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Effects of Long-Term Grazing by Big Game and Livestock in the Blue Mountains Forest Ecosystems

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ABSTRACT

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The effects on eastside forest ecosystems from long-term grazing by large mammals are assessed, because long-term herbivory can reduce or increase ecosystem productivity. The assessment emphasizes elk and cattle in the Blue Mountains of northeast Oregon and southeast Washington. Histories of populations of large mammals and their effects in the Blue Mountains are described. Maximum populations of domestic livestock in the Blue Mountains occurred about the turn of the 20th century, declined by 1940, and increased slightly to the present. Livestock grazing on Federal livestock allotments declined from 1915 through 1950, and remained relatively stable since. Elk herds, which existed in relatively low numbers prior to Euroamerican settlement, were decimated by the late 1800s. Hunting restrictions and translocations resulted in increased herds, and hunting was re-instituted in 1927 in Washington and in 1933 in Oregon. Elk herds grew to high density levels by 1980. Long-term heavy use by domestic livestock, primarily cattle, and elk has changed ecosystem processes. There is empirical evidence that persistent herbivory by large mammals caused moderate to severe reduction of shrubs and forage productivity in a variety of logged and unlogged forest communities, with subsequent effects on frequency of wildfire and conifer seedling establishment in some plant communities. Long-term herbivory was shown to have alternative effects by either improving or reducing wood-fiber production by reducing competition from understory plants or reducing soil fertility. The changes in plant communities caused by the herbivores may have had negative feedback effects to productivity of both elk and cattle. Cattle do not achieve desired weight gains on summer allotments. Empirical studies on forage quality and livestock nutritional status support a view that large domestic and wild mammals subsist on suboptimal forage conditions most of the year in the Blue Mountains. Survival of elk calves appears low, partly as a result of density-induced shortages of high-quality forage. The reduced calf production appears to be exacerbated by low adult bull:cow elk ratios, which reduces calf survival via delayed and lengthy birthing periods. The low bull:cow ratios are a result of reduced cover due to logging and increased access to hunters due to logging roads. Reduced big game productivity has led to restrictions on hunting opportunities, with concomitant losses in revenue to local economies. In addition, the dense elk herds, in concert with forest management activities on federal lands, have resulted in increased use by elk on private lands, where they damage crops. The paper identifies adaptive management experiments that could identify options for-clarifying the complex relationships between herbivores, vegetation, and ecosystem processes and identify management options for restoring forest health.

Keywords: Adaptive management, big game, Blue Mountains, cattle, density-dependence, ecosystem, elk, grazing, herbivory, livestock, nutrient cycling, ungulate.

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INTRODUCTION

Management programs developed to restore and sustain forest health must use socially and economically acceptable methods. Assessing past management practices can help identify acceptable options for overcoming current forest health problems. Here, we assess the effects of long-term grazing by livestock and big game animals on forest ecosystem processes. Such assessment is appropriate because long-term herbivory by large mammals may either reduce or increase ecosystem productivity (Crawley 1983, Gessaman and MacMahon 1984), including that of forests (Pastor and others 1988).

We conduct this assessment from the view that large-scale systematic disturbances, primarily logging and fire suppression, have profoundly influenced vegetation patterns and vegetation-herbivore interactions. We emphasize the Blue Mountains of northeastern Oregon and southeastern Washington because of the 130-year history of livestock use in an area rich in big game animals. We assume that results from the Blue Mountains represent, to various degrees, other forests in the interior Northwest. We emphasize cattle and elk (see appendix A for scientific names) because they are numerous and widespread and because long-term information is available on both species and their habitats. We also emphasize plant-soil-animal interactions, including nutrient cycling and feedback mechanisms that influence animal population performance. These topics are relevant to both economic development and an understanding of ecological processes.

First, we describe ecosystems important to large herbivores, and summarize management histories and trends among elk and livestock populations in the Blue Mountains. Next, we review published scientific literature that provides a basis for predicting the effects of cattle and elk on forested ecosystems. Then, we review local studies to determine the accuracy of predictions from the literature. Finally, we use the results to suggest management options that might be tested by adaptive management experiments (Waiters 1986) within a comprehensive program for restoring forest health.

IMPORTANT ECOSYSTEMS FOR LARGE HERBIVORES IN THE BLUE MOUNTAINS

Assessing herbivory begins with describing the major ecosystems that are grazed. Kuchler (1964) described 10 ecosystems for the Blue Mountains, based on their potential vegetation. Garrison and others (1977) described 11 ecosystems that were generally similar to those in Kuchler (1964); they distinguished mountain meadow ecosystems and excluded Kuchler's grand fir--Douglas-fir class. Thomas and others (1979) described 15 ecosystems important to wildlife in the Blue Mountains.

Franklin and Dyrness (1973) described eight major forest and woodland vegetation zones and several steppe and shrub-steppe associations for the Blue Mountains. They paid particular attention to successional variation in subalpine grasslands, mountain meadows, and riparian communities. Other workers subdivided the major ecosystems into vegetation communities and associations (Hall 1973, Johnson 1959, Johnson and Clausnitzer 1992, Johnson and Simon 1987).

The most important ecosystems for large herbivores in the Blue Mountains are those at mid-elevations. These primarily include open plant communities in ponderosa pine and Douglas-fir zones, and mixed conifer communities at higher elevations. Large herbivores often graze early seral stages heavily after timber harvesting in the mixed conifer zone (Skovlin and others 1989), and they also graze in timber stands. Steppe and shrub-steppe zones at lower elevations and high mountain and subalpine zones at higher elevations also contain plant communities of great importance to large herbivores. The lowelevation zones include grasslands, sagebrush, and juniper woodlands in association with foothills and canyons (Driscoll 1962). These zones are particularly important as spring, fall, and winter range for all classes of ungulates (Sheehy 1987). The high-elevation montane grassland types, which are mixed with forest communities, provide important summer range (Reid 1941).

Mountain meadow communities are interspersed throughout the Blue Mountains, where streams have low gradients and wide flood plains. These communities are important to large herbivores because they produce significant amounts of nutritious forage in late summer and fall (Holechek and others 1982). Mountain meadows comprise not more than one percent of the total summer range for livestock and big game, yet produce up to 15 times more forage than surrounding rangelands (Pickford and Reid 1942a).

MANAGEMENT HISTORY OF LARGE MAMMALS IN THE BLUE MOUNTAINS

Livestock History and Federal Management Practices: 1850-Present

Little historical information about livestock is available before European settlement, although the local Cayuse and Nez Perce Indians kept horses as early as 1730 (Haines 1938). The first extensive exploitation of the forested grasslands occurred between 1843 and 1870, when thousands of cattle were herded over the Oregon Trail (Evans 1991). Journals of early pioneers described large yellow pine forests with grassy glades that looked like fields of grain, and told of a landscape that burned so often no underbrush was left (Wickman and others 1993).

Settlers' livestock primarily used forage along travel routes as they crossed the Blue Mountains to the Willamette Valley in the western Oregon Territory. That pattern changed when eastern Oregon was settled, after western valleys became populated. By 1860, small cattle herds were scattered from Walla Walla, Washington, to Farewell Bend on the Snake River upstream from Hells Canyon (Oliphant 1932). Subsequently, tens of thousands of cattle and nearly as many horses from the Willamette Valley were brought to the area after gold strikes in Canyon City and Auburn, Oregon (Oliphant 1968).

Stockmen moved their animals to the foothills and to more remote regions as homesteaders began tilling what had been cattle winter range in fertile valleys. This gradual expansion of livestock use continued into the early 1870s. Livestock numbers increased eight- to ten-fold from the 1870s through the 1880s, reflecting an influx of transient cattle that were herded from western Oregon to the Great Plains from 1875 to 1885 (Oliphant 1964).

We show (fig. 1) trends in numbers of livestock from 1860 to 1960 in nine Blue Mountains counties (four in Washington and five in Oregon). Compiled from the U.S. Census, Bureau of Statistics (U.S. Department of Commerce 1900) and from the Census of Agriculture Area Reports for Oregon and Washington (State of Oregon 1890), the information reflects the total animal units present in the ninecounty area but does not accurately indicate the proportions of those animals that grazed in the present-day National Forests.

Evidence of changes in range vegetation in the ecoregion that includes the Blue Mountains was recognized as early as the 1870s. In a supplement to the 1880 census (Gordon and others 1883), a group of livestock producers reported:

> ... we find generally in Washington territory and in Oregon that free range pasturage, originally strong and luxuriant, has been injured by overstocking. The pasturage is generally good, except the timbered mountain heights in the northwest, ..., and along the whole extent of the Cheyenne trail for a couple of miles in breadth.

