

Herbivory in the Intermountain West

An Overview of
Evolutionary History, Historic Cultural Impacts
and Lessons From the Past

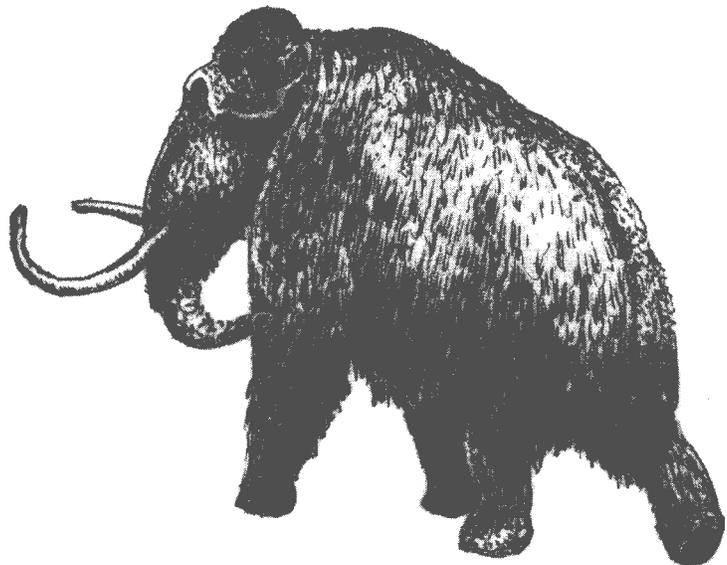
by
Dr. J. Wayne Burkhardt

Station Bulletin 58
of the
Idaho Forest, Wildlife and Range Experiment Station
College of Natural Resources, University of Idaho

This paper was presented at the 1996 Pacific Northwest Range Short Course
January 16-18, 1995, Boise, Idaho

Sponsored by the University of Idaho
Rangeland Ecology and Management Department

Partially funding for this research was provided by the
Columbia Basin Ecosystem Research Project.



Herbivory in the Intermountain West

TABLE OF CONTENTS

INTRODUCTION	1
HYPOTHESES	1
EVOLUTIONARY HISTORY	2
HISTORIC PERCEPTIONS	5
CULTURAL IMPACTS	7
LESSONS FROM THE PAST	8
Characteristics of the Pleistocene Herbivory	8
Prehistoric vs Historic Grazing	11
Multiple Grazers	11
Sedentary Grazers and Confinement Grazing	11
Season-Long Grazing	11
Rotational Grazing	12
Range Readiness	12
Herding	12
Drought Response	13
Dormant Season Grazing	13
Utilization Limits	13
CONCLUSION	14
LITERATURE CITED	14

About the Author:

An alumnus of the University of Idaho (BS, MS, Ph.D), J.Wayne Burkhardt is now affiliate professor of Rangeland Ecology and Management at the University of Idaho, having retired as professor emeritus at the University of Nevada.
He is also a rangeland consultant in Indian Valley, Idaho.

This refereed publication is issued as Contribution number 817 of the Idaho Forest, Wildlife and Range Experiment Station,
College of Natural Resources,
University of Idaho, Moscow, ID 83844-1130

To enrich education through diversity the University of Idaho is
an equal opportunity/affirmative action employer

Artwork by Lorraine Ashland, graphic artist.
Editing and lay-out by Denise Ortiz and Donna Anderson

Printed by UI Printing and Design Services

Herbivory in the Intermountain West

An Overview of Evolutionary History, Historic Cultural Impacts and Lessons From the Past

INTRODUCTION

There has been increasing interest in environmental issues related to land use in the western U.S. over the past decade. Traditional consumptive uses of renewable natural resources are coming under increasing scrutiny, especially on public lands. Certainly a major part of these land use concerns focuses on livestock grazing on public lands. While livestock grazing may be one of humankind's oldest endeavors, second to hunting or food gathering, (Towne and Wentworth 1951) its environmental sustainability is being questioned.

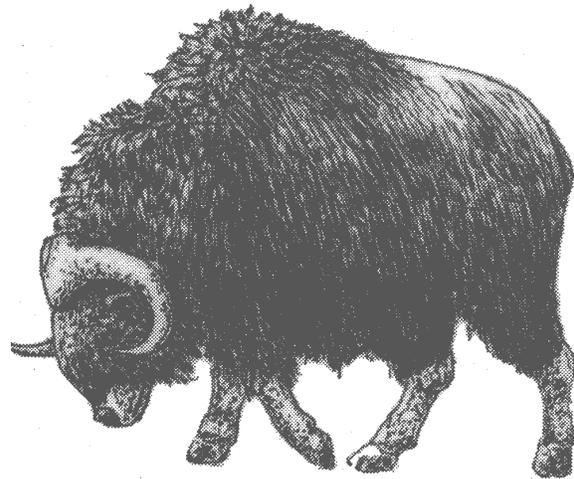
Our experience with historic livestock grazing in western North America provides a mixed track record. While most rangelands remain productive and stable after more than a century of livestock grazing, problems with altered plant communities and eroding streams abound. As a response to those problems there is a questioning of the ecological sustainability of livestock grazing. This paper is a review of the scientific literature relating to prehistoric and historic herbivory on the Intermountain West of North America. This characterization of the nature and role of prehistoric herbivory in comparison to our historic domestic grazing experience can provide useful insight to future management of livestock grazing.

HYPOTHESES

Existing scientific literature in plant ecology and range management, either by omission, implication, or assertion, indicates that large-bodied herbivores were not naturally part of the Intermountain West of North America (Young et al. 1976, Reveal 1979, Mack and Thompson 1982, Daubenmire 1985). The historical record from early European contact with the Intermountain West indicates a landscape largely devoid of large ungulates (Ewers 1959, Kline 1963, Haines 1940, 1967 and 1955, Schroedl 1973). From this experience rangeland managers, plant ecologists

and environmentalists have generally assumed that the flora and fauna of the Intermountain West evolved without significant influence of large herbivores. Indeed the most frequently used reference point in matters of plant community ecology is the plant community protected from herbivores (exclosures). The underlying assumption apparently is that large herbivore grazing is an unnatural impact on the plant community.

There is reason to question the assumption that large herbivores were not a functional component in the formative evolution of intermountain rangelands. Herbivores which include large-bodied grazers are indeed common to terrestrial systems in other parts of the planet. The most notable intact natural system today is in the Serengeti of Africa (McNaughton 1976, 1979, 1988). However, in historic times the plains region of North America sustained a vast natural herbivory characterized by millions of large-bodied grazers. Such natural herbivores, composed of bovids, equids, camelids, proboscideans, and other large herbivores, have developed in mesic as well as arid landscapes and in environments ranging from deserts to grasslands to shrub /woodlands. That the Intermountain West did not evolve a similar natural herbivory, as our post European contact experience suggests, should certainly arouse scientific curiosity. Is the region a biologic anomaly?



Interpretations of our historic experience in the region appears to suffer as a result of narrow temporal limits of post-European contact. Certainly the historic record regarding an obvious paucity of large ungulates is convincing. However, whether ecological conditions at the time of initial European contact in the Intermountain West were normal, "natural", and stable remains largely unquestioned. Plant ecologists and range scientists have generally assumed that ecological conditions immediately prior to European settlement of the West represented the climax or pristine natural state. Departures from those conditions are viewed as human disturbances of the natural system (Young *et al.* 1976).

Certainly determining the normal natural state requires tapping the scientific knowledge of disciplines other than ecology or range science. Archeology, paleontology, and geology provide an opportunity to extend the time frame of consideration well beyond the historic record. A cursory review of the archaeological literature suggests a fertile opportunity to extend our ecological understanding of the Intermountain Region back into the Pleistocene Era. The fossil record would indicate that for several million years the North American continent, including the Intermountain Region, supported a wealth of large ungulates and only relatively recently (the past 10,500 to 7000 years) did that herbivory disappear (Flehart and Hunlett 1977, Butler 1976 and 1978, Agenbroad 1978, and Martin 1986). There is increasing evidence that these late Pleistocene extinctions in North America are not adequately explained by climatic shifts (Wigand, Nowak 1992, Owen-Smith 1987). These findings suggest that the biological conditions in the West at the time of European contact may have been abnormal and unusual (Wagner and Kay 1993).

The issues in question here are of fundamental importance to scientific understanding of western rangeland ecosystems and sustainable land management practices. These issues logically lead to the formulation of several hypotheses which can be

tested against the available scientific data in ecology, archeology, paleoecology and paleoclimatology.

Hypotheses:

Biotic conditions and relationships of the Intermountain West at the time of European contact represented the pristine, stable state ecology of the region.

Rangeland biota of the intermountain region evolved in the absence of large-bodied herbivores and is unadapted to such grazers.

