NATURAL REGULATION OF UNGULATES
(WHAT CONSTITUTES A REAL WILDERNESS?)[1]

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Abstract: The last decade has produced 2 different perspectives on natural regulation of large ungulates. They may be categorized as ungulate-habitat interaction and predator-ungulate interaction. Irruptive behavior—a dramatic oscillation in numbers followed by development of an equilibrium between vegetative biomass and herbivore density where predators are superfluous to the sequence—has been considered a typical pattern of population growth. In other cases, the irruptive sequence has not been implicated in development of an equilibrium. In both cases, the equilibrium implies that either a zootic climax or a zootic disclimax will exist as a natural condition. Other studies have indicated that predation may serve as a population regulating mechanism, without creating zootic climax or disclimax. The spread of man's influence precludes investigation of pristine ecosystems. Before natural regulation of ungulates can be examined in the field, restoration of natural fire regimes and native predators must occur. Likely, no 1 factor consistently regulates native cervidae and bovidae.

The 1970s produced several perspectives on natural regulation of ungulate numbers that have broad implications for management of big game. Impetus for these perspectives arose from a series of independent investigations initiated in and before the 1960s. The perspectives may be placed into 1 of 2 frameworks: those that deal primarily with the ungulate-habitat interaction, and those dealing primarily with the predator-ungulate interaction. This review is a brief critique of these 2 perspectives and a comment on what conditions are required to evaluate natural regulation of ungulates in the field.

Krebs (1972), Lack (1954), and others approach the issue of natural regulation indirectly by stating that wild populations fluctuate within certain limits regardless of the potential rate of increase, and the task is to determine causes that confine a population within these limits. According to Webster's Dictionary (Woolf

1976), "natural" means being in accordance with or determined by nature. Conversely, "artificial" is defined as humanly contrived, often on a natural model. Natural regulation can be defined as that set of controlling mechanisms that serves to limit or control population density in the absence of human influence. This means that natural regulation may take place only in ecosystems where predator, prey, and habitat are uninfluenced by human activity.

UNGULATE-HABITAT
INTERACTION

A major ungulate-habitat interaction theory has sprung from observations of population irruptions. (Irruption has also been spelled eruption. Webster's New Collegiate Dictionary (Woolf 1976) refers to irruptions in animal populations, and Leopold et al. (1947) used irruption.) Caughley's (1970) evaluation of irruptive behavior in Himalayan tahr (*Hemitragus jemlahicus*) in New Zealand led to his

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analysis of similar behavior in other species (Caughley 1976, 1979). He considered a vegetation-herbivore equilibrium to be dependent on grazing influences on vegetative production and/or composition. In the first 3 phases of the irruptive sequence, the tahr population increased to a high, then leveled off, and then crashed; the vegetative biomass dropped in reverse sigmoid fashion. In the fourth phase, an equilibrium between vegetative biomass and herbivore density was reached, with grazing pressure as the driving force. Caughley (1976) concluded that the irruption was the typical pattern of population growth.

Webster's Dictionary (Woolf 1976) defines irruption of a natural population as a sudden upsurge in numbers, especially when natural ecological balances and checks are disturbed. This refers only to the population increase phase: the initial high, subsequent decline, and leveling off are also involved—the "single irruptive oscillation" of Riney (1964:261). For my purposes, irruption may thus be defined as an abrupt increase, initial stabilization, and decline of a population, peaking well above the normal fluctuations and related to an abrupt decrease in limiting factors.

Implications of the irruptive sequence in terms of natural regulation include:

(1) Forage deterioration is a natural condition.
(2) Dieoffs related to deteriorating forage are natural.
(3) Predators may delay or promote the population fluctuations, but are unnecessary.

The question is whether, as Caughley (1979) implies, irruption is the natural pattern of growth for large herbivores. Although Caughley (1976) states that ir-ruptions occur in the presence of predators, all documented irruptions recorded in North America have also been preceded by human interference with the ecosystem in some manner.

