

THE CONCEPT OF OVERGRAZING AND ITS
APPLICATION TO YELLOWSTONE'S NORTHERN RANGE

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Abstract

The management of the large ungulate herbivores, especially elk (Cervus elaphus) and bison (Bison bison) in Yellowstone National Park has been controversial almost since the park's establishment in 1872. A historical review of the concept of overgrazing on Yellowstone's northern range was conducted. A perception of overgrazing that started in the 19-teens and that intensified due to the drought of 1919-1936, was predicated upon the premises that 1) elk increased due to protection within the park, 2) the idea that few elk wintered in the park prior to 1878, and that instead elk had migrated out of the park each winter and 3) that ranching outside the park excluded elk from winter ranges and that unrestricted harvests helped to eliminate migration patterns.

Early application of the concept of overgrazing followed directly from experience in range management. Ungulates were artificially regulated until 1968 when artificial reductions were terminated on the premise that the park elk occurred on an ecologically complete habitat and that their abundance would be naturally regulated - ie. the Yellowstone natural regulation experiment. The Yellowstone hypothesis resulted from theories in equilibrial population ecology developed in the 1960's, and it's associated concept of overgrazing differed from that used by range managers.

We compare the Yellowstone natural regulation hypothesis to four other models or concepts of overgrazing; a) range management, b) wildlife manager, c) the Caughley model, and d) the persistence model. The Yellowstone hypothesis was intermediate in conservatism, rejecting 12 of 19 hypothetical plant, animal or soil responses to grazing. The most liberal model, the Caughley model rejected only four responses. The Yellowstone natural regulation hypothesis was explicit in demanding reference to a balanced or equilibrial state, however since the time of formulation of the hypothesis (Cole 1971) ecologists have found that: a) nature is not necessarily equilibrial and homeostasis may be imprecise especially at small spatial scales and in climatically variable environments, b) populations may be strongly limited by density independent factors, c) multiple equilibria, catastrophes, and even chaotic behavior are possible in systems with non-linear feedback mechanisms and d) mechanisms of persistence or endurance may be of equal or greater importance than homeostasis.

Introduction

The concept of overgrazing is meaningless and overgrazing is not possible in a completely natural system. However, there is widespread concern that Yellowstone National Park is no longer completely natural. In 1986 Congress directed the National Park Service to "start a study on Yellowstone to see whether there is evidence of overgrazing (and) what should be done to avoid that ..." (Congressional Record - Senate, S 12613, September 16, 1986). National Park Service policy also states that "Natural processes will be relied upon to control populations of native species to the greatest extent possible. Unnatural concentrations of native species caused by human activities will be controlled if the activities causing the concentrations cannot be controlled" (U.S. Dept. of Interior 1988).

We suggest that there are three difficulties associated with definition and implementation of the concept of overgrazing. First, the demarcation between proper grazing and overgrazing is not sharp as grazing severity varies along a continuum. Second, overgrazing is defined in the context of a stated objective and specific criteria are related explicitly to that objective. Third, recognition and definition of overgrazing depends on current understanding of plant responses to climate and herbivory, and natural interactions between plants, herbivores and predators. Therefore, concepts of overgrazing depend on the current state of ecological science.

Application of the concept in Yellowstone National Park requires that overgrazing be defined relative to the goal of regulation by natural processes. Definition of overgrazing depends upon ability to identify natural processes and mechanisms of natural regulation. In line with this objective, Yellowstone National Park embarked in 1968 on an experimental program of natural regulation management of the large ungulates of the park's northern range (Cole 1971, Houston 1971). Prior to that date

elk, bison, and antelope were artificially controlled.

The purpose of this paper is to examine the history of the concept of overgrazing in general and as applied in Yellowstone. An historical approach is adopted to reveal the manner in which the concept has changed in relation to changes in natural conditions, changes in human influence on the system over time, and scientific advances. We will review changes in ecological theory that have occurred since the time the natural regulation experiment was formulated (1971) and discuss how those changes might affect the concept of natural regulation. Ecology since 1971 has become more concerned with the validity of equilibrial assumptions (Weins 1977, Connell and Sousa 1983, DeAngelis and Waterhouse 1988), particularly in variable environments and small spatial scales.

We compare concepts of overgrazing as used by a range manager, a wildlife manager, a model of natural regulation (Caughley 1976), the Yellowstone natural regulation hypothesis, and a model of natural regulation that is less dependent on equilibrial assumptions.

History of the Concept of Overgrazing in Yellowstone

1872-1886, Continued Hunting of Elk

Yellowstone National Park was established in 1872. The hunting of elk (Cervus elaphus) was banned in 1883. But from then until the U.S. Army assumed administration of the park in 1886, poaching and market hunting of elk continued. There was no evidence of concern for overgrazing during this period.

1886-1916, Era of Protection by U.S. Army

The Army progressively eliminated the hunting of elk during this period. A protectionist attitude developed toward native ungulates that included supplemental winter feeding and predator control.

The concept of overgrazing was first introduced. In 1887 Lt. Lindsley estimated there was summer range enough for 40000 elk, but only enough winter range for 1/4 that number. In 1895 Acting Superintendent Anderson remarked that a series of mild winters could make elk more numerous than the food supply could support (Houston 1982). The perception was that there were too many elk confined to too small an area (Graves and Nelson 1919). On the other hand Ranger Depuis who worked there from 1910-1924 said, "grass was knee deep and moisture was plentiful". He felt there was plenty of range grass and that the northern range was not overgrazed (Edwards 1931).

1916-1930, Era of Near-Agricultural Philosophy, Dry Weather

Artificial feeding of elk continued near Mammoth and the last park wolf was eliminated in 1926 (Weaver 1978). The perception of an overpopulated elk herd intensified during this period. High wintering densities were felt to be unnatural (Skinner 1928, Cahalane 1941) and due to: 1) protection of elk in the park 2) the idea that few elk wintered in the park prior to 1878, and that instead elk had migrated far down the Paradise Valley each winter 3) ranching development outside the park excluded elk from using these traditional winter ranges while unrestricted hunting eliminated the migration.

The summer of 1919 was very dry and that winter Rush (1932) reported "there was no forage on the winter range at all". Park staff estimated that 6000 animals

starved that winter (Grimm 1945). While Houston later questioned the precise number (1979), clearly a large die-off did occur.

Dry conditions greatly influenced perceptions of overgrazing. An army scout, George Whittaker stated that "During those years of plentiful moisture, no depletion of the range was noticed, but generally dry conditions since 1926 caused the ranges to have a look of apparent overgrazing" (Edwards 1931). The summers of 1919 and 1921 were dry and 1926 was so dry that many natural springs in Slough Creek stopped flowing (Edwards 1931).

