CHAPTER I

HISTORY OF THE NORTHERN HERD: CONTEXT FOR THIS STUDY

THE EARLY YEARS, 1872-1967

Prior to 1968, the National Park Service 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[1] the park's northern winter range, including willow (Salix spp.) and aspen (Populus tremuloides) communities (Skinner 1928; Rush 1932; Grimm 1939, Cahalane 1941, 1943; Kittams 1959; Pengelly 1963; Tyers 1981; Kay 1985; Chase 1986). During this era, the Park Service believed (1) Yellowstone was not a historical elk wintering area, (2) European settlement forced elk to winter in the park, (3) under protection afforded by the park, the elk herd irrupted to over 35,000 animals, (4) those animals proceeded to overgraze the range causing changes in plant species composition and soil erosion, and (5) during the severe winters of the late 1910s, large numbers of elk died of starvation and the population fell precipitously (Houston 1982, Chase 1986, Despain et al. 1986).

After Yellowstone Park was created in 1872, a succession of civilian, military, and Park Service administrators protected "good" animals such as elk and other ungulates while killing "bad" animals like wolves (Canis lupus) and mountain lions (Felis concolor)(Hampton 1971; Haines 1974, 1977; Houston 1982; Chase 1986; Despain et al. 1986). During this period, the Park Service fed hay to wintering elk, mule deer (Odocoileus hemionus), white-tailed deer (O. virginianus), bison (Bison bison), bighorn sheep (Ovis canadensis), and pronghorn antelope (Antilocapra americana). Using traps, dogs, guns, and poison,

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[1]Terms such as "overgrazing," "range damage," and "unnatural" elk population are common in nearly all early government reports about the northern range. Since these terms are value-laden, they are used throughout this dissertation only in their historic context.

government agents eliminated all wolves and most mountain lions from the park by the late 1920s. After this had been accomplished, the Park Service came to believe that its eradication of native predators had permitted the northern elk herd to irrupt and overuse its range.

Now convinced that the unnaturally large elk population was destroying Yellowstone's northern range, the Park Service began reducing the herd by trapping and transplanting elk to areas outside the park. Live trapping began in the 1910s-1920s and intensified during the 1930s. From 1934 to 1968, nearly 11,500 elk were moved from the northern herd by this method (Erickson 1981). However, agency officials concluded that live trapping alone could not reduce the herd to within the range's estimated carrying capacity of 5,000 animals, so rangers began shooting elk in the park to further reduce the herd (Kittams 1959; National Park Service 1962, 1963; Houston 1982; Chase 1986; Despain et al. 1986).

This program was called direct reduction, and from 1949 to 1968 the Park Service shot over 13,500 elk on the northern range (Erickson 1981). To help reduce the herd, the Montana Department of Fish and Game (since renamed the Department of Fish, Wildlife, and Parks) instituted a special, extended late hunting season north of the park to harvest migrating elk. From 1934 to 1968, sport hunters killed over 43,700 elk when those animals left the park's protection. As removals in the park intensified, sport hunters outside the park generally killed fewer and fewer elk (Table 1). Occasional severe winters forced large numbers of elk to leave the park, and during those years, sport hunters shot more elk, which, at times, confounded the general trend.

During the winter of 1961-62, Park Service rangers shot 4,309 elk on Yellowstone's northern range. By 1967-68, an aerial census of the northern range recorded only 3,172 elk (Erickson 1981, Houston 1982). The combination of government rangers killing elk in the park, a declining elk herd, and falling sport harvest outside the park generated intense public outcry and heated political debate over how best to manage the northern herd (Olsen 1962, 1968; Trueblood 1963). The situation quickly evolved from a local problem to a nationwide concern. The national media seized upon this issue when Montana Congressman Arnold Olsen (1962) wrote an article entitled "Yellowstone's Great Elk Slaughter" for Sports Afield magazine. From a reading of newspaper accounts and events of the day, there is little doubt that politics overshadowed scientific decision making (L. Pengelly, pers. commun. 1984)[2].

The issue reached a head in March 1967 when Gale McGee, U.S. Senator from Wyoming, chaired a subcommittee of the Committee on Appropriations to solicit opinions on how best to manage Yellowstone's northern herd (U.S. Senate 1967). In fact, an accommodation was reached prior to the hearing. As the first order of business, Senator McGee announced that the Secretary of Interior and the Director of the Park Service had just agreed to stop "the direct kill of elk in the park" (U.S. Senate 1967:1).

At that hearing, the Director of the Park Service (pp. 11-18) reiterated his agency's position that an unnaturally large elk population was destroying Yellowstone's northern range and had to be controlled. In support of the Park Service, A. Starker Leopold (UC Berkeley) stated (pp. 19-21):

> In short, our concern was the--recommending to the Secretary [of Interior] and to the parks, the long-term maintenance of this habitat.
>
> Now, the reduction and the control of elk numbers is obviously the keystone to maintenance of the habitat. The priorities of public hunting outside the park, first, trapping, second, and direct reduction, third, which we recommended, I am amazed to find had been recommended as early as 1915. This was unknown to me--that the Boone and Crockett Club had come up with exactly the same formula 40, 50 years before.
>
> I have no reason whatsoever to alter my views that this is the manner in which that herd has to be regulated. . . . Again, we recommended that direct control continue. And I have not changed my mind on this. If I were posed with the same problem again, this is exactly what I would

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[2]The full names and addresses of all the people who provided personal communications for this dissertation are found in Appendix A.

Table 1. Northern Yellowstone elk herd removals, 1935-1990.

Date	Number of elk killed by sport hunters outside park	Number of elk killed and live-trapped in park
1935-39	11,700	2,341
1940-44	9,132	874
1945-49	9,373	237
1950-54	5,035	2,820
1955-59	5,430	6,075
1960-64	760	9,273
1964-69	2,350	4,656
1970-74	206	0
1975-79	2,650	0
1980-84	5,866	0
1985-89	7,016	0

Adapted from Erickson 1981. Data after 1981 are from Chrest and Herbert (1982, 1983, 1985) and Montana Fish, Wildlife, and Parks (pers. commun. 1990).

> recommend.
>
> I would like to put into perspective, Mr. Chairman, the fact that what you are dealing with here, the question of too many of a grazing animal on a protected area, a park, is a universal problem on national parks throughout the world, not just throughout the United States. . . .
>
> Now, if we are going to protect our national parks here, or California, or Uganda; the maintenance of this balance between vegetation-eating animals and the vegetation is absolutely essential. And this is one tool that will be in use a hundred years from now, sir; direct reduction, I think.

The Director of the Park Service (p. 34) added that his agency would not let the northern herd "get out of hand" and that because of the public outcry, in the future the northern herd would be controlled only by live-trapping and sport hunting outside the park to prevent range abuse. At that hearing, the Governor of Wyoming (pp. 4-6) and Montana's representative (pp. 44-51) both stated that their respective states would accept, for transplant, as many live elk as the Park Service could deliver. However, Earl Thomas of the Wyoming Game and Fish Commission (pp. 35-43) sounded a note of caution when he pointed out "we [Wyoming] do not need them [Yellowstone elk] . . . We have elk in most of the historic elk ranges in Wyoming." But he added "We are so opposed to the direct reduction methods that we have said we will accept any amount of elk that the park can deliver to us."