The St. Matthew Island reindeer (*Rangifer rangifer*) irruption (Klein 1968) occurred on a 332-km² island in the middle of the Bering Sea where no predators occurred, and in an introduced population. The Himalayan tahr population was introduced onto New Zealand vegetation that had evolved in the absence of ungulates; no natural predators were present. In the absence of food habits and forage utilization data, we must assume that the tahr were responsible for the decline of tussock grass (*Chionochloa* spp.) and increase in bluegrass (*Poa* spp.). The Kaibab deer herd irruption was related to reductions of heavy livestock grazing, extensive vegetation modification attributable to livestock, and intensive predator control (Caughley 1970), which reflect high human intervention.

None of the irruptions reported by Leopold et al. (1947) occurred without human interference with either the predators, the habitat, or the ungulates. The Isle Royale moose (*Alces alces*) irruption of 1921–36, based on crude estimates of populations and locations of 24–40 dead moose per year, occurred in the absence of wolves (*Canis lupus*) (Mech 1966). Wolves were present in low numbers and were hunted in Riding Mountain National Park when the elk irrupted (Banfield 1949, Blood 1966). Wolves were also present in Algonquin Park, Ontario, but were hunted and trapped during a reported white-tailed deer (*Odocoileus virginianus*) irruption (Leopold et al. 1947).

In terms of deciding whether the irruptive sequence is a natural phenomenon as defined, evidence is obviously scanty.

Evaluations will require complete or reasonably intact ecosystems including predators that are relatively undisturbed by man.

Practical implications involved go far beyond questions of yield and carrying capacity discussed by Caughley (1979). Forage deterioration occurs coincidentally with the irruption. Essentially the commonly used forage species and other preferred species will decrease in availability. This may mean highlining of browse, reduction of browse heights below prevailing snow levels, changes in growth form (highlining, clubbing), decrease in productivity (after an initial increase stimulated by browsing), and ultimately changes in species composition favoring less palatable species or outright reduction in density of all browse. Herbaceous vegetation will change in the direction of decreased vigor (seed-stalk numbers, heights, culm height). Composition will favor plant species that have growing points below the level available to the grazer, and often long tap roots. A range ecologist will judge such sites as deteriorated (Ellison 1960), whether this is natural or not. However, if this occurrence is to be expected in the truly natural situation, then by definition it must be accepted in natural areas, national parks, and wilderness as a process that should be allowed to occur.

Cole (1971) postulated that ungulate populations were regulated naturally by a combination of intraspecific competition and periodic severe weather, which affected forage availability. Mortality was directly related to population size and inversely related to available winter food. Cole's study was based on investigations of bison (*Bison bison*), elk (*Cervus elaphus*), and moose in national parks of the United States' Rocky Mountains. Intra-

specific competition is a density-induced factor; weather effects on forage availability are partially density-independent.

A zootic climax is formed when vegetation and the dominant herbivore form a dynamic and interlocking system (Daubenmire 1968:237). When a natural ungulate-vegetation interaction forms a zootic climax, no unidirectional vegetation *trend* is implied. Rather, the interlocking system prevents vegetation from changing to conditions that reflect absence of the dominant herbivore.

Presumably, the sites on which zootic climaxes naturally occur would have evolved through time in the presence of ungulates; no retrogression from a more productive state need be implied. Conversely, a zootic disclimax would exist in stage IV of Caughley's ungulate-vegetation model, where some dynamic equilibrium has been reached. This implies retrogression and depends on continuing disturbance. Although this may be a natural condition, it is often artificially induced. Thus, there is a useful distinction to be made between a zootic climax and a disclimax from the standpoint of natural ungulate-vegetation interactions.

As a corollary to Cole's hypothesis, some relatively snow-free areas used in winter would be considered zootic climaxes. Houston (1976) concluded from photographic evidence that such areas in Yellowstone National Park were stable over long time periods—in some cases nearly a century—rather than actively deteriorating. Thus, a vegetation-herbivore equilibrium could be postulated for the situation of the Northern Yellowstone elk and their habitat.