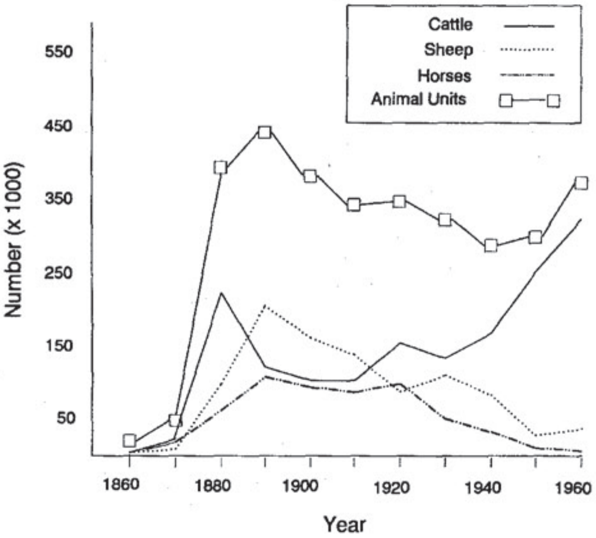

Figure 1. Trends in livestock numbers in the Blue Mountains of northeastern Oregon and southeastern Washington, 1860-1960. Information for this chart was compiled from the U.S. Census Bureau of Statistics, U.S. Department of Commerce, and from the Census of Agriculture Area Reports for Oregon and Washington, Washington, DC: U.S. Government Printing Office.

Gordon and others (1883) believed that forested rangelands were stocked at perhaps four times their sustainable capacity by 1880, and they had been subjected to such intensive grazing for the previous 10 to 15 years. Gordon and others (1883) wrote that eastern Oregon grazing land, “Probably,.., will not now support more than one-third of the cattle that it fattened five or seven years ago.” Domestic sheep continued to increase, however, a result of high prices for wool. Sheep production peaked in the 1890s (fig. 1), and numbers of cattle and horses stabilized or declined. Total animal numbers were at an all time high of almost 450,000 animal unit equivalents (an animal unit equates five sheep with one horse or cow).

Consequences of continued high stocking rates included loss of stable vegetation cover, which resulted in erosion on steep slopes (Fording 1931). Tree reproduction was browsed and trampled along stock routes and in key foraging areas. Exposed mineral soil led to establishment of tree seedlings (Rummel 1951). Grazing removed vegetation that, when dry, became fine fuels. Thus, grazing in the ponderosa pine zone altered the conditions under which ground fires previously controlled establishment of dense stands of pine seedlings (Hall 1977). In doing so, grazing probably contributed to changes in fire frequency in the ponderosa pine zone. Intensive grazing also led to establishment of alien, often noxious, plants (Branson 1985).

Although the apparent range destruction alarmed government officials and stockgrowers, large livestock herds continued to graze public lands until the Forest Reserves were established. The Forest Reserve Act of March 1, 1895, created the Forest Reserves specifically to protect water and produce trees.

The National Academy of Sciences (1898) focused national attention on unregulated grazing in the Forest Reserves in a report to the Secretary of the Interior. That report alleged that mass destruction of natural resources had occurred, particularly by transient sheep. Sheep grazing was banned, except in Oregon and Washington, where studies had shown sheep grazing was not detrimental (Coville 1898). Enforcement was difficult at best, however, and livestock trespassed widely on mountain summer ranges. Range wars erupted as sheep and cattle producers feuded over limited forage resources (Griffiths 1903).

The creation of the U.S. Department of Agriculture Forest Service in 1906 helped to enforce regulations and eliminate trespass. Although grazing was not mentioned as an allowable practice in Forest Reserve legislation, the Secretary of Agriculture instructed the Chief Forester (U.S. Department of Agriculture 1905) to, “...

see to it that the wood, water, and forage of the reserves are conserved and wisely used." Rules and regulations for livestock grazing on Forest Reserves were specified shortly thereafter. Forest Service personnel and stockgrowers negotiated agreements on range division by class of livestock, permit application procedures, periods of use, grazing fees, dates of allowable grazing, and commensurability (Tucker 1940). Commensurability meant that property of a participating ranch had to have the capacity to provide adequate forage for livestock when they were not grazing on Federal allotments.

Management for productive herds required accurate estimates of the numbers of animals on the range. The first reliable record of livestock grazing for the Wallowa Reserve was in 1911 (Tucker 1968). Previous boundary changes, allotment consolidations and inability to stop animal trespass reduced the accuracy of counts. Trespassing animals probably accounted for 25 percent or more of the use on this reserve (Tucker . 1968).

Attempts to balance forage supply with livestock demand resulted in a 70 percent decline in livestock use on the Wallowa and Whitman Reserves (now the Wallowa-Whitman National Forest) from 1911 to 1970 (fig. 2). Most of that decline was due to reductions in sheep (table 1).

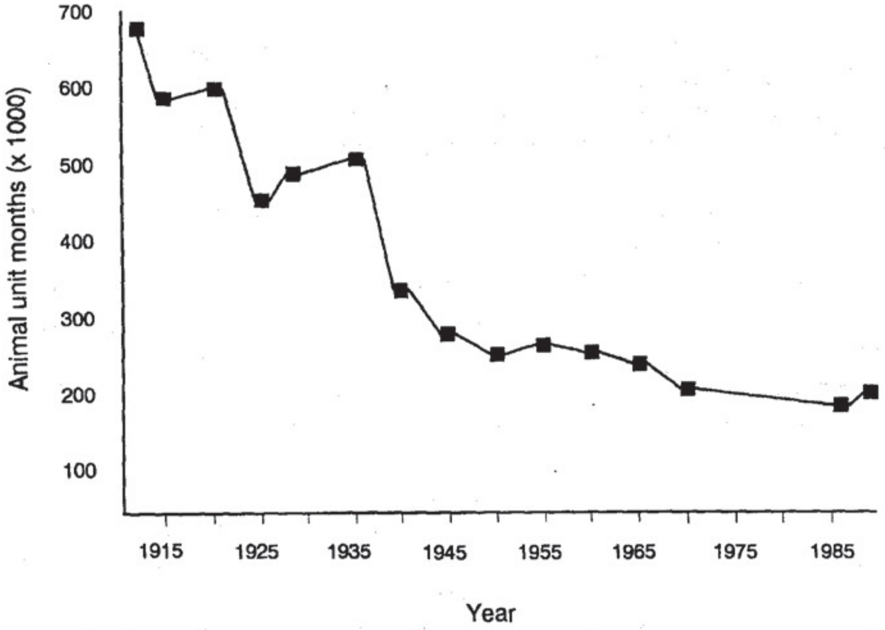

Figure 2. Trends in livestock use on the Wallow-Whitman National Forest, 1911-90.

Table 1-Numbers of cattle and domestic sheep grazing on the Wallowa Reserve, Oregon, 1911-1961 (from Tucker 1968)

Year	Cattle	Sheep
1911	13,625	121,740
1921	23,830	67,203
1931	9,654	71,213
1941	8,121	41,764
1951	9,780	15,276
1961	11,255	16,447

Federal agencies needed improved technical information for managing range lands under the new regulations. Sampson (1914) investigated plant succession on depleted subalpine fir forested grasslands on the Standley sheep allotment on the Wallowa National Forest in 1907. Sampson (1913) recommended varying the period of use of ranges, and he experimented with domestic grass seedings to restore the productivity of the range (Sampson 1908). Methods of open range sheep production were compared with conventional herding systems. Open range production, which means that sheep were not tended by herders with dogs that returned sheep to a camp or corral each evening, appeared to be economical only if predators were eliminated (Jardine 1910). Also, Fleeting (1910) investigated the influence of livestock grazing on tree regeneration on the Malheur National Forest.

Steffens (1915) conducted a range reconnaissance survey in 1914 to locate and map the distribution of forage supplies. He found cheatgrass, an introduced annual grass, on only six areas within portions of 12 square miles (sections) on the former Imnaha Reserve and adjacent private lands (memo to files from Melvin H. Burke, Assistant Range Examiner, Wallowa National Forest, November 19, 1938). Cheatgrass presently occurs on nearly every section below about 3000 ft elevation.

Livestock numbers increased slightly on Forest allotments after World War I, reflecting a policy change to increase food production. New policies eased restrictions on livestock numbers and season of use to such an extent that abusive grazing practices occurred. A report to Congress in 1935 revealed some degree of forage depletion on most of the forested mountain summer ranges (U.S. Senate 1936). The areas and amount of depletion (fig. 3) were based on departure from what was assumed to have existed in the absence of livestock grazing. Livestock use on National Forests in the Blue Mountains, as represented by trends on the Wallowa-Whitman National Forest, has remained relatively stable in recent years (fig. 2).

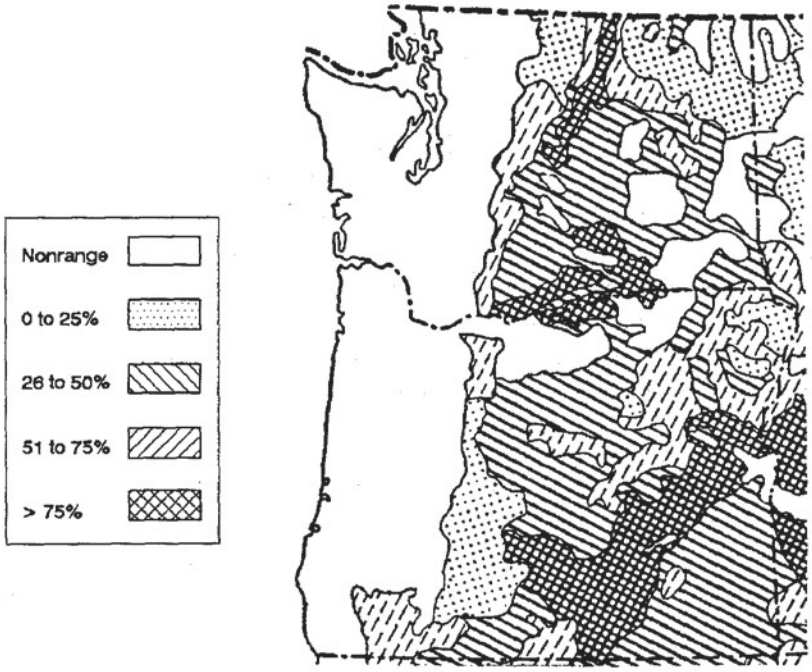

Figure 3. Extent of forage depletion on ranges of eastern Oregon and Washington, 1935 (Senate Document 199, The Western Ranges).

