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Scientific Contract Report

Preface

The following report was prepared by University scientists through cooperative agreement, project science staff, or contractors as part of the ongoing efforts of the Interior Columbia Basin Ecosystem Management Project, co-managed by the U.S. Forest Service and the Bureau of Land Management. It was prepared for the express purpose of compiling information, reviewing available literature, researching topics related to ecosystems within the Interior Columbia Basin, or exploring relationships among biophysical and economic/social resources.

This report has been reviewed by agency scientists as part of the ongoing ecosystem project. The report may be cited within the primary products produced by the project or it may have served its purposes by furthering our understanding of complex resource issues within the Basin. This report may become the basis for scientific journal articles or technical reports by the USDA Forest Service or USDI Bureau of Land Management. The attached report has not been through all the steps appropriate to final publishing as either a scientific journal article or a technical report.

Paleoecological Relationships
of
Prehistoric Equus in the
Intermountain West

An Overview With
Implications for
Management of Wild
Horses and Burros

by

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INTRODUCTION

It is ironic that wild free-roaming horses and burros have become a source of so much contention in public land management. These creatures have a long tenure on the rangelands of western North America and are at the center of our western culture and tradition. Affinity for the wild horse and burro is pervasive throughout the American public. This interest in wild horses and burros cuts across virtually all segments of our society; urban and rural or eastern and western folks all share this interest. Few other public lands aspects have the potential for such a positive public identity and appeal. The mythical wild horse is inexorably interwoven into the fantasy and fascination the American society has for the "Ole West" and "Cowboys." Wild horses and burros are a symbol of our roots. As an image maker, the wild horse and burro program should have exceeded Smokey Bear.

However, in the absence of a common philosophical foundation on how free-roaming, large grazing animals should be managed, the wild horse and burro program has instead been tugged to and fro by conflicting special interest agendas to no one's satisfaction. The wild horses and burros have literally been used to create conflict over public rangeland use. Public land ranchers claim wild horses take livestock forage; environmental and humane activists attempt to block population control in the hopes that the horses will graze livestock off the public lands; and wildlife advocates claim feral horses are competing with "native" fauna for limited habitat.

Amid all this controversy there is a need for a better philosophical and ecological understanding of the role of large free-roaming herbivores in the rangeland ecosystem. After more than a century of experience with large animal grazing on the western rangelands, our track record is less than an unqualified success. While most rangelands remain productive with range trends generally stable or improving; problems with altered plant communities and eroding streams abound. Perhaps it is appropriate to question the naturalness and ecological sustainability of both livestock and wild horse grazing.

As a part of that analysis this paper is a review of the scientific literature relating to prehistoric and historic herbivory in the Intermountain biome of western North America. Hopefully, characterization of the nature of that prehistoric herbivory and the role of large grazing animal in the biotic complex will provide a better model for future wild horse and livestock grazing management.

EVOLUTIONARY HISTORY

Flora and Fauna of the Intermountain West

The coevolution of warm-blooded animals and the flora appears to have began about 60 million years ago with the extinction of the dinosaurs. However, the origins of current Intermountain flora dates back to the late Miocene, 12-20 million years before present (B.P.). Prior to the uplift of the Cascade-Sierra Cordillera the Great Basin and Columbia Plateau were vegetated by hardwood-deciduous and conifer forests (Tidwell et al. 1972 and 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 block the Pacific storm track, the landscape to the east became progressively more xeric and seasonal (Tidwell et al. 1972). The temperate forests were slowly being replaced by shrub land 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 families as Chenopodiaceae, Gramineae and Compositae all important plant families in the deserts and shrub lands of the Intermountain region today. Gray (1964) reports the earliest fossil pollen record of Artemesia (sagebrush) to be in late Miocene deposits in northeastern Nevada. By the end of the Miocene (about 12 million years B.P.) much of the Intermountain West had become distinctly more arid and was vegetated by xeric woodlands (Tidwell et al. 1972).

During the Pliocene (2-10 million years B.P.) the CascadeSierra 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 million years B.P.) the flora of the Intermountain Region was essentially the same as our modern flora (Tidwell et al. and Barnosky 1981). During the climatic fluctuations associated with the glacial-interglacials periods plant species migrated longitudinally and elevationally in a compensatory action (Nowak et al. 1994 and Tidwell et al. 1972). On the basis of the plant fossil record, pollen studies and the pack rat middens it appears that many of the plant species which comprise the current Intermountain flora have existed in this region at least since the beginning of the Pleistocene (2 million years) (Barnosky 1987).

Evolution of the flora most certainly was not the only biological event occurring during the past 20 million years. Concurrently with this floral evolution was the appearance of the myrid of new animal species (Kurtin and Anderson 1980 and Martin 1990). The neo-tropical 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 mega fauna. The fossil record indicates that grazing herds of elephants, mammoths, rhinos, camels, horses, burros, ground sloths, and many other grazers and browsers roamed throughout western North America for several million years (Kurtin and Anderson 1980; Grayson 1982; Webb 1977). Prehistoric cattle were also part of this faunal assemblage. Several genera from the Bovidae family including Bos (cattle) have been found in the North American Pleistocene fossil record (Martin 1986). The fossil record of these herbivores and the associated predators (sabre-tooth tigers, cave 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 mega fauna resulted from the coevolution of flora and fauna over several million years. This biotic complex successfully existed throughout North America despite numerous major climatic fluctuations. 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) states "based on the sizeable biomass of elephants, bovids 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) goes on to state "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."

Prehistoric Horses in North America

The fossil record indicates that horses first evolved in North America about 60 million years ago and from there spread to other continents (Denhardt 1975). Ancestors to our modern horse were some of the early mammals to develop after the dinosaur extinctions of the late Mesozoic. During this long evolution the horse underwent astounding bodily changes. It evolved from a tiny forest dwelling browser into the large bodied, fleet plains and plateau grazer with which we are now familiar.

The modern horse (Equus caballus) and the burro (Equus hemionius) had both evolved by the Pleistocene (2 million years before present) and are well represented in the fossil record of

Ice Age fauna. Equus fossils of the Pleistocene have the same skull and skeletal features as our modern horses (Denhardt 1975, and Evans et al. 1977) which has changed very little since the Ice Ages.

After having evolved and thrived in North America for about 60 million years, the entire geneus Equus became extinct during the late Pleistocene (Willoughby 1974, Martin 1986, and Fleharty and Hulett 1977). Several fossil recovery sites from Nevada date Equus extinctions (youngest recovered fossils of Equus) from 9700 to 13,000 years before present (B.P.) (Table 1).

Table 1: Equus Extinction Dates in Great Basin

(from Grayson 1982)

Location	Youngest Fossil Date
Crypt Cave, Nevada	9,700 ± 200
	10,000 ± 220
	10,700 ± 240
Fishbone Cave, Nevada	11,200 ± 250
Gypsum Cave, Nevada	8,527 ± 256
	10,075 ± 550
	10,902 ± 446
	13,310 ± 210
Tule Springs, Nevada	11,500 ± 250
	13,100 ± 200

Numerous other fossil sites such as Catlow Valley Cave, Paisley Five-Mile Point #3 and Fort Rock Cave all in Oregon provided similar dates for the youngest horse fossil remains (Grayson 1982). In fact the fossil record indicates that horse became extinct throughout North America by 7800 years B.P. (Willoughby 1974, Grayson 1987 and 1991, Martin 1970 and 1990). As stated by Fleharty and Hulett 1977, "the complete removal of North American horses ... represents a loss of a lineage of grass eaters, without the loss of the grass.

Pleistocene Extinction

Just as the fossil record reveals the coevolution of the Pleistocene flora and fauna and the existence of these widespread natural herbivories on each continent; the fossils also record the demise of the mega fauna (Martin 1986; Fleharty and Hulett 1977; Owen-Smith 1982 and Grayson 1991). In western North America the fossil record indicates that the majority of large herbivores and their associated predators became extinct between 10,500 and 7,000 B.P. This massive extinction over an extremely short time period removed over 70% of the Pleistocene mega fauna in North America (Martin 1986). Similar extinction occurred in other continents but at somewhat different times. North America lost 33 out of 45 genera of large fauna during this late Pleistocene extinction (Martin 1986 and 1990). From 7,000 year B.P. to the present the depauperate remnants of the Pleistocene mega fauna include bison, elk, moose, deer, antelope, and bighorns. 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 implications of the Pleistocene extinctions on current efforts to comprehend our western ecosystems is tremendous, even if not yet recognized. 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. Ecologists, range scientists, land managers and environmentalists (largely unaware of the fossil record) 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 pervade all facets of land management and ecology in the country.

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 as yet to replace what was lost. This hardly appears to have been a normal evolutionary event.

The demise of the Pleistocene mega fauna 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 and 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 mega fauna 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 extinction were primarily driven by human predation is gaining scientific proponents (Fleharty and Hulett, Denevan 1992; Martin 1970, 1986, 1990; Graham 1986; Burney 1993; Owen-Smith 1987). It now appears that the first humans immigrated to North America from Asia crossing the Bearing Straits land bridge during a glacial period at least 12,000-15,000 years B.P. Apparently it took about 1500 to a few thousand years for this new super predator, hunter man, to populate the new lands and begin to dramatically impact the mega fauna. 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 1989; Fleharty and Hulett 1977). Whatever the cause, the extinction by 7,000 years B.P. of most large herbivores and predators left a natural rangeland grazing ecosystem, which had existed several million years, with many vacant large fauna niches.

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 vicinity of the America's, European descendants 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). Numerous ecologists and biologists attributed the scarcity of bison in the Intermountain region to environmental constraints of the 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 1800s stand in stark contrast to the Pleistocene fossil record of the Intermountain Region (Schroedl 1973 and Grayson 1982). Certainly bison and the other members of the Pleistocene mega fauna roamed the entire Intermountain Region at least until the extinction of 7000 B.P.

A review of the literature reveals emerging evidence indicating 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 7000 years up to the Indian acquisition of the horse and rifle. Butler (1976 and 1978) discusses 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. Van Vuren and Bray (1985) presents 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 reports that bison remains recovered from 22 archaeologic sites in the Columbia Basin provides evidence of bison present from the late Pleistocene until just prior to historic times.

Based on the archaeologic/fossil record it seems evident that bison survived the Pleistocene extinctions of 7000 years ago 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.

HISTORIC PERCEPTIONS

At the time of European man's arrival in the Intermountain West (ca 1800), he found a vast region vegetated largely by open shrub stands with an abundant perennial grass understory. Climatically, the shrubs and junipers could out compete 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, antelope and some deer and elk (Rickard et al. 1977). In parts of the Intermountain Region game animals were spare enough that early explorers sometimes had difficulty acquiring sufficient food (Young and Sparks 1983).

It is on the basis of this historical experience that we have formulated 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 adverse impacts of livestock or wild horse or burro 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 because the Intermountain Region evolved without an abundance of large herbivores, therefore the native plant communities were not adapted to support such grazers in the form of cattle, horses and sheep and burros. This has become 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 has 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 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 of our underlying ecological assumptions. First, did biologic conditions of the western landscapes at the time of European contact (ca 1800) represent the stable natural state - the end product of evolutionary and ecological adjustments or the climax biologic communities? Considered in the context of the Pleistocene extinctions and the continually changing climatic conditions (Eddy 1991 and Nowak et al 1994) of the Quaternary period (the past 2 m.y.), climax or pristine biotic communities hardly seems a relevant concept. 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 (Nowak 1994). Indeed 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). 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 is no longer acceptable. A more appropriate paradigm is needed.

Implicit in our vegetation concepts such as pristine, climax or virgin forests is that of 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 communities pre-European contact. For example Savage (1991) and Denevan (1992) detail evidence of major human impacts upon the North American landscape pre-European contact. Denevan refers 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 is not adapted to large animal grazing. Again the fossil record, as we currently understand it, stands in direct contradiction of the 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 7000 years has the large bodied herbivores and predators not been part of this continent's 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 7000 years in which they were absent. Tidwell et al, (1972) considers our present flora to be essentially the same as that of the Pleistocene. If one would equate the 2 million years of the Pleistocene in which large herbivores influenced plant adaptation to one calendar year; then the adaptive time period without large herbivores is about 31 hours out of that year.

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 size grazers such as antelope and bighorn, 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 marine and terrestrial ecosystems and is basic to biologic diversity and energy flow in these systems. In grasslands, shrub steppes, woodlands savanna and arctic tundra throughout the world, complex herbivories evolved which 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 webb 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.

If indeed the Intermountain flora evolved over millions of years with large herbivores (as the fossil records indicate) and in recent time those animals became extinct; is it possible that wild horses, burros and other livestock could now represent a potentially functional replacement for the mega fauna? It appears that since the continental extinction of mega fauna by 7000 B.P. and the regional extinction of bison in the late 1700s there would indeed be unoccupied large herbivore niches. Certainly it would seem that cattle and horses are large bodied herding animals with generalist grazing habits which might compliment the more selective browsers and grazers such as antelope, deer, elk and bighorn. Cattle could occupy closely the bison niche and horses as well as burro's were indeed part of the original mega fauna. Perhaps exotic grazers from other continents could be imported to fill vacant niches as has been done in Texas. The idea of surrogate herbivores has previously been suggested by other authors (Martin 1970; and Fleharty and Hulett 1977) and has left some ecologists and environmentalists, who may have been unaware of the fossil record, aghast.

After something more than a century of experience with domestic and feral livestock grazing in the Intermountain Region, it should be possible to judge the functionality of these surrogate grazers. If we were to do so on the basis of the current environmental uproar over livestock and wild horse 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 has 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 and wild horses, 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 stressed the forage plants, consumed all the annual growth of grasses and fire-proofed the sagebrush steppe. The inevitable consequence was an increasing shrub or woodland aspect to the vegetation 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 a permanent flora 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).

Consequently in the lower elevation portion of the sagebrush steppe, due to the continuous carpet of fire-stemmed annual grass, flammability is now higher and fire frequency in recent years has increased. 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 grazing does not prevent or reverse this change (Svejcar and Tausch 1990). At the higher elevation on more mesic sagebrush sites such as mountain big sagebrush--Idaho fescue, cheatgrass is not as well adapted. Dominance of cheatgrass occurs only as the result of disturbance, such as poor grazing practices.

On these sites, "pristine" plant communities remain the potential and the current vegetation on nearly all of these sites.

Juniper has existed in portions of the Intermountain Region for thousands of years as the rim-rock monarchs standing watch over this plateau country. Changes in the extent and distribution of juniper have occurred through geologic times as a response to shifting climatic conditions (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 since- about the 1880's western juniper has been extending its range from the fire-safe rim-rocks and rock outcroppings into. the valley slopes and bottoms (Burkhardt and Tisdale 1976). This change, while producing an increasingly green landscape, is the demise of productive wildlife, wild horse and livestock habitat. As young juniper stands thicken, 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 higher elevation sagebrush ranges (Burkhardt and Tisdale 1976). Settlement of the West and subsequent heavy livestock grazing essentially fire-proofed these ranges thereby creating safe havens for the establishment of juniper seedlings. Fire prevention and control programs in more recent years have assured the continuing demise of these productive rangelands.

Riparian areas have been heavily impacted partially by livestock grazing but 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 negatively and positively by a century of livestock grazing. Bighorn sheep have suffered set backs most likely due to transmitted livestock diseases and to "brushing up" of much of their range. Deer populations expanded phenomenally as the result of shrub increases in the sagebrush steppe. Antelope, elk and moose populations have made remarkable increases in the past 3 decades despite continued urbanization of winter ranges and increasing sport hunting demands. These increases are the likely result of improving habitat created by more conservative and better managed livestock grazing of the past 3 decades. Certainly range condition at least on uplands over much of the Intermountain Region has improved over conditions of the early 1900s and the trend continues (USDI-BLM 1990 and Burkhardt 1991). Exceptions to this pattern of improvement are for the most part those areas dominated by preadapted exotic annual plants and those ranges where juniper or shrub encroachment have eliminated the native herbaceous understory plants (woody plant monoculture) Additionally some riparian areas are in declining condition.