During the early 1960s, contemporary animal welfare groups were not yet in existence or were silent on the Yellowstone elk situation. Thus, most of the opposition to killing elk in the park did not come from animal rights activists, but from sport hunters. They apparently did not object to the killing per se, but to the fact that it was being done by government agents. What the sport hunters really wanted was to do the killing themselves. Though this probably was on the back of everyone's mind at the time of the U.S. Senate (1967) hearing, only Burton Marston (pp. 57-60) of the Izaak Walton League suggested "Let's try hunter harvest" in the park to control Yellowstone's northern herd. Others (pp. 66, 71) testified they were "unalterably opposed to any open public hunting in Yellowstone National Park." This sentiment was shared by Yellowstone's Chief Naturalist (McIntyre 1962) who, in 1962, had presented a paper entitled "The threat of public sports hunting in Yellowstone and other national parks."

After the hearing when emotions had cooled and the participants had time to measure the ramifications of their public statements, a representative of Wyoming called Yellowstone Park and reiterated his Governor's pledge to take all the live-trapped elk Yellowstone could provide, and reportedly said, "But why don't you give them to Montana first?" At the same time, Montana called the park and reportedly said "Why don't you give Wyoming first crack at all those elk?" It seems the respective livestock associations of each state had informed their governors that they did not want any more elk out on their public lands to compete with their livestock for their forage (L. Pengelly, pers. commun. 1984). Elk were not live-trapped from the northern herd after 1967-68 (Erickson 1981). So, the Park Service could not shoot elk in Yellowstone, could not give away live-trapped elk, and would not let sport hunters into the park. Since they had also eliminated large predators, how could the agency control (limit) the northern herd?

NATURAL CONTROL

On September 19, 1967, the National Park Service (1967a) released a short statement entitled "Management objectives for northern Yellowstone Park." In that document, the agency stated:

> The primary purpose of Yellowstone National Park is to provide present and future visitors with the opportunity to see and appreciate the natural scenery and native plant and animal life <u>as it occurred in primitive America</u>.
>
> Primitive scenes with a variety of wildlife species only result from allowing <u>natural regulatory processes between plant and meat-eating animals to take place</u>. Where natural processes have been lost from a park, attempts must be made to reestablish them. The following [are our] management objectives . . .
>
> Encourage an understanding of the elk's role <u>in maintaining a "balance of nature"</u> in the park where it serves as a food source which determines the abundance and variety of wild meat-eating animals and birds within the park.
>
> Rely upon the combined action of <u>native predators and</u>

> periodic adverse weather to naturally regulate elk numbers whenever possible. . . .
>
> Limit park control operations to duplicating the action of natural predation which relieves severe overuse of vegetation and reduce extreme fluctuations in animal numbers. [emphasis added]

On December 5, 1967, the National Park Service (1967b) issued another statement entitled, "Natural control of elk" in which it added:

> Elk have lived in the Yellowstone region thousands of years before modern man arrived on the scene. The elk could not have persisted over this span of time if natural control processes had not existed to keep the animals in balance with their plant food sources.
>
> Historical and recent knowledge on the subject tells us that elk populations can be naturally controlled, within limits set by winter food, by periodic severe winter weather and native predators. . . .
>
> The occurrence of uncompensated predation deaths relieves grazing pressure on vegetation and severe food stresses on elk populations at critical times. End results are a smoothing of elk population fluctuations, which would be more extreme in the absence of effective predation.
>
> In summary, periodic severe winter weather, native predators and the elk population itself interact to naturally control elk numbers within limits set by winter food. [emphasis added]

On December 7, 1967, the agency issued an "Administrative policy for the management of ungulates" (National Park Service 1967c) in which it stated:

> The primary purpose of Yellowstone National Park is to preserve, and at the same time provide visitors opportunities to see and appreciate, the natural scenery and the native plant and animal life as it occurred in primitive America. A portrayal of primitive America is defined as having natural conditions where scenery and "balance of nature" in ecosystems are not altered by man.
>
> The most favored form of management is to rely upon natural controls to regulate animal numbers whenever possible. This automatically results in a balance of nature, preserves the aesthetic and scientific values of the park ecosystem, and enhances visitor opportunities to see and photograph animals that have not learned to fear man. [emphasis added]

While these documents are unsigned, they may have been written by Yellowstone biologist Glen Cole. The agency presented no citations or data to support its new concept. The agency repeatedly alluded to a "balance of nature" in which predators through uncompensated mortality interacted with severe weather to keep animals "in balance with their plant food sources." Without supporting evidence, the Park Service also repudiated its long standing belief that the northern range was never a historic wintering area for large numbers of elk.

In June 1968, Cole wrote a short paper on "Elk and the primary purpose of Yellowstone National Park" in which he made the following statements:

> The primary purpose of Yellowstone National Park is to preserve natural ecosystems and the opportunity for visitors to see and appreciate natural scenery and native plant and animal life as it occurred in primitive America. [p. 1] . . .
>
> Accumulated knowledge on natural ecosystems tells us that the Northern Yellowstone elk and other native wildlife would have had to be in some dynamic balance with each other, their food sources and the environment several thousand years before modern man first visited the region. . . . Native predators such as the grizzly bear, mountain lion, grey wolf, etc., were abundant. It would seem unlikely that the elk in this several thousand year old ecosystem would suddenly present problems, unless some very disrupting influence occurred. Records indicate man was responsible.
>
> . . . The first major disrupting influence on the Northern Yellowstone elk resulted from man progressively eliminating the grey wolf and cougar between 1870 and 1925. . . .
>
> Recognition that native predators assisted in maintaining natural balances in the park ecosystem came too late, and the native grey wolf and mountain lion have yet to reestablish themselves in significant numbers. [pp. 2-3] . . .
>
> The combined action of native predators and weather should be relied upon to control elk which winter in the more remote interior of Yellowstone National Park. [p. 5, emphasis added]

Cole (1968) provided no citations or data to support these statements.

During 1968, Yellowstone biologist William Barmore wrote a letter to his supervisor, Glen Cole, in which he raised several questions regarding the new direction taken by Yellowstone's elk management. Barmore (1968a) said:

> I think we should recognize, however, that the factual basis for these hypotheses is far less than adequate to warrant "strong" belief that they are correct. In other words, I believe we could choose other data of similar factual "depth" and reliability and support other hypotheses that could take us most any other way we want to go with elk management or any other kind of management.
>
> . . . Thus we are abruptly "scrapping" current objectives with no stated justification or supporting information. Past objectives were based on supporting information that indicated relationships between elk, their habitat, and associated wildlife were different from what

> existed in primeval times; that ecological changes since the early 1900's were "unnatural." I believe similar justification must be provided to support the proposed change in direction. I feel sure that we will be called upon to provide this justification. I seriously question whether we can come up with a satisfactory explanation of the proposed change on the basis of objective information available at this time. . . . But I think we are being less than completely "scientific" or completely objective and honest by proposing a drastic program switch without saying why.
>
> I think the weight of currently available information gives greater support to the interpretation that elk-habitat relationships the past 50 years or more have been "unnatural" rather than "natural." Again, this is not to say that more intensive study may not indicate a different interpretation that is more correct. But it does raise the question as to what is the basis for a reinterpretation of the problem at this time? . . .
>
> The point I want to make is that I think new interpretations and approaches to management should be based on better information than previously available, and should be clearly stated when management recommendations are made.