Research since the 1940s provided managers with a scientific basis for range management. More than 75 publications dealing with ungulate grazing on forested rangelands resulted from studies on the Starkey Experimental Forest and Range (Skovlin 1991). Methods for monitoring and judging changes in range condition or range succession have come into standard use (for example, Pickford and Reid 1942b, 1946, Reid and Pickford 1946), although they are difficult to interpret on grazed forested sites because of relatively rapid succession. Studies on grazing capacities and rangeland sustainability determined proper grazing intensity on key forage plants (for example, Pickford and Reid 1948). The recommendation has continually been revised downward, based on longer, more highly controlled studies (Strickler 1969).

Studies conducted in subalpine areas show that foraging by summering elk and sheep can exceed the allowable use on several grasses and grasslike plants (Pickford and Reid 1943). These authors also provided a model for judging subalpine range condition based on plant composition and production (Pickford and Reid 1942a). That model continues to guide determinations of the long-term sustainability of grazed subalpine rangelands in the Blue Mountains.

Research and management efforts helped restore productivity to abused rangelands, and recovery of some areas over the past 50 years has been striking. Improvements on one allotment, the Tenderfoot Basin allotment, have been chronicled since the late 1950s (Reid and others 1980, Reid and others 1991, Strickler 1961). Sheep continue to graze this allotment irregularly, with evidence of continued recovery. Mule deer and elk, in particular, have increased use of this allotment.

Range condition on the Standley sheep allotment in the Minam River drainage has been monitored since 1908 (Sampson 1909, Strickler and Hall 1980). Sheep numbers on this allotment declined by over 90 percent from those at the turn of the century, and sheep have not used this allotment regularly since 1980. Recovery is evident, although some sites contain vegetation in early stages of secondary succession.

Range research since the middle of this century has centered on determining proper seasons of livestock use, grazing systems, and stocking for various ecosystems (Skovlin and others 1976). In 1950, fewer than one in five National Forest cattle allotments in eastern Oregon and Washington was managed by systems other than season-long grazing. By 1970, more than three of five allotments were at least managed under a deferred rotation system (A. Denham, pers. comm.).

The Wallowa-Whitman National Forest (1980a, b, c, d; 1981) evaluated condition and trends in grazing allotments within five Oregon Department of Fish and Wildlife (ODFW) Wildlife Management Units. These subjective evaluations suggest that ranges in allotments in the Starkey and Minam Units were generally in satisfactory condition. Information was lacking from allotments in the Imnaha Unit, and many allotments within the Snake River and Chesnimnus Units were judged in unsatisfactory and declining condition. The poor conditions in the Snake and Chesnimnus Units were believed to be a result of poor livestock management practices before the Forest was established. The subjective evaluations for the Snake and Chesnimnus allotments also suggested that combined use by big game and livestock was at or above the ability of the range to sustain productivity.

Recent concerns for aquatic and terrestrial wildlife, water quality, and fisheries led to studies on the proper grazing intensities in riparian and wetland habitats (for example, Kauffman 1982, Kauffman and others 1982, Skovlin and others 1977, Skovlin 1984). Current research at the Starkey Experimental Forest and Range features habitat use and forage resource partitioning among cattle, deer, and elk (Johnson and others 1991). Relatively little research has evaluated dynamics of managed forest sites that are grazed.

History and Management of Elk in the Blue Mountains

The archeological record indicates that elk have been present in the Columbia Basin and probably adjacent forest zones for at least the last 10,000 years (McCorquodale 1985). They were relatively common after 1840, when settlers traveled the Oregon Trail (Bailey 1936, Shay 1954, Thwaites 1905). Elk were an important subsistence resource for Native Americans prehistorically (McCorquodale 1985) and for the early Euro-American settlers (ODFW 1992). Unregulated subsistence and market hunting, however, which coincided with initial livestock grazing and land cultivation, nearly extirpated elk from the Blue Mountains by the late

Table 2-History and management of Rocky Mountain elk in northeast Oregon and southeast Washington

Date	Comments[1]
Early 1800s	Elk not present in abundance (historical accounts).
Late 1800s	Market hunting resulted in elk scarcity (3, 4, 5, 7, 8).
1899	Oregon legislature prohibits selling elk meat, apparently resulting in a 10-year ban on hunting (3, 4, 8).
1905	Hunting briefly re-opened in eastern Oregon (3, 4, 8).
1909-1932	Hunting seasons closed; elk populations increased. (3, 4, 5, 8).
1912	Twenty-two elk from Jackson, WY, released in Wallowa County, OR (1, 2, 4, 8).
1913	Twenty-nine elk from Yellowstone National Park (YNP) released, Pomeroy, WA (2, 6, 9).
1913	Twenty-five elk from YNP released near Walla Walla, WA (2, 6).
1916	Seven hundred and ten elk estimated to occur in Baker, Umatilla, Union and Wallowa Counties, OR (1, 10).
1918	Fifty YNP elk released near Walla Walla, WA (2).
1924	Complaints about competition between elk and livestock begin (3).
1926	Elk population for Blue Mountains at 3,663 (1).
1926	Elk population for Wallowa County, OR, estimated at 669 (1).
1927	Hunting season first opens for elk in southeastern Washington (2, 9).
1931	Thirty YNP elk released near Dayton, WA (2, 9).
1932	Estimated 3,000 elk in Wallowa County (2).
1933	Estimated 11,030 elk in Oregon (1).
1933	Hunting re-instituted in Oregon; 23-25 October for 2-point or larger bulls; parts of Baker, Wallowa, Union, Umatilla Counties; 579 elk killed (3, 4, 5, 7).
1934-37	Ten-day mid-November season in Oregon; 550-750 antlered bulls killed (3, 8).
1937	Six hundred and twenty elk reported through Whitman National Forest check stations (5, 8).
1939	First antlerless season; 379 females killed (3).
1940	Between 50-150 elk harvested in southeastern Washington since 1927 (9).
1941	General either-sex hunts, Oregon; unrestricted hunters; 3,741 elk killed (9).
1949	A total of 26,000 hunters in Oregon killed 8,685 elk, including 6,071 antlerless elk (3).

Table 2-History and management of Rocky Mountain elk in northeast Oregon and southeast Washington (continued)

Date	Comments
1955-1963	Hunters and elk harvest continue to increase. (3)
1964	Separate tags required for eastern and western Oregon; extensive intrastate translocations of elk into the 1970s (3).
1970s	Elk populations increased by 45% during the decade; bull ratios declined; 19-day season, last 5 days of which included antlerless; >65,000 hunters (3).
1972	Declining bull ratios led to limited-entry permits for bulls; 3,295 permits for antlerless elk, increasing to 10,675 by 1978. (3)
1979-1985	Split hunting seasons to disperse hunting pressure; bull ratios improve by 25%; small increase in populations; 16,000 Rocky Mountain elk killed; antlerless tag numbers nearly double; > 75,000 hunters (3).
1981	Oregon adopts management objectives for elk density and cow-calf ratios (3).
Post 1985	Concern for increased road access, reduced cover and bull escapement. Hunter numbers declined to > 70,000 (3).

[1] Numbers in parenthesis refer to the following references:

1. Bailey, V. 1936. The mammals and life zones of Oregon. North American Fauna, No. 55, Washington, DC: U.S. Department of Agriculture, Bureau of Biological Survey. 416 p.
2. Couch, L.K. 1953. Chronological data on elk introductions in Oregon and Washington. Murrelet 16:3-6.
3. Edwards, D. 1992. Draft elk management plan. Portland, OR: Oregon Department of Fish and Wildlife. 79 p.
4. Gildemeister, J. 1992. Bull trout, walking grouse and buffalo bones-oral histories of northeast Oregon fish and wildlife. La Grande, OR: Oregon Department of Fish and Wildlife. 64 p:
5. Huff, R. 1953. Early day game conditions. Memo to files, Jan. 19, 1953, Regional Office, W-Supervision-General. Baker City, OR: On file at Supervisor’s Office, Wallowa-Whitman National Forest, 9 p.
6. Bobbins, R.L.; Redfearn, D.E.; Stone, C.P. 1982. Refuges and elk management. Pages 479-507. In: Thomas, J.W; Toweill, D.E., eds. Elk of North America: ecology and management. Harrisburg, PA: Stackpole Books. 479-507.
7. Skovlin, J.M. 1991. Fifty years of research progress: a historical document on the Starkey Experimental Forest and Range. Gen. Tech. Rep. PNW-GTR-266. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 58 p.
8. Shay, R. 1954. Immigrant elk: the story of two early-day elk transplants to Wallowa and Clackamas counties. Oregon State Game Commission Bulletin. 1954:3-8.
9. Tucker, G.J. 1940. History of the northern Blue Mountains. On file with: Pomeroy Ranger District, Umatilla National Forest, Pendleton, OR. 169 p.
10. Tucker, G.J. 1968. History of the Wallowa National Forest. 3 volume unpublished document. On file with: Supervisor’s Office, Wallowa-Whitman National Forest, P.O. Box 907, Baker City, OR. 97814.