And now back to the hypothesis regarding the suitability of horses, burros and livestock to function as surrogate mega fauna. At best this seems a mixed bag. The 100 plus year experiment has not been a complete failure or success. The fire proofing 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 "Smokey Bear." Additionally some of the riparian problems result from poor livestock distribution (however, watering places in the African Serengeti 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 has produced some positive changes. However, as surrogate mega fauna our wild horses and livestock grazing experiment leaves a lot to be desired.

LESSONS FROM THE PAST

If our livestock and wild horse grazing experiment has been less than a 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 (and at considerable risk) to characterize functional features of the Pleistocene mega fauna 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 and wild horse management.

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. The Intermountain Region was and is arid due to the Sierra-Cascade rainshadow. Because of elevation and the predominately winter Pacific storm track, precipitation was largely cold season. This produced a shrub steppe vegetation in the valley and foothills and coniferous forest in the mountains. Cool season bunchgrasses predominated and climatically 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 6 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 prairie region offered the Pleistocene herbivores a very different environment than those same species encountered west of the Rocky Mountains. The plains which lie east of the Rocky Mountains are arid to mesic and receive precipitation from the winter storm track off the Pacific Ocean and the Arctic cold fronts. Summer moisture comes from cyclonic Gulf of Mexico storm systems. Consequently the prairie region has 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 grazing season. The Prairie landscape is noted for its 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 mega fauna was apparently very tolerant of a wide range of environments. Other significant features of this faunal assemblage included hoofed, herding herbivores with both grazer and browser species. Grazing habits apparently included both selective and generalists. The Pleistocene mega fauna was also characterized by a diverse array of large and small herbivores and predators much like the Serengeti today.

Just as today, there would have been an inherent difference in total productivity both floral and faunal. The Prairie Region is more productive due to growing season precipitation. Annual aboveground 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 grazer 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 differential 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 the 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 production/ reproduction in large herbivores. Cured forage protein content is generally maintenance or submaintenance 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 or 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. Likely all three of these options were capitalized upon. Given the mountain valley topography and the numerous stream systems it would be possible for herbivores to extend the green feed period available to them throughout the entire summer.

It seems obvious that herbivory in the Intermountain Region had to develop seasonal grazing patterns. Literally following the melting snows up the mountain in the spring and beating the drifting snow back off the mountain 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 smaller bodied native ungulates that survived the Pleistocene extinctions. In fact even our wild horses and livestock, after centuries of domestication, exhibit these same behavior patterns in mountain/valley landscape if given the opportunity.

It is easy to comprehend the functional advantage to the herbivore of seasonal grazing in the Intermountain Region extended green period/protein availability. 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 serve 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; and Jansen 1982 and 1984). The functional relationships of herbivores to plants range from influencing plant completion in the community and seed dispersal/planting to nitrogen mineralization, carbohydrate reallocation and compensatory growth.

Certainly for as pervasive and enduring as herbivory is in the biologic world, the process must serve a purpose beyond simply filling paunches with grass.

In regards 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 follow greenup from winter ranges in the valley to summer ranges in the mountains would allow the bunch grasses and forbs to regrow and set seed after the animals moved on. This would have assured reproduction and carbohydrates storage in bunchgrasses. It would also have allowed for the accumulation of cured grasses on the 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 served the plant community. Seed dispersal and dormancy release after passage through the animals digestive track and seed planting are ail by products of dormant season foraging (Jansen 1982 and 1984). All of these are much more important to the cespitose 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 breaking soil surface crusts which are so common to Intermountain soils and litter incorporated into the soil. As Allan Savory has so effectively and frequently discussed, the hoof action of herding animals in arid regions can improve nutrient and water cycling.

It is possible that the Pleistocene predators would 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 well have been tempted to "keg-up" in these favorable environments during the heat of summer. Yet we do not see strong tendencies to do so in the surviving native grazers such as elk, deer or antelope. Perhaps the effectiveness of predators along the densely vegetated stream bottoms discouraged Pleistocene herbivore from using riparian areas as social centers. Similar predator-prey- topofloral relationships have been noted in modern African herbivories (Bell 1971). Predation may well have prevented sedentary herding behavior.

The evolutionary process of functionally matching flora and fauna to each other and the physical environment certainly involves diversity of herbivores and vegetation. Floral or fauna monocultures are unusual and temporal in natural ecosystems. The diversity of the Pleistocene herbivores which the fossil record indicates roamed the Intermountain region would seem appropriate to the diversity of the region's vegetation. The array of selective and generalists 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 stabilized species composition within plant communities and maximized herbivore biomass.

Wild Horse and Burro Management

Bringing back the Natives

The reintroduction of Equus caballus and E. heminius back into North America in the early 1500s by Spanish Conquistadors represents perhaps the earliest recorded effort by humans to reestablish extinct faunal populations. Inadvertent as that event may have been, it is notable for its success. Indeed, today populations of wild horses and burros thrive over much of the public rangelands of the western U.S. This is ample testimony to the statement by Fleharty and Hulett (1977) that the extinction "of North American horses, for example, represent the loss of a lineage of grass-eaters without the loss of the grass" ... "Certainly nothing happened at the end of the Pleistocene to destroy horse habitat." Tidwell et al. (1.972) considers the Intermountain flora of the Pleistocene to essentially be the flora of today. On the basis of several lines of evidence currently available, it appears that the wild horse and burro habitat niches remained essentially vacant for nearly 8000 years following the late Pleistocene extinctions (Martin 1970, Willoughby 1974, Grayson 1987). European contact with North America in the early 1500s set in motion a partial reoccupation of those riches.

The return of horses and burros back to North America, after having evolved and thrived in North America for millions of years and after immigrating to other continents before going extinct in North America, was indeed a notable event. Horses and burros have a longer tenure claim in North America than several of our "native faunal' such as bighorn sheep or bison which are both Asian immigrants. It is remarkable that public land management policy has been to remove horses and burros from several National Parks and some cases other public lands. They are considered feral or exotic species that are encroaching on so called "native" wildlife habitat. Such management policies are much at odds with the known fossil record. “... in strictly genealogical terms, it is clear that certain supposedly "alien" mammals have a valid prior claim to the continent. At higher taxonomic levels some of the "natives" are considerably less American then certain foreigners" (Martin 1970).

The wild horse and burro education program should strive to increase public awareness of the remarkable North American heritage of these animals. Programming should celebrate the long evolutionary history, the extinction and the reintroduction of wild horses and burros in North America. That is important historical and philosophical backgrounding on which the WH&B management program should be based.

Missing Links

Significant and successful as was the repatriation of the continentally extinct Equus in North America, there remain fundamental biologic problems. The horse was but one grazer in a complex web of herbivores and predators which over millions of years had achieved some level of mutualism/ facilitation/ competition between each other and their respective habitats. Like the horse many of the other faunal components of this herbivory became extinct and have not been reintroduced or substituted.

In regards to wild horse and burro management, the loss of predator components of the Pleistocene herbivory is particularly significant. That complex of large bodied herbivores evolved with a variety of equally sizeable predators. The short-faced bear, sabre-toothed cat, dire wolf and a host of other carnivores likely provided functional roles in that grazing ecosystem. Natural herbivories evolved on virtually all terrestrial landscapes from deserts to tundra. Predation as well as grazing and/or browsing are the common biologic processes to each of these. Beyond just facilitating energy flow through the ecosystem, predators provided the population checks, fitness screening and herding incentives necessary to assure sustainability of the herbivory. In a sense predators were the grazing herd managers or cowboys.

Population checks on large herbivores is essential to herd stability and sustainability. The excess young, the infirmed or unwitting and the aged are systematically removed from the herds. In the absence of this removal, grazer populations overwhelm their forage resources to the demise of themselves as well as other members of the herbivory. In the Pleistocene mega fauna, the diverse array of predators which coevolved with the herbivores performed this function. In post Pleistocene, big game herds the population checks are both four-legged and two-legged predators. With domestic grazers, the excess and the unfit are removed each year by the herdsmen. Removal of the annual excess from the grazing herds is essential to stability of the entire complex (fauna and flora). In the absence of this function, population explosions, habitat destruction and herd die-offs characterize the herbivory.

When Europeans brought the horse back to North America, they did so minus the natural predators which had been an integral part of the Pleistocene herbivory. It would seem ecologically and perhaps even morally incumbent upon man, since we can no longer bring back the extinct predators, to at least prudently provide that functional role in our management of free-roaming horses and burros. The WH&B. Act (PL92-195) specifically directs the

Secretaries to protect, manage and control these animals on public lands in a thriving ecological balance. If the Pleistocene herbivory provides the model, then the essences of the wild horse and burro management program should be to assure the functional roles of population control and fitness. Nothing less is acceptable if we are to maintain the grazing ecosystems (thriving ecological balance) on our public lands.

WH&B management should assure that horse and burro herds (as well as the other herbivores) exist within the capacity of their ranges. The production of excess young (the annual herd increase) should not exceed the outlet capacity for these animals and they should be removed from the herds. Warehousing of unadopted or excess horses and burros either on or off of public lands is symptomatic of a management program out of balance ecologically, politically and economically. Such management is also outside the letter and intent of the law.

In a natural herbivory system, predation is directed primarily at the young, the infirmed or unwitting and the aged portions of the herbivore population. This maintains a breeding herd of largely fit, mature animals which possess the collective herd behavioral knowledge necessary for survival. It would seem prudent for the WH&B management program to emulate, so far as possible, this natural population control function. Breeding herds should be maintained on the range and in the absence of "effective natural predators" population control should be directed at the excess young and the old or infirmed.

Multicultural Herbivories

or

"Political Correctness" on the Range

It is obvious from the fossil record of the past or from the "natural" systems of today that monocultures, either floral or faunal, are abnormal and temporal on terrestrial landscapes. They are not sustainable, as we have learned in agriculture, without energy inputs. Yet much of our livestock grazing and to some extent our wild horse management practices on public lands tends toward single or dominant species herbivores. The Intermountain Region provides a great variety of landscapes vegetated by a diverse array of woody and herbaceous plants. Certainly such an environment would provide niches for a variety of generalists and selective grazers and browsers. Single or dominant species herbivores would concentrate grazing pressure on a portion of the plant community. This creates competitive shifts in the plant community and lower carrying capacity.

Too often we think only in terms of competition between multiple herbivores. Volumes of research has been published which deals with competition between livestock and big game or horses in terms of food habits or security cover (Krysl et al. 1984a and

1984b; Vavra and Sneva 1978). While some of this is certainly appropriate; the relationship between multiple herbivores goes beyond just competition. At least the fossil record of the Pleistocene certainly is suggestive of some degree of mutualism and facilitation among herbivores. Research in the Serengeti has demonstrated this complex relationship among multiple herbivores using the same rangelands (MacNaughton 1976, 1984). The management histories at several state game ranges (Bridge creek in Oregon and Sand Creek in Idaho for examples) illustrate mutualist relationships between cattle and elk. Cattle grazing is now used to precondition forage for elk use by increasing palatability and protein content.

In the political turmoil surrounding public land management and the WH&B program, there have been numerous efforts to create wild horse or burro sanctuaries. Regardless of the political attractiveness of such ideas, the ecological wisdom is lacking. The fossil record of the complex grazing ecosystem that was North America for millions of years provides no such model.

Useful Tools or Bandaides

The goal of the WH&B management program should be to allow horse and burro herds to graze public rangelands in as "natural" a regime as possible. That would appear to reflect the intent of the WH&B Act as well as allow these animals to follow their instinctive grazing habits. In the Intermountain Region that most often would ,be some form of seasonal migrations. Given the elevational relief, and the short growing season of this region; native game, horses and even livestock instinctively follow the green up the mountain in spring and the drifting snow back down in the fall. As previously discussed this grazing strategy in the Intermountain Region is ecologically functional, serving both the vegetation and the herbivore.

In an effort to better manage livestock grazing on public lands, range managers have applied a number of grazing strategies and tools that in some cases are counter to this natural grazing system of the region. The application of these tools to livestock allotments may well affect the manner in which horses or burros graze. Obvious examples include allotment boundary and rotational pasture fencing, and water developments. Less obvious but no less at odds with seasonal grazing would be the application of deferred/rotational grazing, range readiness criteria and utilization limits. If we look to the Pleistocene herbivory as a model there are no analogues to these grazing management tools. Where are the indications in the fossil record of prehistoric rangers enforcing rotation, range readiness or utilization limits on the Pleistocene mega fauna?

The WH&B management program and the livestock grazing program should at least provide some opportunities to experiment with the

Pleistocene model. Rangeland herbivories are extensive, nomadic or migrational ecosystems. Yet our every effort over the past 50-75 years at better grazing management has been toward greater intensification, confinement and specialization. Perhaps wild horses and burros, the rangeland ecosystem and our society would benefit from some new yet very old approaches to management of grazing ecosystems.

CONCLUSIONS

The modern horse (Equus caballus) and burro (Equus hemionius) have a most unique history in North America. Perhaps no other animal can claim to have evolved in North america over the past 60 millions years, spread to other continents only to become extinct on the continent of its origin by 7000 years B. P. and finally to be reintroduced back to America in historic times. Horses and burros may be the first successful human reintroduction of a continentally extinct species. The tenure claim of horses and burros to North America exceeds that of several of our highly vaunted big game species. Certainly wild horses and burro are a living legacy of North American rangelands and are a part of our public land heritage.

Until their extinction, horses and burros were part of a complex grazing ecosystem which developed and sustained itself for several million years on the rangelands of North America. The fossil record indicates that this North American herbivory, the Pleistocene mega fauna, exceeded the modern Serengeti for faunal diversity. Between 10,500 and 7,000 years ago massive extinctions removed most of the larger bodied fauna from the system. There are indications that these extinctions were related to the arrival of the first humans to North America.

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 the fossil record, assumed that the biologic conditions at the time of European contact were pristine or climax. This view has shaped the development of range science and land management profoundly. The underlying assumption has been that the Intermountain biome was largely unadapted to large herbivore grazing. Consequently, livestock grazing management has largely 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 our wild horse and burro management as well as livestock grazing is functional within the parameters of the biologic system.

Characterization of the Pleistocene herbivory provides a potential model for functional wild horse and burro management grazing.

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Peer Review Comments

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Herbivory In the Intermountain West. An Overview of Evolutionary History, Historic Cultrual Impacts, and Lessons from the Past

and

Paleoecological Relationships of Prehistoric Equus in the intermountain West. An Overview with Implications for Management of Wild Horses and Burros

Specific comments are addressed to the contract report entitled ***Herbivory in the Intermountain West: An over-view of Evolutionary History, Historic Cultural Impacts, and Lessons from the Past*** (hereafter simply called 'the report'], and all page numbers are from that report. However, in many respects the two reports are nearly identical, so comments and criticisms generally apply to both.

The reports (at least as provided to me) are anonymously authored. The first person pronouns scattered throughout the reports (e.g*., I, we, our*) are inappropriate for documents without authors. Either the pronouns need to be deleted or the author(s) should be identified. If the later, the author(s) need(s) to consistently use either singular or plural pronouns.

I do not know if there were authors or an author. However, for the sake of convenience, hereafter I am using the singular (hereafter called 'the author]. Anything in double quotations marks is a direct quotation. If a quotation is unattributed or if only page numbers are given, then it is directly from the report.

I have found a number of serious flaws in both reports, which I discuss in detail below. These include faulty conceptualization of processes of natural selection and evolution, reliance on unsubstantiated or weakly substantiated assumptions, arguments built on scientifically unsupported premises, a failure to present all alternatives concerning controversial issues, a propensity to present a single alternative as if it were the only point of view found in scientific literature, presentation of scientifically unsubstantiated opinions as if they were scientifically tested and accepted, and inconcise or unconventional uses of scientific terminology. Current versions of the reports are scientifically invalid, and should not be considered for use as a framework on which to base management decisions without almost complete revision.