In 1969, Cole published a report on "The elk of Grand Teton and southern Yellowstone National Parks" where he had worked prior to beginning his duties in Yellowstone. Cole (1969a) concluded:

> Original predator and scavenger populations probably played an important role in reducing the extreme highs and lows in elk population fluctuations [p. 51] . . .
>
> Winter habitats that were interspersions of different physiographic sites and/or vegetation types provided increased opportunities for an elk population to remain in some dynamic equilibrium (ecological homeostasis) with its main food sources. Such ecologically complete habitats obviously had carrying capacity relationships where "the whole was greater than the sum of its parts." The elk's variable use of different habitat units, general food habit, protection from snow, and the capacity of native plants to withstand periodic heavy use appeared to preclude free-ranging animals from progressively depleting their main winter food sources.
>
> . . . Periodic "high" mortality of subadults, adult males, and other animals with limited energy reserves would not represent a loss of biologically essential population members and would be predestined to occur in an elk population that was largely environmentally regulated. . . .
>
> The logistic curve relationship between population growth and environmental resistance may have been first expressed by Verhulst in 1833 (Allee, et al. 1959). Accumulated knowledge since this date further establishes that cyclic environmental changes, which alternately result in less or more resistance to population increases, cause animal numbers to fluctuate around some mean. Directional changes which consistently offer less environmental resistance permit upward trends in population numbers. Consistently more environmental resistance causes downward

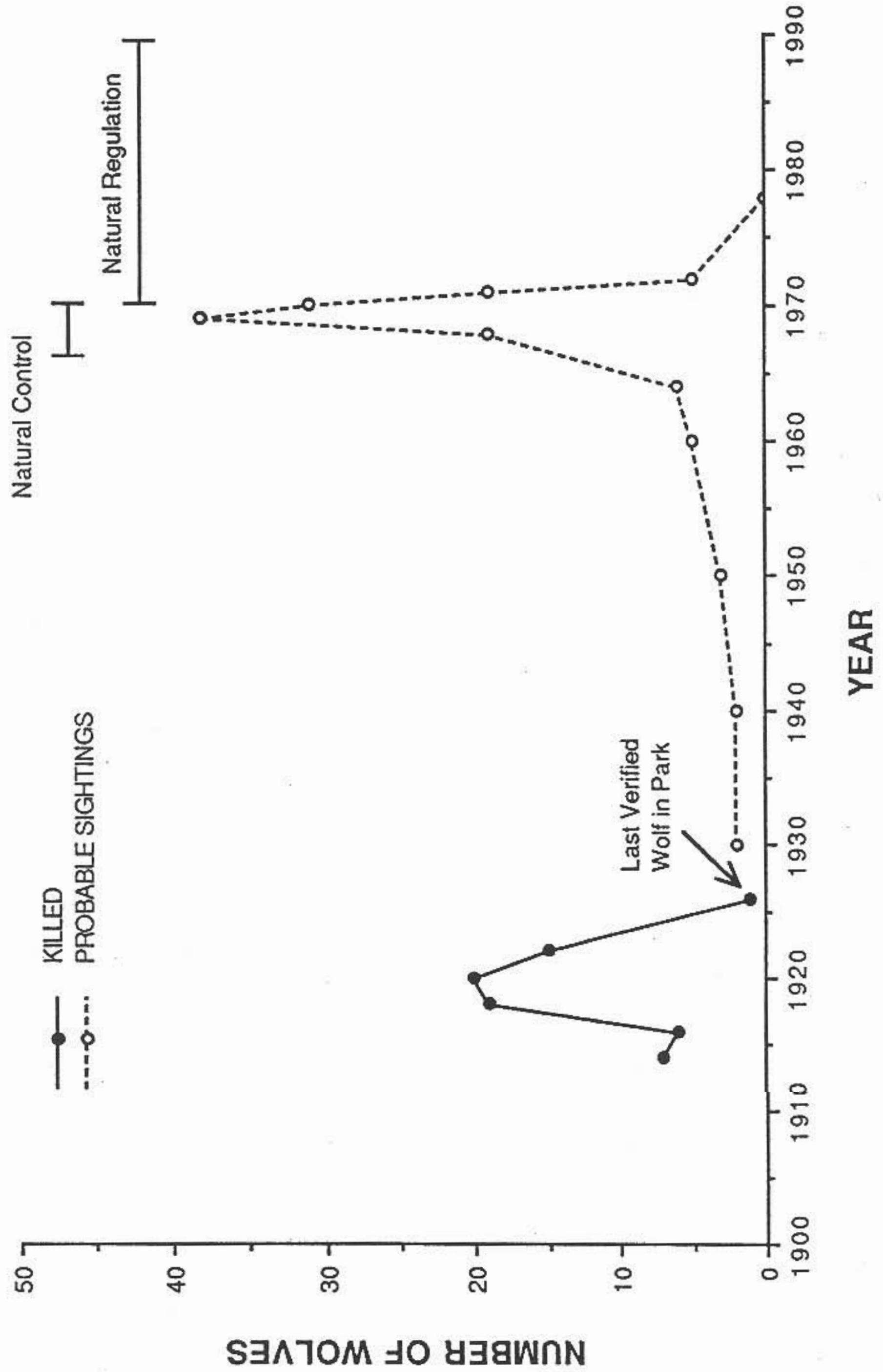
> population trends. [p. 60] . . .
>
> Accumulated knowledge on the organization of life in natural communities tends to assure that past elk populations were regulated to the extent that they could not, by themselves, progressively deplete food sources which limited their numbers.
>
> . . . Original predator populations probably reduced the intensity of intraspecies competition within an elk population during more severe winters. The extent to which this occurred would have relieved energy stresses and smoothed elk population fluctuations. [p. 61, emphasis added]

Again, Cole repeatedly cited "accumulated knowledge" without identifying that knowledge. His only citation was to the logistic growth model. He also assumed that "ecological homeostasis" or "the balance of nature" would preclude free ranging animals from progressively depleting their food resources. Under this new policy of "natural control," the Park Service still clearly believed that large predators were important in limiting ungulate populations. Even though Yellowstone's last verified wolf sighting was recorded in 1926, during the "natural control" period, the number of probable wolf sightings increased dramatically (Fig. 1).

WHAT IS "NATURAL REGULATION"?

In the early 1970s, the Park Service abandoned its policy of "natural control" in favor of a new concept termed "natural regulation." Under this paradigm, the agency reversed its position and claimed that large predators never limit ungulate populations. Once this new policy was adopted, the number of "probable" wolf sightings dropped markedly (Fig. 1). Chase (1986:119-141) accused the Park Service, and Cole in particular, of fabricating wolf sighting reports to support their former "natural control" policy. In Chase's view, when the Park Service "needed" large numbers of wolves in Yellowstone to bolster their "natural control" policy the agency saw them (Fig. 1), and when wolves were no longer required under the new "natural regulation" paradigm, the agency "saw" fewer and fewer until it finally admitted there were no wolves in Yellowstone (U.S. Fish and Wildlife Service 1987, Singer

Fig. 1. The average number of wolves killed in Yellowstone Park by 2-year periods from 1914 to 1927 and the average number of "probable" wolf sightings in the park from 1930 to present. Data points for "probable" wolf sightings represent 1930s, 1940s, 1950s, 1960-64, 1964-67, 1968, 1969, 1970, 1971, 1972-77, 1978-present. Adapted from Cole (1971a) and Weaver (1978).