Domestic livestock (horses and cattle) introductions to the intermountain region represent a partial replacement of the extinct Pleistocene megafauna.

Domestic livestock, introductions to the intermountain rangelands has resulted in significant destabilizing impacts to the system.

Characterization of Pleistocene herbivory in the intermountain region would provide a model for management of domestic livestock grazing.

EVOLUTIONARY HISTORY

The co-evolution of warm blooded animals and the flora appears to have begun about 60 million years ago with the extinction of the dinosaurs. However, the origins of current intermountain flora date back to the late Miocene, 12-20 million years before present (BP). Prior to the uplift of the Cascade-Sierra Cordillera the Great Basin and Columbia Plateau were vegetated by hardwood-deciduous and coniferous forests (Tidwell et al. 1972, Axlerod 1966). Such temperate flora probably flourished in a mild climate of 35-50 inches of rainfall with little seasonality.

By late Miocene, as the Cascade-Sierra uplift began to impede the Pacific storm track, the landscape to the east became progressively more xeric and precipitation more seasonal (Tidwell et al. 1972). The temperate forests were slowly being replaced by shrubland and deserts. Regional pollen records indicate a distinct increase in herbaceous angiosperms during the Miocene (Gray 1964 and Gray and Kittleman 1967). These

include species from such plant families as *Chenopodiaceae*, *Gramineae* and *Compositae*, all important plant families in the deserts and shrublands of the intermountain region today. Gray (1964) reported the earliest fossil pollen record of *Artemisia* (sagebrush) to be in late Miocene deposits in northeastern Nevada. By the end of the Miocene (about 12 million years BP) much of the Intermountain West had become distinctly more arid and was vegetated by xeric woodlands (Tidwell et al. 1972).

During the Pliocene (2.5-10 million years BP) the Cascade-Sierra underwent the greatest uplift, rising as much as 5,000-6,000 feet in the Cascades and more in the Sierra (Tidwell et al. 1972). This active mountain building also accelerated desertification by intensifying the rain shadow on the leeward side of the mountains. Precipitation decreased to levels similar to historic times and with a similar seasonality (Tidwell et al. 1972). With substantially less growing season moisture the intermountain flora increasingly shifted toward shrub lands at the lower elevations and coniferous forests in the mountains. The fossil record indicates that by the beginning of the Pleistocene Ice Ages (2.5 million years BP) the flora of the intermountain region was essentially the same as our modern flora (Tidwell et al. 1972, Barnosky et al. 1987). During the climatic fluctuations associated with the glacial-interglacial periods plant species migrated longitudinally and elevationally in a compensatory action (Nowak et al. 1994, Tidwell et al. 1972).

Concurrent with this floral evolution was the appearance of a myriad of new animal species (Kurtin and Anderson 1980, Martin 1990). The neotropical forest-dwelling creatures of the early to mid-Cenozoic era slowly evolved into the rich faunal assemblage. This fauna has come to be known by scientists as the Pleistocene megafauna. Common Pleistocene fossil genera and species found in the intermountain region include *Mammuthus columbi* and *M. primigenius* (Columbian and woolly mammoths); *Equus* (various species of horses and burros); *Camelops* (yesterday's camel); *Megalonyx* (Jefferson's ground sloth); *Bison antiquus* and *B. latifrons* (extinct bison); and at least a dozen other genera of large

mammals, both herbivores and carnivores. The family *Bovidae* was represented by four genera, *Bootherium* and *Symbos* (woodland musk oxen); *Eucerantherium* (brush oxen) and *Bison* (Kurtin and Anderson 1980, Grayson 1982 and 1993, Webb 1977, Martin 1986, Martin and Klein 1984, Mead et al. 1986, Guthrie 1990). This faunal assemblage of grazers and browsers roamed throughout North America for several million years. The fossil record of these herbivores and the associated predators (sabretooth tigers, short-faced bears, and dire wolves) have been found from Mexico to Alaska in environments ranging from the hot and cold desert systems through the shrub steppe and woodlands to the forest and tundra.

The Pleistocene megafauna shaped the coevolution of flora and fauna over several million years. This biotic complex successfully existed throughout North America despite numerous major climatic fluctuations (Martin 1984, 1986). Glacial and interglacial climatic pulses may have effected local or regional and seasonal grazing habits of these herbivores. Compensatory action analogous to changes in plant species distribution may have occurred (Edwards 1992, Fleharty and Hulett 1977). Martin (1970) stated that "based on the sizeable biomass of elephants, bovines and zebra in protected parts of Africa ... plus the great number of mammoth, mastodon, bison and horse teeth found in the fossil deposits of North America, it seems fair to assume that ... the natural Pleistocene vertebrate fauna on this continent (North America) was also abundant." Martin (1970) also stated, "The Pleistocene game-carrying capacity of western North America must have equaled and very likely exceeded, the 40 million units of livestock which it now supports."

Just as the fossil record reveals the coevolution of the Pleistocene flora and fauna and the existence of these widespread natural herbivores on each continent, the fossils also record the demise of the megafauna (Martin 1986, Fleharty and Hulett 1977, Owen-Smith 1982, and Grayson 1991). In western North America the radiocarbon dates of most common genera found in the fossil record indicates that the majority of large herbivores and their associated predators became extinct between 12,000 and 10,000 BP. This massive extinction over an extremely short time period removed over 70% of the Pleistocene megafauna in North

America (Martin 1986). Similar extinction occurred on other continents but at somewhat different times. North America lost 33 out of 45 genera of large mammals during this late Pleistocene extinction (Martin 1986, 1990). From 7,000 years BP to the present the depauperate remnants of the Pleistocene megafauna include bison, elk, moose, deer, pronghorn, and bighorn sheep and mountain goats. To date, neither evolutionary substitution (for which there has been far too little time) nor immigration have filled the empty niches in this natural herbivory (Martin 1970).

The unrecognized implications of the Pleistocene extinctions on current efforts to comprehend our western ecosystems is tremendous. Underlying nearly all aspects of land management is the assumption that the fauna and flora of North America at the time of European contact was in a pristine natural state of balance. Largely unaware of the fossil record, many ecologists, range scientists, land managers and environmentalists have assumed that this so called pristine balance was the end product of millions of years of coevolution of plants and animals. The concepts of climax pristine and natural have pervaded all facets of land management and ecology in the U.S.

When the system is in balance, i.e. all the available niches occupied, extinctions and evolution of new forms occur somewhat equally. The late Pleistocene extinction far exceeded replacement and it affected only the larger fauna. Smaller creatures and the habitat remained. Immigration or ecological substitution has not yet replaced what was lost. This hardly appears to have been a common evolutionary event.

The demise of the Pleistocene megafauna has perplexed scientists for many years. Climatic change during the last major deglaciation period which would have caused environmental stress for the "ice-age" fauna has commonly been advanced as the driving force behind the Pleistocene extinctions (Martin 1986, Grayson 1987 and 1991). However, certain features of the extinction are not well explained by the climatic theory. Differential timing of the extinction between continents and the

apparent lack of effects on small fauna and flora are difficult to explain under the climatic theory. Equally troublesome are some of the most recent interpretations of past climatic fluctuations which suggest that the Pleistocene megafauna survived several early periods of glacial and interglacial climatic pulses which were more severe than that of 10,000 years ago (Grayson 1991).

More recently the theory that the Pleistocene extinctions were primarily driven by human predation is gaining scientific proponents (Flehart and Hulett 1977, Denevan 1992, Martin 1970,1986,1990, Diamond 1992, Wilson 1992, Alcock 1993, Burney 1993, Owen-Smith 1987). It appears that the first humans immigrated to North America from Asia, crossing the Bering Straits land bridge during a glacial period at least 12,000-15,000 years BP Apparently after about 1500 to a few thousand years this new predator, hunter man, populated the new lands and began to dramatically impact the megafauna. An interesting aspect of this extinction theory is that the chronology of Pleistocene extinctions on each of the world continents and major islands occurs shortly after the arrival of man (Martin 1990, Steadman 1995). Whatever the cause, the extinction by 10,000 years BP of most large herbivores and predators left a natural rangeland grazing ecosystem which had existed for several million years, with many vacant niches for large herbivores.

Bison was one of the few really large herbivores to survive the Pleistocene extinctions and vast herds of these animals roamed the American prairies at the time of European contact (Roe 1970). It is ironic that within slightly less than 400 years after Columbus landed in the Western Hemisphere, Europeans all but hunted the North American bison to extinction. At the time Europeans began exploring and settling the intermountain region, bison numbered in the millions east of the Rocky Mountains and were almost nonexistent to the west (Haines 1967, Kingston 1932, Christman 1971). Some ecologists and biologists attributed the scarcity of bison in the intermountain region to environmental constraints of a shrub-steppe which could not sustain vast bison herds (Mack and Thompson 1982, Daubenmire 1985, Johnson 1951). This viewpoint, while consistent with historic conditions of the early 1800's, stands in stark contrast

to the Pleistocene fossil record of the intermountain region (Schroedl 1973, Grayson 1982). Bison and the other members of the Pleistocene megafauna roamed the intermountain region at least until the extinction of 10,000 BP, with bison surviving much longer.

