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AN ECOLOGICAL RATIONALE FOR THE NATURAL OR ARTIFICIAL REGULATION OF NATIVE UNGULATES IN PARKS

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Abstract

The results from studies of both naturally and artificially regulated ungulate populations in four Rocky Mountain parks are reviewed. Study findings on population regulation processes, the role of predators, natural mortality and natality, and ungulate habitat and food relationships suggest that previous assumptions which were the basis for artificially regulating ungulates overestimated the regulatory effects of predators and did not always distinguish natural from human-influenced conditions or changes. The suggested rationale for artificially regulating native ungulates in Rocky Mountain parks is: a human influence that causes unnatural successional trends by restricting ungulates from freeranging over an ecologically complete habitat (1) cannot be removed, (2) can be rectified by artificially regulating ungulate numbers, and (3) that such regulation will not cause greater departures from natural relationships in a biological system than accepting a new equilibrium. The rationale for relying on natural regulation processes in parks is that ungulates are not causing unnatural successional trends, or the antithesis of the rationale for artificial regulation. Fundamental considerations for applying the rationale are presented.

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Introduction

Yellowstone, Glacier, Rocky Mountain, and Grand Teton National Parks are designated as natural areas. The primary objective in such areas is to preserve representative natural environments and native biota as an integrated whole (i.e., ecosystem) for their scenic, educational, cultural, and scientific values. Evolved policies for these natural areas restrict management to protecting against, removing, or compensating for human influences that cause departures from natural conditions. Management that manipulates park biota (i.e., artificial regulation) is to be based on the findings and evaluations from appropriate research.

In retrospect, the rationale for artificially regulating wild ungulates in the subject parks was not always consistent with the objectives or present management policies of natural areas. This was partly due to a paucity of ecological data on ungulate populations that were naturally regulated (i.e., without human influences) and general assumptions that were not critically evaluated.

In substance, these assumptions were: (1) that ungulate populations need to be artificially regulated to compensate for insufficient native predators, prevent progressive habitat deterioration, and/or maintain interspecies equilibriums (mean numerical stability) between large herbivores; (2) that "low" rates of increase in ungulate populations or periodic "high" overwinter mortality were unnatural phenomena; and (3) that the artificial regulation of ungulates would retain the esthetic or scientific values of biological systems to a greater extent than doing nothing.

The results from research on both naturally and artificially regulated ungulate populations within the subject parks, as well as other literature, will be used to evaluate the above assumptions and present an ecological basis for relying on natural or artificial processes. The various studies within parks involved moose (Alces alces), bison (Bison bison), mule deer (Odocoileus hemionus), elk (Cervus canadensis) and other associated faunal species. Some of these ungulate species were associated with what are usually considered large predators: grizzly bears (Ursus arctos), mountain lions (Felis concolor), and small numbers of grey wolves (Canis lupus) (Cole, 1969a). All were associated with the coyote (Canis latrans) and a variety of scavenger species. Except where other references are cited, the author's interpretations for ungulates in general are drawn from research progress reports or publications by Houston (1968, 1969, 1971a), Meagher (1970, 1971), Martinka (1969), Stevens (1970, 1971), and Cole (1969b, 1971a, 1971b). Interpretations were aided by considerations of ecological principles as presented by Elton (1927), Nicholson (1933), Allee et al. (1949), Andrewartha and Birch (1954), MacArthur (1958), and Slobodkin (1961).

Natural Regulation

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).

Unusually severe weather periodically caused higher than usual mortality in ungulate populations by increasing intraspecific competition, energy stresses, or the efficiency of predators. This mortality was also predominantly animals with low energy reserves, but individuals that would have probably survived the usual harsh weather were included. The additional mortality from the effects of unusually severe weather was considered density-independent to distinguish it from the more consistent density-influenced mortality from intraspecific competition.

Winters with less severe weather and/or intraspecific competition allowed ungulate populations to compensate for mortality that was predominantly animals with low energy reserves and return to higher numbers. Compensations occurred from density-influenced natality and/or survival or what Errington (1946) calls compensatory trends. Emigrations also helped to relieve intraspecific competition.

Ungulates that were predisposed to death by intraspecific competition or weather influences provided food for native predator and scavenger species. Predators and scavengers, as an interacting unit, tended to hasten the deaths of ungulates with the lowest energy reserves. Scavenging forced more efficient predators to make additional kills. Exceptions to the usual hastening relationships occurred when unusually severe weather increased the efficiency of grizzly predation by temporarily increasing the vulnerability of elk. Under these conditions, grizzly predation with scavenging served to dampen and extend the interval between elk population fluctuations (Cole, 1971b).

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.

Natality and Mortality

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.

Habitat and Food Relationships

Interpretations of ungulate relationships to their habitats or food sources required considerations of natural selection processes, the ecological completeness of habitats, plant succession, food sources that did or did not limit population numbers, and human actions that changed habitat and food conditions.