NUMBER OF WOLVES
0
10
20
30
40
50
YEAR
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
KILLED
PROBABLE SIGHTINGS
Last Verified
Wolf in Park
Natural Control
Natural Regulation

1989).

Cole (1971b) expounded upon his new concept of "natural regulation" in a paper presented at the 36th North American Wildlife Conference.

> . . . ungulate populations that were naturally regulated (i.e., without human influences) . . .
> Naturally regulated ungulate populations were depressed to lower numbers by density-influenced intraspecific competition and the partially density-independent effects of periodic severe weather. Intraspecific competition increased energy stresses in populations that were at high densities in relation to their available winter food. This directly or indirectly (by predisposing) caused the mortality of subadults or adults with the lowest energy reserves and sometimes lowered the subsequent year's natality (realized reproduction). [p. 417] . . .
> An appropriate summary may be: Over a series of years, naturally regulated ungulate populations were self-regulating units. They regulated their own mortality and compensating natality in relation to available winter food and their population size. Predation on either wintering or newborn ungulates seemed a nonessential adjunct to the natural regulation process because it did not prevent populations from being self-regulated by competition for food. [p. 419]
> Low realized natality, with the recruitment of young in a replacement relationship to low adult mortality, appeared to represent the "best system" for a naturally regulated ungulate population to maintain relatively stable numbers in a frequently harsh environment. The latent potential for high natality allowed populations to compensate for periodic higher than usual mortality that was partly due to severe weather. This mortality, as well as the more consistent density-influenced deaths of animals with low energy reserves, was predestined to occur in naturally regulated ungulate populations. Such mortality would not represent a loss of biologically essential population members and it, as well as low realized natality, are not unnatural phenomena. [pp. 419-420]
> . . . Deductions, from the principle that consistently harmful relationships do not survive the natural selection process (Darwin, 1859) and the concept of density-dependence (Howard and Fiske 1911, and others), led to a hypothesis that populations of native ungulates cannot, ... progressively reduce food sources that limit their own densities.
> In the absence of substantial environmental changes, interspecific competition maintained populations of different ungulate species in some equilibrium with each other and their respective food or habitat niches where they had a competitive advantage. . . .
> Ecologically complete habitats (ECH) for wintering ungulates were complexes of physiographic sites . . . Particular habitat units were ecologically essential to maintain high population densities, but interspersions of different units as an ECH had carrying capacity relationships where the "whole was greater than the sum of

> its parts." [p. 420]
>
> . . . This led to the conclusion that the less available but quantitatively greater food sources on ECH, in combination with successional processes determined ungulate population numbers over time. The variable "rest rotation" use of food sources and habitat units by free-ranging ungulates over a series of years obscured "law of minimum" relationships. [pp. 421-422]
>
> In the absence of human restrictions on their free-ranging use of ECH, native ungulates did not seem to be able to cause retrogressive or secondary succession and, except for limited zootic climax sites, halt primary successional trends. These interpretations applied to populations with or without significant natural predation or human exploitation. The biotic effects of free-ranging ungulates in hastening the replacement of seral vegetation, when stands reached late stages or remnant status, were considered an inevitable natural relationship. . . .
>
> The information reviewed thus far permits some evaluation of previous assumptions that park ungulate popula tions need to be artificially regulated to substitute for native predators, prevent progressive habitat deterioration, or maintain interspecies equilibriums. These assumptions infer that predation by either beasts or man is universally essential to "control" ungulate populations or their biotic effects and prevent one species from displacing another. This inference is not supported by the various studies in the Rocky Mountain parks. [p. 422] . . .
>
> This section applies to native ungulates that were year-long inhabitants or had ecologically complete winter habitats within the subject parks.
>
> . . . The rationale for relying on natural processes to regulate native ungulate populations in parks is that the animals are not causing unnatural trends in biological succession . . . [p. 423, emphasis added]

In this paper, Cole changed his previous concept of "natural control" to one of "natural regulation" in which predation is a "nonessential adjunct" to the regulation of ungulate numbers. Density-dependent homeostatic mechanisms would prevent ungulates from over-using their food resources. Furthermore, "natural regulation" could occur only in an ecologically complete habitat.

Cole (1974) subsequently presented a paper at the annual meeting of the Montana Chapter of The Wildlife Society entitled, "Population regulation in relation to K" in which he explained how he developed his "natural regulation" paradigm. Cole stated:

> By definition, a regulating mechanism or influence causes population size to change. [p. 2] . . .
>
> A more useful equation appears to be
>
> $$\frac{dN}{dt} = rN \left(\frac{K - N}{K}\right)$$

> This is the equation for the familiar logistic curve [p. 3] . . . . Laboratory and field studies have rather firmly established that dN/dt are functions of population density. If "density" is more specifically identified as the process of density-influenced competition, then the hypothesis is also consistent with much of the literature on population regulation. It mainly differs from other hypotheses that populations are regulated by the effects of social interactions, genetic feedback, food deficiencies, or environmental influences by specifically identifying density-influenced competition for K as the process by or through which these become regulatory. [p. 10]
>
> . . . Another often-mentioned justification applied to native ungulates is that hunting is necessary to prevent them from progressively destroying their own K, which is generally defined as food or habitat. This concept apparently assumes that native predators previously held herbivores below K, which now only seems to occur in marginal or low-security level habitats, or that species which have persisted over thousands of years have the capacity to destroy forage sources that determine their own density. The latter is inconsistent with the biological axiom that consistently harmful relationships do not survive the natural selection process.
>
> As near as I can determine, the predominantly North American concept that native ungulates destroy their own K is based on extrapolations from situations where domestic stock or wildlife occurred at artificially high densities due to supplemental feeding or restrictions on dispersals, on arbitrary designations of minor sources of food as K, on interpretations that plant succession toward climax is "deterioration" and due to biotic effects alone, and finally, the "textbook examples" of the Kaibab deer (Rasmussen 1941) and introduced reindeer (*Rangifer tarandus*) on the St. George, St. Paul (Scheffer 1951) and St. Matthew islands (Klein 1968). For alternative interpretations of the Kaibab, read Caughley (1970) and subsequent comments by Burk (1973). [p. 12] . . .
>
> In closing, I would propose that the concept that free-ranging native ungulates can progressively reduce their own K by their foraging alone not be used as a rationale for hunting or for population control within North American national parks. [p. 13, emphasis added]

From the way Caughley (1970) is cited above, I infer that this author influenced Cole's change from "natural control" where predators were important agents limiting elk numbers to "natural regulation" where predators were a nonessential adjunct.

In 1978, a "Symposium on natural regulation of wildlife populations" was held by the Northwest Section of The Wildlife Society. In what apparently was his last paper on this topic, Cole (1983) summarized his ideas about "A naturally regulated elk population."