As the author points out, traditional uses of natural resources are "coming under increasing scrutiny, especially on public lands" (p.1). One of these is domestic livestock grazing. One criticism has been that beef cattle (which the author describes as "being nearly the sole herbivore" (p.32) in the area covered by the report) raised on public lands in the western United States (US) compose only a very small proportion the US herds (Jacobs as cited in Torell et al. 1992). Using data from the US Forest Service (USFS) and Bureau of Land Management (BLM), Torell et al. computed that, in 1990, 15% off cattle in the US were produced on public land ranches (more than 5% grazing capacity from BLM & USFS lands), about 8% of the total US herds were authorized to graze on federal lands, and about 4% of the forage for the those herds was supplied by western US public lands. While these numbers are greater than the 2% cited by some, they are much less than the livestock industry's estimate of 40% (Jacobs and *Newsweek*, respectively, as cited in Torell et al. 1992). No matter how carefully calculated, numbers such as these (coming from within the agriculture and range science academic community) may still be questioned because the integrity and credibility of that community (especially at western US land-grant institutions) have also been questioned (e.g., Fradkin 1979, Johnson 1987, Marston 1990, 1992, Savory 1983, Williams 1991, the report author). Advocates of livestock grazing on public lands must be able to demonstrate that low-impact management is possible, on the basis of careful use of the best available science (not just currently most popular nor limited by subdiscipline, e.g., range, wildlife, or animal science). Use of scientifically unsubstantiated opinions as a basis for management decisions can leave public-land management agencies and their personnel vulnerable to accusations of management by myth.

Since, as the author points out, "our" 100-plus-year livestock grazing experiment "has been less than a success" (pp.23-24), advocates of public-land livestock grazing must be able to demonstrate how ecological costs (Fleischner 1994) can be minimized, not trivialized (i.e., these reports). Introduction of alien taxa (including both traditional domestic livestock and "other exotic grazers from other continents" (P.19)) must always be treated as "a significant ecological change" (p.20), and negative impacts on native plants and animals, on soils and soil organisms, and on all other aspects of the ecosystems must be anticipated and minimized. This will not be done if management decisions are made based on myths, misunderstanding, and misinformation. With these reports, the author(s) and agencies who funded them will be handing those opposing livestock grazing on public lands a strong weapon to use in arguments for removing livestock from public lands.

After pp.2-6, the Hypotheses are never directly addressed again, nor is it stated anywhere whether the author feels they should be accepted of rejected. This should have been done in a Conclusions section. On the basis of best available science, one of the five hypotheses (p.5) cannot be accepted or rejected as worded, two must be rejected (i.e., null hypotheses accepted), and two must be accepted (i.e., null hypothesis rejected) [concepts involved discussed in more detail below]. (1) This is not actually a testable hypothesis. It is a statement about validity of traditional Clements/Dysterhuis succession concepts and philosophical questions about 'pristine'. It needs to be reworded. (2) This hypothesis must be rejected. Best available science provides evidence that large-bodied herbivores were probably not important selection forces in the Intermountain Region. (3) This hypothesis must be rejected. Best available science provides evidence that alien domestic livestock (horses and cattle) cannot be "replacements" for "extinct Pleistocene mega-fauna". (4) This hypothesis must be accepted. Best available science, domestic livestock introductions in the Intermountain Region and. accompanying ecosystem disturbances have produced significant biological impacts. (5) This hypothesis must be rejected. Characterization of Pleistocene herbivory in the Intermountain Region cannot provide a workable model for management of domestic livestock grazing.

The Conclusion (sic) on pp.40-41 is not supported by best available science (see below for more detailed discussion]. (1) There is not compelling evidence that the Intermountain Region "evolved" as a "natural grazing system". (2) It is true that "at the time of European contact with North America the biologic (sic] system was in flux" rather than at "climax"; however, that is the nature of a dynamic system [see discussion of disequilibrium, etc.]. There were no "vacant" niches. Within the discipline of ecology, use of the fossil record and other paleobiological information, as well as archeology, paleoclimatology, etc., is not new. Best available science supports the "underlying assumption" that the Intermountain "biome" was "largely unadapted" to large herbivore grazing. (3) While it may be "time to rethink the fundamentals", there is no reason to attempt to build a reevaluation on scientifically unsupported premises. Herbivory is "part of the natural biologic (sic] system on terretrical (sic] landscapes". However, terrestrial herbivores can range in size from single cells to elephants (Billings 1970). Large-bodied grazers are not part of all natural systems. There is no compelling evidence to support the opinion that they played a significant role in development of contemporary ecosystems in the Intermountain Region, Large-herbivore grazing by alien domestic livestock is not part of natural ecosystems in the Intermountain Region. Biologically, domestic livestock are ± preadapted, ± invasive, alien species. Furthermore, it is recent selective forces (rather than longest) that are reflected in contemporary populations. Selective agents of the Holocene have operated more recently than those of the Pleistocene, and one should expect contemporary taxa to reflect the more recent environment (Baker 1992). Pleistocene herbivory is an inappropriate model because of intervening time, natural selection processes, and differences between alien livestock and native taxa. None of the patchily distributed native Holocene ungulates are as nearly true grazers as the more ubiquitously distributed alien livestock, and it is possible that none of the Pleistocene large herbivores were (see Akersten et al. 1988, McDonald 1981). Alien livestock are very different from native western North American ungulate taxa in behavior, diet, etc., and therefore can have very different impacts. Contrary to the author (p. 19), cattle cannot "occupy closely" niches of either extinct or extant Bison spp. (niches are not space, and cattle exploit resources very differently from bison - see McDonald 1981, Van Vuren 1982), and extinct native Pleistocene Equus spp. were different taxa (therefore had different niches) than modern alien horses. If one genuinely wished to build a model for domestic livestock herbivory in the Intermountain Region on natural selection, evolution, and parameters of the natural biological system, with a focus on 'prehistoric herbivory' (rather than building one based on minimizing and mitigating negative impacts), that model would have to incorporate the most 'similar' (i.e., most biologically similar in size, diet, behavior, etc.) herbivores that might have been a recent selective force experienced by contemporary plant taxa (or their recent ancestors). These 'similar' herbivores would have been some portion of widely scattered, relatively small groups of late-Holocene native ungulate taxa. (The most common, most ubiquitous vertebrate herbivores were Lepus spp. (jackrabbits), not ungulates.] This would mean that numbers of livestock could be no greater than what that might be considered equivalent (sensu Vallentine 1990) to numbers of pre-settlement native ungulates. It would also mean that distribution would be limited to only those areas known to have supported populations of the 'similar’ native herbivores. Numbers of livestock 'allowed' by this model would probably be considerably fewer than actual numbers of livestock currently in the Intermountain Region.

While construction of scenarios and models can an acceptable way to present working hypotheses, they must still be based on best available science. The best models are usually built using parsimony and preponderance, i.e., the most parsimonious model that can be supported by the preponderance of good science. Without good science backing it up, scenarios (e.g., these reports) are nothing more than opinion, and opinion is not an acceptable basis for major management decisions.

Some scientific terminology is used in ways contrary to accepted meaning within the particular discipline where the term originated, and the author's intended usage of other terms is unclear. Many of these are terms that have sometimes been loosely used by others (usually by writers outside the discipline). However, because both reports are built around controversial material, special attention should be paid to precise use of terminology. Where there could be confusion, terms should be defined and a reference given ("sensu"...).

Herbivory is the act of being an herbivore, the consumption of photosynthetic primary producers. It is not a synonym for plant/herbivore interactions. Types of herbivory are frequently imprecisely defined in the literature. As one scans the 'grazing' literature, one finds ***to graze*** is used to mean (1) to consume any type of aboveground production (both woody and herbaceous plants), (2) to feed primarily on herbaceous plants, or (3) to feed primarily on grasses or graminoids (Painter 1995, in press). ***To browse*** is used to mean to feed primarily on (1) woody plants or (2) non-grasses or non-graminoids. In addition, both terms may be used only for defoliation or may include some or all ancillary impacts (e.g., trampling, excrement, pull-up and breakage). A statement such as "grazing is a natural process on all plant communities" (Box & Malechek 1987) takes on different meanings, depending on the definition used. In this review, I use definition 2 (to feed primarily on herbaceous plants) for ***grazing*** and definition 1 (to feed primarily on woody plants) for ***browsing,*** and include ancillary impacts. Strictly speaking, a grass or graminoid specialist is a ***graminivore,*** a subcategory of ***grazer.***

Strictly speaking, communities, ecosystems, biomes, etc., ***develop*** or ***form*** rather than ***evolve.*** In and of themselves, they do not possess genes and, in addition to living organisms, ecosystems also include the physical environment (see Billings 1983). ***Natural selection*** acts on phenotypes, altering gene and genotype frequencies, and ***evolution*** occurs at the population or species level (Arnold & Wade 1984a,b, Cohan 1984, Fowler & MacMahon 1982, Lande & Arnold 1983, Tidwell et al. 1972). Within phylogenies, the term is used with higher taxonomic levels (Stebbins 1974). *Evolution* is an ongoing process, and does not have an "end product". Taxa within a community do not collectively respond to a selection agent; each taxon in a community responds independently to selective agents depending on amounts of intraspecific genetic diversity, etc. Entire regions (e.g., Intermountain Region) do not *evolve.*

An ***adaptation*** is any trait possesses that promotes fitness, was built by selection for its current role, i.e., has direct historic genesis through natural selection (Gould & Vrba 1982). Environments and ecosystems are not *adapte*d, and plant communities do not have *adaptations* (to grazing or anything else). Because of the direct link to natural selection, *adaptation* is limited to organisms, populations, species. **Exaptations** are traits that evolved for other usages (or no function at all) and were later 'co-opted' for their current role (Gould & Vrba 1982). **Aptation** is sometimes used for traits when historical genesis is unknown (Gould & Vrba). Alien plant taxa can be at least somewhat ***pre-adapted*** by selective agents in their original environment to conditions in their new environment (Grant 1977), but not *adapted.* Successful invasions by alien taxa do not occur because native taxa are not 'as well adapted' (by definition the original flora was adapted to the pre-invasion status quo); however, depending on the degree to which alien invader taxa affect the ecosystem once invasion has occurred, the original assemblage may not be adapted to persist in the post-invasion environment (Johnstone 1986). Traits present in a population are not "lost" *per se.* Under a given set of environmental conditions, a trait may be selected for, selected against, or unaffected. Under natural conditions, only in small populations or with traits in very low frequency would neutral traits be disappear completely, except with catastrophe.

Co-evolution involves direct interactions of particular species with one another, i.e., the effects of association of lineages of interacting species (Herrera 1985, Pellmyr 1992), "an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first" (Janzen 1980). Both Herrera and Janzen discussed the frequent misuses of *co-evolution* and pointed out that it should not be used as a synonym for non-species specific animal-plant interactions. An assemblage (e.g., community) of plant species does not ***co-evo***lve with an assemblage of more or less generalist herbivore species, nor do entire regional floras and faunas. **Joint or concurrent evolution** is more accurate.

As used in contemporary ecological theory, a ***niche*** is the set of resources required by a particular species, not the structuring of resources in a habitat (Hutchinson 1957, Johnstone 1986, Whittaker 1970). Therefore, a niche is not *occupied*. The premise behind an *empty* (or *vacant*) *niche* is that there is a ready-made matrix of niches waiting to be filled, which violates the definition. To quote Dr. W. Dwight Billings[1], "when a species becomes extinct, so does its niche" (pers. comm.). The phrase *empty* (or *vacant*) *niche* is an oxymoron; there is no niche if there is no species.

In scientific parlance, a **theory** is a supposition derived from a preponderance of evidence and generally accepted, a ***hypothesis*** is an assumption provisionally accepted, especially as a basis for further investigation. Popular usage gives them similar meaning, but scientists do not generally use them as synonyms. The role of human predation in extinction of Pleistocene mega-fauna is best described as a *hypothesis*.

The prefix ***mega-*** means *large* or *massive* (e.g., *mega-fauna, mega-herbivores*). It is used by Pleistocene paleozoologists (e.g., Lundelius et al. 1983, Owen-Smith 1987, Potts & Behrensmeyer 1992) to describe the largest animals of the epoch, i.e., exceeding 1000 kg adult body mass, Owen-Smith 1987). It does not mean, and should not be used for, *many* or *diverse*.

Terms that presently are (or are becoming) jargon within the (at least parts of) range, livestock, and wildlife management communities need to be defined or explained (and appropriate citations provided). Jargon needing definition or explanation includes (but is not limited to) *cured* [grasses], *encroachment, fire-proofed, fire-stemmed, followed the green, green feed period, greenup, holistic, keg-up, optimization, predator-preytopofloral, prehistoric analog[ue], rangeability, range readiness*. Use of anthropomorphic expressions are unnecessary, unscientific, and present an image that is less than professional. Emotionally charged wording can be inflammatory and is inappropriate. The author should avoid both, deleting such expressions as *aghast, attractive nuisance, conventional wisdom, demise, emotional environmental debate, fatally flawed, flourishes*

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[1] Dr. W. Dwight Billings, professor emeritus at Duke University, is one of the most distinguished and influential American plant ecologists of the past half-century. He and his students have influenced almost every aspect of plant ecology. He has conducted research in the Intermountain Region for more than 50 yrs. However, if his expertise needs illustrating, one can read the introduction to Chapter 15 in Woodwell (see Billings 1990), the introduction to Section IV in Woodwell & MacKenzie (see Billings 1995), or Young (1994),

game [native ungulates], *hardly seems plausible, ludicrous, marriage* (of farming & range livestock), *pervade, prehistoric forest rangers, rim-rock monarchs standing watch, sedentary welfare cattle, thriving, uproar, purpose & serve* [biological processes are not altruistic (they neither 'serve' nor do they have 'purpose'), and herbivores do not 'serve' the plant community, flora, fauna, etc.].

Identities of taxa mentioned in the text are often unclear (e.g., Does "wild ryegrass" refer to *Elymus, Leymus, Taeniatherum*, all three genera in tandem, or just to a single species? Which *Bison* sp. or spp. is(are) discussed? Which Equus sp. or spp.?). To reduce confusion, it is preferable to use scientific names in the text and to include a table of scientific and common names of all plant and animal taxa (extinct and extant) mentioned, with nomenclature sources cited. As a source for both scientific and common names of plants, I recommend the PLANTS[2] database[3]. Nomenclatural conventions (italics, authors, etc.) should be followed.

Although the author repeatedly says that the report is "a ***review of the scientific literature*** relating to prehistoric and historic herbivory in the Intermountain West" (p.1), that it "is a ***review of pertinent scientific publications*** in archeology, paleoecology, paleoclimatology and geology related to [the] hypotheses (p.5), and the result "is ***synthesized with the historic and range science literature***" (pp.5-6), the Literature Cited contains only a small portion of the available literature, is biased toward the author's point of view, and is inadequate even as support the author's opinions (particularly after p.23). Although pp.32-38 apparently represent the "model of prehistory herbivory ... synthesized with the historic and range science literature" (p.5), there are almost no citations, so there is no way to examine the "historic and range literature" (if any) used in the 'synthesis'. Failure by the author to cite significant portions of available literature prevents one from knowing what scientific literature missed versus what was rejected. There is also no way of knowing on scientific basis some literature was accepted (deemed "pertinent", p.5), while most was rejected (much of which might seem 'pertinent' to others).

At no time is it acceptable to attempt to characterize the flora, fauna, vegetation, ecosystem processes, etc., with one or two geographically restricted studies. If for some unexplained reason, extensive citations are undesirable, then the majority of citations should be monographs with extensive literature reviews (e.g., Grayson 1994, Mack 1981, McDonald 1981).