1931-1968, Artificial Regulation of Elk, Drought and Recovery

The drought continued and intensified through 1936. Rush (1932) made a subjective assessment of changes since 1914 and to him it appeared that 1-2" of topsoil had eroded and that the grass was badly disturbed. Browse species were being heavily utilized. In 1933 a grasshopper infestation coincided with dry growing conditions (Wright 1934). LaNoue (1936) summarized the thinking of the day on the range's evidence of deterioration. This included: 1) soil erosion, 2) disappearance of herbaceous cover, 3) damage to tree growth 4) poor elk physical condition at winter's end and 5) periodic large elk winter kill. Grimm (1935) reported erosion and denudation of plant cover aggravated by elk. Willows were dying at Slough Creek due to drought and grazing. The first scientific studies using grazing exclosures indicated that the decrease in plant density from 1930-37 was 43% inside exclosures and 59% outside exclosures (Grimm 1937).

Growing conditions improved in 1937 and grass production nearly tripled by 1942 (LaNoue 1941). Still, Gammill (1939) reported that "the area looks as if part of the grass had been washed away leaving the remaining tufts aboveground level... with bare

soil below". Gammill (1940) also reported a significant increase in plant density, but stated there was only 50% recovery from the drought. Despite the wetter conditions aspen and willow continued to decrease, and in 1943 Grimm reported that the amount of browse from willow and aspen was too small to even factor into elk forage requirements.

Range monitoring started by Rush, Gammill and LaNoue and continued by Kittams through 1958 concluded that: 1) big sagebrush declined dramatically on the part of the northern range (near Gardiner) that is preferred by antelope (Grimm 1945), 2) aspen sprouts were heavily browsed and there was a net decline in shoot height (Kittams 1949, Barmore 1968), 3) willows greatly declined in abundance (Kittams 1948, Wright 1934), 4) sparse vegetative cover and degree of bare soil was a result of soil erosion from overgrazing (Wright 1934, Cahalane 1943), 5) elk were competing with other ungulates (Mills 1935, Gammill 1941), 6) there was retrogression in the grasslands from bluebunch wheatgrass to bluegrasses (Kittams 1948).

Pengelly (1963) proposed that evidence for overgrazing would include: 1) reduced plant cover, 2) more runoff, 3) less organic matter on the ground, 4) drier soil, 5) a drier type of vegetation, 6) less fescue and bluebunch wheatgrass, 7) more space between bunchgrasses, 8) greater relative abundance of more short-statured grass species, 9) increase in perennial forbs, 10) increased wind erosion.

This period of drought and recovery is typified by Wright's (1934) conclusion that the range was in deplorable condition and Kittams' (1952) conclusion that the range was in a seriously deteriorated condition. Superintendent Garrison decided in 1956 that there was a need to restore a balance between ungulates and the range. In 1962 the elk cull was increased dramatically and elk numbers were reduced to less than 3200 by 1968.

1969-Present, Natural Regulation Experiment

In 1968 artificial reductions of elk, bison and pronghorns in Yellowstone were terminated on the premise that most of the park elk occurred on an ecologically complete habitat and that their abundance would be naturally regulated (Cole 1971, Houston 1976). Cole (1971) defined the natural regulation of ungulates on Yellowstone National Park as: "Over a period of years, naturally regulated ungulate populations were self regulating units. They regulated their own mortality and compensatory 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 completion for food."

The natural regulation experiment depended upon the assumptions that: 1) the park elk exist in an ecologically complete habitat, 2) hunting by Indians was insignificant (Houston 1976, 1982), 3) predation by wolves and other predators was non-essential for regulation of populations (Houston 1971, Cole 1971). Bases for rejection of the natural regulation hypothesis included (Houston 1976): 1) eruption of elk population, 2) retrogressive plant succession, 3) competitive exclusion among previously sympatric ungulates, 4) population eruptions among sympatric ungulates, 5) a significant effect of natural predation on elk population fluctuations.

Houston (1982) reached nearly diametrically opposed conclusions on the condition of the northern range relative to earlier reports. He concluded: 1) the decline of sagebrush on the antelope winter range was probably due to removal of heavy livestock grazing, 2) willow decline was probably induced by drier climate, 3) there was no real evidence for widespread soil erosion, 4) fluctuation in abundance of perennial grasses were more the result of fluctuating growing conditions (especially rainfall) than due to

ungulate densities.

The natural regulation experiment has been controversial. Ellig (1975) argued that natural regulation resulted in: 1) chronic famine of elk, 2) adverse effects on other species, 3) accelerated soil erosion, 4) reductions of certain woody species and 5) accelerated streambank erosion. Ellig felt that the northern elk were not controlling their own population sizes and although the impact of predation and Indian hunting was debatable, wolves had likely influenced elk population sizes in severe winters. Cayot et al (1979) concluded that most of the traditional winter range seemed intact and that vegetative conditions on zootic climax sites were natural. Peek (1980) concluded that a test of natural regulation in Yellowstone and the existence of a natural zootic climax vegetation could not be realized as long as fire and wolves were excluded from the system. Caughley (1983) pointed out some fallacies of artificial regulation (culling) to prevent overgrazing. Among these were: 1) increaser plant species can provide ground cover after a bout of heavy grazing, 2) culling during an eruption weakens the system's feedback mechanisms and may delay the ultimate equilibrium, 3) culling may drive the system to a less stable state. Kay (1984), however, concluded that elk in Yellowstone were not being naturally regulated because 1) willow and aspen declines were evidence of retrogressive succession, 2) the elk population had not stabilized even in the 1980s. Kay (1987) also criticized Houston (1982) for having no detailed statement of hypotheses, methods for evaluation and basis for rejection of the natural regulation hypothesis. He argued that since no experimental control for the experiment had been identified, the hypothesis was not falsifiable. Chase (1986) reiterated many earlier concerns. He echoed Garrison's (1956) beliefs that Yellowstone was by nature, a hostile habitat for elk, and that harsh winters and predation by bears, wolves and Indians were the agents for maintaining low elk populations. Chase argued that Yellowstone is therefore, not an intact ecosystem so natural regulation is

not possible. Mahlein (1987) largely supported Chase's contentions, and concluded that excessive human interference with the system early in the history of the Park precluded a complete policy of natural regulation in the present. Baur (1987) disagreed with Chase and indicated that the natural regulation policy was integral to National Park Service policy and could be traced to the agency's origins at the turn of the century. He felt that the solution was not to abandon natural regulation but to implement measures that would contribute to its success.