Caughley (1979) felt that predators were incapable of preventing irruptions, in view of the rapid increase of forage supplies thought to initiate the irruptive

sequence. Leopold et al. (1947) did not consider deer irruptions to be periodic, although Caughley (1976) implied that they are dependent on conditions created where an excess of forage becomes available. General agreement prevails that ungulate populations are externally controlled by changing environmental conditions rather than through intrinsic regulating mechanisms.

The vegetation-herbivore interaction is basically an extension of Lack's (1954:178) food-limiting hypothesis, which is summarized for North American deer as follows: "The numbers of North American deer are limited by food shortage, which causes a rise in the death rate, especially among the young and senile, and a fall in fecundity. The reduction is density-dependent, though precipitated by heavy snowfalls. Disease seems secondary. The effect of predators (scarce because destroyed) is uncertain." Taylor and Hahn (1947) showed that severe drought may also precipitate reductions in white-tailed deer.

A working hypothesis for the continuing research on elk in Yellowstone Park is that predation functions as a nonessential adjunct to the regulation of population size (Houston 1976). Thus, 2 independent investigations emphasize vegetation-herbivore interaction as the prime regulating factor and minimize the role of predation.

PREDATOR-UNGULATE INTERACTION

Studies of wolf predation as a regulating mechanism for moose populations were initiated on Isle Royale in 1958 (Allen 1979). Early in this investigation, Mech (1966) concluded that wolf predation was accounting for the annual in-crease of moose, but subsequent work by Peterson (1977) showed that snow hardness and depths affected the relationship. Crusted snows supported wolves but made travel and feeding difficult for moose and increased the rate of predation. Mild winters favored moose and decreased the rate of wolf predation. Loss of moose to malnutrition during severe winters indicated that a weather-forage relationship was involved in regulating numbers. Although moose could not be considered consistently regulated by wolf predation due to weather-forage interaction, predation was obviously a major mortality factor and may have served to check the increase observed in the 1968–71 period.

Evaluations of mountain lion (*Felis concolor*) predation in the central Idaho wilderness did not implicate this species as a factor controlling mule deer (*Odocoileus hemionus*) and elk populations (Hornocker 1970). However, Hornocker (1970) distinguished between population control and regulation. He defined control as a check on numbers, and noted that regulation involved influences of predation on behavior, dispersion, habitat use, and all factors by which the predator affected its prey.

The northeastern Minnesota wolf population depended primarily on a white-tailed deer population for its main food source (Mech and Frenzel 1971). Following a recent series of severe winters and declining deer populations, wolf predation appeared to be a factor controlling the numbers of this species (Mech and Karns 1977). Deer became extremely scarce and were distributed mainly along the boundaries of wolf pack territories (Hoskinson and Mech 1976). Mech and Karns (1977) expected that declines in deer under these conditions would be

followed by declines in wolf populations, thereby allowing deer to repopulate wolf pack territory centers.

Bergerud (1978) concluded that the gregarious behavior of barren-ground caribou (*Rangifer tarandus*) is related to wolf predation as well as to open habitat. His review of changes in the Nelchina, Alaska, caribou population indicated that wolf predation coupled with hard winters and late springs, plus heavy hunter harvest, were responsible for the decline in the Alaska population in the late 1960s and early 1970s. Lynx (*Lynx lynx*) predation, coupled with infectious disease, was responsible for high losses of caribou calves, and acted as a population depressant in Newfoundland (Bergerud 1971). Bergerud found no evidence to implicate range deterioration in the caribou population declines he investigated, implying that predation (human and otherwise) was the controlling factor.

