CHAPTER XII

SUMMARY OF "NATURAL REGULATION" PARADIGM TESTS AND ALTERNATIVE HYPOTHESES

"NATURAL REGULATION" TESTS

In Chapter 1, I discussed the development of the Park Service's "natural regulation" paradigm and then generated a series of hypotheses from that model which I tested in Chapters 3-11. In this chapter, I will review each of those hypotheses and then summarize the data I have presented which address those questions.

Vegetation

Hypothesis one is the elk and vegetation on Yellowstone's northern range have been in equilibrium for several thousand years and any changes in the vegetation since establishment of the park (1872) are largely due to suppression of naturally occurring lightning fires, climatic change, normal plant succession, or some combination thereof, not significantly to ungulate grazing. More specific hypotheses include the following. (1a) Elk have not been primarily responsible for changes which have occurred in the park's aspen communities. (1b) Aspen is a seral species on the northern range which, in the normal course of plant succession, is replaced by conifers or other vegetation. Aspen does not form climax communities. (1c) If burned, aspen stands will regenerate despite heavy utilization by elk and other ungulates.

In Chapter 3, I compared aspen community dynamics in Eagle Creek outside the park with those of aspen stands in Yellowstone National Park. Most aspen stands in Eagle Creek are multi-aged, are not being readily invaded by conifers, and have understories dominated by cow parsnip or other tall forbs which are characteristic of stable or climax aspen. Aspen stands in the park are dominated by trees 80-100 or more years old because, except where protected, the species has not successfully regenerated for the last 80 or so years due to repeated browsing of aspen suckers. Understories of aspen stands in the park are dominated by introduced grasses and unpalatable forbs which are representative of grazing disclimaxes. The majority of present aspen stands in the park also are not being readily invaded by conifers.

Since Eagle Creek has experienced the same history of fire suppression and climatic change as the rest of the northern range in the park, those factors cannot be primarily responsible for these differences. Moreover, there is a negative correlation between elk numbers and aspen regeneration taller than 2m in Eagle Creek. Thus, it appears reasonable to attribute the inside park - outside park differences to ungulate grazing especially since over the last 50 years fewer elk wintered in Eagle Creek than in Yellowstone Park.

The aspen exclosure data which I presented in Chapter 4 demonstrated that when protected from ungulate browsing, aspen stands develop multi-age structures, are not bark-scarred, and have understories dominated by shrubs or grazing-sensitive forbs which are again characteristic of climax or stable aspen communities. Since fire played no role in stand development inside these exclosures and since the general climate is the same on both sides of the fence, those factors cannot be responsible for the observed differences. Data from Eagle Creek and Yellowstone's exclosures suggest that with few or no ungulates, a significant proportion of aspen present in the Greater Yellowstone Ecosystem today is potentially stable or climax.

Furthermore, historic photos of aspen on the northern range taken ca. 1870-1890 show that those communities most closely approximate aspen inside today's exclosures rather than outside; multi-aged stands, absence of bark scarring, and diverse understories. Thus, conditions inside the exclosures which are protected from ungulates most closely approximate those which existed in Yellowstone prior to European influence and the creation of Yellowstone National Park. None of the early historic photographs show any evidence of elk browsing, high-lining, or bark damage to aspen. Aspen in repeat photographs taken on the northern range has declined approximately 95% since creation of Yellowstone Park and from 1947 to 1988, the number of aspen trees > 2m tall on those northern range photo sites declined by an estimated 85%.

Data on 467 aspen burns which I presented in Chapter 5 support the following conclusions. (1) Under normal conditions, aspen communities will not burn to any great extent until after leaf fall and the understory plants have cured out following a killing frost in late September or early October. (2) Lightning seldom strikes on Yellowstone's northern range or in Jackson Hole during late September or October when aspen stands are usually dry enough to burn. (3) Hence, the lack of aspen regeneration on the northern range and throughout much of the Greater Yellowstone Ecosystem is not due to the suppression of lightning fires. If aspen burned at frequent intervals in Yellowstone and Jackson Hole prior to European influence, the majority of those fires were probably started by Native Americans. (4) Moreover, data from prescribed burns clearly demonstrates that low-intensity, frequent fires will not regenerate aspen stands subject to ungulate use in winter, even when the use levels are moderate. Burned aspen stands will not produce regeneration taller than 2m if they are subjected to heavy elk browsing.

Repeat photographs (see Chapter 8 above) show that 84% of the aspen stands pictured in photos dating to the 1880-1910 period have now been heavily invaded by conifers. This would suggest that much of the original aspen in Yellowstone was seral and that its replacement represents normal plant succession. This could lead one to conclude that succession has been more of a factor in the decline of Yellowstone's aspen than ungulate browsing. However, in my opinion, this would not be entirely correct.