> The study tested three hypotheses that were developed from previous studies and reviews of literature (Cole 1971

> and 1974). The first was that the elk population was naturally regulated on a year-to-year basis by its density-influenced competition for space, food or mates; and the additive effects of harsh weather. [p. 77] . . .
>
> The second hypothesis was that the elk population could not by its actions alone progressively reduce sources of forage that determined its density. . . . Presumably, feedbacks on potential increase rates from density-influenced competition for space and food prevented this elk population from <u>having consistently harmful effects on the vegetation that sustained its numbers</u>.
>
> The third hypothesis was that predation with associated scavenging (which forced more efficient predators to make additional kills) was not essential to, but assisted, the natural regulation process.
>
> . . . My restatement would be that <u>predation</u>, with associated scavenging, <u>was not essential to the natural regulation process</u>, but was accommodated by the elk population. [p. 78, emphasis added]

Houston (1971) reiterated many of Cole's views on "natural regulation." In 1971, Houston (1976a) listed the specific hypotheses being tested in Yellowstone. He also listed the methods which would be used to evaluate those hypotheses and the bases on which they and presumably "natural regulation" would be rejected. Houston began his paper by noting:

> . . . Current research is designed to test hypotheses which relate to ungulate habitat relationships, biotic succession, and <u>ecological homeostasis</u>. . . .
>
> The primary purpose of Yellowstone National Park, as a natural area, is <u>to maintain a representative ecosystem in as near pristine conditions as possible</u>. [p. 11]
>
> . . .The major concern in posing hypotheses was that they be capable of being tested and rejected, and I have not always used a formal null form (Ghent 1966). Stating hypotheses capable of unequivocal support or rejection is a problem in ecology, <u>and I suspect that those being used to guide this research program could generate lively discussions on the basis for rejection, the separation of causes from effects, the possibility of circular arguments, etc</u>. [pp. 11-12]
>
> . . . The basis for rejecting the hypothesis would be departures from natural conditions in interspecies homeostasis which resulted from an elk population eruption (<u>Caughley 1970</u>), retrogressive plant succession, or trends toward competitive exclusion among populations of sympatric native herbivores. [p. 18]
>
> . . . The hypothesis concerning sympatric herbivores will test the concepts that the natural regulation or effects from hunting the different segments of the elk population <u>will not result in competitive exclusion because of interspecific competition</u>, and that populations of herbivores associated with elk will also be naturally regulated.
>
> . . . A continuing analysis of predator-prey relationships (including rates of predation and scavenging,

> prey selection, etc.) will be used to evaluate the hypothesis that in a variably harsh environment such as Yellowstone's, predation functions as an assisting but nonessential adjunct to the regulation of ungulate population sizes [p. 19]
>
> . . . A fundamental hypothesis is that the density, composition, and successional trends of vegetation on the range do not depart from natural conditions, or that departures have not resulted from grazing by native ungulates. . . . The corollary under study is that native ungulates on ecologically complete habitat do not have a capacity to progressively deplete food supplies that ultimately determine their own densities. Stated more specifically, no unnatural effects upon vegetation will result from the natural regulation of the resident segment of the elk population. [p. 20, emphasis added]

In "A comment on the history of the northern Yellowstone elk," Houston (1975a) cited Caughley's 1970 paper to support his reinterpretations of elk population dynamics in the park.

> Subsequent reports and publication built upon and reinforced a largely incorrect historical account of the northern Yellowstone elk in a manner analogous to that reported by Caughley (1970) for the Kaibab deer of Arizona. [emphasis added]

In a letter to Montana Outdoors, Houston (1975b) again cited Caughley's 1970 paper to support Yellowstone's "natural regulation" management.

> To [referring to the State of Montana] cite the Kaibab deer myth as support for interpretations of ungulate ecology in 1975 suggests a failure to keep up with current literature in the field.

Caughley's herbivore-vegetation model was first published in 1976 and Houston (1979) apparently incorporated some of those ideas into his concept of "natural regulation."

> Caughley (1976) has pointed out that the interaction of ungulates with vegetation typically leads to a stable equilibrium (i.e. the system returns to equilibrium when displaced) at an ecological carrying capacity. A range of lower sustained yield densities may be imposed, down to or below economic carrying capacity (which produces a maximum sustained yield). [p. 270]

In 1982, Houston published his book entitled The Northern Yellowstone Elk: Ecology and Management which summarized his work in the park. He had this to say about "natural regulation":

> The general hypothesis being tested was that vegetation-ungulate equilibria appropriate to the park were possible without cropping ungulates in the park. This was operationally difficult to test, so more specific

> hypotheses were developed. One such was that vegetation on ranges occupied by elk did not depart from pristine conditions because of grazing by the elk--i.e., progressive "range deterioration" was not occurring. [p. 2] . . .
>
> The interaction of ungulates with vegetation typically leads to a stable equilibrium at an ecological carrying capacity (Caughley 1976b, 1979). A range of lower sustained yield densities may be imposed upon a population, down to or below economic carrying capacity (which produces a maximum sustained yield). As Caughley has pointed out, these concepts and their implications are not widely recognized. This has led to confusion in the management of ungulate populations--particularly those in national parks. Ecological carrying capacity (Kl) characterized by a higher standing crop of animals and a lower standing crop of edible vegetation, is usually the level that is relevant in national parks. Economic carrying capacity (Kc), characterized by much lower standing crops of animals and higher standing crops of vegetation, is of primary interest to range managers, whose objective is to maximize the yield from herds of livestock, and to game managers, whose objective is to maximize the hunting harvest from wild ungulates. [p. 62] . . .
>
> The concept of population regulation through density-dependent factors has been reviewed by Sinclair (1977), who also demonstrated such regulation from field studies of the African buffalo. A brief and oversimplified consideration of how current ideas of population regulation apply to the northern Yellowstone elk seems appropriate here. Borrowing Sinclair's terminology, a population is considered to be regulated when the attributes of natality, mortality, or dispersal show negative feedback from population density. This means that density-dependent responses increase the percentage mortality or reduce natality as a population grows. Populations may be limited by the availability of a resource such as food or by other external agents such as predation. A resource-limited population might be regulated by intraspecific competition that affects natality, mortality, or dispersal in a density-dependent fashion. [p. 67] . . .
>
> In the particular case of the northern Yellowstone elk, the absence of a wolf population does not justify resumption of human predation in the park. . . . It is unfortunate that a viable wolf population does not occur in Yellowstone, but their absence may not be as serious as sometimes suggested insofar as their effects upon elk numbers are concerned. [p. 195, emphasis added]

While citing Cole, Houston (1982) apparently relied to some extent on Caughley's plant-herbivore model instead of the logistic equation. Not only is Caughley cited on pages 62, 131, 134, and 196, but in his acknowledgments, Houston stated that Caughley reviewed Chapter 5 on elk population dynamics. Subsequently, Houston, Caughley and two others co-authored two papers under the pen name Macnab (1983, 1985) which discussed ungulate-vegetation relationships and improving wildlife science. Neither experimental management nor "natural regulation" are listed in Houston's (1982) index.

Referring to "natural regulation" Meagher (1985) wrote,

> At first, this approach was simply a moratorium, while we examined our scientific data. It was apparent that there were very little data, so the moratorium became a scientific experiment, testing whether modern man's actions are required within the boundaries of the park to regulate herd numbers.

While Cole and Houston had previously stated they were testing the "natural regulation" paradigm, as near as I can determine, this is the first time any Park Service employee referred to agency policy as a scientific experiment. This was after Chase (1983) accused the agency of mismanagement and failing to follow accepted scientific standards.

In 1986, Park Service employees (Despain et al. 1986) published a book entitled Wildlife in Transition: Man and Nature on Yellowstone's Northern Range. Since I have reviewed this popularly written book elsewhere (Kay 1987), the following quotations will be confined to what is "natural regulation"?