Other investigations have demonstrated that predation may serve to depress ungulate population numbers, including investigations in Texas on white-tailed deer-coyote (*Canis latrans*)-bobcat (*Lynx rufus*) interactions (Cook et al. 1971). Virtually all these investigations indicate that predator-prey interaction is affected by environmental factors such as snow conditions or drought, which in turn affect the nutritional state of the prey by varying the availability and quality of forage. Still, there is no question that the presence of an effective predator population affects prey population dynamics and behavior. Keith (1974) concluded that because early records did not reflect heavy or extensive range deterioration by bison, and because recent grazing and browsing pressure on native plants appears unprecedented, ungulates appear to lack self-regulating mechanisms. Large

predators can account for an appreciable amount of total mortality; removal of predators will result in population increases.

UNGULATES ASSOCIATED WITH CLIMAX VEGETATION

Virtually all North American ungulates are associated with climax vegetative communities across portions of their range. Wildfire would be a common, large-scale abiotic force that would exist in the natural situation. Natural fire frequencies and the response of forage species to burning would dictate the ungulate response. Timing and intensity of fires can cause a wide range of detrimental to positive responses on herbaceous species productivity, but positive responses are usually short-lived (Vogl 1974). Fire frequencies can range from as high as 1 every 4–5 years to virtual absence (Weaver 1974). In areas where fire frequency is extremely high and plant response is short-lived, response of ungulates may merely be shifts in habitat use to areas most recently burned without changes in productivity or numbers. Further, to the extent that burns would promote local shifts in distribution and temporarily increase productivity of the herbaceous vegetation, the possibility exists that zootic disclimaxes or zootic climaxes might not be created. Wolves and other predators could affect local distributions, timing, and duration of use of areas as Murie (1944) and Hornocker (1970) have suggested. Adverse weather and snow conditions could further suppress responses to fire by ungulates in these circumstances and would affect vegetation response. As fire frequencies decrease, the possibility for zootic climaxes or disclimaxes to develop would

seem to be greater, dependent upon the weather and predator component.

Houston (1975) could find no evidence that an irruption of elk occurred in Yellowstone National Park during historical times. Fire frequencies on this bunchgrass winter range were 20–25 years, with larger intervals between the 8–10 major fires occurring in the last 300–400 years. Thus, Caughley's Stage IV, the dynamic vegetation ungulate equilibrium, depicts the currently prevailing condition. This is not natural because wolves are absent and fire has been effectively suppressed for decades, but it may have existed even when fire and wolves were present.

For ungulates occupying climax or near-climax vegetation under natural conditions, the 2 major factors that could cause irruptions are extremes in weather conditions and wildfire. A wide range of ungulate population responses could be expected. Local shifts in habitat use to areas of higher-quality forage created following burning may be the most common situation without additional population responses. The effect of predation is predicted to decrease the amplitude of natural fluctuations in response to fire and weather-induced habitat change. Table 1 summarizes potential relationships of weather, fire, vegetation, predators, and ungulates on ungulates.

UNGULATES ASSOCIATED WITH SERAL VEGETATION

North American cervidae, except caribou, are known to increase when long-lived seral shrub communities develop following fire in many coniferous and deciduous forest habitats. If the irruptive sequence is characteristic of ungulates, then it is with cervids occupying these

highly dynamic systems that such population behavior would be most likely in the natural situation.

Species adapted to occupation of such habitats should be capable of rapidly dispersing to newly created habitats, and have higher innate capacities for increase than species adapted to occupy less transitory situations (Bendell 1974). However, the characteristics of rapid dispersal and higher innate capacity for increase seem controvertible. Moose and deer species frequently produce twins, but elk do not. However, age at sexual maturity is similar for elk, mule deer, and moose (1 year for females). Evidence of rapid dispersal capability in moose (Peek 1974), mule deer (Robinette 1966), and white-tailed deer (Hawkins et al. 1971) exists, but similar evidence for elk is less conclusive. Investigations by Brazda (1953) and Craighead et al. (1972) suggest interchange occurs between adjacent elk herds in Yellowstone National Park that consists of unidirectional movement by some individuals, indicative of dispersals. Colonization of shrub-steppe in central Washington by elk, from at least 96 km distant, indicates a dispersal capability (Rickard et al. 1977). None of the records suggests that elk are able to colonize new habitat as rapidly as moose or deer, but this capability is related to number of potential dispersers (often yearlings) in the population as well as population density.