Evidence indicates that bison survived the Pleistocene extinctions and continued to exist in the intermountain region as well as the prairies until just prior to the European explorers of 1800-1830. Agenbroad (1978) reported an extensive buffalo jump site on the Owyhee River of southwestern Idaho which yielded evidence of use for 7,000 years up to the Indian acquisition of the horse and rifle. Butler (1976, 1978) discussed evidence of abundant bison in eastern Idaho from the late Pleistocene to historic times. In the Great Basin, Grayson (1982) concluded that bison were widespread until historic times. And Bray (1985) presented evidence that bison were widely distributed over eastern Oregon and abundant in at least one locale from the late Pleistocene until shortly after 1800 when they became regionally extinct. Schroedl (1973) reported that bison remains recovered from 22 archaeological sites in the Columbia Basin provide evidence of bison presence from the late Pleistocene until just prior to historic times.

Based on the fossil record it is evident that bison survived the Pleistocene extinctions of 10,000 BP and continued to populate the shrub-steppe landscapes of the entire intermountain region until the late 1700s or early 1800s. The regional extinction of bison at this time may well have been in part related to native hunting made more effective with the availability of horses.

HISTORIC PERCEPTIONS

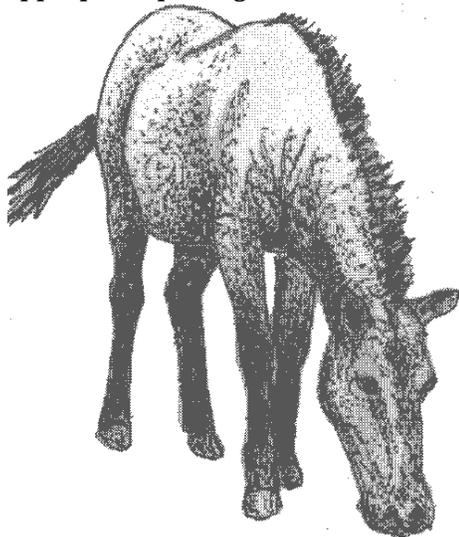
At the time of European man's arrival (ca. 1800) the Intermountain West was a vast region vegetated largely by open shrub stands with an abundant perennial grass understory. Climatically, the shrubs and junipers could dominate the herbaceous species creating dense shrub or woodland stands with meager understory. Periodic lightning and Indian-set fires shifted the vegetation back to a perennial grassland and kept the adjacent juniper woodland largely restricted to the more rocky, fire-safe sites (Burkhardt and Tisdale 1976). The landscape of the early 1800s supported scattered herds of bighorn sheep, pronghorn, and some deer and elk (Rickard et al. 1977). In parts of the intermountain region, game animals were scarce enough that early explorers sometimes had difficulty acquiring sufficient food (Young and Sparks 1985).

It is on the basis of this historical experience that we have formulated many of the concepts which underlie the sciences of ecology and range management. The conditions encountered at the time of European exploration and settlement have been considered the pristine natural state. Frequently scientists and land managers have related the apparent adverse impacts of livestock grazing in the intermountain region to the obvious absence of large herbivores in the region prior to settlement (Daubenmire 1970, Tisdale 1961, Mack and Thompson 1982, Young and Sparks 1985). The scientists reasoned that the intermountain region apparently evolved without an abundance of large herbivores and the native plant communities were not adapted to support such grazers in the form of cattle, horses, and sheep. This has been the conventional wisdom. Virtually all undesirable changes in the plant communities of the intermountain region are considered the result of livestock grazing in an environment not adapted to large herbivores.

There is no question that substantial modifications of the historic plant communities of intermountain rangelands have occurred since European settlement (Mack 1984, Young et al. 1987, Burkhardt and Tisdale 1976). But, it is still an open question as to whether these changes are the direct consequence of large herbivore grazing in an unadapted ecosystem. From a theoretical perspective, and given what is now known

of the evolutionary history of the intermountain region, a more critical analysis of cause and effect would seem appropriate.

The evolutionary history of western North America, as indicated by what is now known of the fossil record, raises fundamental questions about at least two common ecological assumptions. First, did biologic conditions of the Intermountain West at the time of European contact (ca 1800) represent the stable natural state? That is, were the existing plant communities the end product of evolutionary and ecological adjustments (i.e. climax)? Considered in the context of the Pleistocene extinctions and the continually changing climatic conditions (Eddy 1991, Nowak et al. 1994 a & b) of the Quaternary period (the past 2 million years), the concept of climax or pristine biotic communities hardly seems valid and some ecologists are already questioning this concept (Tausch et al. 1993, Johnson and Mayeux 1992, Laycock 1991, Denevan 1992, Sousa 1984, Sprugel 1991, Box 1992). Certainly vegetation has been in a state of flux over the past 30,000 years in the western U.S. if woodrat middens are indicative (Betancourt et al. 1990, Nowak 1994 a & b). The current effort toward ecosystem management, if it is to have more than just political significance, must consider these issues. The hypothesis that biotic conditions and relationships of the Intermountain West at the time of European contact represented the pristine, stable state ecology of the region certainly no longer are acceptable (Wagner and Kay 1993). A more appropriate paradigm is needed.



Implicit in our vegetation concepts such as "pristine" or "climax" is the "natural" world untouched by man. Aside from the issue that man, too, is a part of the "natural" world, there are other problems when we apply those concepts to the North American landscapes and biotic conditions prior to European contact. For example, Savage (1991) and Denevan (1992) detailed evidence of major human impacts upon the North American landscape pre-European contact. Denevan referred to the pre-1492 landscape as "humanized" by a population much greater than that encountered 200-300 years later during the colonization of North America.

A second questionable assumption common to ecology and range management is that the lack of large herbivores in the intermountain region at the time of European contact is evidence that the region's evolutionary history and ecology did not include and therefore has no adaptation to large animal grazing. Again the fossil record, as we currently understand it, stands in direct contradiction to this assumption. The record indicates that for several million years North American rangelands, including the Intermountain West, sustained a faunal assemblage equal to the African Serengeti (Martin 1970). Only for the past 10,000 years have the large-bodied herbivores and predators not been part of the intermountain region's native biota. Furthermore, there is increasing evidence that the extinction of these large animals was related to human predation rather than evolutionary and ecological accommodation to environmental conditions.

Regarding the plant species and plant community adaptations to herbivory, the several million years in which large herbivores were present on the landscape would seem more formative than the 10,000 in which large herbivores influenced plant adaptation to one calendar year, then the adaptive time period without large herbivores is about thirty-one hours or less than two days out of that year. While management decisions are made in decades and centuries (ecological time), the adaptive characteristics and coevolution aspects of biota were shaped over millions of years (evolutionary time).

As previously noted, the Pleistocene extinction of the mega-fauna did not completely remove herbivores from the landscape or herbivory from the plant community. Medium-sized grazers such as pronghorn and bighorn

sheep, as well as bison, continued to graze the western landscape including the intermountain region until at least the late 1700s. From this perspective it hardly seems plausible that the intermountain flora would have lost its adaptation to herbivory and become intolerant of large herbivores.

Herbivory is a fundamental biologic process in aquatic and terrestrial ecosystems and is basic to biologic diversity and energy flow in these systems. In grasslands, shrub steppes, savanna woodlands, and arctic tundra throughout the world, complex herbivores evolved that are characterized by a diversity of floral and faunal species. Typically the variety of environmental niches are occupied by a diverse array of minor and mega-herbivores and their associated predators. These function in a complex biologic web involving mutualism, facilitation, competition, and optimization (MacNaughton 1976, 1979 and 1985, Owen and Weigert 1981, Sinclair 1982). It would seem unusual and abnormal for the intermountain biome to have evolved differently. Nature abhors a vacuum.

The intermountain flora evolved over millions of years with large herbivores until, in recent time, those animals became extinct. Is it possible that livestock could now represent a potentially functional replacement for the megafauna? It appears that since the continental extinction of most megafauna by 10,000 BP and the regional extinction of bison in the late 1700s, unoccupied large herbivore niches would remain. Cattle and horses are large-bodied herding animals with generalist foraging habits that can complement more selective browsers and grazers such as pronghorn, deer, elk, and bighorn sheep. Cattle could closely occupy the bison niche and horses were part of the original megafauna. Perhaps exotic grazers from other continents could be imported to fill vacant niches as has been done in Texas (Demario et al. 1990). The idea of surrogate herbivores (Martin 1970, Fleharty and Hulett 1977) has left aghast some ecologists and environmentalists who may have been unaware of the fossil record.