While no one has time to review all available literature, I found that there was a general lack of breath and depth in biological literature used, as well as an over-dependence on unpublished, popular, and quasi-scientific materials (e.g., *American West, Earth Quest, Fremontia, Range, Rangelands, Scientific American*), cited where science should be. In addition to the biological journals that were cited (*Annual Review of Ecology & Systematics, American Naturalist, Biological Conservation, BioScience, Ecology, Journal of Range Management, Nature, Oecologia, Oikos, Paleobiology, Quatemary Research*), pertinent research can be found in a wide range of peer-reviewed basic and applied biological journals, including (but certainly not limited to) *Advances in Ecological Research, Agro-Ecosystems, American Journal of Botany, American Journal of*

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[2] Plant List of Accepted Nomenclature, Taxonomy, & Symbols

[3] USDA National Plant Data Collection Center, P.O. Box 74490, Baton Rouge, LA 70874-4490

Zoology, American Midland Naturalist, Annals of Botany, Annals of the Missouri Botanic Garden, Botanical Gazette, Botanical Review, Bulletin of the Torrey Botanical Club, Canadian Journal of Botany, Ecology, Conservation Biology, Ecological Applications, Ecological Modeling, Ecological Monographs, Environmental Management, Environmental Pollution, Evolution, Evolutionary Ecology, Grass & Forage Science, Great Basin Naturalist, Journal of the American Society of Agronomy, Journal of Applied Ecology, Journal of And Environments, Journal of Biogeography, Journal of Ecology, Journal of Forestry, Journals of the Linnean Society, Journal of Mammalogy, Journal of Vegetation Science, Journal of Wildlife Management, Journal of Soil & Water Conservation, Madrono, New Phytologist, Plant & Soil, Taxon, Trends in Research in Ecology & Evolution, Southwestern Naturalist, Vegetatio Weed Science. References I provide (while more extensive than those in the reports) are certainly not comprehensive (hence the frequent use of 'e.g.').. I suggest using the 34 pages of references in Grayson (1993) as a source for additional pertinent literature for paleoecology of the Intermountain Region. Given the large amount of literature available in range science, there is no excuse for the very low numbers of citations used to support very broad generalizations, particularly in the second half of the report. By using references included in recently published range science books (e.g., Heady & Child 1994, Heitschmidt & Stuth 1991, Vavra et al. 1994, Vallentine 1990), the author could have substantially augmented the currently unimpressive array of scientific literature cited.

With limited exceptions, the author has chosen to replace evidence from scientific literature with opinions, apparently mostly his/her own, but occasionally attributed to someone else (e.g., Savory, p.30, & cited popular literature). Regardless of how "effectively and frequently" an opinion is expressed (by Savory *or anyone else*), it still needs to be substantiated by data collected in a scientifically acceptable manner. Savory (1988, pp.542-543) has chosen to not conduct 'demonstration' tests of his controversial hypotheses. In addition, he is very critical (as evidenced by letters to the editor in Rangelands, personal communications to authors, etc.) of those who criticize his opinions or his lack of scientific research to back them. His critics range from environmentalists to academics to resource managers (e.g., Bartolome 1989, Bock et al. 1993, Fleischner 1994, Jacobs 1991, Noss & Cooperrider 1994, SkovIin 1987, 1994). There have been a number of studies that have tested his opinions on "herd hoof action" (p.30) and reported negative results (e.g., Abdel-Magid et al 1987, Dormaar et al. 1989, McCalla et al. 1984, Warren et al. 1986, Weltz et al. 1989, Winkel & Roundy 1991).

Although there are numerous late-Pleistocene and Holocene paleobotanical studies, using pollen, middens, etc., the author attempts to characterize dynamics of that period in the entire Intermountain Region with only a single study of several middens from a geographically restricted area in west-central Nevada (Nowak et al. 1994). Although Nowak et al. is a good paper, it is not by itself adequate for the entire region. Studies from all parts of the region need to be examined and several different syntheses should be compared before any conclusions should be drawn (e.g., Baker 1983, Bamosky et al. 1987, Betancourt 1987, Delcourt & Delcourt 1993, Grayson 1993, Heusser 1983, Mack et al. 1976, 1978a,b,c,d, 1979, Mehringer 1967, 1985, Mehringer & Wigand 1985, 1986, 1987, 1990, Neilson 1987a,b, Nowak et al. 1994, Spaulding et al. 1983, Thompson 1990, Van Devender et al. 1987, Wells 1983, 1987). Despite the large number of studies of shrublands and woodlands that have been conducted in the Intermountain Region (focus of several federal agency-sponsored symposia, e.g., Everett 1987, McArthur & Welch 1986), the author also attempts characterize all shrublands and woodlands in the Intermountain Region using only Nowak et al. (1994) and a single geographically restricted study of contemporary Juniperus populations (Burkhardt & Tisdale 1976). Again, a much larger, more diverse literature sample is necessary, covering the diversity of vegetation types in the region, e.g., all types of grasslands, shrublands, and woodlands, especially those that might be impacted by livestock in the Intermountain Region (see Barbour & Christensen 1993, Billings 1990, 1994, Holmgren 1972, Sims 1988, West 1988, & citations therein).

The paleoecological scenarios presented are the author's conjectures about past climates, flora, and fauna. Construction of scenarios is acceptable, as long as they are built on best available science and present alternative views when there is controversy (e.g., Grayson 1993). The quality of any scenario is directly dependent on the quality of the supporting documents. Primary supporting documents need to be scientific literature, not unpublished materials (e.g., Fleharty & Hunlett's unpublished "independent study", which should be dropped entirely) nor popular publications (e.g., *American West, Fremontia, Range, Rangelands*). While popular publications serve many useful functions, they are rarely peer-reviewed and requirements for publishing 'opinion' pieces in them are less strenuous (e.g., permitting publication of opinion without reference to supporting scientific literature) than they would be for publishing 'opinion' papers, position papers, or review articles in *American Naturalist, Ecology, Ecological Applications, Madrotlo, Oikos*, etc. These journals require substantial scientific documentation to support opinions and put them through the same type of peer-review processes as research papers.

Using unsupported or weakly supported opinions to buttress conjectures is little better than having no supporting literature at all. This is especially true when they are opinions voiced by someone without demonstrated expertise (e.g.., has little or no formal training, has not published on the topic in peer-reviewed journals, nor is not actively doing scientific research) in the scientific field about which he/she is writing, particularly when those opinions are disputed by respected scientists in the field. For example, while Stephen Edwards is probably quite knowledgeable on fossil gymnosperm paleontology or botanic garden management, he has no demonstrated expertise on any of the subjects discussed in the cited article (Edwards 1992), and he often provides no supporting scientific literature for opinions expressed therein. Well-respected experts in applicable fields, including Drs. G. L. Stebbins[4] and H. G. Baker[5], have questioned many of his opinions. Because of the differences in expertise, Bakers (1992) & Stebbins' (1992) opinions *prima facie* carry more weight. Baker and Stebbins have written numerous important, highly regarded papers and books, many of

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[4] Dr. G. Ledyard Stebbins, professor emeritus at the University of California is a member of the United States Academy of Science (the highest peer recognition available to a US citizen). His expertise in evolutionary botany is globally recognized and he has greatly influenced the contemporary concepts of evolution. A list of his well known, frequently cited publications would take several pages.

[5] Dr. Herbert G. Baker, professor emeritus at the University of California, is a fellow of the Royal Linnean Society. His expertise in and influence on evolutionary botany is globally recognized. A list of his well known, frequently cited publications would take several pages.

which are (at least in part) relevant to these reports (e.g., Baker 1955, 1965, 1972, 1974, 1978, Baker & Stebbins 1965, Stebbins 1950, 1952, 1956, 1966, 1969, 1974, 1978, 1980, 1981, 1983).

Not only does the information provided by Baker (1992) and Stebbins (1992) need to be discussed when Edwards' opinions are used, so should both sides of all other controversial topics. Failure to present all alternatives concerning controversial issues and the propensity to present a single alternative as if it were generally accepted and/or the only alternative available in scientific literature are major shortcomings of the reports. When the author prefers one alternative over others, all alternatives should be presented, then scientific literature should be used to support why the chosen alternative is preferred.

Given how often what is in the reports does not agree with what is in the cited publication, it would appear that either the author has not critically read some of the materials cited, or he/she has cited papers used as citations by others (without checking the original). (in fact, some basic tenets of careful citation are violated frequently enough that I have attached an undergraduate biology course handout on the topic.)

On the basis of the ecological literature and the ecologists I have known over the past 20 years, I have to take exception to some of the author's veiled rebukes of ecology and ecologists. No doubt some ecologists (individually or as a group within a subdiscipline) may be out of touch with current concepts; however, the author portrays ecology and ecologists (particularly plant ecologists) as generally being so. Statements (and tone set by them) such as "the concepts of climax, pristine, and natural ***pervade*** all facets of land management and ecology in the country" (p.10) and "***implicit*** in our vegetation concepts such as pristine, climax or virgin forests is that of the 'natural' world untouched by man" (p.15) (emphasis mine) are inappropriate, denigrating, unnecessary, unprofessional, and generally inaccurate,

Ecologists have always been integrators and synthesizers, as well as experimenters, observers, and modelers, bringing together data and concepts from many disciplines (e.g., genetics, systematics, physiology, soil science, climatology, geology, physics, chemistry, archeology) (Billings 1970). One early major attempt to do an integrated ecological synthesis was, *The Grassland of North America* by Malin (1947, 1984). Cain's (1944) book devoted 144 pp. to Paleoecology (Part 11, Chapters 3-10). Such synthesis is an inherent part of ecology, rather than a new approach to it.

The author contends that "by omission, implication, or assertion, the plant ecology scientific literature indicates that large herbivores were not naturally part of the fauna of Intermountain Region" and that plant ecologists have "generally assumed" that the flora and fauna of the Intermountain Region "evolved" without .significant large herbivores" (p.1). Ecologists are not "unaware *of* the fossil record" (p.10). [I'm not sure how "the science of ecology" can be "largely unaware of the fossil record" (p. 40). 1 don't think that 'science' can be cognizant or incongnizant.] The presence of large herbivores generally has not been ignored as much as it has been put into perspective in relation to other environmental forces. Those selection agents that have operated most recently are the ones most likely to be reflected by contemporary populations *of* modern taxa. There is not sufficient scientific evidence *of* sufficient numbers of large herbivores recently enough for most evolutionary ecologists to consider them significant over a wide area of the Intermountain Region (at least until settlement and introduction of alien livestock). Rather than being "conventional wisdom" (p.1 5), these concepts are based on best available science. Perhaps "recently" and "significant numbers" are crux. *Recently*, in evolutionary time, is of course dependent on generation times of taxa. The general accord that there was a lack of "significant numbers of large herbivores" is based on best currently available science. The general consensus is that after the extinction of Pleistocene mega-fauna, large herbivores were relatively scarce and patchily distributed in the Intermountain Region, so their selective influence was probably geographically restricted. The title of Mack & Thompson's (1982) often cited paper was Evolution in steppe with few large hooved mammals, not without any, [See below for more detailed discussion of Pleistocene and Holocene herbivores.]

Contemporary plant ecologists do not necessarily "generally assume that ecological conditions immediately prior to European settlement of western North America represented the...pristine natural state" (p.3). Nor is this new. In 1947, Malin discussed the myth of the pristine "state of nature" on the Great Plains and attempted to devise less culture-laden terminology (Swierenga in Malin 1984). Despite use of such terms as "virgin", "pristine", or "relatively undisturbed", most ecologists recognize today's communities and ecosystems as being the product of three major forces: evolution, human disturbance history, and present dynamic processes (Forman & Russell 1983). In a recent paper, Billings (1983) pointed out that although, until the mid-Pleistocene, Earth's biota evolved and formed communities and ecosystems without man as a constituent or as an influent, human influence is now ubiquitous. Although humans have affected parts of North America over the past 15+ millennia, the effect is documented in written history over only the past 3-4 centuries (Forman & Russell 1983). Probably none of western North America can be considered free of human influence, i.e., "pristine" (Milton et al. 1994). However, exponentially increasing human populations and increasing abilities of humans to exploit resources have greatly magnified their effects on ecosystems. In the past few centuries, humans have become able to cause disturbances without parallels in nature except those created by large climatic shifts over geologic time (Bazzaz 1983). It is not necessarily "implicit in our vegetation concepts" that “the natural'" world is "untouched by man" (p.16). Early humans were an integral part of natural ecosystems; modern humans modify ecosystems or create new ones they can dominate (Billings 1970). [For a more detailed discussion of humans &'natural', see Rolston 1994.] Despite objections the author might raise (p.3), large-scale human-caused disturbances are outside what is generally regarded as 'natural' (Bazzaz 1983). Humans have become increasingly more able to alter or to destroy, directly or indirectly, natural ecosystems (Bilfings 1983). Indirect effects can be subtle, and changes may not be visible for a long time. An ecosystem can be "picked apart bit by bit, species by species, slowly and then more rapidly" and may be gone or irretrievably damaged before changes are recognized (Billings 1983).

It is the author's contention that a "less provincial setting, both spatially and temporally" than the Intermountain Region at the time of European contact (p.2) should be used as a reference point for evaluating large alien herbivores in the Intermountain Region. I discuss 'temporal' setting below. However, 'spatial' setting must also be addressed. The Serengeti may be a relatively "intact natural system” (p,3). However, it is also an inappropriate model for the Intermountain Region. When developing a model for management of a temperate region in North America, there are obvious problems with extrapolating from an equatorial African region (1) distantly geographically and geologically separated, (2) with different amounts and distributions of rainfall, temperature regimes, and seasonality than the Intermountain Region, (3) where annual migrations of native herbivores leave areas ungrazed for at least half the year, during dry season, (3) where rhizomatous and stoloniferous grass taxa dominant and the few bunchgrass taxa are sparsely distributed and genetically short, (5) with plant and animal taxa that are only distantly related phylogenetically to those in the Intermountain Region. The inappropriateness of extrapolating from the Serengeti to the Intermountain Region becomes more apparent when one considers that the author does not think that extrapolating from the Great Plains to the Intermountain Region would be appropriate because of the dissimilarities (pp.25-28), even though they are not distantly separated geographically, both have temperate climates, and they share plant and animal species. [For alternative views to those cited on 'grazing lawns' and on the Serengeti "system" (p.3), see Gordon & Lindsay (1990), Westoby (1985, 1986).]

There is no reason why the relatively low numbers of patchily distributed native Holocene ungulates (see Petrides 1960) in the Intermountain Region and Southwestern Deserts should be regarded as a biological “anomaly" (p.3). All Pleistocene mega-herbivore species in the Americas, Europe, and Australia became extinct during the Pleistocene/Holocene transition (Owen-Smith 1987). During the Holocene (before European settlement), there were few large herbivores in what is now California (Baker 1978) nor Argentina (Sala et al. 1986). New Zealand had no large herbivores before introduction of livestock and red deer (Billings 1970, Walter 1979). The Great Plains grasslands, although of Holocene origin, probably preceded the only true grazing bison (Axelrod 1985, McDonald 1981, see discussion below).

Using a less spatially provincial setting as a reference point for evaluating large alien herbivores in the Intermountain Region needs to include examination of effects of domestic livestock grazing in other parts of the world (including those with recent histories of substantial numbers of native herbivores). According to Walter (1979), livestock ranching in the pampas has left almost nothing of the original vegetation. Walter (1979) pointed out that, in addition to significant livestock-related changes in vegetation observed in North America, there have also been major changes in vegetation (including desertification, conversion from perennial vegetation to annual grasslands, loss of woody vegetation) in large areas of Africa, Asia, Australia, Europe, and South America, as well as on islands, such as New Zealand and Curucua. Most breeds of livestock introduced into western North America originated in Europe. Most extra-Mediterranean European grasslands date back only a few thousand years, beginning with grazing and browsing of cattle in woodlands (Scholz 1971). In many parts of Europe, such grasslands are artificial (meadows & pastures), created by destruction of forests and woodlands to make raising of livestock more efficient (Scholz 1971). There is no reason to believe that, even if large-animal grazing were a natural part of an ecosystem, **alien** livestock would not require intensive management to minimize negative impacts. Livestock and native herbivores can be substantially different in behavior, diet, etc. (by definition, no two species have completely overlapping niches), and even in parts of the world with longer histories of native and livestock herbivory than western North America, livestock have negatively impacted vegetation.

In the Introduction, the author states (without supporting scientific literature) that, in western North America, "while most rangelands remain productive and stable after more than a century of livestock grazing, problems with altered plant communities and eroding streams abound" (p.1). Both the continued productivity and the stability of western North American arid and semi-arid ecosystems have been challenged in the scientific literature. Progressive losses in productivity and diversity on and and semi-arid ecosystems have been attributed to overuse, of these lands by a narrow suite of domesticated herbivores (Milton et al. 1994). Arid and semi-arid ecosystems and those with a relatively short exposure to mammalian herbivory appear to be more sensitive to domestic livestock than mesic ecosystems and vegetation types that developed with mammalian herbivores (Mack & Thompson 1982).