Population increases following fire are often delayed. Bendell (1974) concluded that the irruption of moose in the Kenai, Alaska, in 1920, following the fires of 1890–1910, was not correlated with the abundance of food. The peak elk population in the Selway River, Idaho, region occurred at least 20 years after the major fire of 1919 (McCulloch 1955)—long after

Table 1. Some potential influences of weather, fire, vegetation, predators, and ungulates on the ungulate-vegetation-predator relationship. Control, regulation, or no effect on ungulate numbers may result.

Variables	Fire	Vegetation	Predators	Ungulates
Weather (precipitation, snow)	Intensity of burn. Size of burn, duration, season, intervals.	Production, and composition. Availability to grazers.	Prey vulnerability, predator distribution, natality, survival, numbers.	Distribution, nutritional status, natality, survival, numbers.
Fire	Fuel reductions influence fire frequency and intensity.	Production— composition.	Prey vulnerability predator distribution, natality, survival, numbers.	Distribution, nutritional status, natality, survival, numbers.
Vegetation	Crown or ground fire intensity, duration, season, and interval.	Plant succession, species composition.	Prey vulnerability, predator distribution.	Distribution, nutritional status, natality, survival, numbers.
Predators	By altering prey distribution, hence the grazing regime, fuel amount is affected.	By affecting prey distribution, hence grazing regime, production or composition is affected.	Dispersion, behavior, survival, numbers.	Distribution, behavior, survival, numbers.
Ungulates	Grazing influences fuel distributions, hence fire frequency, size, timing, and intensity.	Productivity—increase or decrease. Species composition.	Distribution, behavior, numbers.	Nutritional status through intraspecific competition, behavior.

shrub development had reached its maximum. Mule deer appeared to increase and decline more rapidly than elk in that area, implying that competition for a common forage base may have been involved. However, elk populations were apparently low prior to the large fires and may have required a long period to increase to the levels that ultimately resulted. These delays may be contrasted with the 5-fold increase of moose on the Little Sioux burn in Minnesota within 2 years after the 1971 fire (Peek 1974). Although dispersal was implicated as the initial cause of this increase, subsequently higher production and survival was noted on the burn by Irwin (1975). A 400% increase in moose 3–6 years after the 1947 Kenai fire was reported by Spencer and Chatelain (1953). Black-tailed deer (*Odocoileus hemionus columbianus*) response to fire also was rapid (Taber and Dasmann 1957), but had no lasting effect in California chapparal, which grows so quickly it excludes post-fire forage.

As is the case of documented irruptions, no ungulate responses to fire occurred in environments that were intact or relatively uninfluenced by man. The Kenai wolf population was low in the early 1900s, as were predators in general in Idaho during the increase in elk herds. Wolves were present on the Little Sioux burn, but were feeding primarily on white-tailed deer. The virtual absence of substantial burns since 1936 on Isle Royale has undoubtedly affected the moose-wolf interaction there.

Population density is involved in irruption because, even if most ungulates are tolerant of crowding, range expansion will be most rapid when numbers are high. At high population densities, the number and perhaps proportion of dispersers in a population will be high. Although the presence of genotypes with a proclivity for dispersing is undocumented in ungulate populations, their existence in small mammal populations (Myers and Krebs 1971) suggests this possibility. Frequency, intensity, and vegetation response to wildfire will also affect the irruptive potential of a population. Finally, predators, competitors, parasites, and diseases may also depress the increase, and delay or prevent an irruption.