After something more than a century of experience with livestock grazing in the intermountain region, it

should be possible to judge the functionality of these surrogate grazers. If we were to do so only on the basis of the current environmental uproar over livestock grazing on public lands, it would certainly seem that the idea is fatally flawed. However, the emotional environmental debate and some of the scientific discussion have been less than discerning in attributing cause and effect to historic adverse environmental changes. An objective evaluation of the surrogate herbivore hypothesis necessitates closer scrutiny of the historic changes which have occurred on intermountain rangelands.

CULTURAL IMPACTS

European settlement of the intermountain region eventually brought about three ecologically significant changes. These were the introduction of new herbivores in the form of domestic livestock, the subsequent reduction in the role of fire, and the introduction of preadapted exotic flora. Simply filling the vacant large herbivore niche with cattle and horses did not necessarily represent a significant ecological change. However, the intense stocking levels and the shift of foraging patterns from seasonal (native herbivores "followed the green" up the mountain) to season-long use stressed the forage plants and consumed all the annual growth of grasses, thereby fireproofing the sagebrush steppe. The inevitable consequence was an increase in shrubs and woodland at the expense of herbaceous species. In the lower elevation or drier part of the sagebrush steppe the lack of fire and decades of season-long grazing have created sagebrush monocultures.

Additionally, the inadvertent introduction of preadapted exotic plants, especially cheatgrass (Mack 1984), resulted in an irreversible floristic change in the warmer/drier portion of the sagebrush steppe. In those areas of the shrub steppe with mild, wet winters and early hot, dry summers (essentially the Wyoming big sagebrush sites) cheatgrass is better adapted than the native perennials (Melgoza et al. 1990). In this environment, regardless of livestock grazing, cheatgrass and other Mediterranean annuals have largely replaced the herbaceous understory. The pelican refuge on the ungrazed Anaho Island in Pyramid Lake is a good example (Svejcar and Tausch 1990, Tausch et al. 1994).

Consequently in the lower elevation portion of the sagebrush steppe, due to the nearly continuous carpet of fine-stemmed annual grass, flammability is now higher and fire frequency in recent years has increased (Bunting 1987). With more frequent fires, the shrub overstory has been eliminated and prevented from reestablishing, thereby creating an annual grassland (Young et al. 1987). This change from sagebrush bunchgrass to sagebrush-annual grass to annual grassland has occurred widely in the more xeric, lower elevation portion of the sagebrush steppe, especially in loamy/silty soils. Conservative livestock grazing or no livestock grazing does not prevent and cannot reverse this change (Svejcar and Tausch 1990). At higher elevations on more mesic sagebrush sites, such as mountain big sagebrush/Idaho fescue, cheatgrass is not as well adapted. On these sites dominance of cheatgrass occurs only as the result of disturbance, such as poor grazing practices. On nearly all of these sites, "pristine" plant communities currently exist and represent the potential vegetation (Tausch et al. 1995).

Juniper has existed in many areas of the intermountain region for thousands of years as the rimrock monarchs. Changes in the extent and distribution of juniper have occurred through geologic time as a response to shifting climatic conditions (Miller and Wigand 1994, Nowak et al. 1994). However, significant increases in juniper have more recently been occurring which apparently are not a response to climatic changes. Photographic records and juniper stand age patterns clearly demonstrate that western juniper has been extending its range from the fire safe rimrocks and rock outcroppings into the valley slopes and bottoms since about the 1880s (Burkhardt and Tisdale 1976, Miller and Wigand 1994). This change, while producing an increasingly green landscape, leads to the demise of productive wildlife and livestock habitat. As young juniper stands become dense, understory forage plants (both shrubby and herbaceous) are eliminated. Fire history studies suggest that the encroachment of western juniper onto sagebrush-grass sites is a direct result of the diminished influence of fire on these sagebrush ranges (Burkhardt and Tisdale 1976). Settlement of

the West and subsequent heavy livestock grazing essentially fireproofed these ranges thereby creating safe havens for the establishment of juniper seedlings. Fire prevention and control programs in more recent years has assured this continuing vegetational change.

Riparian areas have been heavily impacted, partially by livestock grazing, and also by roadway construction, channelization, reservoirs and diversions, urbanization, and in some situations by natural geomorphic/hydrologic processes (Masters and Burkhardt 1991).

Wildlife have been affected both negatively and positively by a century of livestock grazing. Bighorn sheep populations have declined largely due to "brushing up" of their habitat. However, deer populations have expanded phenomenally as the result of these shrub increases in the sagebrush steppe (Leopold 1950). Populations of pronghorn, elk, and moose have made remarkable increases in the past three decades (USDI-BLM 1990) despite continued urbanization of winter ranges and increasing sport hunting demands. These increases are the result of improved habitat created by more conservative and better managed livestock grazing of the past three decades. Certainly range condition, at least on uplands over much of the intermountain region, has improved over conditions of the early 1900s and this trend continues (USDI-BLM 1990, Burkhardt 1991). Exceptions to this pattern of improvement are for the most part those areas dominated by pre-adapted exotic annual plants and those ranges where juniper or shrub encroachment have eliminated the native herbaceous understory plants (woody plant monoculture). Additionally many riparian areas are in degraded condition.

Again consider the hypothesis regarding the suitability of livestock to function as a surrogate for the lost Pleistocene megafauna. At best our livestock experience seems a mixed bag. The one hundred-plus-year experiment has not been a complete failure or success. The fireproofing of shrub steppe rangelands in which fire previously played a functional role was, at least early on, the result of livestock stocking intensity and season-long grazing. More recently this problem relates to agency fire control programs. Additionally, some of the

riparian problems result from poor livestock distribution (however watering places in the African Serengeti and elk or buffalo wallows in the West look much like our livestock watering areas).

Application over the past 30-40 years of more conservative stocking levels, range readiness, rotational/deferred grazing, and range revegetation projects have produced some positive changes. However food, fiber, economical, and cultural considerations aside, as surrogate megafauna our livestock grazing experiment leaves much to be desired.

LESSONS FROM THE PAST

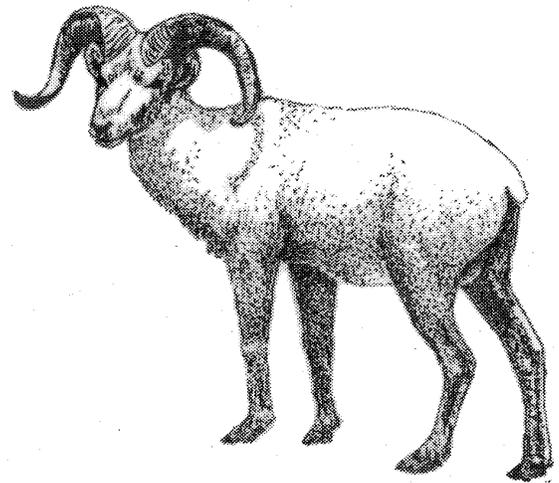
If our livestock grazing experiment has been less than a resounding success, perhaps we should consider why. Conceptually the idea of filling vacant herbivore niches in a natural herbivory with surrogate grazers seems reasonable. Certainly, given sufficient time, that is exactly what the evolutionary and immigration processes would do. To understand why it hasn't worked better, I wish to attempt to characterize functional features of the Pleistocene megafauna herbivory and compare those to our livestock grazing practices. Admittedly the task of functionally characterizing a complex biologic process that is thousands of years extinct is daunting but the temptation is irresistible. My sincere hope is that this effort will stimulate further inquiry and eventually lead to more sustainable and environmentally sensitive grazing practices.

Characteristics of the Pleistocene Herbivory

In several respects the arguments that the intermountain region biota evolved under different conditions than that of the North American prairies are correct (Platou and Tueller 1985). Then, as now, the two regions were very different environmentally by reason of geography and climate. The intermountain region was and is arid due to the Sierra Cascade rain shadow. Pacific storms are predominantly cold season which support shrub steppe vegetation in the valley and foothills and coniferous forest in the mountains. Cool season bunchgrasses form the understory, and because of

the predominantly cold season precipitation, woody species could dominate the herbaceous understory. However, periodic fires favored the understory plants. Due to the winter precipitation pattern, the spring growing season, except for riparian vegetation, was short (about six weeks). As stated by Tidwell et al. (1972) the flora of the Pleistocene is essentially the flora of today. The landscapes offered much topographic relief just as today in the form of sheltered valleys and canyons below high mountains and plateaus.