First, the available historical photos may not be representative of the original aspen in the park. As noted in Chapter 4 (above), nearly 49% of the aspen stands which I measured in the park did not have any conifers in them (Table 9). Despite a diligent search, I was unable to locate any 1880-1910 photographs of those aspen stands. In Yellowstone, most aspen communities are located at the grassland-forest ecotone and they extend from near the valley floors one-half to two-thirds the way up the surrounding mountain slopes. In general, aspen stands at higher elevations are more susceptible to conifer encroachment than are stands at lower elevations (Mueggler 1988). Since most of the aspen depicted in 1880-1910 photos are at higher elevations, this may bias that sample.

Second, as discussed in Chapter 3 (above), aspen stands subjected to repeated ungulate browsing may be more susceptible to conifer encroachment than ungrazed stands. For instance, Wyoming State range specialist Jeff Weinstein concluded that ungulate grazing-induced deterioration of aspen communities was a prerequisite for conifer invasion. My data on conifer encroachment rates inside and outside the park (Table 9) support this conclusion since fewer aspen stands in Eagle Creek are being invaded by conifers than are aspen stands in the park. Some or even a majority of the original aspen in Yellowstone was most likely seral to conifers, but I also believe that one-third to one-half were potentially stable or climax if they had not been repeatedly browsed by large numbers of elk.

Third, plant succession with large numbers of elk is different from succession with only a few or no elk. Based on aspen-stand dynamics inside exclosures and in Eagle Creek, even seral aspen stands (those being readily invaded by conifers) are able to repeatedly produce stems > 2m which grow into mature trees. Thus, even seral aspen can maintain its presence on a site while it "waits" for the next fire to remove the encroaching conifers. However, in Yellowstone Park repeated elk browsing has eliminated any new aspen stem growth > 2m tall (Table

5). I searched several areas depicted as aspen on 1880-1910 photos without finding any aspen trees or any aspen suckers. Conifer invasion plus repeated elk browsing since 1900 has apparently eliminated some aspen clones which had probably existed on those sites for several thousand years via vegetative regeneration.

Fourth, even if Yellowstone's seral aspen stands had burned once or more since 1900 reducing or eliminating conifer encroachment (eg. if the Park Service had not suppressed fires and eliminated aboriginal burning), elk would, in all probability, still have prevented any aspen stems from growing > 2m tall. In addition to the aspen burn data I presented in Chapter 5, I established 131 photo points containing 765 frames in aspen stands on Yellowstone's northern range burned by the 1988 wildfires. I also established permanent 2x30m belt transects on which I recorded the number and height of all stems. Despite post-fire regeneration rates approaching 200,000 suckers per ha, during the following winter, elk and other ungulates browsed all of the new stems to within a few centimeters of the ground (Kay unpub. data). Unless there is a drastic decline in elk numbers, I do not believe that any of these burned aspen stands will be able to regenerate successfully.

Thus, the data which I have presented in Chapters 3, 4, 5, and 8 do not support Hypotheses 1, 1a, 1b, or 1c and I rejected them. The decline of aspen on Yellowstone's northern range is due primarily to repeated elk browsing not climatic change, successional trends, or fire suppression.

Hypothesis 1d is the decline of tall willows on the northern range is due primarily to natural factors such as climatic change, normal succession, and fire suppression, not browsing by elk.

The data on tall willows which I presented in Chapters 6, 7, and 8 may be summarized as follows. (1) Tall willow communities have almost entirely disappeared from the northern range since establishment of Yellowstone Park. (2) Willows protected from ungulates exhibit significantly greater growth and canopy-coverage than unprotected plants, and in physical stature resemble the willows which existed in the park during the late 1800s. (3) Short, repeatedly browsed willows common on the northern range today are not ecologically equivalent to the former tall willows. (4) Repeatedly browsed willows produce no male or female aments; hence, they do not produce any seeds. In contrast, tall willows protected from browsing produce an average of over 300,000 seeds per m^2 of female willow canopy-coverage. Without seeds, willows cannot colonize newly created habitats, and as the existing willows die of old age, disease, insects, or other causes, willows will eventually disappear. Thus, the virtual elimination of willow seed production by ungulates indicates that those herbivores are not in long-term equilibrium with the park's vegetation.