1880s. The State government and private groups responded by banning both elk hunting and the selling of elk meat, and by translocating elk from other areas (table 2).

The earliest official elk census in the Blue Mountains was apparently made in 1916, when the total population for Baker, Umatilla, Union, and Wallowa counties was estimated at 710 animals (Bailey 1936; Tucker, n.d.). The next recorded census was in 1926, when the population for Wallowa County was estimated at 669 and that for the entire Blue Mountains was 3663 (Bailey 1936). Some of the animals used in deriving the 1916 estimate may have been survivors or offspring from translocations of elk from Yellowstone Park to Pomeroy and Walla Walla, Washington (table 2). Likewise, the 1926 estimate in Wallowa County explicitly included both native animals and the survivors and offspring from earlier transplants, according to Shay (1954). The total elk population in the Blue Mountains probably did not contain more than a few thousand animals in the 1920s.

More recent records paint a vastly different picture. In the 20 population management units in northeastern Oregon (fig. 4), which roughly correspond to the four counties in the population estimates of 1916 and 1926, ODFW estimated the aggregate winter population in 1980 at 58,500 animals. Therefore, the residual and translocated elk herds grew into one of the largest regional populations in North America. Below, we review the management practices that fostered such growth.

In Oregon, elk management generally has consisted of several decades of no legal hunting followed by years of conservative legal harvests to facilitate population growth (table 2). Management from 1889 through 1932 focused on increasing herd size. No hunting was allowed during this time, except for a short period between 1905 and 1909. Bull-only hunting was reauthorized in 1933. Legal harvest of females was reauthorized in 1939, so the female segment of the regional population probably grew relatively unchecked for 30 years. General either-sex hunting prevailed for the next 30 years. In the early 1970s, concern for overharvest led to the first limited-entry hunts. The development of split seasons followed in 1979 in an effort to accommodate increasing numbers of hunters.

Surveys were initiated shortly after World War II to monitor elk populations. Survey procedures were standardized by 1953 to estimate density of animals on winter range (in terms of elk sighted per mile of survey route) and winter ratios of bulls to cows to calves on selected herd ranges. Monitoring was gradually expanded to other areas; in 1960, the system of population management units (fig. 4) was established. Population surveys were conducted from vehicles and horseback until 1960. Some surveys were conducted by using fixed-wing aircraft in the early 1960s; by 1965, aircraft were used in all management units. Management objectives for winter density and bull:cow:calf ratios were adopted by the Oregon Fish and Wildlife Commission in 1981, and ceilings were set on the size of some populations (ODFW 1982). Estimates for winter densities since 1953 (fig. 5) showed pronounced increases for most populations, particularly prior to the 1980s.

Recent management on behalf of elk populations has expanded to include habitats. Recommendations for winter and summer thermal cover have been adopted by the National Forests to enhance elk distribution and use of landscapes (Thomas and others 1979, Thomas and others 1988b), and to reduce harassment from recreationists (Skovlin 1982). Concern also has grown for the vulnerability of elk to hunting in managed landscapes, mostly focused on increased access to hunters as road densities increased and hiding cover was reduced by timber harvests (Christensen and others 1991). High numbers of elk hunters also have been implicated (Vales and others 1991).

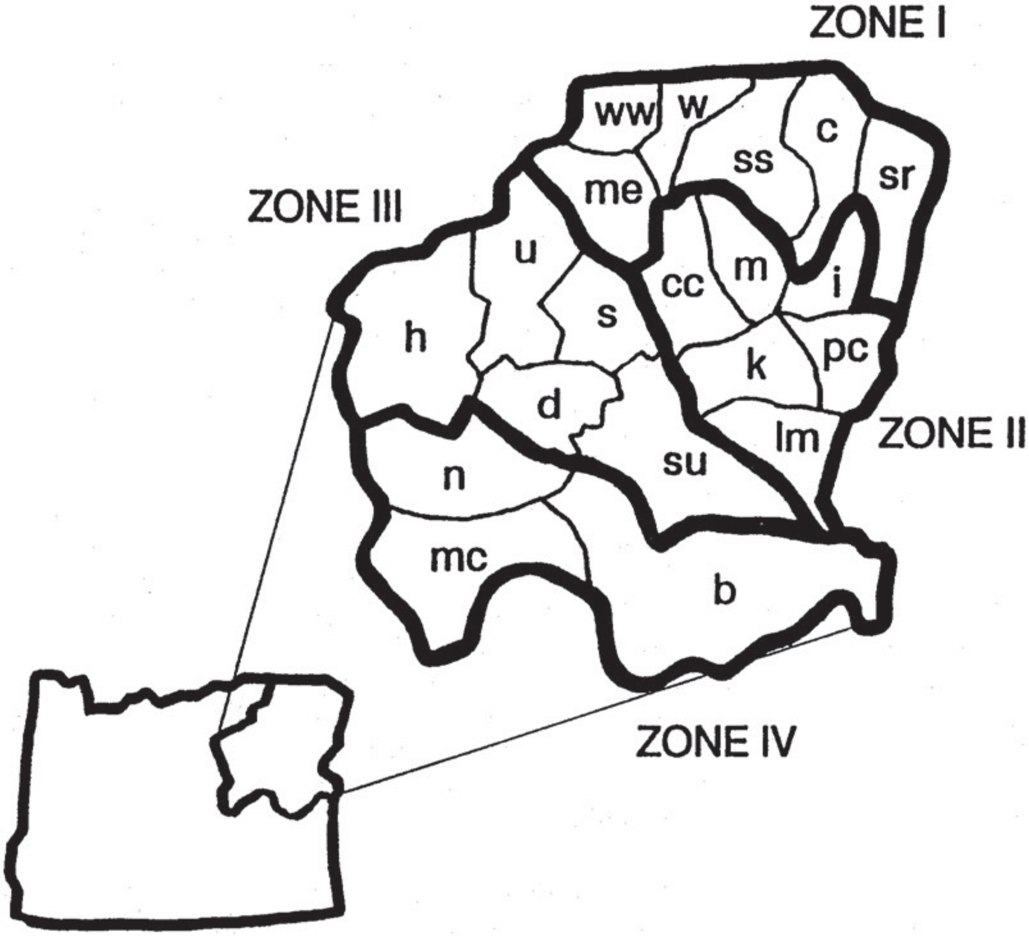

Figure 4. Game management zones and units in northeastern Oregon: Zone I (sr = Snake River, c = Chesnimnus, ss = Sled Springs, w = Wenaha, ww = Walla Walla, ME = Mount Emily); Zone II (m = Minam, i = Imnaha, cc = Catherine Creek, k = Keating, pc = Pine Creek, lm = Lookout Mountain); Zone III (u = Ukiah, s = Starkey, h = Heppner, d = Desolation, su = Sumpter); Zone IV (n = Northside, mc = Murderer's Creek, b = Beulah).