The fossil record (Frick, 1937; Péwé and Hopkins, 1965), suggests that the ancestors of present day ungulate populations arrived in central North America 10 to 20 thousand years before primitive man, and approximately 30 thousand years before modern man. 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, without overriding successional influences or habitat limitations imposed by man, 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. Changes in food or habitat conditions that favored certain ungulate species over others occurred from fires or floods that temporarily reversed plant succession, or the long-term trends of primary plant succession since the retreat of the last glaciers. Plant succession from pioneer substrates, in combination with interspecific competition, probably caused general trends in biological succession as shown by Figure 1.

Ecologically complete habitats for wintering ungulates (ECH) were complexes of physiographic sites such as bottomlands, upland swales, and different slope exposures and interspersions of different vegetation types and plant successional stages. Such habitats provided contingencies for ungulates to obtain food and maintain relatively stable populations in variable and periodically harsh environments. 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."

Ungulates that freeranged over ECH fully utilized the most available food sources, such as limited ridgetops or other sites that were relatively free of snow each winter. Such use maintained stabilized biotic disclimaxes or conditions that Daubenmire (1968) and Houston (1971a) describe for zootic climaxes. Trees that bordered or occurred within openings which furnished relatively greater quantities of forage to wintering ungulates were variously "high-lined" as a zootic climax. These and other zootic climaxes on sites that remained relatively free of snow were suggested to be natural by

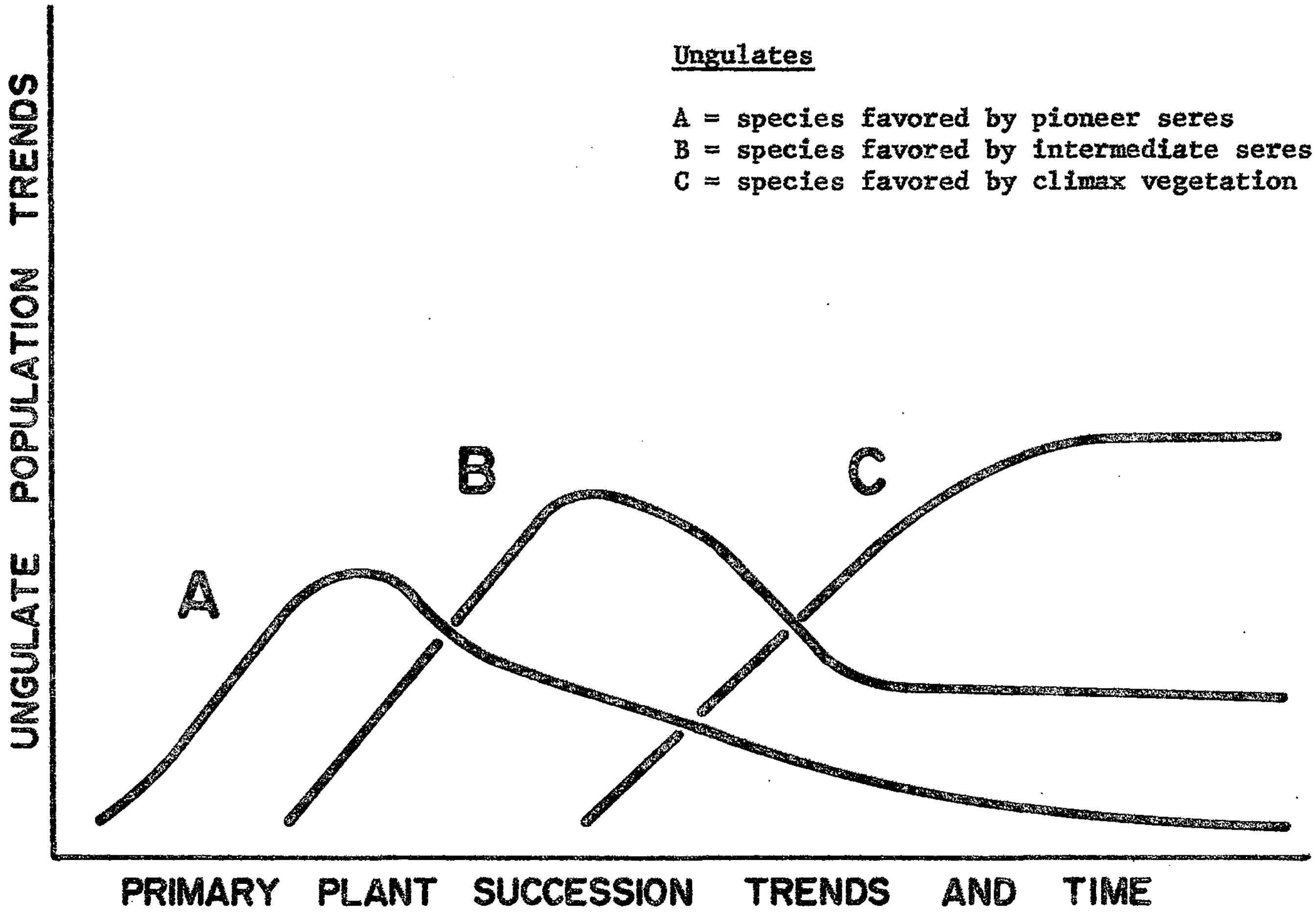

Figure 1.--Theoretical biological succession which results from primary plant succession and accompanying interspecific competition.

comparing present conditions with 1871 to early 1900 photos. Less available (due to partial or complete snow cover), but quantitatively greater food sources on other habitat areas were variably utilized by ungulates as a result of weather influences, animal preferences, or foraging actions (pawing snow or prior use).