Historical Developments in Range Ecology

When Roosevelt first recommended scientific management of Yellowstone elk in 1915, the science of range ecology was just emerging. After decades of open range livestock exploitation, the task of identifying overgrazing had become a necessity. Overgrazing was viewed as a condition resulting from "a stocking rate that kept plants so grazed down that they could neither develop nor get essential elements from the air" (Barnes 1913).

Natural revegetation of degraded rangelands was studied on the basis of plant growth requirements and life histories (Sampson 1914). Concepts of a natural succession of plants towards a climax equilibrium were developed (Clements 1916) and these concepts were implemented to determine the degree to which grazing had caused retrogression from the equilibrium state (Sampson 1919). Clementsian climax concepts have constituted the framework for range studies for quite some time (Weaver and Clements 1938, Dyksterhius 1949, Parker 1952).

While succession-based classification may measure departure from theorized climax, it does not necessarily provide a relationship between current stocking rate and the

direction or rate of departure (trend). Determination of overgrazing is based on observations of effects of stocking rate on range trend, as determined through trial and error (grazing trials). Stocking rates are implemented to achieve a balance between retrogressive effects of grazing and natural tendencies of succession towards climax. Thus in the final analysis, "no accurate method of grazing-capacity determination has yet been devised which does not rely upon extensive experience founded upon comparable range of proved grazing capacity" (Stoddart and Smith 1955).

The conceptual background of early range management is relevant to historical accounts of overgrazing in Yellowstone. Range science developed following widespread degradation of rangelands by livestock through unregulated grazing. This was followed by a period of drought and recovery from drought. In both periods external perturbations had clearly moved the system away from a perceived state of balance, as judged by reference to the prior idealized climax vegetation. A clear pattern of retrogression from climax to bare ground had been outlined. This framework, based on deviation in vegetation state from an ideal equilibrium has been the basis for most Yellowstone overgrazing statements. Unfortunately, many of the early overgrazing statements were based on subjective judgement relative to this framework rather than controlled studies of changes in condition (trend) as affected by stocking rate (ie. grazing trials).

This concept of overgrazing can be difficult to implement in the context of the objective of the natural process mandate for National Parks. First, it presumes that an ideal balance between vegetation and herbivores is maintained by anthropogenic control. If climate change shifts the appropriate balance, stocking rate must be adjusted by the rancher. Anthropogenic mis-manipulation of stocking rate may result in retrogression or range deterioration, but there is no parallel in natural systems. If stocking rate is not under anthropogenic control, then this concept of overgrazing is

ambiguous and of limited value. However, if the National Park is in fact not a naturally regulated system, then the concept becomes more relevant. The second problem is that this concept assumes the equilibrium will always shift continuously and reversibly. As Westoby et al. (1989) argued, this may not be a valid assumption. A third problem is that the concept fails to account for temporary but natural imbalance arising from imperfect adjustments of herbivores to changes in climate and vegetation.

Experimental and Explanatory Approaches

Experimental approaches have been used to determine grazing tolerance and its causes at the level of a single plant or sward. Many experimental approaches have strived for a physiological basis for defoliation response. An era of grazing and defoliation experiments was summarized by Jameson (1963). Some of the earliest and most important studies along these lines were: Aldous (1930), Sampson and McCarty (1930), Parker and Sampson 1931), Crider (1955) and Weaver and Darland (1947). Recently, knowledge of the physiology of individual plant species has come to be recognized as an important prerequisite for proper range management (Sosebee 1977). Specific traits and mechanisms that are responsible for plant resistance or tolerance of herbivory, or lack thereof, are well known (Youngner 1972, Archer and Tieszen 1980, McNaughton 1983, Caldwell 1984). However, biological variability is high and specific cases are often poorly known. Some of the resistance or tolerance conferring traits may have arisen as adaptations for other purposes, such as ability to withstand arid and semiarid climates and many traits are in fact highly interactive processes (Coughenour 1985). The concept of compensatory growth, supported by a thorough review of underlying mechanisms (McNaughton 1979,1983), represented a significant departure

from the simple view that plants are harmed in direct proportion to the biomass removed. Detailed systems modeling of interactions between physiological processes and morphometric traits (Coughenour et al. 1983a, 1983b, Coughenour 1984) established that a quantifiable mechanistic basis for herbivory responses can be formulated.

Numerous grazing exclosures erected as early as 1930 in Yellowstone have been used more for monitoring than for hypothesis testing or mechanistic explanation, however, dominant grass species of the Northern Range have been studied in a more controlled manner outside of Yellowstone (eg. McIlvanie 1942, Blaisdell and Pechanec 1949, Pond 1957, Mueggler 1972) and more explanatory, hypothesis-driven studies are now in progress on the northern range.

Developments in Population and Community Ecology

Equilibrium Views Give Rise to Natural Regulation Hypotheses

The concept of overgrazing in Yellowstone post-1970 is largely derived from theories of natural population regulation.

While the term "carrying capacity" was used by early range managers in reference to an appropriate stocking rate, ecological usage is more accurately traced back to Malthus, who in 1798 hypothesized that there were intrinsic limits on geometric human population growth. Later (1838) Verhulst formulated a logistic population model with a parameter (K) representing the maximum population size due to an absolute limit on rate of food supply (Hutchinson 1978).

This theory led to the concept of intrinsic balance between the size of a consumer population and its food resources (Nicholson 1933). Nicholson deduced that since there are observable relations between population sizes and resource abundance, there must

be an underlying tendency toward balance between the two. Nicholson argued that the controlling factor on population must ultimately be some process which acts proportional to population density, particularly increasing competition for limiting food. Most ecologists in the 1930s and 1940s adhered to this hypothesis of density-dependent regulation (Krebs 1972). Lack's (1954) book on natural regulation was very influential in promoting this view.

Mathematical analysis was also applied to predator-prey interactions (Lotka 1925, Volterra 1926). This theory predicted that damped cyclic population fluctuations or stable limit cycles would occur about a theoretical equilibrium between predators and prey. A substantial body of mathematical theory arose in the 1960s and 1970s based upon assumptions that population dynamics are controlled principally by this type of biotic interaction (predation and competition). The underlying assumption was always an intrinsic equilibrium or balance between biotic components. The mathematical conditions leading to stable oscillations, dampened oscillations or divergent oscillations in predator-prey systems were graphically developed by Rosensweig and MacArthur (1963).