The hypothesis that vegetative modification is a consistent result of the irruptive sequence may be questioned. The moose population in northeastern Minnesota at the time Peek et al. (1976) investigated it was unhunted, and wolves were present. Habitat had been altered through logging, but this may be considered an influence analogous to fire with respect to moose. At a time when the population of moose had appeared to be in stage II, the high point of the irruption, no forage deterioration could be documented. Limiting factors included wolf predation, the parasite *Parelaphostrongylus tenuis*, and severe winter conditions that reduced calf survival; data were too few to analyze mortality in detail. As D. L. Allen (21 February 1980, pers. commun.) notes, this may not be an example of an irruption.

Although the woody vegetation showed obvious, extensive browsing pressure, it could not be considered deteriorated. Intensity and sustained browsing pressure over a 3-year period were within limits that individual plants could withstand without decreasing in productivity. These results are at variance with those on Isle Royale before wolves were present (Krefting 1951) and when wolves were present (Peterson 1977). Moose populations in the 1970s on Isle Royale were about double those observed in north-

eastern Minnesota. The 2 ecosystems are quite different. Isle Royale has no white-tailed deer, and presence of *Parela-phostrongylus tenuis* is low or absent; significant fires and logging are absent. Opportunities for moose to disperse are limited. Logging and other factors listed above have been constant on the north-eastern Minnesota range in varying degrees; the area has been extensively influenced by man.

IMPLICATIONS

Irruptive behavior most likely occurs in environments naturally subject to massive, abrupt changes in forage quality and quantity. Caughley (1976) presents enough evidence from field investigations to indicate that irruptive behavior is an expected occurrence in the presence of human intervention. Human intervention may occur at any or all trophic levels, and may be a current or historic condition that still affects the population. However, whether irruptive behavior occurs under natural conditions is left unresolved. This issue may seem academic, given man's pervasive interference. However, in some areas large herbivores are by law and policy presumably allowed to be naturally regulated. If irruptive behavior is the natural process, then development of zootic disclimaxes may be considered natural. This could extend, under extremes, to soil erosion and extensive site deterioration. In the absence of irruptions, if the herbivore-vegetation interaction evolves zootic climaxes as a result or cause of natural regulation, then this condition, too, is natural.

Until a truly intact ecosystem with little human influence can be restored for investigation, conclusions about what naturally regulates native herbivores seem premature. Even then, a few case history studies will not necessarily elucidate the entire range of conditions involved. Natural regulation of these species is rarely due to 1 factor or complex of factors even within the same population.

The potential for intact systems lies mainly in the larger national parks and wilderness areas. Isle Royale, Glacier, and Yellowstone national parks, Selway-Bitterroot Wilderness, River-of-No-Return Wilderness, Boundary Waters Canoe Area, the larger Canadian national parks, the Canadian Archipelago (Miller et al. 1977), and possibly some Alaskan areas are places where such conditions are most likely to be approximated. In all cases, restoration of a natural fire regime and/or the native complement of predators and reduction of human interference is needed.

Aside from ethical questions (which are ultimately most critical) and legal aspects concerning resource stewardship, is the goal of total ecosystem reestablishment of any practical significance? To the extent that investigations of these systems can serve an important role in understanding man's impact on wildlife and the landscape, not to mention man himself, there is no question that the goal is worthwhile. Although management (of which preservation is a form) of these areas will be very different from others where populations are exploited and other factors are modified, natural evolutionary processes still should be understood and considered when population or habitat manipulation is attempted.

Very often resource management is based on an unrecognized underlying hypothesis. In the case of native ungulates, the hypothesis that a weather-forage complex regulates populations is implicit in much habitat and population manipulation. The alternative—that predation

controls populations—is widely accepted also. Fires are generalized as promoting increases, whereas predators cause decreases or promote stability. Perhaps Oliver Wendell Holmes stated the situation best: "The chief end of man is to frame general propositions and no general proposition is worth a damn" (Flesch 1966:132).

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