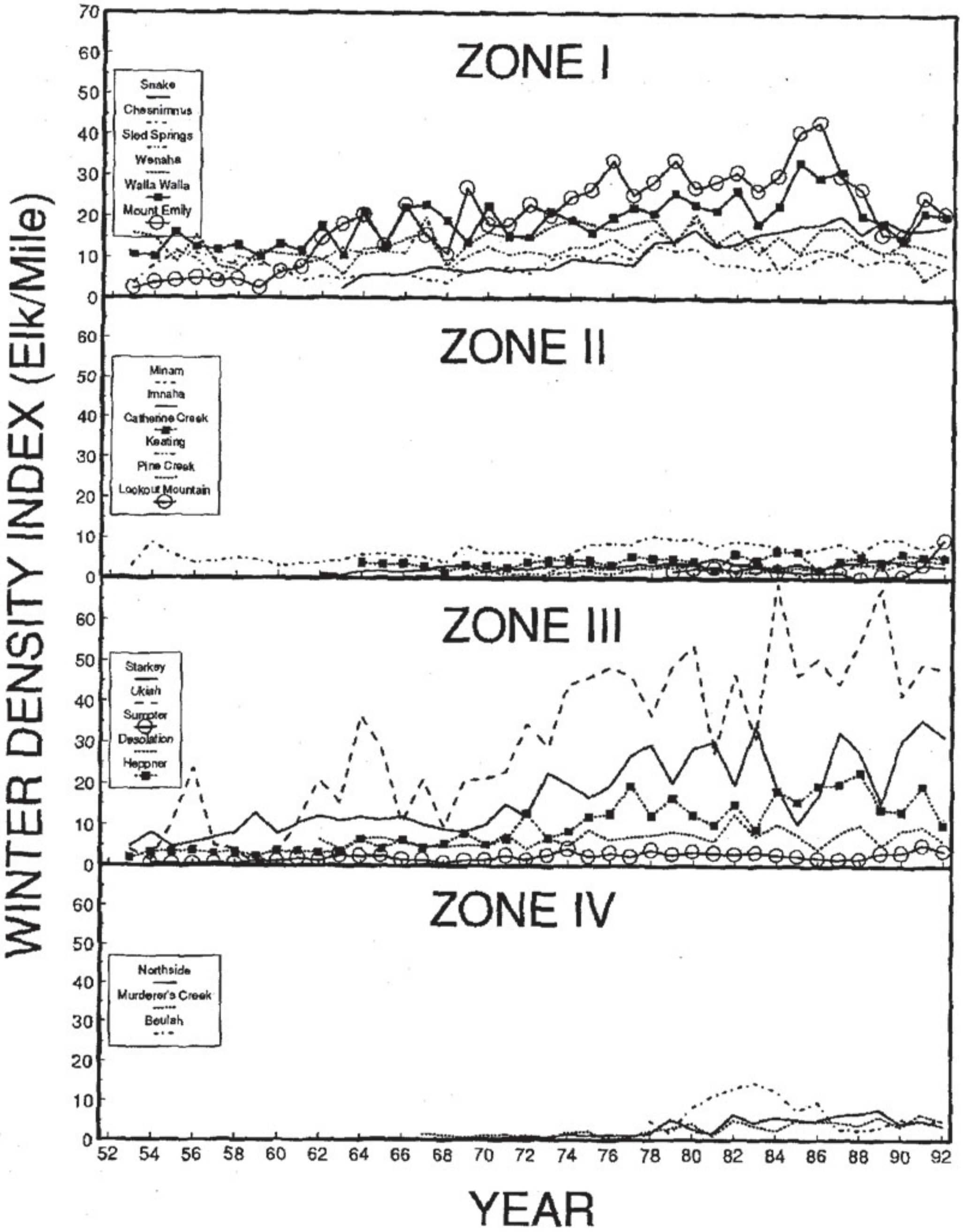

Figure 5. Recorded annual density indices, by zone and unit, in the northeastern management area of Oregon, 1953-92. Pre-1960 data were derived by summing data for herd range samples nested within the current Game Management Units. Source: Oregon Department of Wildlife annual reports, 1953-92.

RELATIONS OF LARGE HERBIVORES TO ECOSYSTEM PROCESSES

Large herbivores influence ecosystem processes beyond reducing the standing crop of vegetation, compacting soil, or removing preferred forage species from plant communities (Crawley 1983, Gessaman and MacMahon 1984). Soil-plant-herbivore systems are highly interactive, with massive feedback between the dynamics of both the vegetation communities and the herbivore populations. Herbivory by large African ungulates strongly influences such ecosystem processes as energy flow, nutrient cycling, and the frequency and extent of wildfires (McNaughton and others 1988). Such soil-plant-animal systems cannot be understood without close consideration of the large mammals (Naiman 1988), and population dynamics of the large mammals cannot be understood without considering them in an ecosystem context (fig. 6).

Interactions between large herbivore populations and their environments are summarized in the concept of carrying capacity. Caughley (1979) defined two types of carrying capacity: economic and ecological. Economic carrying capacity is the density of animals, held constant by harvesting, that provides maximum sustained yield, as measured in weight of animals or net revenue. Ecological carrying capacity is the density of ungulates that could be sustained if they were not harvested. Carrying capacity can also be expressed as a characteristic composition and density of vegetation.

Vegetation production and composition and animal densities fluctuate (Caughley 1977) in the process of interacting with each other and weather. This natural process limits the range of alternative populations that can be maintained via hunting or other harvesting (Caughley 1979). Range managers seek to maximize revenues by maintaining livestock densities at economic carrying capacity. Such management accepts little or no change in vegetation composition, and annual vegetation production fluctuates primarily with precipitation. Range managers typically classify animal densities that are above economic carrying capacity as overpopulations (Caughley 1979).

Populations of wild ungulates that are hunted may be maintained below, equal to, or above economic carrying capacity. Populations that are not hunted, such as wild ungulates living entirely in National Parks are expected to exist at densities near ecological carrying capacity (Houston 1982). As populations increase toward ecological carrying capacity, vegetation production may decline, and composition may be modified (Houston 1982). Composition of plant communities may be affected by low ungulate densities as well, through selective foraging.

Below, we summarize literature on soil-plant-animal relations and develop predictions for the Blue Mountains Ecoregion. We reiterate that these relations are complex because both wild and domestic ungulates are harvested, and fire control and previous logging have modified vegetation communities. Such large-scale disturbances create new dynamic equilibria between herbivores and vegetation.

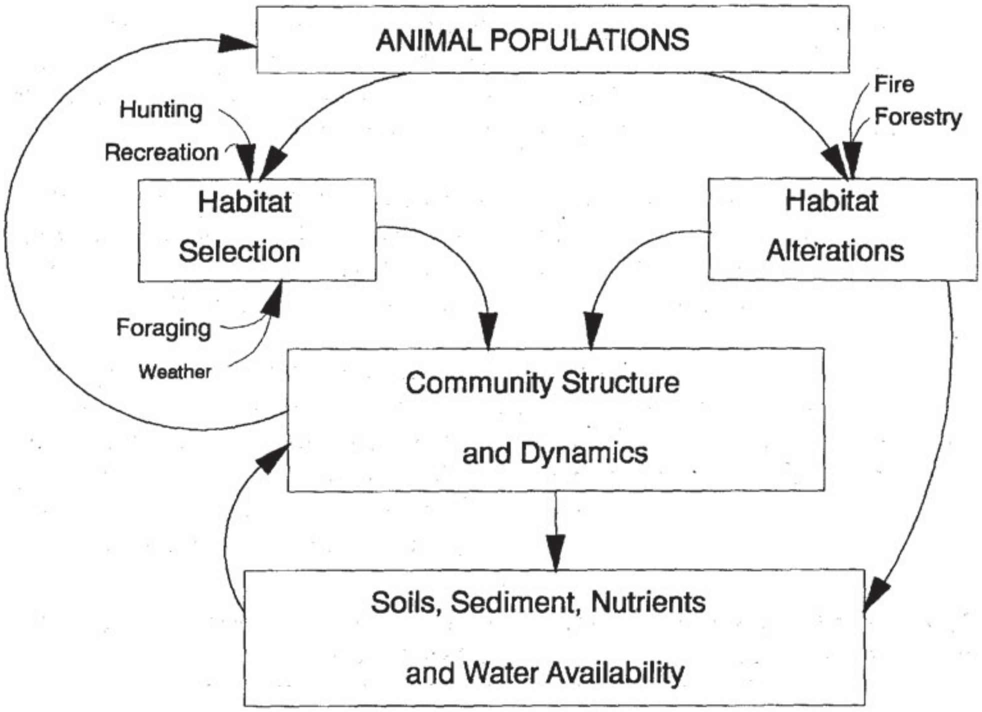

Figure 6. Herbivores influence ecosystem dynamics by their foraging and by physical habitat alterations. These effects are transmitted to the community, resulting in long-term changes to biogeochemical cycles (after Naiman 1988).

Predicted Effects of Large Herbivores on Plants and Soils in Forests

The effects of livestock and big game herbivory on forest stands have received little attention by National Forests, despite graphic examples of substantial effects in some areas (for example, Rasmussen 1941, Pastor and others 1988). Pastor and others (1988) documented significant effects to forest ecosystem processes from browsing by moose on Isle Royale, Michigan. Exclosures, or fenced plots where moose were not allowed to browse, have been maintained on the island for over 40 years. Aspen, paper birch, mountain ash, and mountain maple were significantly taller inside the exclosures than in browsed plots. Exclusion of browsing by moose also resulted in significant increases in litter depth in two of three exclosures, and in significant increases in six of eight soil properties: soil carbon, total nitrogen (N), cation exchange capacity, field nitrogen availability, potentially mineralizable nitrogen, and microbial respiration rates.

The long-term decline in nitrogen availability on Isle Royale may have subsequently shifted ecological carrying capacity for moose. For example, reduced nitrogen availability may delay the rate of recovery of shrubs from browsing, increasing the rate of re-invasion by spruces. Balsam fir is browsed so intensely that the historic fir-dominated forests are unlikely to return (Brandner and others 1990). Decline in soil nitrogen might cause browsed plants to produce greater quantities of secondary compounds (tannins), which may further impede herbivory by depressing digestive functions (Bryant and Chapin 1986). Such changes may also depress soil microbial activity, further reducing nitrogen availability (Pastor and others 1988). The moose population probably would decline in the absence of major disturbances to the conifer overstory, resulting in a new ecological carrying capacity.

Studies show that browsing by white-tailed deer reduces the abundance of certain conifers (Frelich and Lorimer 1985, Marquis 1981), and reduces thickness of the litter layer on the forest floor in eastern deciduous forests and mid-western northern hardwood-hemlock forests. Conversely, Ross and others (1970) found that high densities of white-tailed deer in Minnesota forests promoted dominance by conifers that were not browsed, including red pine and eastern white pine. Allison (1990) found that deer negatively influenced the reproductive biology of plants such as Canada yew.