The plains and prairie regions offered the Pleistocene herbivores a very different environment from those the same species encountered west of the Rocky Mountains. The plains which lie east of the Rocky Mountains are arid to mesic and receive some precipitation from the winter storm track off the Pacific Ocean, the Arctic cold fronts. However significant summer moisture comes from cyclonic Gulf of Mexico storm systems. Consequently, the plains and prairie regions have a preponderance of spring-summer rainfall when temperatures are warm enough for plant growth. As a result, prairie vegetation is a grassland dominated by rhizomatic/stoloniferous warm season graminoids favored by a long growing season. The prairie landscape is noted for weather extremes and vast expanses with little elevational change or topographic relief and its weather extremes.



The Pleistocene fossil record indicates that these two very different environments were populated by exactly the same set of faunal species. The Pleistocene

megafauna was apparently tolerant of a wide range of environments, perhaps more so than some of the large African herbivores today. This faunal assemblage included hoofed, herding herbivores with both grazer and browser species (Hansen 1978, Mead et al. 1986). Grazing habits apparently included both selectivists and generalists. The Pleistocene mega fauna was also characterized by a diverse array of large and small herbivores and predators much like the African herbivores of today.

Just as today, there would have been an inherent difference in total productivity, both floral and faunal. The prairie environment is more productive due to growing season precipitation. Annual above-ground plant production in the grasslands (650-2400 lbs/ac) is about double the productive capacity of intermountain rangeland (240-1200 lbs/ac) (Platou and Tueller 1985). Certainly faunal biomass or stocking rates would have reflected this disparity of carrying capacity.

When the differences between the intermountain and prairie environments are considered, it seems certain that the grazing herds would have developed very different grazing strategies in the different environments. Prairie herbivores would likely have been nomadic grazers with little distinctive seasonal patterns or definitive home ranges. The long summer growing season and the mix of cool and warm season grasses would have provided sufficient green forage to assure adequate protein intake necessary for successful reproduction in the large herbivores. The lack of elevational relief and long growing seasons would provide little incentive for the herds to develop seasonal grazing patterns. Forage quantity and predators were the incentives to herd movement. The prairie was likely a vast region of wandering herds of grazers and scattered predators.

This contrasts sharply with the manner in which herbivory likely occurred in the intermountain region. Due to short growing season on intermountain upland ranges this likely would have been a protein deficient environment for large herbivores as previously suggested by Johnson (1951) as well as Mack and Thompson (1982). Green forage is required to support growth and

reproduction in large herbivores. Cured forage protein content provides only maintenance or submaintenance nutrition levels for herbivores, especially the larger ones. Six weeks of growing season is an insufficient green forage period to support late stages of gestation, lactation, and recycling in most herbivores. In the intermountain region the grazing herds would have been forced to extend the green feed period to maintain adequate protein intake. This could easily have been accomplished by "chasing the green up the mountain," by seeking out riparian areas as the summers progressed, and by browsing on the numerous woody plants which retain protein content better than grasses. Probably all three grazing strategies were utilized. Given the mountain valley topography, the shrubby vegetation, and the numerous riparian systems, it would have been possible for herbivores to extend the green feed period available to them throughout the entire summer.

It seems obvious that herbivores in the intermountain region had to develop seasonal grazing patterns. Literally this would have been following the melting snows up the mountains in the spring and beating the drifting snow back down the mountains in the fall. Here forage quality and adverse late fall weather were the incentives that drove herd migrations. Those migrations were likely definitive and repeatable patterns rather than nomadic wanderings. Seasonal home range behavior probably developed. All of these grazing behavior patterns are certainly displayed by native ungulates that survived the Pleistocene extinctions. In fact even livestock, after centuries of domestication, exhibit these same behavior patterns in mountain/valley landscape if given the opportunity.

It is easy to comprehend the nutritional advantage to an herbivore of seasonal grazing in the intermountain region. However, if particular grazing behaviors are to be sustainable over millions of years as was the Pleistocene herbivory, then those foraging patterns must also functionally benefit the vegetation. Numerous authors have investigated the relationships of herbivory to flora (McNaughton 1976,1979,1986,1988, Holland et al. 1992, Belsky 1986, Page and Whitman 1987, Jansen 1982,1984). The functional relationships between herbivores and plants include influencing interspecies plant competition, seed dispersal and planting, nitrogen

mineralization, carbohydrate reallocation, and compensatory growth. Certainly, for as pervasive and enduring as herbivory is in the biologic world, the process must provide positive interactions with forage species and serve a purpose beyond simply filling paunches with grass.

With regard to the seasonal grazing habits of intermountain herbivores this strategy appears advantageous to the plant community in several ways. Early spring grazing where the herds simply followed "green-up" from winter ranges in the valley to summer ranges in the mountains would have allowed the bunchgrasses and forbs of the sagebrush steppe to regrow and set seed after the animals moved on. This would have assured reproduction and carbohydrate storage in bunchgrasses. It also would have allowed for the accumulation of cured grasses on the sagebrush-grass covered uplands to fuel periodic summer fires. These fires would have checked woody plant encroachment and favored the herbaceous understory (Burkhardt and Tisdale 1976).

Fall grazing by the herd returning to lower elevation would also have positively impacted community. Seed dispersal and dormancy release after passage through the animals' digestive tract and seed planting are all byproducts of dormant season foraging (Jansen 1982, 1984). All of these are much more important to the caespitose grasses of the intermountain region which reproduce by seed than they would be to the sodgrasses of the prairie. Additional beneficial effects resulting from herd hoof action during the dormant season would include incorporating litter in the soil and breaking soil surface crusts which are so common to intermountain soils. Additionally, the hoof action of herding animals in arid regions would have improved nutrient and water cycling (Savory 1988).

In the sagebrush-bunchgrass uplands of the intermountain region, a seasonal grazing pattern ("following the green") was biologically functional. Perhaps it was even a requisite strategy for sustainability of this arid to semiarid environment. Seasonal grazing provided the nutritional needs of the herbivores, allowed periodic fires to control woody plants and facilitated stand maintenance in

bunchgrasses. These three processes are likely the basis for sustainable grazing in the shrub-steppe. The more mesic montane environment of the mountainous summer ranges were perhaps less fragile, more productive, and more tolerant of summer-long grazing (Savory 1988). At these higher elevations summer moisture is more prevalent, thereby supporting a much longer growing season than occurs at lower elevations. Additionally, herbaceous vegetation tends to be composed of more rhizomatous species and perhaps somewhat less dependent on seed reproduction.

Pleistocene predators may also have provided a functional role beyond just herbivore population control and fitness. With the steep terrain of much of the intermountain landscape and the availability of green forage and water in the many riparian corridors, Pleistocene herbivores might have had tendencies to "keg-up" in these favorable environments during the heat of summer much as livestock do today. Yet strong tendencies to do so are not evident in the surviving native grazers such as elk, deer, or pronghorn. Neither are such tendencies evident in African herbivores. Perhaps predators hunting along the densely vegetated stream bottoms discouraged Pleistocene herbivores from using riparian areas as social centers. Similar predator-prey-topoflora relationships have been noted in modern African herbivores (Bell 1971). Predation may well have prevented sedentary herding behavior by the Pleistocene herbivores.

The evolutionary process of functionality between flora and fauna and the physical environment certainly involved a diversity of herbivores and vegetation. Floral or fauna monocultures are unusual and temporal in natural ecosystems. The diversity of Pleistocene herbivores and predators that roamed the intermountain region would seem appropriate to the diversity of the region's vegetation. The array of selective and generalist grazers and browsers would have dispersed the impacts of foraging across virtually all plant species within the shrubby/herbaceous plant communities. Functionally this would have maintained a diversity of plant species within plant communities and optimized herbivore biomass as is evident in Africa today.

Prehistoric vs Historic Grazing

Range livestock grazing has most often been viewed from the animal perspective, i.e. adequate forage quantity and quality. When the plant perspective has been considered grazing has been largely thought of as something that was done to plants (a disturbance). From a management perspective we have simply tried minimize the adverse effects. Given the evolutionary history of the intermountain region it could be argued that grazing and fire, rather than being disturbances to the natural system, are indeed requisite functional processes of a healthy ecosystem. One hundred or more years of experience with livestock grazing in the intermountain region suggests that domestic grazing, as it has been conducted, has not been a completely functional replacement for the Pleistocene herbivory. A comparison of historic grazing strategies with possible features of the prehistoric herbivory is pertinent.