Plant ecologists do not necessarily "generally assume that ecological conditions immediately prior to European settlement of the West represented the climax state" (p.3). Contrary to the author's apparent impression (p.16) that ecologists are just beginning to question traditional views of *succession* (including associated concepts such as *climax, stability*, etc.), As conceived by Clements (1916), introduced to range management by Sampson (1919), and revised by Dyksterhuis (1949), these views actually have been in dispute for as long as they have been around, beginning with Cowles (1911), Shreve (1914), and Gleason (1917) (see review in Joyce 1993). Gleason (1926) and Malin (1947) were early proponents of models more similar to 'modern' models than to Clements'. By the mid-1950s, community ecologists were abandoning Clements' views on succession and climax and were testing alternatives (Joyce 1993). One problem that has been identified with traditional succession is that change is seen as directional and deterministic (caused by time and therefore self-dependent), rather than non-directional and stochastic (causes being system dependent, with space-time probabilities - a unifying theme in "successful" scientific theories) (Johnstone 1986).

A "more appropriate paradigm"[6] (p.16) has available for some time. Disequilibrium (sensu Davis 1984), dynamic equilibrium (sensu Webb 1986), non-equilibrium (sensu. Westoby et al. 1989), or unstable equilibrium (sensu Malin 1984) models have replaced traditional Clements/Dyksterhuis succession as a method of understanding vegetation change. [Choice of term varies, in part, related to time scale. For the convenience of using a single term, I have chosen to use disequilibrium in this review.] The ecological literature has contained discussions of these models since at least the 1960s (see review in Laycock 1991). The conceptual bases for the models allow for a range of alternative states, discontinuous and irreversible transitions, dynamic communities, and stochastic events playing a large role in determining vegetation composition (Milton et al. 1994, Westoby et al. 1989). Conceptual frameworks for ecosystem change have suggested that the probability of reversing grazing-induced change may be inversely related to amount of disturbance involved in the transition (Milton et al. 1994), with the same amount of energy being required to alter species composition of vegetation as is required reverse the process (George et al. 1992, Gordon & Forman 1983). It has only been in the past decade or so that these models have been applied to resource management in western North America (e.g., George et al. 1992, Joyce 1993, Laycock 1991, Milton et al. 1994, Westoby et al. 1989). One seminal

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[6] **Paradigm:** *any pattern or example* (Funk & Wagnalls Standard Dictionary. 1983. Harper & Row, Publ., New York)

paper in the transition from Clements/Dyksterhuis succession to contemporary models in resource management was Jameson's (1987) model for *Juniperus* woodlands, which was ignored by the author, perhaps because it does not support the simplistic single model (pp.14,20-22) for all shrublands and woodlands in the intermountain Region (based one paleobotany paper and one *Juniperus* community paper).

"Biologic [*sic*] conditions at the time of European contact in the West" (p.4) may not have been at Clements/Dyksterhuis "climax", however, based on current literature and disequilibriurn models, there is no reason to believe they were "abnormal" (p.4). Paleobiological and paleoecological literature for the Intermountain Region (e.g., Baker 1983, Bamosky et al. 1987, Betancourt 1987, Delcourt & Delcourt 1993, Heusser 1983, Mack et al. 1976, 1978a,b,c,d, 1979, Mehringer 1967, 1985, Mehringer & Wigand 1985, 1986, 1987, 1990, Neilson 1987a,b, Nowak et al. 1994, Spaulding et al. 1983, Thompson 1990, Van Devender et al. 1987, Wells 1983, 1987) indicates a strongly climatically influenced dynamic equilibrium, and the author offers no scientific literature that counters this. In geological terms, European contact occurred during the transition between the Neo-Boreal and Recent episodes, Holocene epoch, Quaternary period, Cenozoic era (nomenclature follows Bryson et al. 1970, Graham 1993, Tidwell et al. 1972). The level at which one examines dynamics over geological time influences one's. perceptions of 'fluctuating', 'stable', 'steady', etc., in natural vegetation (Ritchie 1986). Rates of change are dependent upon a number of factors, including inertia (sensu Cole 1985).

If stability is resistance to change imposed by external forces (Margalef 1969), then it does not seem to follow that ecosystems with altered plant communities are "stable" (p.1). In the Intermountain Region, alterations in plant communities over the past century have been dramatic. Post-settlement human-induced community and ecosystem alterations have been caused by domestic livestock grazing, tree and shrub removal, altered fire regimes, agricultural conversion, and accidental and deliberate introduction of alien plant taxa. As a result of post-settlement human-induced changes, only small remnants of some vegetation types remain and others have a relatively high proportion of alien plant taxa in their floras (Banner 1992).

The summary of the pre- to mid-Miocene regional flora is so simplified as to be misleading (p.6). Tidwell et al. (1972) do not limit the pre- to mid-Miocene climate to a "mild ... with little seasonality" (e.g., see discussion of late Paleozoic), nor was the vegetation always "hardwood-deciduous and conifer forests". And there apparently was considerable change through time. The author would have better served everyone if he/she had simply cited some of the available literature (e.g., Axelrod & Raven 1985, Axelrod & Ting 1960, Chaney & Axelrod 1959, Graham 1993, Tidwell et al. 1972, & citations therein).

A flora is a list of plant taxa found at a site, in a region, etc. When Tidwell et al. (1972) that the early Pleistocene flora 'was essentially the same" as the modern flora what the statement was intended to convey was that the same families and genera and sometimes species were present somewhere in the Intermountain Region. One should not read into it that elevational, latitudinal, or longitudinal ranges of taxa were the similar to contemporary ranges, nor that assemblages of taxa were similar. And, in a region that is rich in Poaceae (& other groups with relatively indistinguishable pollen), over a time period where paleoflora studies are heavily pollen-dependent, "essentially the same" is relative.

Samples of fossil floras based on pollen give an indication of presence of taxa but evidence of abundance or dominance can be unreliable (wind-borne pollen is over-represented, animal-vectored pollen can be greatly under-represented) (Pielou 1991). Usually pollen cannot be identified below genus, sometimes not below family (Pielou 1991). For example, Poaceae pollen is not identified below family, so fossil pollen floras can only report presence or absence of 'grass'. Asteraceae pollen can be difficult to identify to genus. Even when generic identification can be made, there can be difficulties with extrapolating further. *Artemisia* pollen is generally identified to genus. In a genus with herbs, subshrubs, and shrubs with broad modern ecological ranges (alpine to near sea-level), presence of *Artemisia* may provide little ecological information. Middens provide more information about some difficult groups (e.g., grasses). Identification based on other plant parts can sometimes be made more readily. Middens are only useful for relatively modern studies (e.g., past 40,000 yrs). Betancourt et al. (1986) found that midden floras are subject to food preferences of herbivore taxa, so that even sympatric middens can yield different results. The best reconstructions are probably those made with multiple data sets (e.g., Betancourt et al. 1986, Mehringer & Wigand 1990). Community or vegetation type is sometimes inferred from habitats of modern congeners of fossil animals. However, in western North American, this does not work well for *Bison* (see McDonald 1981) and may not work well for other fossil mammals (e.g., see Akersten et al. 1988).

While Pleistocene/Holocene Intermountain Region floras contain many of the same families, genera, and species found in the Region today (p.7), there has undoubtedly been intra-taxon genetic change and speciation, as well as recurring community re-assemblage. Data from late-Pleistocene/Holocene paleobotanical and paleoecological studies in the Intermountain Region (e.g., Baker 1983, Bamosky et al. 1987, Betancourt 1987, Delcourt & Delcourt 1993, Heusser 1983, Mack et al. 1976, 1978a,b,c,d, 1979, Mehringer 1967, 1985, Mehringer & Wigand 1985, 1986, 1987, 1990, Neilson 1987a,b, Nowak et al. 1994, Spaulding et al. 1983, Thompson 1990, Van Devender et al. 1987, Wells 1983, 1987) provide evidence of dynamic systems, with each individual taxon responding independently to environmental conditions. Samples taken at any single time represented in a profile would provide a 'snapshot' of a different taxonomic assemblage. Late-Quaternary plant associations have been in continuous flux, and plant communities have been ephemeral assemblages of species that have disassembled and reassembled into new combinations (Delcourt & Delcourt 1991, Potts & Behrensmeyer 1992).

While the fossil record can "indicate" presence of mammoths, rhinos, camels, horses, burros, ground sloths, etc., it usually provides little direct evidence as to which were "grazers" and which were social animals in "herds" (p.8). These are sometimes inferred sometimes inferred from modern congeners or apparently closely related genera. However, in western North American, this does not work well for *Bison* (see McDonald 1981) and may not work well for other fossil mammals (e.g., see Akersten et al. 1988). While Martin's hypothetical carrying capacities for Pleistocene large herbivores (p.9), calculated using extrapolated numbers from very small databases (see Grayson 1993, Table 7-1, Figure 7-2) and additional data from very different environmental conditions and taxa in Africa, make an interesting academic exercise. However, lack of hard data from the Intermountain Region about numbers, behavior, diets, etc., for the herbivores, together with documented environmental changes since the Pleistocene would make these precarious estimates (at best) on which to base management decisions.

Although the author says that, according to the fossil record of the Intermountain Region, "bison and the other members of the Pleistocene mega fauna roamed the entire Intermountain Region" (p.12). Based on that fossil record, Lundelius et al. (1983) said that "many of the large herbivores may have existed in smaller populations more isolated geographically than those in the Great Plains", and maps of Pleistocene Bison distributions in McDonald (1981) have few, widely scattered localities west of the Rocky Mountains.

The author is either unaware of the monographer of North American Bison (McDonald 1981) or chose to ignore him. However, since the author provides extremely limited documentation to support opinions in disagreement with McDonald's well documented and widely accepted work, on the basis of best available science one must accept the latter. North American Pleistocene *Bison* spp. were considerably different from extant Holocene *Bison bison*, which became a recognizably distinct taxon ca. 5000 yrs BP, evolving *in situ* in the Great Plains (McDonald 1981, Meagher & Meyer 1994). Morphological traits and spatial and temporal distribution of remains imply three general habitat types occupied by different *Bison* taxa in the late Quaternary: forests and woodlands, savannas and wooded steppes, and open grasslands (McDonald 1981). Morphology implies different feeding habits. *Bison latifrons* probably was a relatively nonsocial browser/grazer living in forests and woodlands. The large head of *B. latifrons* apparently was held higher and oriented more forward than the head of other *Bison* spp., indicating that eye-level browsing would have been more mechanically efficient and lest costly than grazing. *Bison antiquus* apparently was a somewhat more social (small, discrete groups) grazer/browser living in savannas wooded steppes Its head was oriented higher than *B. bison* but not as high as *B. latifrons. Bison bison* have a downward rotation of the head, eye placement that facilitates maintaining herd contact and predator watch, and shorter limbs than the extinct taxa, and a more complex social organization. McDonald thought that they are probably the only North American *Bison* sp. adapted to pure grasslands. Neither the extinct North American Pleistocene *Bison* spp. nor extant European wiscent (*Bison bonasus*) are grazers. Akersten et al. (1988) also concluded that diet of *Bison bison* may be atypical for genus. The time period at which *B. bison* is a recognizably distinct taxon (ca. 5000 yrs BP) post-dates early to mid-Holocene date now recognized for development of a regional grassland in the Great Plains (earlier open vegetation was forest parklands to open woodlands) (Axelrod 1985). It would appear that evolution of grazing bison tracked development of true grasslands, and may have been only marginally concurrent. Several facts that indicate that they are not an obligate grassland animals, particulady that much of their pre-settlement secondary range was forest or wooded steppe and that they browse when woody vegetation is available (McDonald 1981).

Human predation may have been a contributing factor in the Pleistocene mega-herbivore extinction However, Martin's overkill hypothesis (p.9,11,17) is controversial, and is generally considered to be, at best, a partial explanation (see discussion in Grayson 1993). Owen-Smith (1987) presented an alternative hypothesis he called the "keystone herbivore hypothesis". Axelrod (1985) felt that large browsing fauna may have contributed (with drought and fire) to the late-Pleistocene/early-Holocene vegetation transformations, contributing to formation, at least in the Great Plains, of habitats to which they were not suited. Belovsky (1986) suggested that more xeric conditions might have made foraging energetics of mega-herbivore species untenable. Climatic change is generally accepted to be the most parsimonious explanation for the Pleistocene extinctions, with human predation as a contributing factor for some taxa (e.g., Grayson 1993, McDonald 1981, Potts & Behrenmeyer 1992). Contrary to the authors statement (p.10), the Pleistocene extinctions included not only mammalian mega-herbivores but smaller mammal taxa, bird taxa, and members of other animal groups, as well as plant taxa (Delcourt & Delcourt 1993, Grayson 1993, Lundelius et al. 1983, Owen-Smith 1987, Pielou 1991).

There is no evidence that, when the animals became extinct, "the habitat remained" (p.10). As Pielou (1991) pointed out, with the disappearance of ice sheets and pluvial lakes, all habitats changed. Paleobotanical evidence from the intermountain Region (e.g., Baker 1983, Bamosky et al. 1987, Betancourt 1987, Delcourt & Delcourt 1993, Heusser 1983, Mack et al. 1976, 1978a,b,c,d, 1979, Mehringer 1967, 1985, Mehringer & Wigand 1985, 1986, 1987, 1990, Neilson 1987a,b, Nowak et al. 1994, Spaulding et al. 1983, Thompson 1990, Van Devender et al. 1987, Wells 1983, 1987) indicates significant fluctuations in plant distributions during the several millennia over which the extinctions occurred (Grayson 1993, Potts & Behrenmeyer 1992). Although individual taxa may be influenced by biological inertia (sensu Cole 1985), the evidence indicates that at no time has the entire biotic environment been static.

The author offers no literature to support the contention that "when the system is in balance, i.e. all the available niches occupied, extinctions and evolution of new forms occur somewhat equally" (p.10). The author also provides no evidence as to why the author thinks that the Pleistocene extinctions "hardly appears to have been a normal evolutionary event". The author should consider the following: (1) every species has a nonzero probability of extinction within a given unit of geological time; (2) any two dissimilar species have different probabilities of extinction from any particular cause or the same unit of time; (3) every species is characterized by a non-zero probability of giving rise to one or more distinct species in a given unit of evolutionary time; (4) the probability that any particular species will give rise to one or more new species depends not only on its environment by also on the specific features of that species (Fowler & MacMahon 1982). Generation time, body size, environmental changes (e.g., ice ages), interdependence (e.g., food source, trophic web) can all be factors in speciation and extinction (Fowler & MacMahon 1982). [See Fowler & McMahon on Pleistocene extinctions.]

Because of controversy about the time of human migration to North America (see discussion in Grayson 1993), a literature citation is needed (p.1 1).

The author states that "a review of the literature reveals emerging evidence indicating that bison survived the Pleistocene extinctions and continued to exist in the Intermountain Region as well as the prairie until just prior to the European explorers of 1800-1830" (p.1 3), but attaches no citations, which are needed to determine if any such literature exists. Later, the author again states that bison "survived the Pleistocene extinctions...and continued to populate shrub steppe landscapes of the entire Intermountain Region until the late 1700's or early 1800's" (p.13), and "the Pleistocene extinction ... did not completely remove herbivores from the landscape or herbivory from the plant community. ...bison continued to graze the western landscape including the Intermountain Region until at least the late 1700's" (p.18). Pleistocene Bison spp. and the species found in the Intermountain Region in the late Holocene (*B. bison*) are different taxa (Butler 1978, McDonald 1981). The genus *Bison* survived, but only in the form of a single new species.

To support continuous occupation, the author says that "Agenbroad (1978) reported an extensive buffalo jump site on the Owyhee River which yielded evidence of use for 7000 years However, Plew (1987) pointed out that "a review of the archaeological, ethnographic and faunal evidence questions whether the Five Fingers and "Y" Buffalo Jumps described by Agenbroad (1976) are bison jumps. A more probable explanation is an identification of communal artiodactyl hunting facilities." Contrary to the author, *B. bison* residency west of the Rocky Mountains apparently was discontinuous (Van Vuren 1987). Butler (1978) reported a 3000-yr mid Holocene gap in documented residence. The best evidence is that the strictly Holocene species *B. bison* evolved in situ on the Great Plains and periodically migrated from there westward across the Snake River Plains (McDonald 1981, Van Vuren 1987).