The sites and food sources that native ungulates maintained in a zootic climax stage on ECH appeared to be too limited (less than 5 percent by area or about 1 percent of total food in three studies) to have "law of minimum" (Taylor, 1934) relationships to population numbers. This led to the conclusion that the less available but quantitatively greater food sources on ECH, in combination with successional processes (Figure 1), 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.

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.

Native ungulates did cause secondary plant succession and accelerate primary succession when they were artificially concentrated or prevented from using habitat units that were essential to maintain natural equilibriums. Ungulate species that caused secondary succession lowered their own habitat carrying capacity and sometimes increased interspecific competition. Biotic effects that accelerated primary succession hastened inevitable changes in biological systems that favored certain species more than others.

The information reviewed thus far permits some evaluation of previous assumptions that park ungulate populations 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.

The above assumptions probably resulted from overestimating the regulatory effects of native predators and interpreting all successional changes, biotic effects, or interspecific competition that involved ungulates as departures from natural conditions. These interpretations could have also been influenced by situations where ungulates did cause departures from natural conditions because they were artificially concentrated or restricted from using habitat units that were essential to natural equilibriums.

Artificial Regulation Effects

The artificial regulation of ungulate populations mainly differed from natural processes to the extent that human exploitation substituted for natural mortality, caused uncompensated mortality, or conditioned animals to avoid humans. The extent that human exploitation reduced the density-influenced mortality from ungulate populations could be expected to reduce the more consistent food sources for a native predator and scavenger fauna. Prolonged uncompensated mortality progressively reduced the most vulnerable population segments and maintained ungulate densities in relation to human-determined habitat security levels, instead of forage carrying capacities.

The regulation of ungulate populations by sport hunting, helicopter trapping, or controlled shooting resulted in avoidance behavior toward humans that was not present in naturally regulated populations. Contrasts were greatest in species that formed relatively large social groups with leader-follower relationships (elk, bison, pronghorn antelope (*Antilocapra americana*)). Conditioned avoidance behavior from prolonged hunting along park boundaries restricted the freeranging of ungulates to the extent that the animals initiated both secondary plant succession and accelerated primary succession.

Ecological Rationale

This section applies to native ungulates that were yearlong inhabitants or had ecologically complete winter habitats within the subject parks. Other ungulates that regularly ranged outside these parks were managed under the rationale that sustained hunter harvests could substitute for most predestined natural mortality and maintain higher than natural natality rates.

The ecological rationale or justification for artificially regulating native ungulates within the Rocky Mountain parks is considered to be as follows: A human influence that causes unnatural trends in biological succession by restricting ungulates from free-ranging over an ECH (1) cannot be removed, (2) can be rectified by artificially regulating ungulate numbers, and (3) that such regulation will not cause greater departures from natural relationships in an interspecies system than accepting a new equilibrium. 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, or the antithesis of the rationale for artificial regulation (1-3).

A fundamental consideration in applying these rationale is that the presence of humans must be distinguished from their significant ecological effects (Houston, 1971b). The latter mainly occurs when humans divert sufficient amounts of energy or substances to or from a native biota to change species numbers or ecosystem roles. The permanence of human effects should be assessed from an awareness that ecosystems can "repair themselves" after severe natural catastrophies. Other considerations are that primary plant succession changes toward or into the next sere cannot be reversed by eliminating biotic effects. Also, regulating one ungulate species may allow other herbivores to have the same end effects.

Accepting a new equilibrium that occurred with accelerated primary succession may result in fewer departures from natural relationships in interspecies systems than artificially regulating a dominant herbivore on a sustained basis. The ecological role an absent or poorly represented predator species once had may be wholly or partially reinstated by other species in the secondary consumer niche.

Discussion

The foregoing rationale was largely suggested from quantitative field studies of ungulate habits, population dynamics, and ecological relationships. These first began in 1962. Tests of appropriate hypotheses are still being carried out on a continuing basis to permit critical evaluations over time. The paper's intended purpose is to show that the objectives of preserving or restoring the esthetic and scientific values of representative natural ecosystems or their community units require broad ecological considerations. It also shows that a rationale which relates to National Park Service objectives will be considerably different from those where native ungulates are intentionally managed as a harvestable crop. Research which tests the appropriateness of the Rocky Mountain rationale to large herbivores in other parks is encouraged.

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