- **Multiple Grazers**

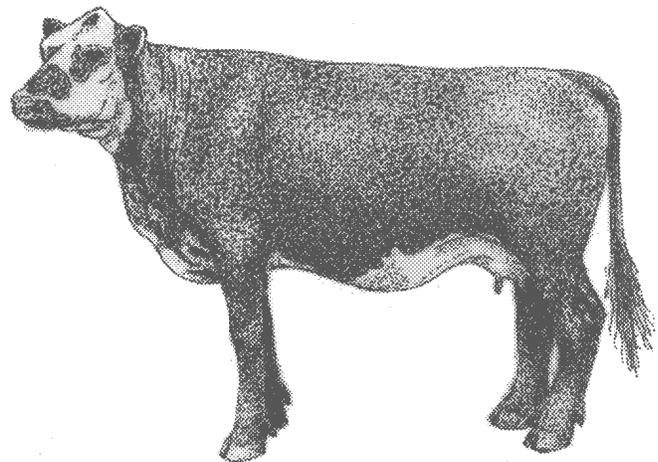
Livestock grazing has differed from prehistoric grazing in some obvious ways. More often than otherwise livestock grazing tends to be somewhat monocultural. Especially in recent years the conversion from sheep to cattle has resulted in cattle being nearly the sole herbivore. This puts grasses at a disadvantage in the shrub-grass steppe. On other ranges, cattle, wild horses, and deer, elk, or antelope provide some vestige of a diverse ungulate herbivory. An indication of the mutualistic relations between multiple grazers and the plant community can be seen in the grazing history of several state game ranges. After World War II the state game and fish agencies in each of the western states began to purchase private ranches for critical big game ranges. These were operating cattle ranches which biologists deemed critical elk or deer winter range. Upon acquisition of the ranches, the biologists removed livestock to supposedly enhance the respective critical big game range. After 10-20 years it became obvious that big game use of these acquired ranches was shifting to adjacent private ranches where livestock were still grazed. On the supposed critical game ranges the vegetation had become rank and

less palatable or nutritious for lack of a generalist herbivore. Eventually "managed" cattle grazing programs were reintroduced to these game ranges. Examples include Sand Creek in Idaho, Bridge Creek in Oregon and Fleecer Mountain, the Blackfoot, the Wall Creek, and the Blacktail in Montana.

- **Sedentary Grazers and Confinement Grazing**

In the interest of developing an animal more efficient at converting forage to meat, we have used genetics, breed selection, and husbandry to create sedentary welfare cattle, square blocks of immobile protein so to speak. Animal scientists and husbandrymen have paid too little attention to "rangeability." While such breed development may have an immediate economic advantage, environmental sustainability as regards rangeland grazing is questionable.

Compounding the problem of breed development has been our tendency to change extensive/open rangeland grazing into an intensive confinement operation. We have spent forty years fencing the open range in an effort to mitigate adverse impacts of cattle grazing. Range scientists and range managers (this author included) have directed too much attention to mitigating grazing problems (merely treating symptoms) and insufficient effort at understanding the functionality of herbivory in the biologic world. Grazing should be more than just something done to plants. If we manage livestock grazing to more closely emulate the original system there should be less need for such bandage approaches.



- **Season-Long Grazing**

Livestock grazing in the West developed largely as season-long with heavy stocking rates. European experience in mesic herbaceous systems suggested that approach. Congressional land policy during western settlement assured that approach (Young and Sparks 1985). There are two problems here. As discussed previously, prehistoric herbivory was necessarily seasonal (following "greenup" elevationally) in the Intermountain West. Season-long cattle grazing, especially under heavy stocking, interfered with herbaceous perennial plant carbohydrate storage and seed production. Perhaps more significant, this approach fire-proofed the range, thereby greatly favoring woody plants. For example fire chronologies dating back to 1600 from the Owyhee Plateau clearly indicated that subsequent to stocking these ranges with cattle in the 1880's, fires, which frequently burned the area prehistorically, then ceased to burn. Shrubs and juniper then began suppressing herbaceous plants (Burkhardt and Tisdale 1976). Under season-long grazing grasses had no opportunity to provide a standing crop of fine fuel to carry fires.

- **Rotational Grazing**

In recent decades range management strategies have recognized the problems of heavy season-long grazing. Stocking rate reductions averaging over 50% since the 1930's (Wagner 1978) have occurred and rotational/deferred grazing has become common. The stocking reductions were largely appropriate and likely have contributed to improving range conditions over the past couple of decades. Rotational/deferred grazing, while helpful, is probably little more than a bandage. There does not appear to be any prehistoric analogue to rotational or deferred grazing strategies in the intermountain region as there may have been in the prairie system.

- **Range Readiness**

Another widely applied management practice intended to correct livestock grazing problems has been the concept of "range readiness." Public land agencies, especially the Forest Service, have fought

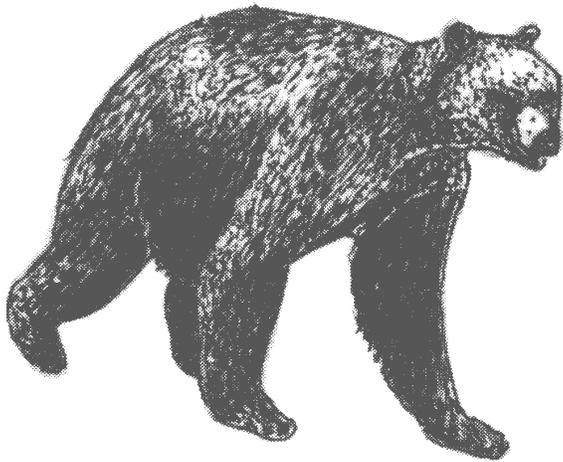
many bitter battles with ranchers over attempts to delay spring grazing until grasses have 4-6 inches of new leaf growth. Early spring grazing has been considered a *prima facie* cause of poor condition rangelands. Yet there appears to be no Pleistocene analogue to this concept. In actuality, the application of range readiness in the shrub steppe postpones grazing until the critical reproductive period of native bunchgrasses such as wild ryegrass and bluebunch wheatgrass. These bunchgrasses are most intolerant of reproductive-period tissue removal on an annual basis (Stoddart 1946). This intolerance is not surprising given the fact intermountain bunchgrasses evolved under the selective pressure of early spring and dormant season herbivory. Fortunately the damage which the application of range readiness could have caused was partially offset by rotational and deferred grazing strategies where the bunchgrasses were only periodically subjected to flowering period grazing. There does not appear to have been anything in the Pleistocene herbivory that was analogous to our concept of range readiness. The concept runs counter to the instinctive nature of native and domestic ungulates. There are no indications in the fossil record of prehistoric forest rangers deterring woolly mammoths from eating green grass.

Perhaps a cautionary note regarding early spring grazing is appropriate. From a functional standpoint, it is the timing of grazing cessation rather than initiation that is operative here. It is paramount that early spring grazing cease while there is sufficient growing season (primarily soil moisture) left to assure plant regrowth and seed production. In a practical sense for the shrub steppe that equates to the grazing herds slowly but continuously grazing toward higher elevations rather than remaining in a particular pasture for an appreciable duration.

- **Herding**

Livestock grazing on rangeland of the intermountain region has become integrally tied to base ranches or farms. These base ranches have often become intensive irrigated farms used to produce winter hay for the livestock that graze rangelands during the summer. Such farming operations can deflect management attention away from grazing operations and the rangeland "pasture" becomes little more than a summer

"day care" for the cattle while the cowboy farms. To some degree farming and rangeland grazing are incompatible endeavors, with each demanding full-time attention. In terms of functional livestock grazing, fences may not be an appropriate substitute for a good saddle horse. Given the sedentary nature of most range cattle, especially during the hot summer season, perhaps there is a need for man to provide the predator-herding function. In unattended fenced pastures, creek bottoms become attractive to many creatures including cattle. The Pleistocene model suggests that rangeland grazing should be more extensive and nomadic.



- **Drought Response**

Periodic and prolonged droughts are common climatic conditions of the intermountain region today just as they likely were during the Pleistocene. Typically, land managers attempt to reduce livestock grazing pressure with the onset of drought. Such actions as shortening the grazing season or reducing stocking levels are apparently driven by concern for the vegetation. However, it is questionable how drought-dormant forage plants benefit from early livestock "takeoff" dates. As soon as favorable growing conditions return we immediately return to normal stocking and grazing seasons.

Prolonged drought would have affected both the Pleistocene herbivores and their habitat. Logically, such prolonged droughts would have initially resulted in heavier to severe overgrazing followed by

eventual herd die-offs. Once the drought gave way to more favorable growing conditions, there would have been a lag of several years before the grazing herds again increased in response to more favorable forage conditions. This lag period would have provided drought-stressed vegetation a recovery period. This scenario would suggest that perhaps we should reconsider our livestock management response to drought.