This equilibrial predator-prey theory was the underpinning of the theory of ungulate population regulation which influenced formulation of the Yellowstone Natural Regulation experiment. Caughley's (1970, 1976) analyses of the phenomena of ungulate population eruptions due to introduction or colonization of new habitat, followed by damped oscillations and minor subsequent eruptions due to disturbance was influential in the Yellowstone hypothesis. Sinclair (1977) found this body of theory useful in his studies on population control in African buffalo following release from Rinderpest disease. This model was viewed as being relevant for Yellowstone because of the potential effect of release of elk from decades of artificial regulation.

Non-Equilibrium Views Prior to the Natural Regulation Hypothesis

Although the equilibrium-dynamic systems theory is highly developed, it is not the only relevant framework for ecology. A earlier, different school of thought (Uvarov 1931) espoused the theory that climate ultimately controls population size, but this school apparently fell into disrepute when the Nicholsonian view emerged (Krebs 1972). An accumulation of empirical data later led Andrewartha and Birch (1954) to support the theory once again. This theory proposed that population sizes could be determined primarily by extrinsic abiotic controls affecting the time that growth rate remains positive, and by periodic density independent mortality.

Later an attempt was made to fuse the density dependent (DD) and density independent (DI) views (Huffaker and Messenger 1964) by theorizing that DI is important in variable environments where intrinsic growth rate is more important, and DD is important in predictable environments where competition is important.

Post-Natural Regulation Views of Ecological Systems

A series of important developments have occurred since the original formulation of the Yellowstone natural regulation experiment. Equilibrium predator-prey theory was the foundation for Noy-Meir's (1975) mathematical analyses of the way range vegetation stability varies as a function of manipulated, fixed stocking rate. Depending on the responses of plant growth and herbivore intake to plant abundance, range vegetation could be forced to extinction, achieve a low production steady-state (equilibrium) with livestock, or achieve a high production steady-state with livestock. Sudden transitions from the high to the low steady state could arise, which have since been interpreted in the light of catastrophe theory (May 1977).

Another group of ecologists, working with insect defoliators and fisheries (Holling 1973, Peterman et al 1979), developed a theory of multiple stability domains. As long as the system remained in a given stability domain, it would tend to move towards the equilibrium in that domain. The theory also allowed for continual shifting of boundaries of domains due to processes of natural selection. The models of Caughley also recognize multiple stability domains (Caughley 1976, 1979). Along these lines, Walker et al. (1981) found multiple stability domains in analyses of savanna grazing systems. They hypothesized that periodic heavy grazing may promote changes in species composition that reduces sensitivity to future episodes of heavy grazing.

More recently, theory of catastrophes and stability domains has shown that chaotic behavior arises with certain parameterizations, or in response to periodic forcing (climate); or systems may exhibit chaotic sensitivity to initial conditions. This is paradoxical because these systems are mathematically deterministic, with non-linear, density-dependent feedback control (Schaffer and Kot 1985). Predators and prey may exhibit odd shaped, and seemingly unpredictable dynamics about an underlying "strange attractor". Although population sizes fluctuate non-periodically or chaotically, order and stability still exist because movement is confined to the attractor domain.

A more non-equilibrium view has been recently suggested as more useful for explaining transitions among vegetation states (Westoby et al. 1989). These authors maintain that equilibrium based models of succession have limited ability to predict sudden, catastrophic changes in species composition. Instead, it is more useful to admit such changes are likely, and to identify the sets of conditions or rules which govern these transitions.

The idea that non-equilibrium dynamics may be caused by density-independent effects on populations is supported by a large body of more recent evidence. For example, Weins (1974,1984) convincingly argued that the world is often non-equilibrium

because the underlying assumption that biotic interactions exclusively govern community patterns is often false. Weins also suggested that there is a gradient from non-equilibrium to equilibrium systems spanning the range from climatically variable habitats that are unsaturated with competing organisms to predictable habitats that are nearly saturated with competing organisms.

An evaluation of the evidence needed to judge ecological stability (Connell and Sousa 1983) indicated a continuum of dynamical variability, with no clear boundary between equilibrial and non-equilibrial systems. The authors concluded there were few examples of stable periodic oscillations, and no evidence of multiple stability domains. They suggested that long term persistence with bounded stochastic variation was a more meaningful concept than stability about an equilibrium point.

Developments in ecological theory since formulation of the natural regulation hypothesis (Cole 1971) have incorporated equilibrial and non-equilibrial views into a more globally applicable framework. A thorough review (DeAngelis and Waterhouse 1987) has shown that simple deterministic equilibrial models are insufficient due to instabilities caused by non-linear feedbacks and time-lags in biological interactions, and stochasticity and density independent effects, and forcing by fluctuating environments. Persistence under non-equilibrium may be facilitated by herbivore movement from grazed to ungrazed areas, or by an ability of plant populations to survive at low densities (DeAngelis and Waterhouse 1987) or as an ungrazeable reserve (Noy-Meir 1975).

Non-equilibrial processes are extremely important in pastoral ecosystems of arid and semi-arid environments that are often strongly controlled by external forces rather than internal biotic interactions (Ellis and Swift 1988). These ecologists argued that assumptions of strong biotic interaction between livestock and plants have often resulted in ineffective or adverse range management policies. They found that periodic

drought inevitably reduces plant and herbivore populations, but compensatory response mechanisms promote endurance, recovery and long term persistence.

These concepts are relevant in Yellowstone because: a) variance in winter severity directly affects elk (Houston 1982, M. Boyce in prep.) and bison (Maegher 1971,1973) (eg. severe winters in the mid-late 1800's, mild winters over the last several years), thus causing large shifts in the number of animals per unit of plant growth; b) long-term climate and fire histories may have caused long-term change in vegetation that is not limiting to elk but is nevertheless eaten (ie. browse); c) time-lags in herbivore responses to rapidly decreasing food supply are possible - for example drought may have reduced the ability of plants to withstand grazing in 1919 before a die-off that winter and; d) migration patterns are labile rather than immutable (Maegher 1989), therefore increases in use of certain areas may cause vegetation changes simply because of local changes in grazing pressure.

Effects of Spatial Scale

Stable equilibrium states should not be viewed as a fundamental property of ecological systems except by extrapolation to large spatial scales (Deangelis and Waterhouse 1987). As spatial scale increases, more local instabilities are averaged, dampened, or compensated for - so that the idealized level of stability may only be achieved at large spatial scales. Brown and Allen (1989) also pointed out that grazing impacts are highly scale dependent. While negative effects may accrue to individual plants, effects at the community or ecosystem scales may be neutral or positive.

