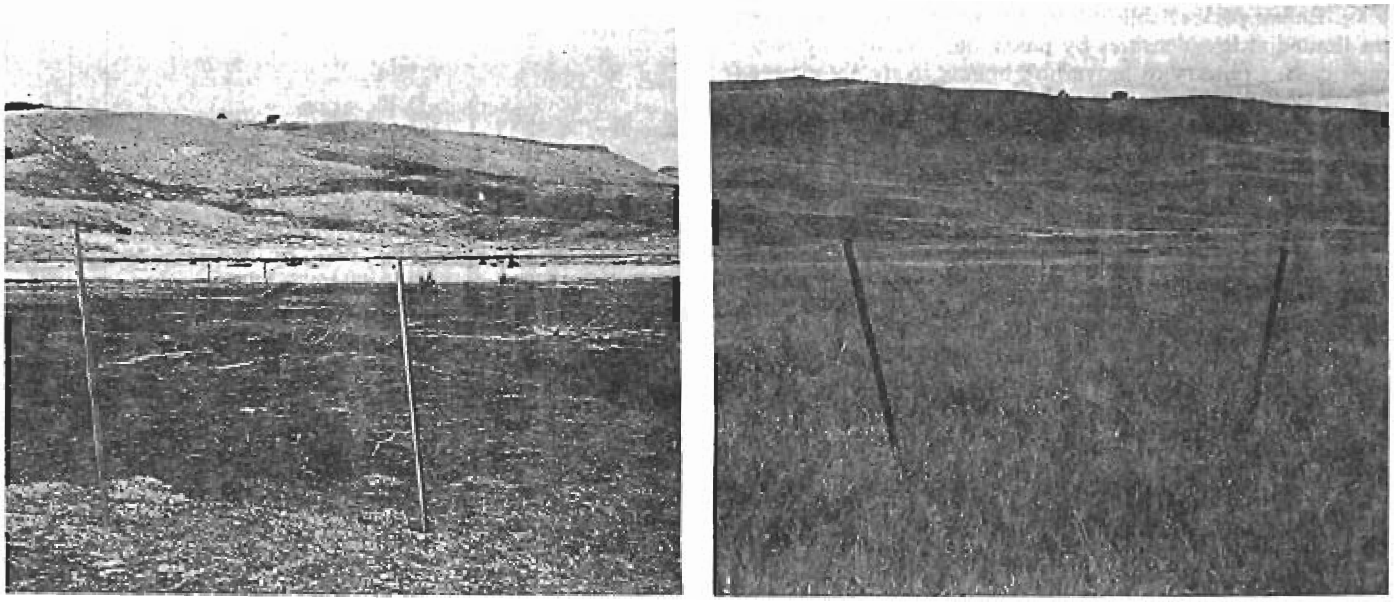

Fig. 3. Repeat photoset of a willow community burned by Yellowstone's 1988 wildfires. (a) The fire was so intense that it consumed nearly all the above-ground woody material. Also note the burn pattern on the far hillside. Due to heavy ungulate use, there was not enough fuel to carry the fire, except in swells or other depressions where snow accumulates and prevents grazing by the park's elk and other ungulates (Kay, in press a). (b) That same area in 1993. Willows are still present, but because of repeated browsing by Yellowstone's elk, have not increased in height. Photos by Charles E. Kay.

under duress. That is not the case and tall willows (> 2 m) are common outside the park, even on ranges grazed by domestic livestock (Rosgen 1993, Kay 1994c). Moreover, repeat photographs taken outside the park do not show the drastic decline of willows that has occurred in the park, except where large numbers of wild ungulates or livestock concentrate (Kay unpub. data—repeat-photo study in progress for the Agricultural Research Service in the Centennial Mountains along the Montana-Idaho border west of Yellowstone National Park).

Elk Reductions

As discussed earlier, when the Park Service thought that too many elk were destroying Yellowstone's northern range, the agency shot elk in the park to reduce herd numbers. By the late 1960s, the northern herd had been reduced to an estimated 5,000 animals——today populations range from 15,000 to 25,000. Singer et al. (1994) contended that those herd reductions did not have a significant impact on northern range willow communities. That is not what was concluded at the time. According to Barmore (1981:357), "By the late 1960's, the growth form and condition of *Salix* sp. on most of the winter range began to more closely resemble the less heavily browsed conditions of the late 1800's and 1900's."

Based on growth in newly enclosed stands, it takes heavily browsed willows approximately 10 years to reach their full biological potential (Kay 1990), which is longer than the period of time Yellowstone's elk herd was substantially reduced. It is likely that early herd reductions did not last long enough for willows or other woody species to fully recover (Kay 1990, 1995b).