Strong evidence is also lacking for the author's contention that bison were abundant and widespread. According to Van Vuren (1987), of at least 44 localities in eastern Washington and Oregon and Southwestern Idaho, only one (Malheur Lake) had evidence of more than a few individuals, the only indication of bison having been even locally common in a very large area. Plew (1987) stated that, with one exception, archaeological evidence of *Bison* in Idaho is restricted to the Snake River Plain, which is also the area with the majority of historic reports (Butler 1978). Only three *B. bison* skulls have been found in all of Nevada (Van Vuren & Deitz 1993). Reher (11978) felt that even the Green River Basin was "marginal" habitat for *B. bison*.

It is true that "Pleistocene extinction of the mega-fauna did not completely remove herbivores from the landscape" (p.18). However, after extinction of the Pleistocene mega-fauna, all species of ungulates apparently were relatively scarce and patchily distributed in the Intermountain Region (Mack & Thompson 1982, Mead et al. 1991, Plew 1987, Van Vuren 1987, Van Vuren & Bray 1985, Van Vuren & Deitz. 1993, Young 1994). The most common, most ubiquitous vertebrate herbivores were *Lepus* spp. (jackrabbits), not ungulates (Young 1994).

Much more literature needs to be cited to support the contentions about pre-settlement vegetation (p.14) and post-settlement changes (pp.20-24) in the Intermountain Region. At no time is a single geographically restricted paleolbotanical study (Nowak et al. 1994) and a single geographically restricted study (Burkhardt & Tisdale 1976) sufficient to characterize millions of acres.

Herbaceous species do not "climatically" compete with shrubs and trees (p.14), e.g., plants cannot compete for climate. If what the author meant was that, because of the climatic conditions at the time Europeans arrived in the Intermountain Region, shrubs and *Juniperus* were at a competitive disadvantage, he/she needs to support that opinion (and others on this page) from the scientific literature. These generalized statements are much too broad to be supported by a single citation. The author needs to provide scientific evidence that the pattern is region-wide and applies equally to all shrublands and woodlands. How does he/she know that statements about competition, climate, fire, etc., apply equally to all types of shrublands and woodlands in the Intermountain Region? What general, region-wide climatic conditions were controlling factors? What is the evidence? What effect, if any, do different species make? The author's opinions are contradicted by much of the Great Basin shrubland/woodland research, including Jameson (1987), and much of the late-Holocene paleoecological literature (e.g., Mehringer & Wigand 1987). How would the author reconcile those differences?

The author's opinion that several million years over a more distant past should be "more formative" than the more recent 7000 yrs (p.17) is contradicted by evidence proved by studies of interpopulational genetic differences in Great Plains grass species with differences in grazing histories of less than 50 (very recent) years (e.g., Carman & Briske 1985, Jaramillo,& Detling 1988, Painter et al. 1989, 1993, Peterson 1962, Polley & Detling 1988). Natural selection can occur over relatively short periods of time in even in long-lived organisms. As one eminent evolutionary botanist (Baker 1992) has explained, "the selective agents of the Holocene operated more recently than the Pleistocene factors, and we can expect that ***present-day taxa will reflect the more recent environment*** (emphasis mine). Selection is a ubiquitous, continual feature of natural populations, but the predictability, frequency, and regularity of selective forces may be highly variable (Loveless & Hamrick 1984, Endler 1986). Each population of each species responds independently of other populations and other species to environment conditions. Even if there had been an extended history of herbivory in the Intermountain Region during the Pleistocene, there is no reason to assume that any *adaptations* acquired by plant taxa during that period would necessarily be maintained in their descendants in modern populations.

While retention of traits acquired in the Pleistocene in response to a hypothetical grazing history is unlikely in plant taxa in the Intermountain Region, there is the small possibility that a few populations of some native taxa may exhibit some small amount of grazing resistance (*sensu* Briske 1986). Populations of native grass species that exhibit any amount of resistance to livestock herbivory may have already possessed an evolved strategy to reduce negative impacts of all types of damage (Belsky et al. 1993), may have exapted traits (e.g., fire or drought resistance), or may recently have developed (if local genetic diversity included some individuals with appropriate traits) genetically based locally adapted 'ecotypes' (Hamrick 1982, Jaindl et al. 1994). All of these are more plausible than maintenance, for several millennia and through major environmental changes, of herbivore-resistance traits in taxa that may not have been forage for extinct herbivores. Given the small numbers and scattered distribution of native Holocene ungulates, only on a local level would ungulate herbivory have been even a somewhat predictable selection agent. The native ungulates have different diets than livestock, so the selection pressure they provided would have influenced different plant taxa. There is considerable difference between the selective effects of being eaten and that of reduced competition because one's neighbors are eaten. Thus, differences in animal diet and behavior are important. And one cannot assume that effects of one animal taxon will be similar enough to another for substitution to have little negative impact. Hard data are necessary.

In natural ecosystems, plant performance is influenced not only by climate, fire, herbivory (both above and belowground),but also by interactions with competitors, symbionts, nurse plants, pollinators, seed dispersers detritivores, and structure and origin of soil. Activities of herbivores can alter all of these, leading to changes in ecosystem function (Milton et al 1994). Intensively grazing and trampling can cause a reduction in plant and litter cover, can reduce infiltration of water, increase runoff, erosion, and spatial arrangement of nutrients (Milton et al. 1994). The author skims over most of these.

Page 18 is full of examples of reckless use of terminology, There was not nor is there now something that could be described as "the plant community" in the Intermountain Region. Landscapes are not grazed, although grazers may be found in (or on) one. Floras are not adapted. Adaptations aren't lost. "Herbivories" do not evolve, nor are they "characterized by a diversity of floral and faunal species". Niches cannot be occupied. Biomes do not evolve. And, while "nature abhors a vacuum", the post-Pleistocene Intermountain Region was not ecologically vacuous. This empty cliche is meaningless here, and does not belong in what should be a science-based document.

As the distinguished British ecologist Dr. M. J. Crawley (1987) has pointed out, "some controversies seem destined to run forever", including the hypothesis that herbivory benefits 'herbs' (to which it seems has been added that predators benefit prey and, by harassing the prey, 'benefit' the environment in general), Despite protestations to the contrary, in nearly all cases of these alleged benefits are based on blatantly grou-selectionist arguments (Crawley 1987, Gordon & Lindsay 1990). There is no compelling evidence that the act of grazing *per se* increases fitness of grasses or any other plant taxa (Crawley 1993, Vicari & Bazely 1993). There is very little (if any) evidence that herbivorous mammals 'manage' the resources they utilize (Gordon & Undsay 1990).

The author states that "minor and mega herbivores and their associated predators ... function in a complex biologic [*sic*] webb [*sic*] involving mutualism, facilitation, competition and optimization" (p.18). Plant/plant and herbivore/herbivore interactions do involve competition and possibly facilitation. There is no unequivocal evidence for plant/large-herbivore mutualisms or 'optimization' (mutualisms *can* be found as **part** of a complex biological web, in tandem with all other parts of the ecosystem, e.g., lichens in cryptobiotic crusts, mycorrhizal associations, legume roots & bacterial nitrogen fixers).

Westoby (1987) pointed out that the main way in which a plant benefits from herbivory is if its neighbor is grazed while it escapes damage. While there is little doubt that grazers greatly influence the outcome of competition between different plant species, there is considerable difference between the effects of being eaten and that of reduced competition because one's neighbors are eaten.

The possibility of plant/large-herbivore mutualisms was debated (and, for evolutionary ecologists, pretty well laid to rest) in a series of papers in *Oikos* (e.g., Bleken & Ugland 1984, Herrera 1982, Inouye 1982, Nur 1984, Owen 1980, Owen & Wiegert 1976, 1981, 1982, Silverton 1982, Stenseth 1978, 1983, 1984a,b, Thompson & Uttley 1982). In order for a relationship to mutualistic, individuals of both taxa participating must have greater fitness than individuals of the same taxa that are not (Belsky et al. 1993, Herrera 1982). There is **no unequivocal evidence** that large-animal herbivory increases plant fitness (i.e., those plants contribute more genes to the next generation). [The only study that purports to show this (Paige & Whitham 1987) has problems that need to be considered before it is used as supporting literature, which are discussed below.]

If the relationships were mutualistic, plants have few if any herbivore-inhibiting traits (Herrera 1982). Although it has been argued that grasses in particular are poorly defended (Owen & Wiegert 1981, McNaughton 1983, Coughenour 1985), members of the Poaceae are not chemically depauperate, but actually contain a wide variety of secondary compounds that can and do deter herbivory (Herrera 1982, Redak 1987, Vicari & Bazely 1993). Many grass species and parts of grass plants (particularly seeds) produce a large array of secondary compounds that have been shown to have some negative effects on herbivores, particularly invertebrates (Redak 1987, Vicari & Bazely 1993). Silica functions as a defense against invertebrate herbivory, but evidence that it plays a significant protective role against contemporary vertebrate herbivores appears to be inconclusive (Vicari & Bazely 1993). Over 240 species of grasses, as well as rushes and sedges, contain (possibly mutualistic) symptomless endophytic fungi, many of which produce ergot and other alkaloids (Vicari & Bazely 1993), including *Leymus cinereus* (Scrbner & Merr.) A. Löve (syn. *Elymus cinereus* Scrbner & Merr.) (Cronquist et al. 1977).

The author points out that "traditionally livestock grazing has been viewed primarily from the animal perspective" (p.32). This has also been the problem with herbivore 'optimization' studies. As Verkaar (1986) pointed out, "the scope of most studies ... has been limited to aboveground production, expressed as standing crop from an agricultural viewpoint or seen as edible food from the viewpoint of a biologist studying animal intake." Although is well established that above- and belowground plant parts are of equal importance (Cody 1986) and that grazing is a whole-plant phenomenon (Holland & Detling 1990), plant/large-herbivore studies usually focus only on the relatively small portion of plant biomass (particularly perennial plant biomass) that is aboveground (Fitter 1989, Painter & Belsky 1993, Verkaar 1986). Herbivore 'optimization'[7] (purported positive effects of grazing on plant productivity, with productivity of plants being greater than non-grazed plants, for at least some grazing intensities) is usually defined in terms of an increase in aboveground net primary production (see discussion in Painter & Belsky 1993). If the author is serious in suggesting that there is a need for "a more holistic[8] approach" (p.1), the place to begin is with citing papers that study **whole-plant** responses, not just the 5-25% that is aboveground. Although there is evidence that some plants sometimes partially (or even occasionally completely) compensate for lost tissue, there is no compelling evidence for **whole-plant** overcompensation (i.e., 'optimization') nor for increased plant fitness in grazed plants, except under very specific conditions, rarely seen in nature (Belsky 1985, 1986, Belsky et al. 1993, Crawley 1993, Ellison 1960, Jameson 1963, Painter & Belsky 1993, Verkaar 1986).

Paige & Whitham (1987) is one of the few studies that purports to demonstrate both grazing-related 'mutualism' and whole-plant 'optimization'. However, in addition questions raised by Crawley (1987), there are other problems with this study. First, it is a study of a single 'population' (unless results are repeatable, one must always be cautious of extrapolating from a single population to a species, extrapolations beyond that are even less prudent). When Bergelson & Crawley (1992a,b) attempted to replicate Paige & Whitham's

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[7] For more information concerning *herbivore optimization* see Belsky (1986), and literature cited therein

[8] **Holism:** *the theory that the whole, especially a living organism, is more than the sum of its parts* (Funk & Wagnalls Standard Dictionary)

experiment in 14 populations of *Ipomopsis aggregata* (Pursh) V. Grant[9], they could never get the same results. The branching pattern following loss of the main shoot (which Paige & Whitham credited with being the mechanism involved and which they associated only with herbivory) has also been observed to occur when the apical meristems of monocarpic[10] *Ipomopsis* spp. plants are damaged by fungus or freezing (M. Price, N. Wasser, D. Wilken, pers. comm.), supporting the hypothesis of Belsky et al. (1993) of a more generalized response to damage rather than a specific response to grazing. In addition (and possibly the most problem)[11] I, the Fern Mountain 'population' Paige & Whitham studied actually consists of two species (*Ipomopsis aggregata* & *1. tenuituba* (Rydb.) V. Grant] plus intermediates (Grant & Wilken 1988)[12]. Since Paige & Whitham did not voucher their herbivory study nor send specimens to an expert for identification, It cannot be determined if the plants used were all of one taxon, or if the sample was composed of both species, with or without the intermediates. [The pollination study (Paige & Whitham 1985) was probably from of a mixed sample - most parsimonious explanation for the results, based on specimens cited in Grant & Wilken 1988 (D.H. Wilken, pers. comm.)]. Composition of experimental sample would strongly influence results, particularly if each treatment group had a different mixture. The results reported by Paige & Whitham (1987) may be related to phylogeny or to a generalized damage response rather than to grazing.

Alien livestock are functionally different from native Pleistocene mega-fauna. Environmental conditions in the Intermountain Region considerably different today than they were when the mega-fauna was a functional part of the environment of the Intermountain Region. Introducing alien cattle and horses was not "simply filling the vacant large herbivore niche" (p.20). And, it is biologically impossible for livestock to "represent a potentially functional replacement for the mega-fauna" (p.19). Livestock are not, functionally or otherwise, "surrogate[13] herbivores", "surrogate grazers", or "surrogate mega fauna" (pp.19,23,24). The definition of surrogate requires that there be something for which livestock (biologically) can 'substitute', in this case

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[9] Identification confirmed by D.H. Wilken (see footnotes 11-12)

[10] Monocarpic plants are those which flower once then die. These include annuals and rosette-forming perennials [including *Swertia radiata* (Kellogg) Kuntze (syn. *Frasera speciosa Griseb*.), which can live as a rosette for nearly a century before flowering only once].

[11] It is again a question of comparative expertise.

12 Dr. Verne Grant, professor emeritus at the University of Texas, is a recognized expert on the systematics and biology of several groups of North American plants, especially the family Polemoniaceae in general and the genus *Ipomopsis* in particular. He has published influential work in systematics, evolution, pollination biology, speciation, etc., is world famous. He is the species 'author' for a number of *Ipomopsis* spp. and subspp., including *1. aggregata* & *1. tenuituba.*

Dr. Dieter H. Wilken, director of research at the Santa Barbara Botanic Garden and adjunct professor ant the University of California, is a recognized expert on systematics and biology of several groups of North American plants, especially the family Polemoniaceae in general and the genus *Ipomopsis* in particular. He is well known and well respected for his work in systematics, evolutionary biology, floristics, etc. He was project manager and a major contributor to *The Jepson Manual., Higher Plant of California*. He was also a contributing author to Flora of the Great Pains and has contributed treatments to the forthcoming *Flora of Arizona* and *Flora of North America.* He is the author of the *Ipomopsis* treatments in all of these. He is already involved in the preliminary processes of the *Flora of Oregon* project. He is a fellow of the Royal Linnean Society.

[13] **Surrogate:** *a substitute, deputy* (Funk & Wagnalls Standard Dictionary)

something that has not existed (a very similar grazer living in the Intermountain Region under contemporary environmental conditions).

If cattle and horses actually "complimented" pronghorn, deer, elk, and bighorn sheep (p.19), then interspecific competition and negative impacts should be similar to those reported for native herbivores (e.g., bison, pronghorn, elk, etc.) on the Great Plains (e.g., Krueger 1986, Wydeven & Dahlgren 1985). Either there has been no research on livestock/native-ungulate interactions in the Intermountain Region or the author has entirely ignored it (p.23), and provided only his/her opinions. The presence of livestock should have no greater impact (than large native ungulates) on other native animals, which does not appear to be the case (reviewed in Fleischner 1994, with the author providing no references that refute). The introduction of any alien taxon, whether it be *Agropyron desertorum*, *Bromus tectorum*, domestic livestock, or "other exotic grazers from other continents" (p. 19), **definitely does** "necessarily represent a significant ecological change" (p.20).

The author lists "three ecologically significant changes" related to European-American settlement of the Intermountain region: introduction of domestic livestock, introduction of alien plant taxa, and change in the role of fire. [The author lists the last as "reduction (p.20), but also discusses increased fire frequency on p.21. 'Change' seems more accurate.] Why these three and not others? What literature supports these as the "significant" changes?