Persistence of small scale ecosystems may depend on the states of and interactions with other surrounding small scale systems to achieve stability at the larger scale. While intermixing of regional herds in the Yellowstone-Teton region may normally be

minimal (Cole 1969, Houston 1982), infrequent instabilities could conceivably result in dispersion. Thus, while the northern range plant-herbivore system may be non-equilibrial, the larger scale system of regional herds may be stable as a whole. Local seasonal movements can also be important as a means of regulating animal density in relation to local spatial and temporal variability of plant resources. Thus an ecologically complete habitat "provided contingencies for ungulates to obtain food and maintain relatively stable populations in variable and periodically harsh environments" (Cole 1971), and "interspersed of different habitats" provided a carrying capacity that was "greater than the sum of the parts" (Cole 1969, 1971).

Predator Control and Food Limitation

Overgrazing could occur if an herbivore population is normally controlled by predators rather than limited by food, and predator control is removed. The question of whether herbivore populations are food limited or predator controlled has not been resolved. This question is critical to the natural regulation hypothesis which assumes food limitation is critical, with predation as an unnecessary adjunct (Cole 1971). Food seems to limit herbivore populations in many grazing ecosystems (Bobeck 1977, Sinclair 1977, Sinclair and Norton-Griffiths 1983, Sinclair et al 1985, Skogland 1985, Fryxell 1987), however predators seem to be more limiting in other systems (Caughley 1976, Smuts 1978, Bergerud et al. 1983, Messier and Crete 1985, Borner et al. 1987, Fryxell et al. 1988).

The question of whether predators control large mammals is a topic of debate at present (Sinclair in press, Bergerud et al 1983, Messier and Crete 1985). Supportive evidence is that: 1) bear predation on newborn caribou (Rangifer tarandus) (Singer 1986), moose (Alces alces) (Franzman et al. 1980) and elk (Shlegal 1973, Singer and

Harting unpubl. data) can be very significant; 2) unregulated wolf increases coupled with severe winters and in some cases harvesting by man has resulted in decreased ungulate populations (Gasaway et al 1983, Bergerud et al. 1983, Messier and Crete 1985). There is a recent (i.e. 1970's onward) growing perception that predator control is more important in N. America (Keith 1974, Bergerud 1988), as many wolf populations increased following cessation of wolf control programs.

However, evidence of true regulation is lacking (Sinclair in press). Predator numbers and predation rates may simply be small relative to the rate of herbivore increase. Alternatively, multiple equilibrium theory predicts that herbivores may be held near a lower steady state by predation but herbivores may escape predator control and become limited instead by food at a higher equilibrium. Predators may hold prey into the lower "predator pit" (Walker and Noy Meir 1982, Messier and Crete 1985), but periodic eruptions may occur if herbivore intrinsic rates of increase are high and if herbivore reproduction responds rapidly to a favorable variation in climatic conditions. Another question is whether periodic herbivore movement beyond predator territories may decrease effectiveness of predator control (Sinclair 1979, Fryxell et al. 1988).

In 1960 it was argued (Hairston et al. 1960) that herbivores must be predator limited because uneaten vegetation is abundant. This argument has since been questioned. Many studies have shown that all plant material is not really food. Plants are often unpalatable because of high concentrations of secondary or other indigestible compounds or low concentrations of protein and minerals. Carrying capacity for large herbivores cannot be computed without considering the frequency distribution of food ranked by quality (Hobbs and Swift 1985). The temporal aspect of food quality is important as well, as the duration of the non-growing season may strongly influence ungulate survival (Fryxell 1987). Calculations which account for food quality distributions and temporal duration are needed for accurate prediction of food

limitation.

Comparison of Different Hypotheses Relevant to Overgrazing

Scope, Models and Ground Rules

The concept of overgrazing employed by an idealized range manager, a wildlife manager, by the Caughley model (Caughley 1970,1976,1979), and by the hypothesis of natural regulation as implemented in Yellowstone (Houston 1971, Cole 1971) differ with respect to their acceptance or rejection of various consequences of herbivory (Table 1). The objectives of range and wildlife managers are maximum sustained production of herbivores. The natural regulation hypothesis aims for preservation of natural processes. These three are clearly based on an equilibrial view, but differ in that the equilibrium may be artificially or naturally achieved.

The Caughley model was derived from equilibrial predator prey theory. It accommodates an initial disequilibrial condition provided this is followed by damped oscillation and convergence to equilibrium. This model recognizes multiple equilibria, and distinguishes full-scale eruptions due to colonization of new habitat or release from disease or predation, and sub-eruptions which are induced by some minor change in habitat or animal density (Caughley 1979).

We also suggest a model that might be termed the persistence model, that puts even more emphasis on the importance of climatically driven variance, accommodates intrinsic instability of population dynamics due to time lags, climatic forcing, unique climatic events and unique combinations of climate and herbivory. This does not

preclude a role for feedback regulation through food limitation; it simply implies that regulation may be imprecise or even ineffective in many cases, especially in variable environments. Disequilibrium at small spatial scales may be natural, but there must be demonstrated mechanisms of persistence that ensure long term stability and ecosystem-level integrity. The persistence model is based on concepts of Connell and Sousa (1987), DeAngelis and Waterhouse (1988), Ellis and Swift (1988) and Westoby et al. (1989).

This comparison will only consider effects induced by herbivory. Direct effects of climate or fire on vegetation are not considered, and none of the criteria can be applied without removing their confounding effects. More specifically; changes in browse species abundance due to climate or fire, and changes in range plant abundance and composition, or resultant effects on soil erosion due to drought will be presumed to be accounted for. Whether or not these effects have been disentangled in Yellowstone is beyond the scope of this paper.

Interactions between grazing and climate are possible. Grazing may reduce ability of plants to withstand climate change or climate change may reduce ability to withstand grazing. The persistence model would recognize that climate change could rapidly reduce vegetation and a time lag in herbivore population decrease could result in a period of grazing that is heavy in relation to food supply. None of the other models explicitly treat interactions, so there is little point in considering them here. Interactions could be very important, however.

The possibility that predation was important for elk population regulation prior to wolf removal and extirpation of Indians is important from all points of view except the range manager, who would actually encourage predator removal. Unfortunately, we cannot be certain whether wolf and Indian predation were effective agents of control in prehistoric time. Archeological evidence may establish the existence of significant Indian

predation on elk, but it is essential to establish the rate of such predation, and the variance of the rate to argue its effectiveness. Efforts in this area are under progress (C. Kay, pers. corres.).

The intent of the natural regulation and the persistence hypotheses is preservation of natural processes. Given the fact that wolves and Indian hunting are presently lacking in Yellowstone, the current situation can only be considered a valid test of these hypotheses if predator control was ineffective in the past.