(5) Ungulate browsing has changed the stature and abundance of willow communities on the park's northern range, and may well have changed animal communities typically associated with those riparian habitats. Entire communities have been affected, not just willows. (6) The near elimination of beaver may well have had a marked negative feedback effect on the extent of willow communities by lowering water tables and reducing stream flows. And (7) the decline and current suppression of willows over the entire northern range is due primarily to frequent, repeated ungulate browsing, and not climatic change, plant succession, or suppression of lightning fires. These findings do not support Hypotheses 1 or 1d.

Hypothesis 1e is other deciduous shrubs such as serviceberry, chokecherry, buffaloberry, rose, and river birch have not been adversely affected by the level of elk use which has occurred on the northern range since 1872.

As I discussed in Chapters 4 and 7, deciduous shrubs protected from ungulates exhibit significantly greater growth, canopy-coverage, and berry/seed production than plants exposed to the level of ungulate browsing which exists on Yellowstone's northern range and in Jackson Hole. Since unprotected deciduous shrubs produce virtually no berries or seeds, they cannot be in long-term equilibrium with their ungulate herbivores. Early historical accounts indicate that prior to European influence and the creation of Yellowstone Park, deciduous shrubs produced large quantities of berries. Therefore, the present lack of berries in Yellowstone was not the condition prevailing in presettlement times. Thus, these findings do not support Hypotheses 1 or 1e.

Hypothesis 1f is ungulate high-lining of conifers on the northern range is natural and not a sign of "overgrazing." Conifers showed extensive high-lining by elk when the park was established.

In Chapter 8, I presented evidence which demonstrated that none of the conifers on the northern range or throughout Yellowstone Park show evidence of ungulate high-lining in ca. 1870-1890 photographs. Conifers at Mammoth Hot Springs photographed ca. 1872 show no signs of ungulate use and suggest that large numbers of resource-limited elk did not winter there as far back as 1800. Moreover, early photographs of more palatable willows and aspen also show no signs of ungulate browsing or high-lining. Early pictures do show that some conifers lacked their lower branches, but that was due to fire pruning or human high-lining, not ungulates. Based on these data, Hypotheses 1 and 1f are not supported.

In summary, none of the data which I have presented support the hypothesis that elk and vegetation on Yellowstone's northern range have been in equilibrium for the last 200 or so years, as assumed by the Park Service. Instead, (1) prior to 1880, aspen, willows, and conifers seldom experienced ungulate browsing, (2) from 1900 to 1920, those same species showed increasing evidence of repeated elk use, (3) repeated ungulate browsing eliminated most tall willows by the 1950s, and (4) repeated elk browsing has prevented regeneration of unprotected aspen stands since approximately 1900. In short, the condition and trend of the woody vegetation on the northern range support the earlier view that Yellowstone was not historic winter range for resource-limited ungulates and that under protection afforded by the park, the elk herd increased significantly and altered the vegetation. This evidence does not support Houston's (1982) interpretation of elk-vegetation interactions in Yellowstone.

Sympatric Herbivores

Hypothesis two is sympatric herbivores have not been competitively excluded by elk. More specific hypotheses include the following. (2a) Elk have not excluded beaver from the northern range due to interspecific competition for food, primarily willow and aspen. Beaver were always rare in Yellowstone Park and any changes in their population is due to factors other than elk. (2b) Over the last several thousand years, the relative abundance of elk and other ungulates on the northern range has not changed.

Based on the evidence which I presented in Chapters 3-8 on the elk-induced changes in aspen and tall willows which are the primary food plants for beaver, and the demonstrated drastic reduction in beaver numbers over the northern range, ungulate browsing has clearly acted to competitively exclude beaver from Yellowstone. Beaver were once common on the northern range and throughout the park. The decline in the beaver population paralleled the decline in tall willows and aspen.

Moreover, the decline of aspen and tall willows probably had an adverse effect on populations of other species normally associated with those habitats such as white-tailed deer, birds, small mammals, and aquatic species. Thus, entire plant and animal communities, not just tall willows or aspen, 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. Grazing-induced short willow, aspen, and deciduous shrub associations are not ecologically equivalent to the unbrowsed or lightly browsed communities which occupied those same areas prior to the creation of Yellowstone Park.

Keating (1982, 1985) argued that the growing elk population on Yellowstone's northern range had a negative impact on sympatric bighorn sheep populations while others have suggested a similar correlation between increasing elk numbers and declining mule deer populations (Chase 1986). Houston (1982:156-185) denied that Yellowstone's elk had adversely impacted any other ungulate species. Unfortunately, the 1870-1990 population estimates for the other ungulate species which occupy the park are unreliable. However, based on the historic source material I discussed in Chapter 9, indications are that mule deer and bighorn sheep were more common relative to elk ca. 1830-1870 than they are in Yellowstone today.