> And here it is important to explain the relationship between management and research. Most researchers, whether they work for a chemical company, a state fish and game agency, or a federal service, have some philosophical attachment to at least some of their employer's goals. But the responsible researcher dare not let those attachments (or the employer's demands) get in the way of objective research. Scientific research and management policies are different things. Park Service research projects are not aimed at simply supporting some established policy. Park Service researchers are not obligated to somehow prove that some management direction is the right one. That's not science; it's public relations. What Park Service research is in fact aimed at is testing and thereby helping to refine policy. It is not this process that has been taking place on the northern range, and it is the results of the test that occupy much of the rest of this book.
>
> What is going on is called "experimental management." It is, in the simplest of terms, management that is conducted as a scientific experiment so that the results can be evaluated. . . . The "great experiment," as it is sometimes called, is a test of just to what extent we can let the giant and complex ecological setting of the northern range take care of itself without human involvement. [p. 10-11] . . .
>
> One reason many were willing to let "natural regulation" have a test was that ecological science was

> also advancing. Some scientists were getting suspicious of earlier thinking regarding predators. In Yellowstone, park scientists were not convinced that Yellowstone's wolves and cougars could have kept the park's thousands of elk from increasing in numbers, and suspected that the real relationships between the park's animals might be considerably more involved than previously assumed. [p.26]
>
> . . . The important point is that, left alone animals and plants have no choice but to come to some balance. [p. 75]
>
> . . . The possibility that control-killings and transplants might not be necessary after all was intriguing, and stopping those management actions would provide scientists with a rare opportunity to test the earlier management ideas.
>
> Such a test was a startling departure from past practices, and like anything else the Park Service might have done, it had its critics, but the new approach was both scientifically valuable and politically attractive--a hard combination to beat. After all, it had been a combination of science and politics that had caused park managers to kill elk in the first place. [p. 27] . . .
>
> Throughout this book we have emphasized that current management of the northern range is experimental management. Park researchers develop hypotheses based on their best understanding of the range and on current ecological theory, and managers test those hypotheses while researchers monitor the results and then accept, reject, or modify the hypotheses. This kind of management requires more than just constant scientific attention. It also requires a willingness to admit that a theory is wrong. When the current program of natural regulation was initiated as an experiment in the late 1960's. [p. 112, emphasis added]

The wildlife profession has been amazingly silent on Yellowstone's "natural regulation" management either as policy or scientific experiment. Cayot et al. (1979) presented a short review of "natural regulation" in the Wildlife Society Bulletin. She and her co-authors were apparently members of a graduate seminar class at Colorado State University when they visited the park and wrote their paper. Their review was not based on any independent field research. Caughley (1981) referred to Yellowstone's aspen problem and Sinclair (1981) repeated Houston's explanation of the Yellowstone situation nearly verbatim.

Unlike the scientific community, the popular press, with few exceptions, has been widely enthusiastic about "natural regulation." The following comment is typical: "It is a brave and determined policy, an attempt to apply scientific knowledge in an arena where politics and presumption often have dominated" (Blonston 1983).

One could cite hundreds of similar statements which have appeared in the popular press over the years. Aside from their whole-hearted support, most of those writers had at least two other things in common. Few had any scientific training and none had either conducted a detailed analysis of existing data or collected data on their own. Moreover, many popular writers apparently had their own personal concepts of "natural regulation" which often were at odds with Park Service statements. For instance, Wright (1988:192) stated:

> . . . Rather than being a politically expedient policy, the basic premise of natural regulation has been a part of NPS management philosophy throughout the agency's existence.
>
> A more valid criticism of the use of the natural regulation strategy in Yellowstone is its diminution of the role predators play in regulating ungulate numbers.

From the material which I have presented, clearly the Park Service first developed its "natural regulation" policy only during the late 1960s and early 1970s, and according to the people who formulated that paradigm, predation does not regulate ungulate numbers. Furthermore, the agency had been artificially controlling elk numbers up through 1967 with the firm support of the Secretary of Interior's select committee on wildlife management (Leopold et al. 1963). Thus, in my judgement, Wright (1988) and most other popular writers have not had an incisive understanding of what is implied by the "natural regulation" paradigm.

To the best of my knowledge, Chase (1986) is the only author who made a detailed analysis of park management and "natural regulation." He noted:

> With one fell swoop Yellowstone biologists had defined the elk and bison problems out of existence. By a simple change of perspective, without one act of restoration, they had returned the park to its original condition. . . .
>
> Throughout the 1970's they worked on the project, mostly unnoticed by the scientific world. Although they did produce periodic progress reports, most were never published and almost none of the original data collected were readily available to the public. [p. 60] . . .
>
> For the Park Service, this silence was desirable. The task facing Houston and his colleagues was daunting. Justifying the new theory required nothing less than rewriting the entire history of the park. . . .

> This is just what they did. [p. 61] . . .
> By brilliant argument in a single equation, natural regulation had captured the scientific high ground: As an intact ecosystem Yellowstone could come to no harm so long as we did not interfere. It was a simple, compelling idea with which to dismiss criticism: range damage and interspecific competition could not exist. If potential critics believed otherwise, it was up to them to prove that these conditions existed, not up to the Park Service to show that they did not. The burden of proof had shifted from the Park Service to the public. [pp. 63-64] . . .
> That the pristine condition of Yellowstone's ecosystem remained unproven mainly escaped notice. ... And the very inaccessibility of data for and against the theory worked to its advantage. Natural regulation had developed an aura of the occult: only the initiate understood it. Independent scientists who did not know kept silent. [p. 69] . . .
> There was, besides, no stopping a simple idea whose time had come. The ecosystem, it seems, had been restored; and for many Americans the illusion of the park as a primitive ecosystem was too attractive to be denied. "Natural," according to a recent report on marketing, by the 1970's had become the most popular word in America, preferred even to "new" and "improved." Natural regulation was a triumph of packaging. [p. 70, emphasis added]

What is "natural regulation?" As with beauty, "natural regulation" often appears to be in the eye of the beholder. Not only has there never been a precise definition offered by the people who developed and applied this concept to Yellowstone, but there is even disagreement between its advocates. For instance in a letter to Dr. James Teer, Yellowstone resource manager Consolo (1989) criticized the president of The Wildlife Society for implying Yellowstone's present policy was a "no management policy." Consolo (1989) specifically said "the National Park Service has not adopted a 'no management' policy." Yet in an earlier paper, Meagher (1974) stated "bison management in Yellowstone National Park now may be termed 'no management'."

DEFINING "NATURAL REGULATION"

Even though the Park Service refers to its policy as "experimental management" (Despain et al. 1986), the agency has not provided a detailed explanation of what exactly is "natural regulation" nor explained the theoretical basis of that paradigm in recent publications

(Houston 1982, Despain et al. 1986). Thus, any definition of that model's assumptions, hypotheses, predictions, and a priori criteria for acceptance or rejection rests on earlier documents and is subject to interpretation. The definitions of "natural regulation" used in this dissertation follow Houston (1976a) and Cole (1971b, 1974, 1983) or are derived from theoretical concepts exposed by those authors.