The author offers no literature to support his/her opinions on behavior of native herbivores (p.20). What evidence is there that they '"followed the green up the mountain"? Were all native herbivores migratory and all populations in areas where such migrations were possible?

Does the author really mean that there were no fires ("fire-proofed") in higher elevation "sagebrush steppe" and in "juniper" vegetation types after livestock grazing impacted them (pp.20-24)? The contention that "sagebrush steppe" and "juniper" (or parts of thereof) were "fire-proofed" by livestock grazing (pp.20-23) appears to contradict a significant portion of the most recent fire literature (e.g., Billings 1994, Bunting 1994, Pelland 1994, Peters & Bunting 1994, Roberts 1994, West 1994, & citations therein). What evidence does the author have for the existence of lower-elevation or drier-site "sagebrush monocultures" (p.20)? Why are two paragraphs on introduction of alien plant taxa and increases in fire placed between two on "fire-proofing" the same general vegetation types? If these are supposedly two different responses of similar vegetation, then they need to be clearly distinguished. And a great deal more scientific literature needs to be cited for each type of response in each type of vegetation.

The discussion of introduced alien plant taxa needs to be greatly expanded, and discussion added concerning role of livestock in introduction, invasion, and alteration of ecosystems by alien plant taxa. Both need to be heavily literature based. Ecosystems where alien plant taxa dominate or are important members are significantly different ecologically from pre-settlement ecosystems they have superseded. Ecologists are beginning to understand the biology of some alien plant taxa and ecological changes that accompany their proliferation (see Johnstone 1986). Allen plant species have become important components or dominants in many areas of the Intermountain Region. For example, alien taxa make up about 14% of the taxa in the contemporary flora of southeastern Washington and adjacent Idaho (Stuckey & Barkley 1993). Alien grass taxa are particularly notable among the alien taxa in the Intermountain Region, including *Agropyron desertorum* (Fischer) Schultes (syn. *A. cristatum* (L.) Gaertner, *A. fragile* Roth, *A. sibericum*; Willd.), *Bromus tectorum* L., and *Taeniatherum caput-medusae* (L.) Nevski (syn. *Elymus caput-medusae* L.). Many of the alien plant taxa that have successfully invaded or successfully introduced in the Intermountain Region originated in areas with similar climates in eastern Europe and southern Asia, and many have evolved in close proximity to continual human-imposed disturbances related to agriculture, including domestic livestock grazing (Stuckey & Barkley 1993). These together indicate that some (many?) alien plant taxa that have been successful in the Intermountain Region were at least somewhat pre-adapted by selective agents in their original environment to conditions in their new environment.

Bromus tectorum, apparently an accidental introduction, approximates Baker's (1974) definition of an ideal weed. Because it is so widespread and has become such an important part of many ecosystems, *B. tectorum* is one of the better studied alien taxa in the Intermountain Region (e.g., Beatley 1966, Billings 1990, 1994, Bookman 1983, Cline et al. 1977, Evans 1961, Evans et al. 1970, Harris 1967, Hinds 1975, Hironaka 1961, Hulbert 1955, Hull 1963, Hull & Hansen 1974, Hull & Pechanec 1947, Hull & Stewart 1948, Klemmedson & Smith 1964, Mack 1981, 1985, Mack & Pyke 1983, 1984, Morrow & StahIman 1984, Rice & Mack 1991a,b,c, Rummell 1946, Sheley & Larson 1994a,b, Stewart & Hull 1949, Thill et al. 1.979, Wicks et al. 1971, Young & Evans 1973, Young et al. 1969). By the 1890s, *Bromus tectorum* had arrived in the steppe of Washington, and its range expanded so rapidly that by 1930 it had become dominant in most disturbed steppe communities (Mack 1981, Mack & Pyke 1983). The taxon apparently was pre-adapted to the unpredictable environments of disturbed ecosystems that began to develop in the late 19th century in the region (Mack & Pyke 1983). There is no convincing evidence that *B. tectorum* ever relinquishes an area to native taxa once it is established (Daubenmire 1970, Morrow & StahIman 1984). Minimal impact by humans and livestock as long as a century ago on Anaho Island (Svejcar & Tausch 1991) may have provided the few 'safe sites' (*sensu* Harper 1977) it needed begin to invade (Johnstone 1986). Because it is an aggressive competitor, even a few *S. tectorum* plants can reduce growth of both native and introduced grasses, reducing overall productivity of a site (Hull 1963). Once established, fire can create new habitat, allowing it to invade increasingly larger areas.

As its range and abundance have increased over the past few decades, *Bromus tectorum* has created alterations in ecosystems that contradict the author's allegations that shrublands and woodlands have become increasingly "fire-proofed" by livestock grazing (pp.20,22), but confirms allegations of fire converting some to annual grassland (p.20). In early as 1948, Hull & Stewart discussed as *B. tectorum* as a serious fire hazard. It has now become abundant enough to provide fuel for an increase in fire frequencies from ca. 30-70 yrs to less than 5 yrs (Bunting 1994, Pellant 1994,. Whisenant 1990), which can convert shrubland and woodland ecosystems to *B. tectorum*-dominated biotically impoverished (compared with original) annual grasslands (Billings 1990, 1994, 1995). There is some evidence that *Taeniatherum caput-medusae*, also able to fuel and perpetuate unnaturally frequent fires, may also have the potential for causing this type of ecosystem-altering pattern (Hironaka 1994, Peters & Bunting 1994).

Not all alien plant introductions have been "inadvertent" (p.20). Agropy*ron desertorum* was deliberately introduced and enthusiastically promoted (Rogler & Lorenz 1983). In less than a century since it was first introduced *A. desertorum* was seeded into millions of acres in the Intermountain Region (Rogler & Lorenz 1983, Young 1994). One result of this practice apparently was to create more habitat for *S. tectorum* (Young 1994).

The author offers no evidence that Serengeti watering places actually "look much like our livestock watering areas" (p.24). Nor does he/she provide any citations that would indicate that (even if this were what watering holes in the Serengeti looked like), that native herbivores (e.g., elk, deer, pronghorn) ever leave (or, pre-settlement, left) riparian areas and other water sources as negatively impacted as domestic livestock sometimes do. If not, the Serengeti allusion is just a red herring.

While the paleobotanical and paleoecological literature do indicate that during the Pleistocene, the Intermountain Region was very different from the Great Plains, the author's characterization of the Pleistocene Great Plains (pp.25-27) is completely at odds with contemporary paleobotanical and paleoecological literature (e.g., Axelrod 1985, Kaul et al. 1988, Wells 1965, 1970, 1983, Wells & Stewart 1987). The Great Plains grasslands are post-glacial. In the late Pleistocene, parts of the northern plains were glaciated or had periglacial tundra, but much of the northern plains had spruce forest (as far south as Kansas). Southwest of that there was pine woodland (into west Texas & New Mexico) or deciduous woodland (into central Texas). 'Grasslands' were apparently limited to small to moderate patches in semi-open forests and woodlands. The author may think that the Great Plains are "vast expanses with little elevational change or topographic relief"; however, he/she might be surprised if he/she spent much time there. "Badlands', 'breaks', 'scarps', 'mesas', and 'plateaus' can be found throughout the Great Plains (and are fire refugia for trees). There are geological structures like the Devil's Tower (first National Monument) and associated Pumpkin Buttes. East of the Rocky Mountain ranges, one finds ±isolated (generally ±low) mountains (or small ranges) surrounded by the plains, including the Bull Mountains, Crazy Mountains, Judith Mountains, Bearpaw Mountains, and Black Hills. Excluding these mountains, the elevational change is ±4200 ft, with a range of ca. 800-5000 ft, east to west (Kaul 1986). 1 suppose it depends upon how one defines "little elevational change or topographic relief." The present flora is recent, with few endemics (Axelrod 1985, Thorne 1993). The author should have looked further into the literature than the one (inappropriate) citation in this section. [A good peer-reviewed comparative paper for contemporary climate/vegetation relationships between the two regions is Cook & Irwin 1992.]

The Intermountain Region climate during the Pleistocene was not the same as the current climate (p.25). The different conditions north and west of the region would have influenced the climate, as would the large pluvial lakes within it. Since the author provides no references his opinions on climate (Pleistocene or modern), one can only guess why he/she thinks that the growing season for either is/was "about 6 weeks".

It is probably true that total productivity might have been different between the two regions. However, so little is known about the actual vegetation patterns of either or about the actual faunal distributions, that it is extremely speculative (and totally inappropriate) to even consider imposing modern plant production on Pleistocene ecosystems (p.27). Equally speculative and inappropriate are the author's (totally unreferenced) ruminations about the Pleistocene fauna of the Great Plains, e.g., "grazing herds", "nomadic grazer with little distinctive seasonal patterns or definitive home ranges", "incentives … to develop seasonal grazing patterns", and, especially, "a vast region of wandering herds of grazers and scattered predators". With little open vegetation (Axelrod 1985, Wells 1970), "vast regions of wandering herds" seem unlikely. Whether the dominant large fauna were grazers is open to question, given the lack of open vegetation. The *Bison* were not (McDonald 1981).

There is no scientific evidence for "grazing herds" in the Intermountain Region (p.28), despite the author's (unsupported) wishful thinking. Here again, unreferenced ruminations are extremely speculative and inappropriate (pp.28-29), despite how "obvious" they may seem to him/her, e.g., "had to develop seasonal grazing patterns", literally followed the melting snows", "incentives that drove herd migrations", "migrations were likely definitive and repeatable patterns rather than nomadic wanderings", "seasonal home range behavior”, etc.

The author is also on shaky footing when he/she begins to speculate about scientifically unsupported grazing advantages "to the plant community" (pp.29-30), again without much supporting scientific evidence. As Verkaar (1986) pointed out that even after more than a quarter of a century, Ellison's (1960) words are still accurate, "One cannot be very greatly impressed after examining this catalog of presumed contributions of grazing animals to the welfare of range vegetation by the supporting evidence". One can only be even less impressed by a speculative list of supposed benefits that are offered with little or no supporting evidence. As Crawley (1993) pointed out, "it is easy to make up stories … where the Darwinian fitness of a plant might be increased by herbivory. ...However a major body of life-history theory is built on the sensible alternative, supported by a wealth of empirical evidence, that herbivory is deleterious to the individual plants that suffer it; it is often highly deleterious, sometimes much less deleterious, but generally harmful nonetheless." There is no reason to believe that regrowing "after the animals move on" (p.30) is advantageous (except over being continually eaten if they did not move on).

The authors speculation on post-herbivory seedset and "assured reproduction" is contradicted by O'Connor's well-researched paper on local extinctions in perennial grasslands (which could lead to regional rarity or extinctions). O'Connor defined what he called "the extinction-prone perennial grass", palatable obligate seed reproducer (e.g., bunchgrasses) producing low numbers of larger, poorly dispersed diaspores, generally found in and and semi-arid environments experiencing periodic drought. One example he used *Pseuddroegneria spicata* (Pursh) A. Löve (syn. *Agropyron spicatum* (Pursh) Scribner & J. Smith). If one examines the life-history of *P. spicata*, using O'Connor's model, one can see why it has "disappeared from much of its former range". While both drought and grazing are capable of inducing high levels of mortality, neither alone is likely to eliminated established populations. However, together (especially for recurring for a successive number of years) they can lead to death of mature plants and (through failure of replacement) elimination of established populations. Because taxa of this type are obligate seed reproducers, successful recruitment is a function of seed availability, seed germination, and seedling survival. Drought and grazing in tandem can greatly reduce or eliminate seed production (a single defoliation can inhibit seed production in some taxa). Repeated seedless years can diminish the seed bank, grazing (especially trampling) can destroy seedlings. Competition from taxa like Bromus tectorum further reduce seedling success. Mature plants (with high amounts of standing dead) are apparently unattractive to native herbivores (e.g., deer), who may utilize the plants only when this natural protective barrier is removed (e.g., fire). Standing dead as an anti-herbivore mechanism has been reported for other taxa (Ganskopp et al. 1993, Johnson & Nichols 1982, Painter 1987, Sheppard 1919, Weaver 1954, Williams 1897). Under natural conditions, grazing would be occasional pulses (e.g., related to fire frequency). Livestock grazing occurs more frequently than every 30-70 years (original fire frequencies, Bunting 1994, Pellant 1994, Whisenant 1990). Other native bunchgrasses with similar life-histories that might be extinction-prone include (but are certainly not limited to) *Achnatherum hymenoides* (Roemer & Schultes) Barkworth (syn. *Oryzopsis hymenoides* Roemer & Schultes) Ricker) and *Hesperostipa comata* (Trin. & Rupr.) Barkworth (syn. *Stipa comata* Trin. & Rupr.).

Jansen's studies are almost exclusively tropical or hot desert and may have little or no relevance in the intermountain Region. The author cites no literature on the dispersal mechanisms of native plant taxa that might elucidate why these references were included. (See Colliins & Uno 1985, Herrera 1,985, for discussion of Janzen & seeds]. The importance of animals as seed dispersers increases along a xeric to mesic gradient (Collins & Uno 1985). Animal transport may be important for long-distance transport of small seeds (Collins & Uno 1985), but not larger-seeded taxa (including native Intermountain Region grasses) nor many of the other taxa at risk from livestock herbivory. Relatively few plant taxa have seeds that appear to be adapted for external dispersal in animal fur, and the risks of seed destruction by chewing, digestion or predation within dung are significant (Collins & Uno 1985). Deposit in dung tends to move seeds from disturbance to disturbance (Collins & Uno 1985), which might favor invasive taxa over natives. While animals (especially livestock) may not be important vectors for many of the native plant taxa, livestock fur is an important vector for invasive alien taxa like *Bromus tectorum* and *Taeniatherum caput-medusae* (Peters & Bunting 1994). If the author were able to document animal transport as a mechanism important to a particular group of native taxa this would be more interesting (and more important).

While the author may feel that "additional beneficial effects resulting from herd hoof action" include "breaking soil surface crusts which are so common to Intermountain soils" (p.30), a large number of researchers would disagree that the loss of the soil crusts is beneficial. Cryptobiotic (cryptogamic, microflora, microphytic, microbiotic) soil crusts are important elements of and and semi-arid ecosystems worldwide, representing over 70% of living cover in some of these systems (BeInap et al. 1994, Beymer & Klopatek 1992, St. Clair & Johansen 1993). In North America, they are most prevalent in semiarid regions of the Columbia Basin, Great Basin, and Colorado Plateau, extending into hotter, more and deserts (St. Clair & Johansen 1993). Cryptobiotic crusts can be found on a range of soils including (but not limited to) those derived from sandstone, gypsum, limestone, and shale parent material, although development may vary among substrates (BeInap & Gardner 1993). Cryptobiotic crusts consist of eukaryotic algae, lichens, bryophytes, cyanobacteria, and fungi that live on or just below the soil surface (Beymer & Klopatek 1992, St. Clair & Johansen 1993). They stabilize soils and reduce wind and water erosion, aid in water infiltration, improve seedling establishment, increase soil organic matter and nutrients, and increase survival of some higher plant taxa (BeInap 994, BeInap,

& Gardner 1993, BeInap et al. 1994, Beymer & Klopatek 1992, Brotherson et al. 1983, Harper & Marble 1988, Harper & Pendleton 1993, St. Clair & Johansen 1993). Both free-living and lichenized cyanobacteria fix atmospheric nitrogen in significant amounts (St. Clair & Johansen 1993). Trampling, compaction, and other disturbances caused by hooves of domestic livestock have negative impacts on soil crusts, especially during dry periods (BeInap & Gardner 1993, Beymer & Klopatek 1992, St. Clair & Johansen 1993). Recovery rates after damage have been found to often be very slow, possibly centuries for some components (e.g., lichens, mosses) may take centuries (1994). Both cover and biomass of the cryptobiotic crust has been found to be reduced on areas grazed by domestic livestock and exposed soil to increase (Beymer & Klopatek 1992, Brotherson et al. 1983). Significant correlations can exist between cryptobiotic crust cover and the composition of vascular plant communities, so that damage can result in an altered vascular flora (Beymer & Klopatek 1992, Brotherson et al. 1983).