Comparisons Among Models

We compare here, the Yellowstone Natural Regulation Hypothesis (YNRH) to other models with respect to acceptance of each type of herbivory response (Table 1).

Reductions of vegetation biomass by grazing would be inevitably accepted by YNRH and all other models over intraseasonal time periods. Over longer time periods, a range manager would try to maintain maximum sustainable yield, which is achieved at a higher vegetation biomass than would be attained under food limitation.

Decreased vigor of preferred grasses induced by grazing may have to be accepted by YNRH and all other hypotheses to some degree because this is the most sensitive indicator of grazing impact and can arise before reductions in basal area or production (Pond 1957, Mueggler 1975), and certainly before species shifts. Thus it may be a stable condition, and an unavoidable consequence of any level of grazing.

Reduced plant productivity would be accepted by YNRH and all others in a limited degree. A range or wildlife manager might find that animal production is maximized with a small reduction in plant growth. Larger decreases in plant production may be acceptable to other hypothesis because stable equilibria between plants and herbivores would likely occur at submaximal levels of production (Caughley 1979). Browsing that results in some highlining and some reduced tree and shrub growth would also be

treated as above.

YNRH states that heavy browsing which results in plant death should not be accepted because this would represent a deviation from pristine conditions (remember that browse decreases due to climate, hydrology or fire are not under consideration here). This is a very conservative requirement. If browse is not the limiting food, then browse abundance must be assumed to depend on effectiveness of some other mechanism of herbivore population regulation. A wildlife manager may reject heavy browsing to maintain other species that depend on browse for food or habitat. The Caughley model would accept heavy browsing if it is an inevitable consequence of re-equilibration. The persistence model would accept this if it is not a consequence of human activity. The persistence model would not necessarily require duplication of conditions in the late nineteenth century because the plant-herbivore equilibrium may have shifted, may have been unstable, or may never have occurred.

Reductions in growth eventually lead to plant death, and replacement by other species that are more tolerant or better able to avoid herbivory. A shift in species composition does not automatically constitute overgrazing, however.

Let us define some terms. In range management terminology, changes in species composition resulting from variations in stocking rate are called trends in range condition. If there is no trend, the system is assumed to be at equilibrium. A species composition that is in equilibrium with herbivores (zootic climax, [Daubenmire 1968, Cayot et al. 1979]) may differ from a composition that might occur where herbivores are absent. If the equilibrium composition is anthropogenically induced such as through disruptions of migration patterns, it may be viewed as a zootic disclimax (Beetle 1974).

A zootic climax would be acceptable to YNRH and most other models. The concept of a zootic climax has no meaning for a range manager because any equilibrium that is attained is the result of human manipulation. (It could be argued, however, that some

range managers attempt to duplicate a natural equilibrium through trial and error adjustments of stocking rate.) A wildlife manager may find a zootic climax acceptable, but he may also reject it if it results in sub-maximal herbivore production.

YNRH would reject a zootic disclimax because it is unnatural. A disclimax would be accepted by a range manager, provided the new equilibrium does not decrease herbivore production. The wildlife manager may have to reject a disclimax if it is in conflict with other management objectives, and he would clearly reject it if it reduced game productivity. The Caughley model would find a disclimax tolerable because it results in re-equilibration. The persistence model would reject disclimax in the spirit of natural process preservation.

An irreversible declining trend would be unacceptable to all equilibrial views, including YNRH. An anthropogenically-induced, transient (reversible) declining trend would be rejected by the natural regulation model because it is non-equilibrial. A non-anthropogenic (natural) trend brought about by herbivory is not considered possible by YNRH because there should be no natural departures from equilibrium. Transient trends are acceptable by the Caughley model, if they are part of re-equilibration. The Caughley model also allows for periodic minor sub-eruptions that must produce transient trends. A natural transient decline would be accepted by the persistence model, which recognizes that equilibria may not be the norm.

Plant species extinction would be unacceptable to any management trying to sustain integrity of natural systems, however even this may be deemed arbitrary in rare cases because species extinction is also a natural process. A range manager might tolerate extinction of a rare economically unimportant species, though he may also find this to be unethical.

Herbivore population responses can be used to determine overgrazing as well, but

effects of predation must be considered. Release from artificial control may result in an eruption of the herbivore population, followed by equilibration to an unnaturally low level of plant production. If predators can control herbivores but are not present, then the eruption may be a result of lack of predation, or it may be exacerbated by lack of predation. If predators cannot control herbivores, release from artificial control may still result in an eruption due to imprecise feedback due to food limitation.

YNRH does not consider the possibility of predator control, so any eruption due to lack of predation would not be considered possible. YNRH would accept a temporary eruption in the event of release from artificial control if predation were not important because temporary overshoot may be part of re-equilibration. Range managers would not consider release from artificial control. Wildlife management acceptance will depend on responses among plants or other animals, as considered elsewhere. The Caughley model would, of course, accept an eruption followed by re-equilibration. The persistence model would not accept an eruption due to lack of predation because the new equilibrium would be unnatural. If predator control is unlikely however, then the persistence model would accept an eruption.

Acceptance of herbivore immigration or reduced emigration would depend on whether these movement changes were man-induced. YNRH does not consider natural variability in movement patterns, and YNRH also assumed that movement patterns were not affected by humans. Of course, range managers would not accept any uncontrolled animal (livestock) movement in or out of the system. Wildlife management acceptance would depend on effects on plants and other game. The Caughley model could accept any such movement change as a process that could be accommodated by the system through gradual equilibration. The persistence hypothesis accept altered movement only if it can be explained in terms of natural process variability. Persistence may accept, for instance, an immigration due to natural vegetation decline in a former

grazing area.

Competitive displacement of other ungulate species would be unacceptable to equilibrial views, including YNRH, because equilibrial concepts of community structuring through competition and niche differentiation would be violated. Communities may also be structured by predation (Sinclair 1984), but this would not be considered by YNRH. A range manager might find competitive displacement acceptable provided the displaced animals were of no potential use. The wildlife model might reject competitive displacement because he is probably trying to maximize diversity and minimize fluctuation. The Caughley model would accept a community restructuring if it is part of re-equilibration. The persistence hypothesis would accept competitive displacement if it results from natural non-equilibrial processes.

Smaller, thinner and less healthy ungulates would be accepted by YNRH, and Caughley hypotheses because it is an inevitable part of food limitation. These two would also recognize that this may result from climatic effects on carrying capacity. The persistence model would also allow that this may result from climatically induced disequilibrium. However, the persistence model also allows for the possibility of predator control, in which case food stress would be unacceptable. Reduced herbivore production would clearly be unacceptable to wildlife or range managers.