Willow Pollen

Engstrom et al.'s (1991) pollen work on the northern range was cited by Singer et al. (1994) to support their contention that the current state of willows in the park is within the normal range of historical variability. Willow pollen is poorly represented in sediment cores and correlation between a few pollen grains and actual changes in willow communities is questionable. Moreover, Yellowstone's geologist has questioned the validity of Engstrom et al.'s study (Hamilton 1994).

Before park establishment, Yellowstone's northern range had a 25 year fire frequency—that is, an area equal in size to the entire northern range burned every 25 years (Houston 1973, 1982). Thus, it is likely that willow communities once burned at frequent intervals. After willows are burned, however, plants expend resources on vegetative growth, not reproductive activity, so pollen production is reduced for several years. This and other factors, such as high beaver activity, could easily explain any variation in willow pollen production.

Aboriginal Overkill

How then were willows able to flourish in Yellowstone and throughout the Intermountain West for the last 10,000± years? We suggest that the large elk populations assumed under "natural regulation" and by Singer et al. (1994) did not exist until after Yellowstone was designated a national park. Historical journals, old photographs, and archaeological data all indicate that there are now more elk in Yellowstone than at any point prior to 1872 (Kay 1990, 1994a, 1995a, 1995b, in press b; Kay and Wagner

1994). Before park establishment, Yellowstone's elk population was limited at low densities by predation, primarily by Native Americans. Contrary to prevailing beliefs, Native Americans were not conservationists (Kay 1994a, 1995a). Because native peoples could prey-switch to small mammals, plant foods, and fish, they could take their preferred ungulate prey to low levels or extinction with little adverse effect on human populations. In fact, once Native Americans killed off most ungulates, human populations actually rose (Hawkes 1991, 1992, 1993). As Kay (1994a, 1995a) has demonstrated, Native Americans were the ultimate keystone species, and their removal has completely altered ecosystems, not only in Yellowstone, but throughout North America (Wagner and Kay 1993).

It must also be remembered that large numbers of native peoples inhabited the Yellowstone Ecosystem for the last 10,000± years (Hultkrantz 1974, Wright 1984). The claim that Native Americans seldom visited Yellowstoue because they feared the park's geysers and hot springs is false—that myth was invented by early park administrators to promote tourism (Hultkrantz 1979). Yellowstone's original inhabitants were forcefully removed ca. 1878 to reservations in Idaho and Wyoming for the same reason (Haines 1974, 1977).

Conclusions

Singer et al.'s (1994) explanation and hypotheses regarding willows in Yellowstone are not supported by the available data and cannot be sustained. Instead, the decline of willows in the park is due to repeated browsing by unnaturally large elk and other ungulate populations. Prior to park establishment, predation by Native Americans kept ungulates from impacting Yellowstone's plant communities, as those animals do today. By established standards Yellowstone contains some of the worst overgrazed willow communities in the entire West (Platts et al. 1983, 1987; Platts 1991; Patten 1993; Rosgen 1993). Since the condition of willows in the park is also a critical test of Yellowstone's "natural regulation" program, that paradigm must be rejected (Chadde and Kay 1991). Elk browsing has also had a drastic impact on aspen, cottonwood, and other plants in the park (Kay 1990, 1995b; Wagner et al. 1995).

In addition, we find Singer et al.'s (1994) call for more research disingenuous. During the late 1980s and early 1990s, a committee of riparian experts, headed by Dr. Duncan Patten, Secretary of the Ecological Society of America, developed a riparian research plan for the northern range at the request of the Park Service, but their recommendations were not followed (Wagner et al. 1995:103). Besides, as explained previously, the Park Service has not availed itself of recent opportunities to have independent panels review the Yellowstone situatiou.

On the other hand, if the decline of Yellowstone's willow communities is considered to be "natural"—i.e. caused by climatic change or the other factors Singer et al. (1994) and the Park Service have proposed—then ranchers throughout the West should be afforded the same consideration. Dodd (1991) recently proposed that federal land management agencies abandon their riparian standards for livestock grazing based on Park Service claims that Yellowstone is not overgrazed. "Most of the riparian habitat I saw in the Yellowstone Park ... is in bad to terrible shape by USFS [U.S. Forest Service] or Disneyland standards but is good to excellent when judged by sound ecological and naturalness standards (Dodd 1991:10)." Clearly, the resolution of this debate is more than an academic interest.

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