Cole and Houston made several claims for "natural regulation." (1) Predation is an assisting but non-essential adjunct to the regulation of ungulate populations through density-dependent homeostatic mechanisms. Elk and other ungulates in Yellowstone are resource (food) limited. If wolves or other predators were present, they would only kill animals slated to die of other causes, and hence would not limit or lower ungulate populations. (2) 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, "range damage," or soil erosion. The ungulates and vegetation will reach an equilibrium where continued grazing will not change plant species composition. (3) At equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone, this means elk have not caused a decline in the numbers of other ungulates or beaver (Castor canadensis). (4) Density-dependent homeostatic mechanisms will result in relatively stable ungulate populations. Irruptions cannot occur unless there has been a drastic increase in the herbivores' food supply.

Houston (1974, 1976b) first reported the results of his research on Yellowstone's northern range in a two-volume, In-Service, report which saw limited distribution. Later, those documents were combined and appeared in his book (Houston 1982) on the northern herd. However, Houston's earlier reports and his book are not identical. Using primarily Houston's data, Despain et al. (1986) wrote a popularized version of "Man and nature on Yellowstone's northern range." In these works, the Park Service rewrote the history and ecology of elk in Yellowstone.

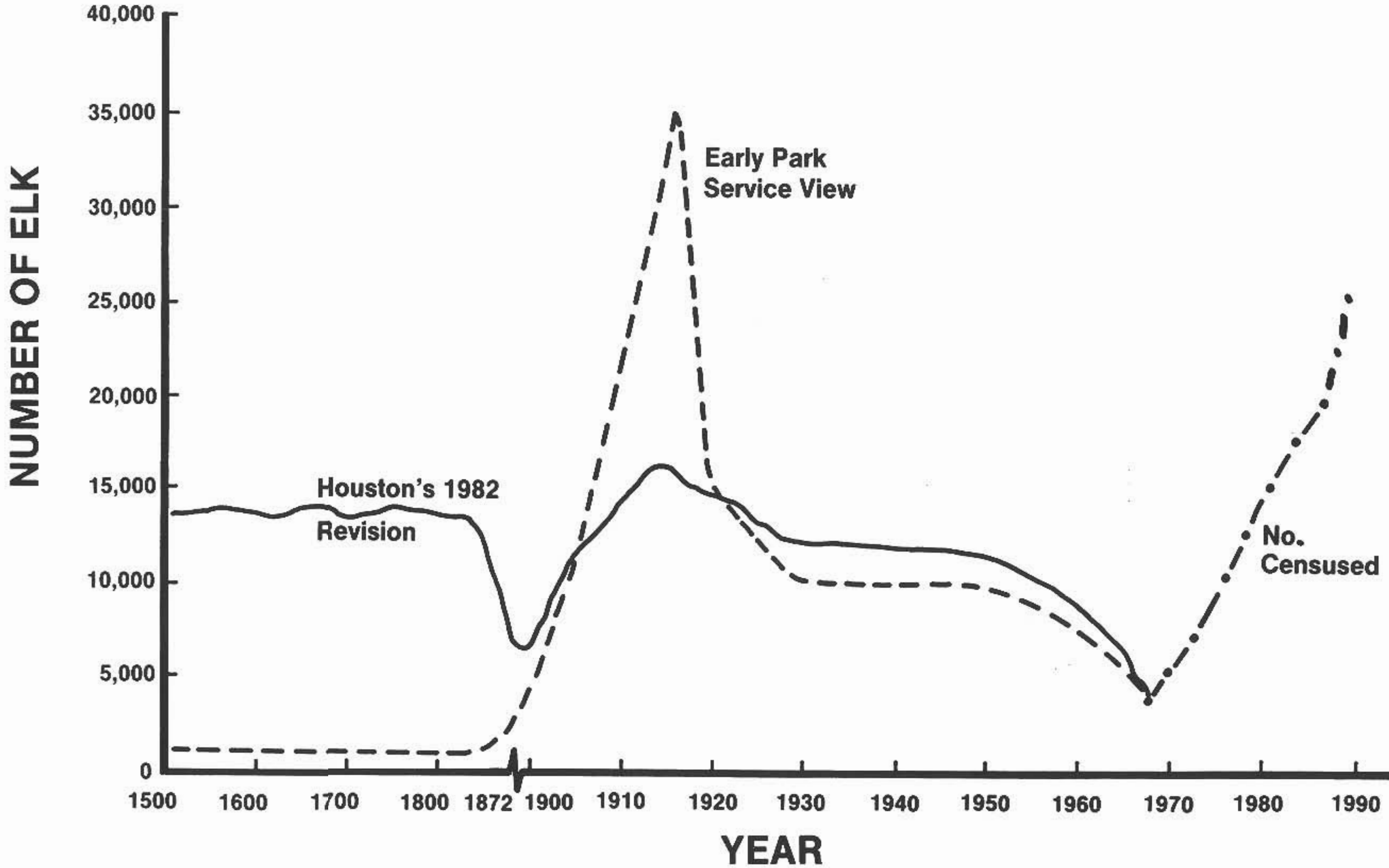
In contrast to earlier (pre-1968) Park Service interpretations, the agency now believes the following (cf. Houston 1982, Despain et al. 1986). (1) Yellowstone has always been a historic elk wintering area. (2) European settlement did not force elk to winter in the park. (3) Yellowstone's northern range is close to being an ecologically complete habitat. (4) Under protection afforded in the park, the elk herd did not irrupt to over 35,000 animals; earlier government counts of 35,000 elk were wrong. (5) There was no massive starvation and elk die off during the late 1910s; again early reports to this effect were wrong. (6) Large numbers of elk (12-15,000) have wintered on the northern range for the last several thousand (8-10,000) years. (7) Because large numbers of elk and the park's vegetation co-evolved for a long period of time, elk, vegetation, and other herbivores have been in equilibrium for several thousand years. Any recent (1872-1990) changes in plant species composition are due primarily to suppression of lightning fires, normal plant succession or climatic change, not ungulate grazing. Specifically, elk have not caused a decline in tall willow or aspen communities. (8) Elk have not competitively excluded other ungulates such as bighorn sheep, mule deer, white-tailed deer, and antelope, or beaver. Either those populations have not declined since the park was established, or if they have, it was not due to elk. (9) Since predation is an assisting but nonessential adjunct to the regulation of ungulate populations which are resource limited, reintroduction of wolves into Yellowstone would have no effect on the already established elk-vegetation equilibrium. Wolves are not necessary to "control" (limit) elk numbers.

The pre-1968 Park Service position, the "natural regulation" paradigm, and current Park Service interpretations regarding Yellowstone's northern herd are summarized in Table 2. Two views of the

Table 2. Summary of past and present Park Service interpretations regarding Yellowstone's northern elk herd and the "natural regulation" paradigm. Adapted from Cole (1971b, 1974, 1983), Houston (1971, 1974, 1975a, 1976a, 1976b, 1979, 1982), and Despain et al. (1986); see text.