Herbivory by cattle also alters the frequency and intensity of wildfires (Madany and West 1983, Zimmerman and Neuenschwander 1984) by removing fine fuels. Herbivory by wild ungulates may have similar influences. Also, grazing by large ungulates can cause nutrient losses from ecosystems via ammonia volatilization (Reuss and McNaughton 1988, Schimel and others 1986).

In summary, the ecological literature indicates that large-mammal herbivory can significantly influence forest ecosystem processes through effects on vegetation composition and productivity, successional rates, and soil-nutrient concentrations. If such patterns are common consequences of long-term herbivory by large ungulates, they should be observable in the Blue Mountains, at least in areas where ungulate populations are high relative to the available forage resources. Potential effects of long-term herbivory by elk and cattle populations in the Blue Mountains are predicted from the literature (table 3).

Table 3-Potential influences of long-term grazing by elk and cattle on ecosystem structure and function in eastside forests of Oregon and Washington

Influence	Selected references
Modify understory composition	Gessaman and McMahon 1984, Pastor and others 1988
Modify understory productivity	Gessaman and McMahon 1984
Alter dominance of conifers	Ross and others 1970, Pastor and others 1988
Alter habitat for other wildlife	Naiman 1988
Alter fire ignition potential	Madany and West 1983, Zimmerman and Neuenschwander 1984
Reduce litter depth	Pastor and others 1988
Compact soils	Crawley 1983
Alter nutrient cycling, energy flow	Gessaman and MacMahon 1984, McNaughton and others 1988
Reduce soil N availability	Pastor and others 1988
Alter cation-exchange capacity	Pastor and others 1988
Depress soil microbial activity	Pastor and others 1988
Decrease soil carbon	Pastor and others 1988

Observed Effects of Large Herbivores on Plants and Soils in the Blue Mountains

Studies with herbivore exclosures in and near the Blue Mountains Ecoregion provide insight on the effects of livestock and big game herbivory on understory vegetative composition (Edgerton 1987; Krueger and Winward 1974, 1976; Tiedemann and Berndt 1972; Zimmerman and Neuenschwander 1984), soil fertility (Tiedemann and Berndt 1972), and establishment and growth of tree seedlings (Kingery and Graham 1990; Weigand and others, in press).

Exclosure studies show that excluding large herbivores results in increases in shrubs. Edgerton (1987) found that shrub cover increased 4-fold in an exclosure in a clearcut grand fir community in northeastern Oregon, but shrub cover outside the exclosure remained relatively constant over an 11-year period. At the same time, grasses increased about 4-fold outside and remained constant inside the exclosure. The effects of grazing on forb production were minor, although forb composition differed between treatments.

Tall shrubs, including Scouler's willow, mountain ash, and mountain maple, and shrubs of medium height, including thimbleberry, Utah honeysuckle, and big huckleberry, were common inside the exclosure but were virtually absent outside by the end of the 11-year period. These changes occurred in the absence of livestock grazing.

Tiedemann and Berndt (1972) reported cover of shrubs averaged five times higher inside an exclosure than outside, whereas cover of herbs did not differ significantly. Their observations occurred where an exclosure was maintained for 30 years in a Douglas-fir community that was clearcut near Wenatchee, Washington. Snowbrush ceanothus and chokecherry accounted for most differences in shrub cover. Big game, primarily mule deer, and livestock, primarily sheep, grazed the plant community outside that exclosure. Krueger and Winward (1974, 1976) reported 18 and 1.4 times greater cover of shrubs inside exclosures than outside, 12 to 14 years after excluding herbivores in northeastern Oregon. Exclosures in their studies were located in both a mature Douglas-fir-ponderosa pine community and in a selectively cut grand fir community, both of which were grazed by livestock and big game.

Additional information on the effects of herbivory on forested plant communities was collected in summer 1992 from four exclosures in the Blue Mountains between Elgin and Troy, Oregon (Tiedemann and others 1992). All exclosures were constructed about 25 years ago in climax grand fir communities in the Blue Mountains: two in clearcut stands, one in a partially harvested stand, and one in an old-growth stand dominated by grand fir. Results have not been summarized completely, but trends described above (a substantially reduced shrub component) were evident (fig. 7, A-F). Plot-based estimates during summer 1992 of four other clearcuts and cursory observations in 10 additional clearcuts that were created 10 to 20 years ago (fig. 8), combined with the available empirical evidence, suggest that suppression of shrubs by herbivores is widespread in the Blue Mountains.

Information on the effects of grazing on soil nutrient profiles apparently is limited to a single study by Tiedemann and Berndt (1972) of an exclosure near Wenatchee, Washington. The authors speculated that removal of shrubs, particularly snowbrush ceanothus, abundant only within this exclosure, might alter rates of nutrient accumulation in soils, because *Ceanothus* spp. can fix atmospheric nitrogen (Youngberg and Wollum 1976, Zavitkowski and Newton 1968). Tiedemann and Berndt (1972) found that herbivory reduced litter, which was 1.4 times greater inside than on the outside. Such differences suggest that soil fertility might differ too, but comparisons of soil fertility did not show significant differences. Long-term effects (for example, longer than one rotation) are unknown.

Figure 7A. Vegetation inside the Motett exclosure, about 18 miles north of Elgin, Oregon, July 1992. The exclosure was constructed in a grand fir community that was clearcut about 25 years ago. Nonconiferous vegetation is dominated by a variety of shrubs. Detailed assessment of vegetation characteristics was presented by Edgerton (1987).

Figure 7B. Vegetation outside the motett exclosure, July 1992. Nonoconiferous vegetation is dominated by bracken fern and western coneflower, both relatively unpalatable to tame elk in grazing trails (see text), and a variety of introduced and native grasses. Edgerton (1972) reported that livestock grazing was excluded from this site.

Herbivory can have important direct economic effects by influencing conifer seedling establishment and growth. Kingery and Graham (1990) examined conifer seedling establishment in three 1-acre exclosures in a Douglas-fir/mallow ninebark community west of Riggins, Idaho. They concluded that grazing by big game and cattle reduced seedling mortality from 35 to 15 percent by reducing competition from grasses and shrubs. Such benefits may be limited, however, because 25 percent of the injury and mortality to pine seedlings was attributed to trampling and browsing of seedlings by deer and elk. Rodents also caused injury to the pine seedlings. Rodent damage was greater inside the exclosures, perhaps because of an abundance of nonconiferous vegetation there.

Persistent grazing by herbivores throughout development of forest stands in the Blue Mountains may improve production of wood fiber by reducing competition from understory vegetation (Krueger and Vavra 1984; Weigand and others, in press; Wheeler and others 1980; Zimmerman and Neuenschwander 1984). If long-term herbivory reduces soil fertility (Pastor and others 1988), however, then removal of competing understory vegetation via herbivory may result in a net loss in the rate of wood-fiber production. Weigand and others (in press) present data supporting that hypothesis. They also suggested that herbivore-induced reduction of shrubs and concomitant increases in grasses and forbs may reduce regeneration of additional seedlings in established ponderosa pine stands.

Figure 7C. Vegetation inside the Hoodoo no-cut exclosure about 10 miles southwest of Troy, Oregon, September 1992. The exclosure was constructed in an old-growth grand fir community about 25 years ago. Understory vegetation is primarily dominated by shrubs such as mountain maple, thimbleberry, baldhip rose, and big huckleberry.

Collectively, these studies suggest that herbivory by large ungulates caused moderate to severe reductions of shrubs in a variety of logged and unlogged forest communities, and that elk and deer can have important effects in the absence of livestock. These studies also show that forest communities in the Blue Mountains respond relatively rapidly to reduced grazing pressure, requiring a decade or less for measurable effects to occur after ungulates are excluded. This ability of communities to respond to reduced herbivory might decline in the future, however. If intensive long-term herbivory suppresses shrub reproduction (Allison 1990, then the potential for natural regeneration of preferred shrubs might diminish as seeds in the soil lose viability. Substantial reductions in shrubs represent an important loss of plant biodiversity.

Studies have not clarified the effects of herbivory on soil fertility in the Blue Mountains, although the premise that reduced shrub abundance will eventually result in reduced soil fertility is reasonable. If soil fertility indeed is reduced, numerous ecosystem processes will be affected, with concomitant effects of production of commodities. If so, an appropriate objective in plans for restoring forest health might include regenerating shrubs and other understory vegetation.

Figure 7D. Vegetation outside the Hoodoo no-cut exclosure, September 1992. Understory vegetation is dominated by low-growing forbs and shrubs, grasses, and common snowberry.

Figure 7E. Vegetation inside the Hoodoo clearcut exclosure, 10 miles southwest of Troy, Oregon, September 1992. This exclosure was constructed in a clearcut area in a grand fir forest stand 25 years ago. Nonconiferous vegetation is dominated by Scouler's willow, common snowberry, big huckleberry, and thimbleberry.

Figure 7F. Vegetation outside the Hoodoo no-cut exclosure, September 1992. Understory vegetation is dominated by a varietyof grasses, low forbs, and shrubs.