An increase in runoff would represent change and thus a departure from equilibrium. This could only be determined by establishing the level of runoff occurring in a condition of plant-herbivore equilibrium, which might include some grazing-induced runoff. Thus, increased runoff would be unacceptable to all but the Caughley and the persistence models. These two would accept transient changes during re-equilibration or natural disequilibrium, respectively.

Similarly, accelerated erosion due to grazing would represent departure from equilibrium, and would be rejected by all equilibrial hypothesis. The Caughley

hypothesis would probably find increased erosion unacceptable because this would be evidence that feedback mechanisms were unsuccessful in preventing system degradation. A very limited increase in grazing-induced erosion would be accepted by the persistence model if it were transient and exacerbated by rare and extreme climatic events.

Discussion

Multiple concepts of overgrazing have been employed in Yellowstone National Park. Confusion has resulted from incompatibilities between assumptions and concepts of range management and equilibrial ecology.

The earliest applications of the concept followed directly from experience in range management. These views were also based on a belief that human activities had resulted in unnatural concentrations of ungulates by disruption of migration. Range management concepts that prevailed through the drought of the late 1920's and early 1930's were based on equilibrial plant succession theory, which depended on definition of a single climatic climax and human adjustment of stocking rate relative to that ideal. As Cole (1974) pointed out, concepts of overgrazing applied to native ungulates seemed to be based on extrapolations from situations where domestic animals were artificially overstocked.

Developments in equilibrial population/community ecology relating to mechanisms of natural population regulation in the late 1950's and early 1960's eventually resulted in formulation of a natural regulation hypothesis. The associated concept of overgrazing differed from that used by range managers. Since the time the natural regulation

hypothesis was formulated, ecologists have also learned that population regulation in variable environments is often non-equilibrial, and that other mechanisms besides homeostasis may ensure long term persistence. Long term persistence of natural systems in spite of variability (Connell and Sousa 1983) is a more realistic concept of nature.

The Yellowstone natural regulation hypothesis was structured primarily around the notion of a dynamic equilibrium. While Cole recognized a density independent effect of severe winter weather (Cole 1969), he later argued that "a problem with using the density independent term is that even though the occurrence and intensity of an extrinsic influence may not be due to population density, density-influenced processes are affected" (Cole 1974). In this view climate acts only on the density dependent term K , i.e. the equilibrium state. Ecology since that time has demonstrated that a) even if extrinsic (DI) factors affect density dependent (DD) processes this may result in instability, b) that DI factors may operate directly on population growth rate (r) and are not limited to effects on DD processes (K) and that c) equilibrial systems are unlikely in variable environments and at small spatial scales. Thus it may be time to reexamine the natural regulation hypothesis in a more modern light.

Comparison of different views of overgrazing revealed strong effects of management objective and context for model development. A production management objective for range and wildlife managers proved paramount, but this was largely incompatible with an objective of natural process regulation. The Caughley model was strongly influenced by a context of ungulate population eruptions following introductions into non-native habitats or release from disease, predation or artificial control.

There were fundamental differences between the two equilibrial self-regulation hypotheses. While Caughley's early work (1970) may have partly inspired the original

natural regulation model (Cole 1971,1974), the natural regulation model departed from the Caughley model in its insistence on reference to a natural presettlement state (Houston 1971,1975,1976,1982), and it explicitly assumes that a certain equilibrial presettlement system can be identified. In contrast, Caughley might find it sufficient if a balance were achieved, even if different from the presettlement equilibrium. The Caughley model accommodates multiple equilibria but the natural regulation hypothesis never employed this concept. The natural regulation hypothesis is therefore considerably more conservative than the Caughley model, but it is also more optimistic (and perhaps unrealistic) in its assumption of a single equilibrium and strict reference to conditions in the late nineteenth century..

Interactions between range plants (ie. grasses, forbs, half shrubs) and herbivores must be distinguished from interactions between browse species (aspen and willow) and herbivores to adequately define overgrazing because limiting food for elk and bison may be grass rather than browse. Caughley (1981) recognized a class of overpopulation which results when a (human) favored plant species is depressed before less favored plant species begin to limit herbivore population sizes. This would be purely aesthetic, and not relevant to the goal of preservation of natural processes. The more serious question here is whether browse species are/were more abundant in the natural system. The persistence model would accept long term oscillations in browse species abundance if herbivore populations are not controlled by browse. However, browse species should not be extinguished by herbivory, and explanations of the causes for natural long-term browse-herbivore asynchrony would be required.

If natural conditions have changed due to climate shift, long term cycles of vegetation or fire or non-equilibrial dynamics, then it may prove impossible to conclude that elk are a natural or unnatural part of the system based solely on their presence/absence just prior to settlement. The assumption that the presettlement state

(ie. 1800-1875) was static and thus represents an appropriate control cannot be accepted at face value because steady-states are not necessarily expected in climatically variable environments or where biotic interactions are intrinsically unstable. Therefore if climate, fire, herbivores and large predators or interactions among these are changing, then there may be no control treatment in the Yellowstone experiment. Similar problems arise in control of confounding variables at large spatial scales and in comparisons to other land areas, even land areas abutting the park. Other methods of strong inference (Platt 1964) may be necessary to attempt falsification of hypotheses of natural regulation. Perhaps we can only erect falsifiable hypotheses for each of the individual mechanisms involved in natural regulation.

The dynamics of plant and herbivore populations must be explainable whether these are equilibrial, non-equilibrial, transient or even chaotic. Shifts in equilibria or departures from equilibria would have to be explicitly related to climatic variability or intrinsic population processes. Mechanisms of persistence in the case of inherent instability, and mechanisms of resilience in the case of climatic responses must be demonstrated.

The possibility that man has disrupted persistence mechanism(s) at a larger spatial scale than Yellowstone (ie. migration) has been a concern since the inception of overgrazing concepts in Yellowstone and long before the natural regulation experiment. To establish this as a valid cause of overgrazing would require firm support of the hypotheses that emigration has been inhibited, that immigration has increased, that non-disrupted movements enhanced persistence and that disrupted movements endanger persistence. Conversely, arguments that normal wintering grounds were outside the park only shift the location, not the fact of population control. Whether animals winter in or out of the park, some natural mechanism that limits population size must be advanced. It is conceivable however, that the overall ratio of winter to summer range

has been altered by human activities outside of Yellowstone Park as has been shown for the Jackson Hole herd (Cole 1969). It was suggested that there should be a balance between summer and winter range in an ecologically complete habitat (Cole 1971). However, the role of this ratio for plant-herbivore balance or the degree of its disruption have not been established in a quantitative fashion for the northern range.