Pre-1968 Park Service position	General principles of the "natural regulation" paradigm	Houston's reinterpretation of the pre-1968 Park Service position
1. Park not historic winter range; elk once migrated up to 80 km north into the Paradise Valley.	1. The species must occupy an ecologically complete habitat.	1. Large numbers of elk always wintered in the park; elk did not migrate into Paradise Valley. Thus, the park is close to being an ecologically complete habitat.
2. Elk caused extensive damage to the winter range. a) South facing hillsides overgrazed. b) Decline in aspen, willows, and other deciduous shrubs due to elk. c) Widespread elk-induced soil erosion.	2. If ungulates and the 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, soil erosion, or changes in plant stature (height).	2. Elk and vegetation in the park have co-evolved for the last 10,000 years; elk have not caused retrogressive plant succession. a) Zootic climax sites are natural b) Decline in aspen and tall willows due to suppression of naturally occurring fires, climatic change, or normal plant succession. c) Accelerated soil erosion has not occurred.
3. During the early 1900s, the elk population irrupted to around 35,000 animals then crashed due to massive starvation.	3. Density, dependent homeostatic mechanisms will result in relatively stable ungulate populations. Irruptions will not occur unless there is a drastic increase in the food supply.	3. The elk population did not irrupt and crash. At most, there were never more than 12-15,000 elk in the northern herd and that population has been relatively stable for the last several thousand years.
4. Predation limits ungulates, but wolves and mountain lions had been exterminated from the park. Native Americans used the park to a limited degree.	4. Predation is an assisting but non-essential adjunct to the regulation of ungulate populations, which are resource limited. By inference, Native Americans did not limit ungulate populations.	4. Elk numbers would not be reduced if predators were reintroduced and thus, the ungulate-vegetation equilibrium would not change if wolves were present. The few Native Americans in the park did not limit elk numbers.
5. The overpopulation of elk caused a sharp decline in the numbers of big-horn sheep, mule deer, white-tailed deer, and beaver.	5. Competitive exclusion of sympatric herbivores due to interspecific competition will not occur.	5. Bighorn sheep and mule deer populations have not declined. The decline in white-tailed deer and beaver numbers are not due to elk.

Fig. 2. Smoothed, historic population trends for Yellowstone's northern elk herd from 1500 to 1967, comparing the early Park Service view with Houston's reinterpretation. Data for 1968-1989 represent the smoothed trend of the actual number of elk counted by aerial censuses. Adapted from Houston (1982:10-25), Kay (1985), Singer et al. (1988a), and Lemke and Singer (1989).


NUMBER OF ELK
40,000
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1500
1600
1700
1800
1872
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
YEAR
Early Park
Service View
Houston's 1982
Revision
No.
Censused

smoothed, historic population trends for the northern Yellowstone herd are presented in Fig. 2. The early Park Service view contrasts with Houston's (1982) reinterpretation for the 1500-1967 period. Since reductions within the park were discontinued in 1968, the northern herd increased from just over 3,100 animals to around 25,000 in 1989 (Singer et al. 1988a, Lemke 1989, Lemke and Singer 1989, Singer 1989).

Park Service biologists attribute the herd's increase beyond Houston's (1982) equilibrium population of 12-15,000 to a series of mild winters (Merrill et al. 1988, Lemke and Singer 1989). Due to a combination of drought, the 1988 fires which burned 34% of the northern winter range, and an average winter, a Park Service-estimated 5,000 elk starved to death during the winter of 1988-89 while an additional 2,200 animals were killed by sport hunters during the late hunt outside the park (Singer et al. 1988b, Lemke 1989, Lemke and Singer 1989, Singer and Schullery 1989). Thus, approximately 1/3 of the northern herd died during the 1988-89 winter.

STUDY OBJECTIVES AND HYPOTHESES

The overall objective of this study is to test several major assumptions and predictions of the Park Service's "natural regulation" model. I generated a series of hypotheses from the "natural regulation" paradigm and then tested them by collecting data from the field or published reports.

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. (1d) 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. (1e) Other deciduous shrubs such as serviceberry (Amelanchier alnifolia), chokecherry (Prunus virginiana), buffaloberry (Shepherdia canadensis), rose (Rosa woodsii), and river birch (Betula occidentalis) have not been adversely affected by the level of elk use which has occurred on the northern range since 1872. (1f) 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.

Hypothesis two is sympatric herbivores have not been competitively excluded by elk. More specific hypotheses include the following. (2a) Over the last several thousand years, the relative abundance of elk and other ungulates on the northern range has not changed. (2b) 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 are due to factors other than elk.

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

The failure of any or all of these hypotheses is grounds for rejecting the "natural regulation" paradigm. Since "natural regulation" is an equilibrium model, it is not necessary to demonstrate that elk have affected all species. If even a few plant species have been negatively impacted by elk since creation of the park, that alone is sufficient to reject the "natural regulation" paradigm.

I chose to study aspen, willows, and other deciduous shrubs on the northern range for five reasons. First, aspen trees lend themselves to age structure analyses which cannot be performed on grasses or forbs. Second, aspen and willow can be clearly identified on old photographs which provide a historic perspective on the condition and trend of those communities over time. Again, this cannot be done with grasses or forbs. Third, woody vegetation is more sensitive to winter use by ungulates than are most grasses or forbs. Fourth, woody plants are less sensitive to variations in yearly climate (mainly precipitation) than are grasses or forbs. Thus, woody plants reflect long-term changes; trends in those communities are not obscured by annual growing conditions, as is often the case with grasses or forbs (Houston 1982). However, in the process of studying aspen and willows, I also measured understory plants in those communities. Thus, I will be able to address changes in entire plant associations.

Finally, structurally diverse woody vegetation provides critical habitat for scores of other species, such as birds and small mammals. Streamside willows are also important in maintaining fisheries habitat. Dense willow and aspen communities provide critical habitat for grizzlies (Ursus arctos), while deciduous shrubs provide critical berry crops for them. Because changes in the woody species I have selected have ramifications far beyond the loss of just those individual plant species, they can be considered barometers of the overall ecological health and diversity of the ecosystem.

This dissertation will begin with a series of five chapters comparing vegetation subjected to heavy elk use with that sustaining light or no elk use. This comparison is achieved in two ways. One is by comparing vegetation outside, but near, the park with that inside the park. In both areas, fire histories, climates, and elevations are similar, but there are fewer elk outside the park. Surprisingly, almost no effort has been directed previously to this kind of comparison where all variables but elk use are roughly comparable. The second means of comparison is measurement of vegetation inside and outside ungulate exclosures throughout the Yellowstone ecosystem.

The key question at the center of the "natural regulation" issue is whether elk and the other components of the system have been at rough equilibrium for millennia, and therefore, whether the current northern range biota is essentially similar to what it was at the time the park was established. Or if the biota has changed since the 1800s, has that change been produced by elk?

As I present data on the contemporary vegetation, I will point out certain implications that bear on the question of whether it is currently in equilibrium. But the real test of whether the system prior to park establishment, including elk numbers, was more like the northern range today or the lightly used or unused areas outside the park and in exclosures is presented in three chapters which synthesize (1) repeat photographs (2) historical reports, and (3) archaeological evidence. The final chapter summarizes the findings and discussions bearing on the original question of testing the "natural regulation" paradigm and offers an alternative hypothesis for pre-Columbian western United States ecosystems.

Establishing whether or not ungulates in Yellowstone are "naturally regulated" is important because (1) it has a bearing on that park's management direction; (2) it has bearing on similar management schemes in other national parks in the United States and around the world; and (3) in a broader context, it is a test of an ecological model which attempts to explain how all ungulate populations interact with their vegetal resources. Furthermore, if "natural regulation" is correct, ungulates do not have to be hunted or preyed upon to prevent them from damaging their environments. This would remove a major ecological rationale for sport hunting and wolf reintroduction.