The substantial literature discussing the negative impacts of domestic livestock is greatly under-discussed (e..g., nutrient export) or trivialized (e.g., riparian areas). Most negative impacts have been discussed in a number of readily accessible papers (e.g., Fleischner 1994, Mack & Thompson 1982 & citations therein) they do not need to be reiterated yet again. However, the effects of dust on plant communities have been until recently under-studied (Farmer 1993). Industrial- and vehicle-generated dust on plant taxa and communities has been the focus most dust pollution research. A rarely considered but potentially important negative impact in arid and semi-arid environments is dust raised by large numbers (herds, & "herd hoof action", p.30) of domestic livestock. Substantial numbers of large animals moving across dry soil often raise considerable amounts of dust. Dust may negatively affect plants in a number of ways, including reducing photosynthesis, respiration, and transpiration, allowing the penetration of phytotoxic pollutants, and inhibiting pollination (Farmer 1993). These and other negative impacts can lead to changes in community structure and composition. Because domestic livestock herds are larger and more ubiquitous than Holocene native herbivores are estimated to have been, the probability for damaging amounts of dust is greater with livestock.

I am not sure how one would investigate "the relationships of herbivory to flora" (p.29), except to see how the list of taxa changed as herbivory was manipulated. That is not the subject of any of the references. Three of the McNaughton papers concerned his Serengeti work and concepts extrapolated from them; the fourth is a response to Belsky's review. The Holland et al. paper combines data and modeling in an ecotype study in a Great Plains ecosystem. Paige & Whitham [misspelled in report] discussed above, involved montane monocarpic herbs. The two Jansen papers are controversial tropical seed studies. None of the references dealt with Intermountain Region plants nor ecosystems. Only Holland et al. dealt with a semi-arid temperate ecosystem. Can the author find no "pertinent" Intermountain Region plant/herbivore interaction studies? If what the author meant was plant/herbivore interactions, and Holland et al. (1992) is pertinent, why aren't Coppock et al. (1983), Holland & Detling (1990), Jaramillo & Detling (1988), Painter et al. (1989, 1993), Polley & Detling (1988), Whicker & Detling (1988)? If one examines the entire series, one sees an interesting picture of Holocene-herbivores/Holocene-grassiand interactions on the Great Plains. It is, however, very different from the one the author paints.

The Intermountain Region is an area of relatively high plant endemism (Thorne 1993). The regional biota includes a number of rare plant and animal taxa, some of which have state and/or federal protection (threatened or endangered). Livestock grazing is one of the land uses that has altered their habitats and put some of these taxa at risk (Yatskievych & Spellenberg 1993). Risk to these taxa needs to be addressed.

The author provides no literature citations for any of the highly speculative opinions expressed on pp.31-34 nor 37-41 (& only 3 in between). Why couldn't the author find any literature to support most of what he/she had to say on 11 pages, especially his/her Conclusion? "Diversity" cannot "roam" (p.31). How is species composition "functionally" stabilized within plant communities (p.31)? By definition, the "relations between multiple grazers and the plant community" are not *mutualistic* (p.33). Are there any publications that verify the post-World War 11, state game & fish stories (p.33)? If so, why aren't they cited? What evidence is there that livestock "disseminate" seeds of anything but invasive alien taxa, and that livestock "plant seeds" at all (p.38)? What evidence is there that "heavy winter grazing or burning is a prerequisite to thriving productive stands" of *Elymus, Leymus, Taeniatherum* (or whatever "wild ryegrass" is), or that "it flourishes under the heaviest winter grazing" (p.38)?

The author, apparently because of his/her mistaken opinions about the history of large animal herbivory in the Intermountain Region, does not seem to think that an exclosures is an appropriate "reference point in matters of plant community ecology" (p.2). There are times when using exclosures or the plants or vegetation growing within them may be inappropriate (see Painter et al. 1989). However, in general, exclosures may be among the most under-rated tools available for understanding livestock herbivory in the arid and semi-arid western North America. While there is an enormous amount of literature on livestock herbivory in western North America, most of it concerns increasing livestock production or increasing forage production to feed livestock., and comparatively little research has been designed to examine what happens when livestock are removed (Painter 1995, in press). There is a genuine need for more, larger exclosures; nongrazed land is relatively rare, and most livestock-free areas are too small for valid comparisons (Sock et al. 1994). Abrupt changes in livestock herbivory (including sudden cessation of grazing) can bring new problems (Painter 1993, in press), so it may be important ‘test' these in exclosures. Crawley (1993) pointed out that, in order to study the role of herbivory in plant fitness, "long-terrn, selective herbivore exclosure and repeated experimental introductions of excess seed will need to be coupled with the analysis of robust, yet simple models of plant dynamics".

The author and others who have accepted the hypotheses around which he/she built the report consider the following statements about hypotheses, controversy, and science:

> "I cannot give any scientist of any age better advice than this: the intensity of the conviction that a hypothesis is true has no bearing on whether it is true or not. The importance of the strength of our conviction is only to provide a proportionately strong incentive to find out if the hypothesis will stand up to critical evaluation " (Medawar in Wenner & Wells 1990).
>
> "It is a common failing - and one that I have myself suffered from - to fall in love with a hypothesis and to be unwilling to take no for an answer (Medawar in Wenner & Wells 1990).

> "Scientists normally receive very little formal training in scientific method or in the philosophy, sociology and psychology of science. Consequently, individual scientists tend to become committed to hypotheses as end products rather than as entities that will be replaced" (Wenner 1993)

> "If the hypothesis is 'attractive,' others may accept it. Given enough time, a subset of the scientific community may treat that hypothesis (rather than the data) as 'fact' and therefore 'not open to question'" (Wenner 1993)

> "Lack of progress in science is never so much due to any scarcity of factual information as it is the fixed mindsets of scientists themselves" (Schram in Vadas 1994).

> "[A]daptionist stories have fallen into disfavor in evolutionary biology and sociobiology because teleological reasoning and theory are not good substitutes for observation and experimental data (*citations*). That is, one cannot validly assume that behavior is adaptive to corroborate theories, although teleological reasoning can have heuristic (and verificatory) value in generating hypotheses about functional adaptations (*citation*). In particular, optimal-foraging behavior..." (Vadas 1994).

> "[P]arsimony (Occam's razor) is well-accepted as a tool in ecology and evolutionary biology, to keep hypotheses simple when greater complexity is unnecessary to explain ecological patterns and mechanisms (*citations*)" (Vadas 1994).

To reiterate, advocates of public-land livestock grazing must be able to demonstrate how ecological costs can be minimized, not trivialized. The introduction of alien taxa (including domestic livestock) must be treated as "a significant ecological change", and negative impacts on native plants and animals, sails and soil organisms, and all other aspects of the ecosystems must be anticipated and minimized. This will not be done if management decisions are made based on myths, misunderstanding, and misinformation. Use of scientifically unsubstantiated opinions as a basis for management decisions can leave public-land management agencies and their personnel vulnerable to accusations of 'management by myth'. And, unless these reports undergo substantial revision, the author(s) and agencies who funded them will be handing those opposing livestock grazing on public lands a strong weapon to use in arguments for removing livestock from public lands.

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January 27, 1995

Dr. Sherm Karl
Interior Columbia Basin Ecosystem Management Project
112 E. Popular Street
Walla Walla, WA 99362

Dear Dr. Karl:

Thank you for asking me to review the following contract reports:

(1) Herbivory in the Intermountain West ... and

(2) Paleoecological relationships of prehistoric equus ...

As you know, due to an oversight in your office, I only received these reports last week with your note asking me to submit my reviews by February 1 st. Due to the time constraint that you imposed and the nature of these papers, I cannot provide you with the detailed review that you requested. While I agree with some of what the author has said, much of his arguments are logically inconsistent, and a detailed rebuttal would be as long or longer than the original reports. Unless you wish to contract for my services, I simply do not have the time to conduct a detailed review of these reports. I will, however, offer a few general comments, but again, I do not have the time to provide you with the citations to support my conclusions. Instead, I have enclosed copies of the following papers, which not only explain my research, but which also contain citations to nearly 2,000 scientific reports.

1. Yellowstone's northern elk herd: A critical evaluation of the "natural regulation" paradigm. I have enclosed the abstract of my 550+ page dissertation and I suggest that you obtain a complete copy, as it summaries ungulate faunal remains recovered from more than 300 archaeological sites in the Intermountain West, including iust about all the Columbia Basin. You may obtain a copy from University Microfilms or if you send me a check or purchase order (made out to me personally, not the University) for $60.00 to cover my costs of photocopying, binding, and shipping, I will then make a copy from my original and send it on to you.

2. An introduction to my Aboriginal Overkill Hypothesis that recently appeared in the journal Human Nature. My Aboriginal Overkill book is under contract to Oxford University Press and will contain detailed chapters on why there

were few ungulates in the Columbian and Great Basins. Each of those chapters will contain well over 100 citations.

3. An abstract of a 405 page report I recently did for Parks Canada on long-term ecosystem states and processes in the southern Canadian Rockies. You will have to write Parks Canada for a complete copy of this report.

4. <u>Aboriginal overkill and native burning: Implications for modern ecosystem management.</u>

5. <u>Long-term ecosystem states and processes in the central Canadian Rockies: A new Perspective on ecological integrity and ecosystem management.</u>

Since the two papers that you asked me to review were written by the same author and set forth the same general arguments and evidence, the following comments apply to both studies.

1. The author must decide whether ungulate populations, prehistoric and historic, were limited by resources (i.e., food) or predation. These hypotheses are mutually exclusive and lead to entirely different views of what grazing/browsing pressure plants evolved with and ecosystems developed with -- also please note that ecosystems do not evolve, only species evolve. While at various points in these reports the author does acknowledge that predators may be important, the underlying assumption of both studies is that ungulate populations, and especially prehistoric populations, were limited primarily by their available food supply.

While the food-limited <u>vs.</u> predator-limited debate has raged for decades, studies over the last 10 years clearly favor the limitation of ungulates by predators, <u>not</u> food. Moose populations throughout most of Canada and Alaska today are being kept by predation at only 10% of the numbers the habitat can support. The same is true of caribou. Food limited populations on islands without predators have densities 100 times greater than on the mainland where wolves and bears are abundant. Dr. Tom Bergerud has even concluded that the sole reason barren ground caribou migrate is to avoid wolf predation, and a similar conclusion has been reached for Africa's Serengeti.

The point of all this is that if ungulate numbers were kept at low levels by predation, then plant species could not have evolved with high levels of herbivory as <u>assumed</u> by the author of these contract reports. Moreover, data suggest that the Pleistocene mega-fauna were also limited primarily by predation, not food. We call them mega-fauna for a reason, because they were very large, but food-limited animals do not achieve large body size, instead they dwarf. Where mega-fauna herbivores reached islands without their predators, those species quickly dwarfed, sometimes by two-thirds or more. Thus, there is little support for the author's food-limited position and since his contract reports are both founded on that <u>assumption,</u> those studies must fall as well.

2. The author basis his abundant mega-fauna hypothesis on the assumption that the Serengeti, with its large numbers of wildlife, is an "intact natural ecosystem" and therefore a valid model of how western North America must have looked in prehistoric times. The Serengeti, though, is not an intact natural ecosystem by instead is a European, romantic, racist view of how Africa should look (see Adams and McShane. 1992. The myth of wild Africa. W.W. Norton).

One of the first thing Europeans did was remove the Serengeti's indigenous peoples. For various reasons, they did not want black Africans in their white national park -- this, by the way, was also done here in the states, Native Americans were forcefully removed from all of our national parks, beginning with Yellowstone in 1878. Now, there have been hominoid predators in Africa for at least 3.8 million years, and our species Homo sapiens evolved in Africa 100,000+ years ago. Thus, there is nothing more unnatural in Africa than a system without hominid predators. Today the Serengeti lacks human predators, as well as the truly large carnivorous predators that hominoids displaced over the last several hundred thousand years. So in the absence of their natural predators, humans and carnivores, large populations of ungulates have built up in Africa, as well as in U.S. national parks, but in no way should that be considered natural or used as a model of how western North America looked in the past.

3. The author also claims that bison and other ungulates populated the Columbia Basin and other areas west of the mountains up until just before the arrival of Europeans ca. 1800. I have reviewed all the available archaeological reports and first person journals of European exploration, and there is absolutely no support for the author's position. A few bison, elk, and other ungulates did inhabit this area at various points during the last 10,000 years, but their numbers were kept extremely low by aboriginal hunting -- please see my Aboriginal Overkill paper. And, in fact, ungulate numbers actually began to increase 500± years ago because that is when European-introduced smallpox and other diseases first began to decimate Native Americans. This is also why even the earliest journals, such as those left by Lewis and Clark, do not describe the way the West was in pre-Columbian times. What Lewis and Clark saw were fewer native people and more ungulates than what existed prior to 1492.

4. It is also the author's contention that plant species, which evolved with high-levels of mega-fauna herbivory, retained their grazing resistant characteristics over the last 10,000± years. That is to say, the author claims that even if there were few ungulates in the Columbia and Great Basins for the last 10,000 years, those plants would still be able to withstand intense defoliation. As with the author's other assumptions, though, the available scientific evidence does not support this contention.

On heavily grazed portions of the Serengeti, for instance, rangelands protected from ungulates change species composition in just a matter of years. Moreover, exclosure studies here in the West have shown that grazed and ungrazed plants of the same species actually have different genotypes, as well as different growth characteristics. So even if we grant that large numbers of mega-fauna once roamed the West, with 10,000 years of virtually no ungulate herbivory our rangelands would have changed markedly. That they have not also argues for low mega-fauna populations.

5. The author also assumes that ungulates in the West followed melting snows and subsequent green-up upslope to secure higher quality food. The author claims that these altitudinal migrations "naturally" rested the vegetation and prevented overgrazing. The author further assumes that ungulates cannot survive, year-round, on low-elevation areas in the West. Again, however, the available evidence does not support any of these assumptions.

First, the author confused proximate and ultimate cause. While some animals may move upslope to secure higher quality foods (a proximate cause), the ultimate (evolutionary) cause of this altitudinal migration is to avoid predation. Moreover, throughout the West where they are not disturbed by humans, large numbers of elk and other ungulates now live yearlong on what we consider to be "winter" ranges. In the hottest driest part of the Columbia Basin, for instance, elk have not only increased at near that species' maximum intrinsic rate of increase, but bulls grow huge record-book antlers indicative of excellent nutritional conditions.

So in conclusion, I do not agree that "Pleistocene herbivory provides a potential model for functional livestock grazing" as envisioned by this author. Moreover, I maintain that fire, and primarily native burning, played a much greater role in structuring pre-Columbian ecosystems than ungulate herbivory. I certainly would not base any management decisions on these two reports or the author's assumptions. I also do not agree with the way this author has defined humans as <u>not</u> being part of natural systems. I am sorry that I cannot offer a more positive response, but I believe the available scientific evidence points to conclusions other than those reached by this author. Nevertheless, perhaps his papers will trigger a rigorous review of these subjects.

If you require any additional information or have any other questions, please feel free to contact me. Again, thank you for allowing me to review these papers and I hope that my comments will help with the development of your Columbia Basin EIS. And finally, I ask that my name be added to your mailing list to receive all EIS documents and supporting reports, as soon as they are available to the public.

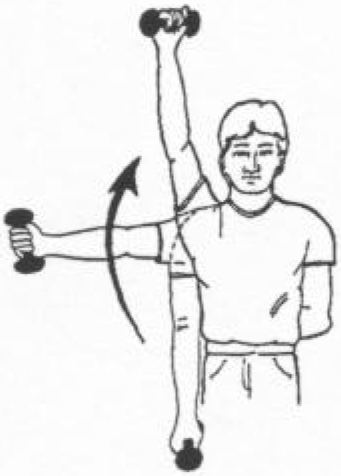
With best regards,

Charles Kay

Charles Kay
Adjunct Assistant Professor,

encl. Personal vitae - - per your request.

SHOULDER ABDUCTION



Exercise 2 of 2

SHOULDER ABDUCTION

1. Stand holding _____ lb weight in _____ hand
2. Raise arm up to the side and overhead as far as you can
3. Hold _____ seconds and slowly lower
4 _____ repetitions, _____ times per day