Historical accounts also indicate that mule deer once summered in areas where they are now extremely rare. Other early accounts suggest that mule deer which once wintered on the park's northern range have been competitively displaced to wintering areas farther down the Yellowstone Valley outside the park. In recent years, few mule deer have wintered inside the park (Singer 1987) while in the past, mule deer commonly wintered in the park (Murie 1940). Moreover, archaeological information (see Chapters 10 and 11 above) strongly suggests that deer and bighorn sheep were even more common (relative to elk) during prehistoric times than they are at present. Thus, these lines of evidence suggest that the relative abundance of elk and other ungulates was dramatically different in the past. These findings do not support Hypotheses 2, 2a, or 2b.

Prehistoric Abundance of Elk

Hypothesis three is large numbers of elk have wintered on Yellowstone's northern range for the last 8-10,000 years.

As discussed above and in Chapters 9, 10, and 11, the historical and especially the archaeological evidence indicate that elk were rare throughout the Greater Yellowstone Ecosystem and throughout the Intermountain West prior to European influence. Moreover, the photographic evidence (see Chapter 8 above) and berry production data (see Chapter 7 herein) clearly demonstrate that large numbers of elk or other ungulates did not inhabit the Yellowstone area ca. 1800-1870. The finding of a few prehistoric elk bones in Yellowstone does not support the Park Service's contention that thousands of resource-limited elk inhabited Yellowstone for the last 8-10,000 years. If large numbers of elk had prehistorically inhabited Yellowstone, those animals should have been killed by Native Americans, should have been transported to habitation sites, and should dominate archaeological ungulate faunal remains. That clearly is not the case, and there are no other data I am aware of which support Hypothesis 3.

CONCLUSION

As noted in Chapter 1 (above), the specific hypotheses discussed above were generated from the Park Service's "natural regulation" paradigm. If any or all of those hypotheses are not true, that is grounds for rejecting the entire "natural regulation" paradigm. Since, I can find no evidence to support any of these hypotheses and all of the available data support the opposite conclusions, I feel compelled to reject the entire "natural regulation" paradigm.

ALTERNATIVE HYPOTHESES

The archaeological evidence suggests that some factor or factors besides resources limited elk and other ungulate populations prior to European influence. While it is beyond the scope of this dissertation to offer an in-depth review of all possible alternatives, in my opinion, the following hypotheses are most tenable. (1) Carnivore predation (wolves, mountain lions, bears) once limited ungulates. (2) Predation by Native Americans limited ungulate populations in pre-Columbian times. (3) Synergism between Native Americans and carnivore predation limited prehistoric ungulate distribution and numbers in the Greater Yellowstone Ecosystem and throughout the Intermountain West. This occurred prior to such European influences as epidemic diseases which decimated aboriginal populations well in advance of actual white contact (Dobyns 1983, Ramenofsky 1987), and the destruction of wolves.

Studies of North American ungulate populations typically focus on whether they are limited by resources, severe winter weather, carnivorous predation, disease, or some combination thereof. In pondering what factors limited ungulate numbers in pre-Columbian times, most authors invoke these same influences. The role of Native American predation is generally not considered, dismissed out of hand, or glossed over with a few cursory statements. I believe that prior to European influence, predation by Native Americans was a major factor limiting the numbers and distribution of ungulates in the Intermountain West, including the Greater Yellowstone area. This hypothesis is based on my analyses of: (1) the efficiency of Native American predation including cooperative hunting, use of dogs, food storage, use of non-ungulate foods, and hunting methods; (2) optimal-foraging studies; (3) tribal territory boundary zones as prey reservoirs; (4) species ratios, and sex and age of aboriginal ungulate kills; (5) lack of aboriginal conservation practices; (6) impact of European diseases on aboriginal populations; and (7) the apparent synergism between aboriginal and nonhuman predation. Accordingly, none of the North American ungulate-predator systems studied to date represents the conditions which existed prior to European influence. The data used to formulate and test this alternative hypothesis are beyond the scope of this dissertation and will be presented elsewhere.

At first glance, the demonstrated lack of elk in archaeological sites appears to negate my aboriginal predation hypothesis. Not only is this not the case but, in fact, the opposite is true. Optimal-foraging theory predicts that high-ranked diet items, such as elk, are more susceptible to "over-exploitation" than low ranked items (see Chapter 11 above). Hence, according to optimal-foraging models, high-ranked items will seldom actually appear in the diet if they are being "over-exploited". Thus, ungulate species unearthed from archaeological sites with the lowest frequency, such as moose and elk, were probably subjected to extreme over-exploitation.