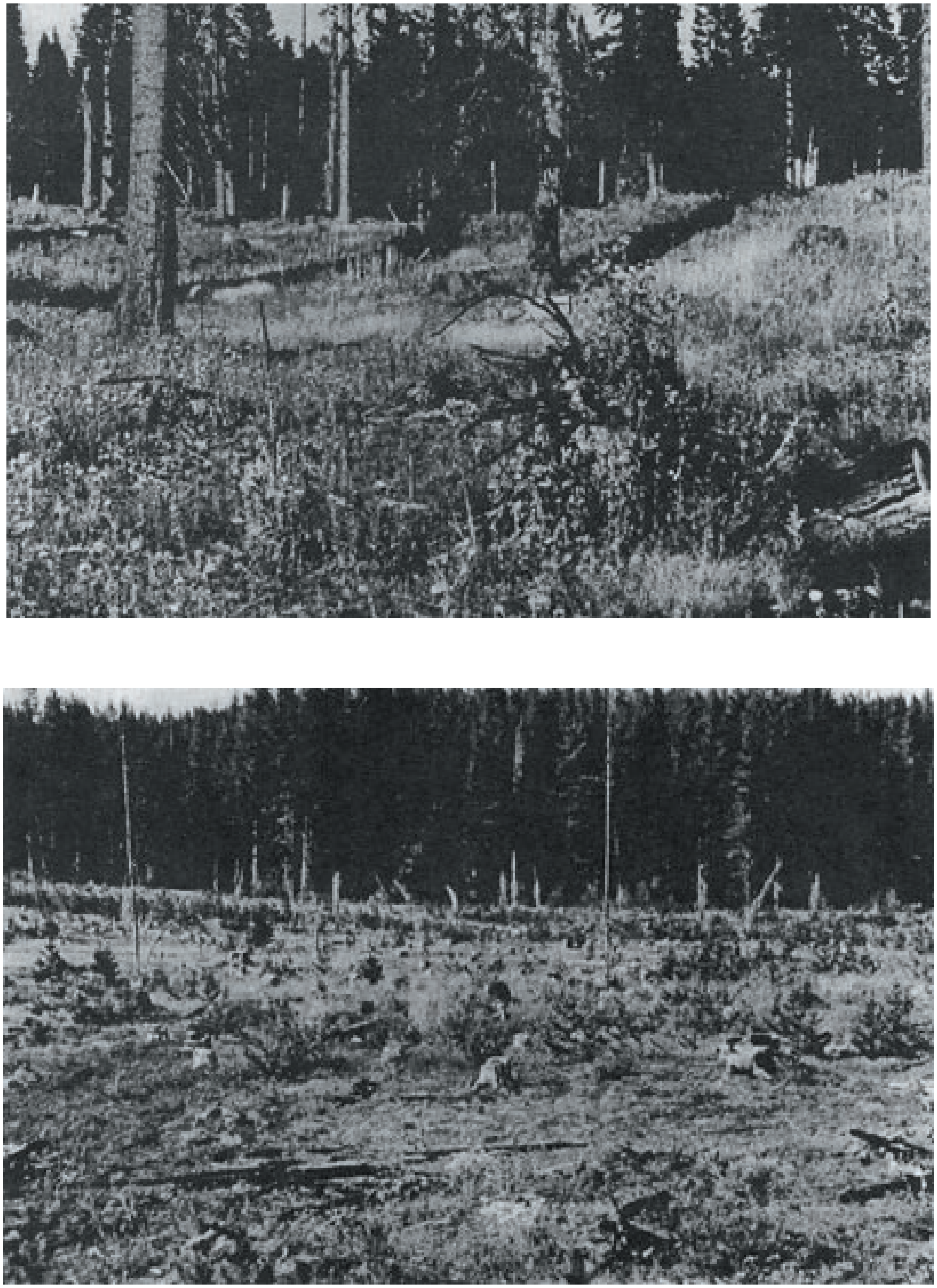

Figure 8. Clearcuts (10-15 years old) 18 miles southwest of Troy, Oregon, September 1992. Note the virtual absence of shrubs, which appears representative of most clearcuts in this area.

Predicted Feedback Effects of Herbivory on Large Ungulate Populations

The prevailing scientific opinion holds that the density of large wild mammals is limited by extrinsic factors, usually the condition of food supplies (Caughley 1987, Sinclair 1977, Sinclair and others 1985), predation (for example, Gasaway and others 1983), or both (Caughley 1976). Sinclair and others (1985) generalized hypotheses that related large-mammal density to forage resources as follows: mortality rate, which increases as population density increases, regulates populations through food shortages. This generalization includes the concept of density-dependence, in which factors that depress population growth act more forcefully as density increases.

In North America, density dependence is believed to occur most frequently in winter, when food is short relative to animal densities. Winter food shortage results in mortality by depressing birth weights and delaying dates of birth (Blaxter and others 1981, Thorne and others 1976, Verme 1969). In fact, CluttonBrock and others (1987, 1988) and Choquenot (1991) concluded that juvenile mortality, through densityinduced food shortage effects on birth weight and date, was the key factor regulating populations of red deer and feral donkeys, respectively. Experimental reduction in density of Rocky Mountain goats led to decreased age at first reproduction and to an increase in the number of young per reproducing female (Houston and Stevens 1988).

Although most work on density dependence has focused on winter food supplies, nutritional status in non-winter seasons is also an important determinant of rates of birth, death, and growth among wild ungulates {Julander and others 1961, Klein 1970, Langvatn and Albon 1985, Reimers 1983). Lactating females require high-energy diets in the growing season to provide adequate milk for their young and to restore their own body weight before the next breeding season (Hudson and White 1985). Summer weight gain is important in reproduction because nutritional status may influence pregnancy rate and because it may influence the age when animals breed. Also, fecundity is related strongly to body weight for females that conceive (Albon and others 1983a, Bartle and others 1984, Glutton-Brock and others 1982, Mitchell and Brown 1974). Further, body reserves built up on summer ranges can determine how long juveniles and adults survive in the subsequent winter (Torbit and others 1985).

The relative influences of summer and winter nutrition on population dynamics of free-ranging large herbivores are unclear. Controlled experiments may be necessary (White 1983) to isolate the effects of numerous interacting factors. Experimental evidence indicates that female red deer on a low plane of nutrition directly after calving experience increased weight loss and produce less milk, which in turn, reduces the growth rates of their calves (Bartle and others 1984, Loudon and others 1984, Sadlier 1980). Mule deer fawns on marginal diets from the time of weaning through December were lighter in weight, deposited less fat, and exhibited reduced skeletal growth compared to fawns maintained on highly nutritional diets (Sadlier 1980). Hobbs (1989) related winter mortality in mule deer to nutritional status in prior seasons.

Fowler (1987) noted that information on density dependence can serve as indices of populations relative to the ability of the environment to support them. Thus, if long-term herbivory has affected plant composition and nutrient cycling in forest vegetation communities, then those changes should cause density-dependent, negative feedback effects to cattle productivity and elk population dynamics. If so, these effects are expected to become more pronounced as animal density increases relative to ecological carrying capacity (Fowler 1987).

Bunnell (1987) reviewed data from 155 populations of the deer family (Cervidae) and expressed the data in terms of simple models relating reproduction and mortality. He noted that elk are less susceptible than other deer species to early predation by virtue of the largest birth weights among the deer family. One consequence of this is that females require relatively high prenatal nutrition (Thorne and others 1976).

Another consequence is alternate-year reproduction among elk on poor ranges (Bunnell 1987). Thus, if density-dependent mortality or fecundity are affecting elk populations in the Blue Mountains, then elk should exhibit many of the characteristics listed in table 4 (adapted from Fowler 1987).

If long-term grazing by livestock and wild ungulates influences summer dietary quality, then several characteristics should be observed among cattle on summer allotments. Such characteristics include reduced growth rates among calves and reduced weight gains among adults compared to past years. Below, we review available evidence and observations from the Blue Mountains Ecoregion that relate to predictions about effects on forage quality, feedback effects on elk population dynamics (table 4), and cattle production.

Table 4-Potential density-dependent feedback effects to large mammal populations that may result from herbivore-induced changes in forage resources in the Blue Mountains

Effect	Selected references
Reduced adult reproduction	Cheatum and Severinghaus 1950, Knight 1970, Carbyn and others 1975, Staines 1978, Kie and others 1980,Clutton-Brock and others 1982, 1985.
Delayed sexual maturity	Buechner and Swanson 1955, Swank 1958, Teer and others 1965, Carbyn 1975, Staines 1978, Kie and others 1980, Houston 1982, Glutton-Brock and others 1985, Skogland 1985.
Reduced juvenile survival	Houston 1982, Sauer and Boyce 1983.
Reduced adult survival	Knight 1970, Carbyn 1975, Fowler and Barmore 1979.
Reduced growth, body size	Klein 1964, Staines 1978, Albon and others 1983a, Cook 1984.
Delayed mating, birthing	McCullough 1969, Kie and others 1980, Hanks 1981, Clutton Brock and others 1982, Teer 1984.
Reduced antler size	Adams 1960, Glutton-Brock and others 1982, 1985.
Reduced length of suckling	Glutton-Brock and others 1985, Skogland 1985.
Changed diet composition	Kie and others 1980, McCullough 1984.
Skewed birth sex-ratio to females	McCullough 1969, Skogland 1986.
Skewed adult sex-ratio to females .	Peek and others 1967, Glutton-Brock and others 1982, 1985.