Recommendations

Understanding and predicting change in ecosystems can be argued to be the most difficult science there is; particularly when we must identify change that is unnatural and irreversible. For example, predictions are now needed for ecosystem level responses to global climatic change. Yet, statistically robust predictions are difficult, because a) the event is unprecedented or comparable events occurred before data were gathered or, b) the scale of the system makes controlled experimentation infeasible or, c) all of the variables cannot be controlled or, d) all important combinations of variables cannot be examined. To address overgrazing criteria that involve herbivore population responses or movements (Table 1) would require experimentation on a scale that is larger than the Yellowstone northern range. A control treatment or replicate treatments would be difficult to find.

In the final analysis, the only definitive answer to a whole ecosystem question can come from whole ecosystem experimentation. Attempts to fuse a theoretical understanding of whole ecosystem responses from an understanding of individual ecosystem components may be of limited success. Interactions between components often cause system dynamics, therefore the interactions must be studied.

A number of steps can be taken, nevertheless, to improve understanding of the northern range grazing ecosystem:

1. Advance falsifiable hypotheses on certain aspects of the system. Controlled experimentation on plants and soils can be used to falsify hypotheses of grazing responses. Paleobotanical records of plant species composition, predator abundance and long term changes in climate and fire can be used to attempt falsification of hypotheses of past ecosystem dynamics. General hypotheses can be tested using data from other comparable ecosystems.
2. Hypothesized mechanisms of interaction between predators, prey and plants should be quantitatively formulated (eg. through numerical simulation) so that they are clearly stated and placed in the proper context of other processes. This formulation should consider: a) consistency with observed historical changes in range condition and the evidence listed above, b) spatial effects and heterogeneity, particularly herbivore movements, effects of landscape heterogeneity on plants, and significance of balance between summer and winter range areas, c) food quality and quantity distributions in time and in space, d) ability of herbivores to endure periods of little or no food, e) effects of food supply on herbivore mortality and natality, f) effects of predation, g) direct effects of climate on herbivores, h) mechanisms of plant responses to herbivory, fire and climate and interactions between these effects over both short and long temporal scales, i) effects of herbivory, fire and climate on nutrient cycling among plant, soil and herbivore. Multiple approaches and sets of working hypotheses would be desirable (Platt 1964) and would provide opportunity for corroboration among models.
4. Concepts of natural regulation should be refined to be consistent with current ecology. Formulation of a natural regulation hypothesis generally appears to be an appropriate framework to detect departures from natural processes that may be occurring on the northern range. The strict comparability to pristine conditions demanded by Cole (1971) and Houston (1976) is rigorous, however, certain of their assumptions about natural conditions need to be reexamined, including:

a) While it has yet to be verified theoretically or experimentally, the possibility that wolves combined with other natural predators may have reduced herbivore numbers needs to be seriously considered rather than assumed not to have been important.

b) Natural regulation should not be predicated on an assumption that the upper winter range is a self-contained system (Houston 1976,1982). Migratory elk from the northern herd apparently do not clearly separate into an upper and lower herd (Singer, unpublished) although an elevational gradient of hunting pressure likely occurs.

c) Natural regulation should not assume that climate controls herbivore numbers only through variable food supply. In particular, variable effects of winter severity on mortality and reproduction as well as the consequences of this under variable climate should be considered.

d) The possibilities that natural systems are not precisely regulated through homeostasis and therefore do not attain static equilibrium should be considered. While the existence of an equilibrium would make it far easier to specify a management goal, this may be unrealistic.

5) There should be an evaluation in the short term of current understanding of population dynamics, the role of predation, and responses of plants to herbivory in recent and ongoing studies in Yellowstone. Conclusions should be related to past evaluations of overgrazing.

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Table 1. Comparison of Yellowstone's natural regulation experiment to other concepts of overgrazing. Specific responses to changes in herbivory level or pattern may either be accepted or rejected relative to goals and assumptions that underlie each definition of overgrazing. Responses may also be accepted under certain conditions (cond.) or accepted in a limited degree (lim.) or rejected because the model does not consider the event possible (rej.-n.c.p.). See text for interpretations.

Concept Employed to Determine Overgrazing

Ecological Observation	Range Manager	Wildlife Manager	Natural Regulation	Caughley Model	Persistence Model
<u>I. Effects on Plant Standing</u> <u>Crop and Production</u>					
1. Reduced Vegetation Biomass	accept	accept	accept	accept	accept
2. Reduced Vigor of Preferred Species (flower no., stem ht.)	accept	accept	accept	accept	accept
3. Reduced Primary Production	limited	limited	limited	limited	limited
4. Heavy Browsing, Severely Reduced Growth of Shrubs and Plant Death	cond.	reject	reject	cond.	cond.
<u>II. Plant Species Shifts</u> <u>(death of some individuals</u> <u>of some species)</u>					
5. Zootic climax	rej.-n.c.p.	cond	accept	accept	accept

6. Zootic disclimax					
a) herbivore production maximal	accept	cond.	reject	accept	reject
b) herbivore production sub-maximal	reject	reject	reject	accept	reject
7. Trend of declining range condition					
a) irreversible	reject	reject	reject	reject	reject
b) transient, anthropogenic	reject	reject	reject	cond.	reject
c) transient, natural	rej.-n.c.p.	accept	rej.-n.c.p.	accept	accept
8. Extinction of a Plant Species	cond.	reject	reject	reject	reject

III. Effects on Ungulates

9. Eruption and re-equil. after release from artificial control					
a) predators can control herbivores but they are absent	rej.-n.c.p.	cond.	rej.-n.c.p.	accept	reject
b) predators cannot control herbivores	rej.-n.c.p.	accept	accept	accept	accept
10. Immigration or reduced emigration					
a) anthropogenic	rej.-n.c.p.	cond.	rej.-n.c.p.	accept	reject
b) non-anthropogenic	rej.-n.c.p.	cond.	rej.-n.c.p.	accept	accept
11. Competitive Displacement of Other Ungulates	accept	reject	reject	reject	limited

12.Submaximal size, health and fertility of individual herbivores	reject	reject	accept	accept	accept
IV. <u>Effects on Soils</u>					
13.Increased runoff, reduced infiltration	reject	reject	reject	limited	limited
14.Increased Erosion	reject	reject	reject	reject	rare cond.