- **Dormant Season Grazing**

Another aspect of the marriage between farming and range livestock involves winter feeding. As discussed previously, dormant season grazing provides functional benefits to the vegetation. Fall/winter grazing as the herds move to lower elevations tends to incorporate litter, break surface crusts, and disperse plant seeds. To the extent that winter feeding of livestock has replaced dormant season grazing these functions are compromised. For some grasses like wild ryegrass heavy winter grazing or burning is a prerequisite to thriving productive stands. This grass which was common in the intermountain region is notably intolerant of summer grazing. It has diminished under decades of summer livestock grazing and flourishes under winter grazing.

Livestock grazing policies of public land agencies sometimes preclude dormant season use if the area was grazed during the spring, the apparent idea being that the plant community should not be subjected to grazing more than once each year. Apparently we are trying to minimize the negatives rather than considering function and purpose.

- **Utilization Limits**

Another disparity between prehistoric herbivory and current management of livestock grazing is the use of grazing utilization limits. For many years the standard range management prescription was take half-leave half. More recently it has become politically popular to impose even more conservative utilization limits (30-40%) on rangeland livestock grazing. When such use levels are reached anywhere on an area, the animals are to be removed. This approach is more political than biological. Seasons of use, rest periods, and vegetation trends are largely ignored. Managing grazing by

utilization standards or guidelines reduces range management from an applied science and an art (Mosley 1985) to a policing action.

Grazing management solely on the basis of conservative use levels does not have the support of the range science community (Sharp et al. 1994, Frost et al. 1994) and for good reason. It is ludicrous to try reducing something as biologically complex as livestock grazing on something as variable as rangelands to a single simple number. Utilization is by definition the percentage removal of total available annual production. If the concept has utility it is only where grazing occurs after annual plant growth is complete. It certainly does not apply to early growing season grazing where grazing ceases before the annual growth is complete (Frost et al. 1994). Conservative utilization limits do not appear to be part of natural herbivores such as in Africa today, the plains bison of the 1800s, or the Pleistocene megafauna. Utilization limits appear to be a human-made concept. The fossil record gives no indication of prehistoric forest rangers attempting to enforce use limits on megafauna.

CONCLUSION

The biota of intermountain rangelands clearly evolved over several million years as a natural grazing ecosystem. The fossil record indicates that this herbivory was comparable to the modern Serengeti in faunal diversity. Massive extinctions at the close of the Pleistocene removed most of the larger bodied fauna from the system.

At the time of European contact with North America the biologic system was in flux. Evolution and species immigration had not yet filled the vacant herbivore niches. The science of ecology, largely unaware of or unconcerned with the fossil record, assumed that the biologic conditions at the time of European contact were pristine or climax. This view has profoundly shaped the development of range science and rangeland management. The underlying assumption has been that the intermountain biome was largely unadapted to large herbivore grazing. Consequently, livestock grazing management has

focused on minimizing and mitigating the negative impacts to the natural system.

Perhaps it is time to rethink the fundamentals. We now know that herbivory, including large grazers, is part of the natural biologic system on terrestrial landscapes, the intermountain region included. Herbivory is a functional process that serves both flora and fauna. Grazing management should be designed to assure that domestic livestock grazing is functional within the parameters of the biologic system. Characterization of the Pleistocene herbivory provides a potential model for the design of functional livestock grazing strategies.

LITERATURE CITED

- Agenbroad, L.D. 1978. Buffalo jump complexes in Owyhee County, Idaho. *Plains Anthropologist* 23:313-221.
- Alcock, J. 1993. *The Masked Bobwhite Rides Again*. University of Arizona Press, Tucson, Ariz.
- Axlerod, D.I. 1966. The Eocene Copper Basin flora of Northeastern Nevada. *Univ. Calif. Publ. Geol. Sci.* 59:1-125.
- Barnosky, C.W., P.M. Anderson, and P.J. Bartlein. 1987. The northwestern U.S. during deglaciation: Vegetational history and paleoclimate implications. *Geology of N. Am. Vol. K-3. North America and adjacent oceans during the last deglaciation*. The Geo. Soc. of Am.
- Bell, R.H.V. 1971. A grazing ecosystem in the Serengeti. *Scientific Amer.* 225:86-93.
- Belsky, A.J. 1986. Does herbivory benefit plants? A review of the evidence. *American Naturalist* 127:870-891.
- Betancourt, J., T. Van Devender, and P.S. Martin (editors). 1990. *Packrat Middens: The last 40,000 Years of Biotic Change*. University of Arizona Press, Tucson, Ariz.
- Box, T.W. 1992. Rangelands, desertification, and Clements' Ghost. *Rangelands* 14:329-331.
- Burkhardt, J.W., and E.W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. *Ecology* 57:472-484.
- Burkhardt, J.W. 1991. Then and now: The Western Range. *Range* 1:12-14.
- Burney, D.A. 1993. Recent animal extinctions: Recipes for disaster. *American Scientist* 81:530-541.

- Butler, R.B. 1976. The evolution of the modern sagebrush-grass steppe biome on the eastern Snake River Plains. Nevada Arch Sur. Res. Paper #6.
- Butler, B.R. 1978. Bison hunting in the Desert West before 1800: The paleoecological potential and the archaeological reality. *Plains Anthropologist* 23:106-112.
- Christman, C.M. 1971. The mountain bison. *Am. West* 8:44-47.
- Daubenmire, R.F. 1970. Steppe vegetation of Washington. *Wash. Agric. Exp. Stn. Tech. Bull.* 62.
- Daubenmire, R.E. 1985. The western limits of the range of American bison. *Ecology* 66:622-629.
- Demarais, S., D.A. Osborne and J.J. Jackley. 1990. Exotic big game: A controversial resource. *Rangelands* 12:121-125.
- Denevan, W.M. 1992. The pristine myth: The landscape of the Americas in 1492. *Annals Assoc. Am. Geogr.* 82:367-385.
- Diamond, J. 1992. *The Third Chimpanzee*. Harper-Collins, New York, N.Y.
- Dyer, M.I., J.K. Detling, D.C. Coleman, and D.W. Hilbert. 1982. The role of herbivores in the grassland. Pages 225-295 *In: J.R. Estes, R.J. Tylor and J.N. Brunken, (eds.) Grasses and Grasslands*. Univ. of Oklahoma Press, Norman, Okla.
- Eddy, J.A. 1991. Global change: Where are we now and where are we going? *Earth Quest* 5:1-5.
- Edwards, S.W. 1992. Observations on the prehistory and ecology of grazing in California. *Fremontia* 20:3-11.
- Ewers, J.C. (ed.) 1959. *The adventures of Zenas Leonard fur trader*. Univ. Okla. Press, Norman, Okla.
- Flehart, E.D., and G.K. Hulet. 1977. Can man survive: An inquiry into the impact of western man on the environment. Independent Study, University of Kansas.
- Freeland, W.J., and D.H. Jansen. 1974. Strategies in herbivory by mammals. *American Naturalist* 108:269-288.
- Frost, W.E., E.L. Smith, and P.R. Ogden. 1994. Utilization guidelines. *Rangelands* 16:256-259.
- Graham, R.W. 1986. Plant-animal interactions and Pleistocene extinctions. p.131-154. *In: D.K. Elliott (ed.), Dynamics of Extinctions*. Wiley, New York, N.Y.
- Gray, J. 1964. Northwest American tertiary paleontology: The emerging picture. *In: Ancient Pacific Floras. Pacific Science Congress Series* 10: 21-30.
- Gray, J., and L.R. Kittleman. 1967. Geochronometry of the Columbia River basalt and associated flora of eastern Washington and western Idaho. *Amer. J. Sci.* 265:257-291.
- Grayson, D.K. 1982. Towards a history of Great Basin mammals during the past 15,000 years. *In: Man and Environment in Great Basin*. SAA Paper #2.
- Grayson, D.K. 1987. An analysis of the chronology of late Pleistocene mammalian extinctions in North America. *Quaternary Res.* 38:281-289.
- Grayson, D.K. 1991. Late Pleistocene mammalian extinction in North America: Taxonomy, chronology, and explanations. *J. World Prehistory* 5:193-232.
- Grayson, D.K. 1993. *The Desert's Past: A Natural Prehistory of the Great Basin*. Smithsonian Institution Press, Washington, D.C., and London, England.
- Guthrie, R. D. 1990. *Frozen fauna of the mammoth steppe*. University of Chicago Press, Chicago, Ill., and London, England.
- Haines, A. 1940. The Western limits of the buffalo range. *Pacific Northwest Quar.* 31:389-398.
- Haines, R.S., Jr. 1955. *The journal of John Workman, 1830-31*. Thesis. Washington State University, Pullman, Wash.
- Haines, F. 1967. Western limits of the buffalo range. *Am. West* 4:4-12 and 66-67.
- Hansen, R.M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. *Paleobiology* 4:302-319.
- Holland, E.A., W.J. Parton, J.K. Detling, and D.L. Coppack. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *Am. Nat.* 140:685-705.
- Jansen, D.H. 1982. Differential seed survival and passage rates in cows and horses; Surrogate Pleistocene dispersal agents. *Oikos* 38:150-156.
- Jansen, D.H. 1984. Dispersal of small seeds by big herbivores: Foliage is the fruit. *Amer. Natur.* 123:338-353.
- Johnson, C.W. 1951. Protein as a factor in the distribution of the American bison. *Geogr. Review* 41:330-331.
- Johnson, H.B., and H.S. Mayeux. 1992. Viewpoint: A view on species additions and deletions and the balance of nature. *J. Range Manage.* 45:322-333.
- Kingston, C.S. 1932. Buffalo in the Pacific Northwest. *Wash. Hist. Quar.* 23:163-172.

- Kline, G.G. 1963. Exploring the Great Basin. University of Oklahoma Press, Norman, Okla.
- Kurtin, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, N.Y.
- Laycock, W.A. 1991. Stable state and thresholds of range condition on North American rangelands. *J. Range Manage.* 44:427-433.
- Leopold, A.S. 1950. Deer in relation to plant succession. *Trans. N. Amer. Wildl. Conf.* 15:571-580.
- Mack, R.N., and J.N. Thompson. 1982. Evolution in a Steppe with few large hoofed animals. *American Naturalist* 119:757-773.
- Mack, R.N. 1984. Invader at home on the range. *Natl. History* 93:40-47.
- Martin, P.S., 1970. Pleistocene niches for alien animals. *Bio Science* 20:218-221.
- Martin, P.S. and R.G. Klein (eds.). 1984. Quaternary Extinctions: A Prehistoric Revolution. University of Arizona Press, Tucson, Ariz.
- Martin, P.S. 1986. Refuting late Pleistocene extinction models. *In: D.K. Elliot, (ed.), Dynamics of Extinction.* John Wiley and Sons, New York, N.Y.
- Martin, P.S. 1990. 40,000 years of extinctions on the "planet of doom." *Paleogeography, Paleoclimatology, Paleoecology* 82:187-201.
- Masters, L.S., and J.W. Burkhardt 1991. The geomorphic process: Effects of base level lowering on riparian management. *Rangelands* 13:280-284.
- McNaughton, S.J. 1976. Serengeti Migratory Wildebeest: Facilitation of energy flow by grazing. *Science* 191:92-94.
- McNaughton, S.J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. *Amer. Nat.* 113:691-703.
- McNaughton, S.J. 1984. Grazing lawns: Animals in herds, plant form and coevolution. *Am. Natur.* 124:863-885.
- McNaughton, S.J. 1986. On plants and herbivores. *Amer. Nat.* 128:765-770.
- McNaughton, S.J. 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature* 334-345.
- Mead, J.I., L.D. Agenbroad, O.K. Davis, and P.S. Martin 1986. Dung of *Mammuthus* in the arid southwest, North America. *Quaternary Research* 25:121-127.
- Melgoza, G., R.S. Nowak, and R.J. Tausch. 1990. Soil water exploitation after fire: Competition between cheatgrass and two native species. *Oecologia* 83: 7-13.
- Miller, R., and P.E. Wigand. 1994. Holocene changes in semi-arid pinyon-juniper woodlands. *Bicent* 44(7): 465-474.
- Mosley, J.C., 1985. Let's not forget the art in range management. *Rangelands* 7:154-155.
- Nowak, C.L., R.S. Nowak, R.J. Tausch, and P.E. Wigand. 1994a. Tree and shrub dynamics in northwestern Great Basin woodland and shrub steppe during the late Pleistocene and Holocene. *Am. J. Botany* 81:265-277.
- Nowak, C.L., R.S. Nowak, R.J. Tausch, and P.E. Wigand 1994b. A 30,000 year record of vegetation dynamics at a semi-arid locale in the Great Basin. *J. Vegetation Science* 5:579-590.
- Owen, D.E, and R.G. Weigert. 1981. Mutualism between grasses and grazers: An evolutionary hypothesis. *Oikos* 36:376-378.
- Owen-Smith, N. 1987. Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* 13:351.
- Paige, K.N., and T.G. Whitham. 1987. Overcompensation in response to mammalian herbivory: The advantage of being eaten. *American Naturalist* 129:407-416.
- Platou, K.A., and P.T. Tueller, 1985. Evolutionary implications for grazing management systems. *Rangeland* 7:57-61.
- Reveal, J.L. 1979. Biogeography of the Intermountain Region: A speculative appraisal. *Mentzelia* #4.
- Rickard, W.H., J.D. Hedlund, and R.E. Fitzner. 1977. Elk in the shrub steppe region of Washington: An authentic record. *Sci.* 196:1009-1010.
- Roe, E.G. 1970. The North America buffalo, second edition. Univ. Toronto Press, Toronto, Canada.
- Savage, M. 1991. Structural dynamics of a southwestern pine forest under chronic human influence. *Annals Assoc. Am. Geogr.* 8:271-289.
- Savory, A. 1988. Holistic resource management. Island Press, Conelo, Calif.
- Schroedl, G.E 1973. The archeological occurrence of bison in the Southern Plateau. Wash. State Univ. Lab of Anthropology. Report of Investigation 51. Pullman, Wash.

- Sharp, L., K. Sanders, and N. Rimbey. 1994. Management decisions based on utilization-Is it really management? *Rangelands* 16:256-259.
- Sinclair, A.R.E. 1982. Does competition or facilitation regulate migrant ungulates in the Serengeti? *Oecologia* 53:363-369.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Ann. Review Ecol. Syst.* 15:353-391.
- Sprugel, D.G. 1991. Disturbance, equilibrium, and environmental variability: What is "natural" vegetation in a changing environment? *Biol. Conserva.* 58:1-18.
- Steadman, D.P. 1995. Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* 267:1123-1131.
- Stoddart, L.A. 1946. Some physical and chemical responses of *Agropyron spicatum* to herbage removal at various seasons. *Utah Agr. Exp. Sta. Bull.* 324.
- Svejcar, T., and R.J. Tausch. 1990. Anaho Island: A relict area dominated by annual invader species. *Rangelands* 13: 233-237.
- Tausch, R.J., P.E. Wigand, and J.W. Burkhardt. 1993. Viewpoint: Plant community thresholds, multiple steady states and multiple successional pathways: Legacy of the Quaternary. *J. Range Manage.* 46:439-447.
- Tausch, R.J., J.C. Chambers, R.R. Blank, and R.S. Nowak. 1995. Differential establishment of perennial grass and cheatgrass following fire on ungrazed sagebrush-juniper sites. *USDA Forest Serv. Intmntn. Res. Sta. Gen. Tech. Rept.* 315:252-257.
- Tidwell, W.D., S.R. Rushforth, and D. Simper. 1972. Evolution of floras in the intermountain region Vol 1. *In: A. Cronquist, A.H. Cronquist, H.H. Holmgren and J.L. Reveal. Intermountain flora.* Hafner Publishing Co., New York, N.Y.
- Tisdale, E.W. 1961. Ecological changes in the Palouse. *Northwest Sci.* 35:134-138.
- Towne, C.W, and E.N. Wentworth. *Cattle and Men.* Univ. of Okla. Press, Norman, Okla.
- USDI-BLM (United States Dept. of Agric., Bureau of Land Managment). 1990. State of the public rangelands 1990.
- Van Vuren, D., and M.P. Bray. 1985. The geographic distribution of *Bison bison* in Oregon. *Murrelet* 65:56-58.
- Wagner, E.N. 1978. Livestock grazing and the livestock industry, p.121-145. *In: H.P. Brokaw (ed.), Wildlife and America*
- Wagner, E.H., and C.E. Kay 1993. "Natural" or "healthy" ecosystems: Are U.S. national parks providing them? *In: M.I. McDonnell, and S.T. Pichett, (eds.), "Humans as Components of Ecosystems.* Springer-Verlag, New York, N.Y
- Webb, S.D. 1977. A history of savanna vertebrates in the new world. Part 1. North America. *Annual Review of Ecology and Systematics* 9:393-426.
- Wilson, E.O. 1992. *The diversity of life.* WW. Norton and Co. New York, N.Y
- Young, J.A., R.A. Evans, P.T. Tueller. 1976. Great Basin Plant Communities-Pristine and Grazed. *Nevada Arch Survey Res. Paper #6.*
- Young, J.A., and B.A. Sparks. 1985. *Cattle in the cold desert.* Utah State Univ. Press, Logan, Ut.
- Young, J.A., R.A. Evans, and B.L. Kay. 1987. Cheatgrass. *Rangelands* 9:266-270.