Evidence of Feedback Effects on Ungulate Productivity in the Blue Mountains

No studies in the Blue Mountains have attempted to demonstrate density-dependent feedback interactions between wild herbivore populations and their food supplies. The first step in any such attempt requires assessing nutrient concentrations in forage and herbivore dietary quality. If nutrient content of large herbivore diets provides for optimal reproduction and growth, then the probability for negative feedback effects on animal productivity is low. If the supply of forage that meets nutritional requirements is not limited relative to herbivore densities, then the probability for negative feedback effects is also low.

When crude protein in forage on summer ranges in teh Blue Mountains is compared to protein requirements of large mammals (fig. 9), forage quality appears adequate during late gestation, marginally adequate during early lactation, and inadequate from peak lactation (mid- to late July) through mid-autumn, although the data vary considerably among studies, forage classes, and vegetation types from which data were collected. The data also suggest that big game may suffer from nutritional deprivation during, late fall and winter; assuming 7 percent protein in forage meets requirements for maintenance (French and others 1955, Mould and Robbins 1981). Protein concentrations in forage in September and October were 7 percent or less, and likely declined further by early winter (assuming little or no fall "green-up" after fall precipitation). If so, big game must compensate in spring and early summer for inadequate protein consumption from late summer through winter. These data also identifythe importance of birthing date: females that give birth in mid-May experience forage conditions superior to those of females giving birth in late June.

These observations on nutritional deficiences in forage ignore the ability of ungulates to acquire high-quality diets by selective feeding. Large herbivores might compensate for such deficiences by selecting plant parts and plant species of high quality. Empirical data from the Blue Mountains (fig. 9) suggest that livestock are unable to compensate, and summer-fall diet. quality is inadequate (Skovlin 1962, Vavra 1983). Cattle weight gains were considered undesirable, and cattle often lost rweight after mid-summer, particularly during years with sub-normal moisture. These studies have not determined that density-dependent feedback effects have reduced productivity of livestock or big game herds in the Blue Mountains; however, they describe a setting in which negative feedback effects might occur.

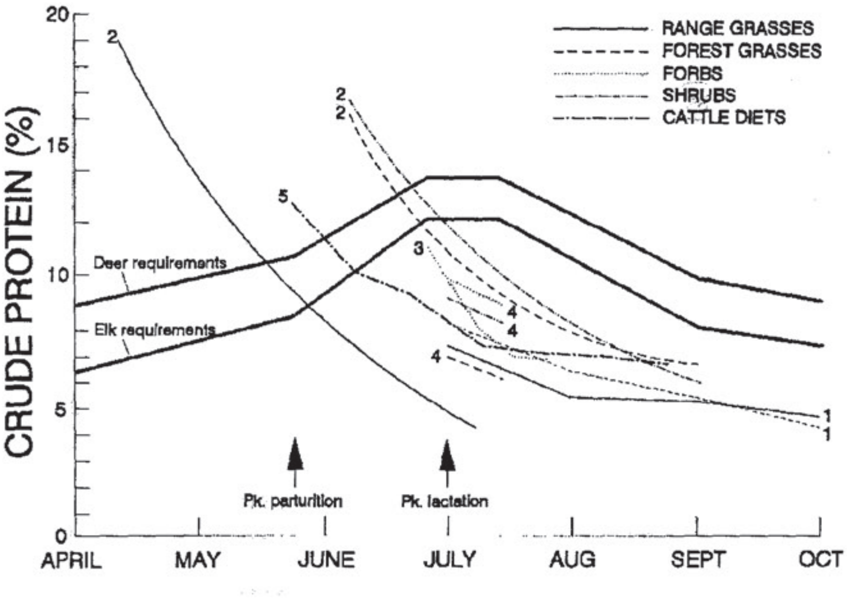

Figure 9. Crude protein of selected forage classes summarized from data sets collected in the Blue Mountains of northeastern Oregon. Numbers along lines identify source of data: 1—Skovlin (1967); 2—Svejcar and Vavra (1985); 3—J. Cook. (unpubl. data collected in 1990 in a ponderosa pine type at the Starkey Experimental Forests near La Grande, Oregon; 4—A. Tiedemann (unpubl. data collected in 1992 at 4 sites in grand fir types between Elgin and Troy, Oregon; 5—Cattle diets reported by Vavra (1983). Deer requirements were based on data for domestic sheep (a 60 kg ewe nursing a single lamb (NRC 1985), and elk requirements were extrapolated, using metabolic weights, from cattle requirements (NRC 1984) to a 250-kg cow elk with a calf. Both sets of requirements were modified to follow the late-gestation lactation curve for elk, described by Robbins and others (1981). Peak parturition (June 8) was based on birth dates of 64 elk calves born at the Starkey Experimental Forest (Irwin and others 1992), and peak lactation is assumed to occur 4 to 6 weeks port-partum (Robbins and others 1981).

Experimental studies were initiated in 1992 to assess summer foraging dynamics of elk, using two tame elk at four exclosures on elk summer range (Tiedemann and others 1992). Data were collected on dietary composition, foraging efficiency, and dietary quality using bite-count methods (Canon and others 1987, Wickstrom and others 1984).

Tall shrubs (such as mountain maple, mountain ash, Saskatoon serviceberry, Scouler's willow) and shrubs of medium height (such as thimbleberry, Utah honeysuckle, rose, and big huckleberry) comprised 80 percent of tame elk diets inside the exclosures, but comprised about 35 percent of the diets outside the exclosures (fig. 10). Elk concentrated their browsing on shrubs in May, where shrubs were available, even when grasses and forbs were abundant and likely of relatively high quality. Forage consumption rates tended to be higher inside the exclosures (fig. 11), although differences were not statistically significant. Elk foraging outside the exclosures consumed significantly less forage per meter traveled, particularly in September, and traveled at significantly faster rates than inside the exclosures. Thus, elk traveled greater distances to compensate for lower shrub availability outside the exclosures. This suggests that ecological carrying capacity is lower outside the exclosures where shrubs had been reduced by selective herbivory.

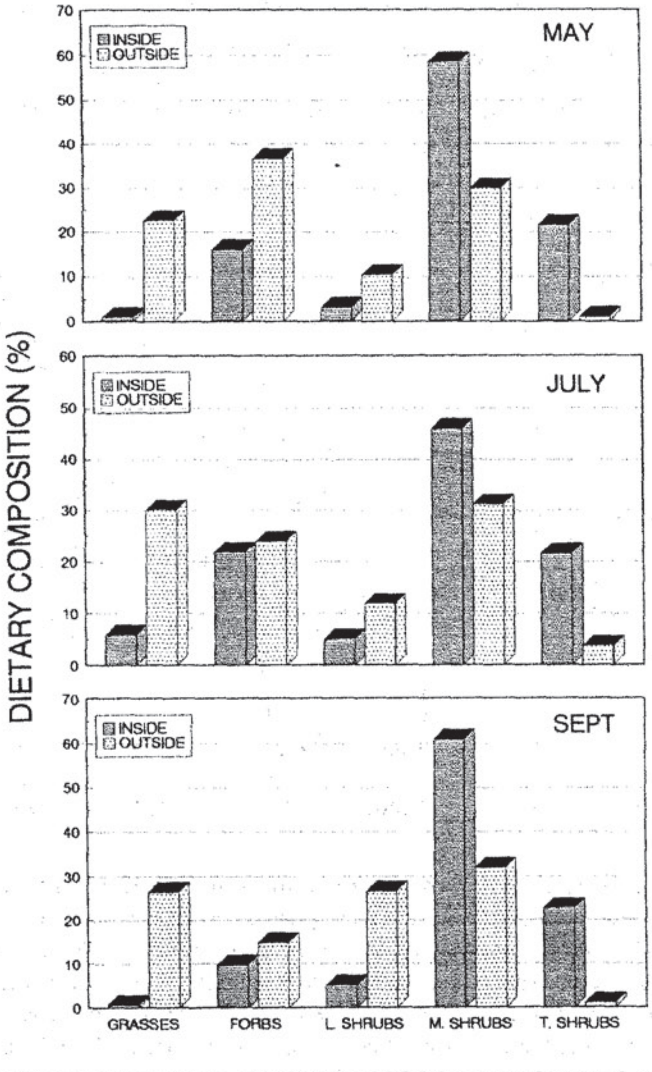

Figure 10. Dietary composition of two tame elk during 1992 in experimental grazing trials inside and outside four exclosures on elk summer range in the Blue Mountains between Elgin and Troy, Oregon. Differences between treatments (grazed vs. ungrazed), time sampling (May, July, and September), and treatment x time interactions were tested using multivariate, repeated measures ANOVA. The cattle- and big game-proof exclosures were constructed about 25 years ago in grand fir communities, two in clearcuts that now support sapling and pole-sized trees, one in a partial cut dominated by mature grand fir, and one in an old-growth stand of grand fir.

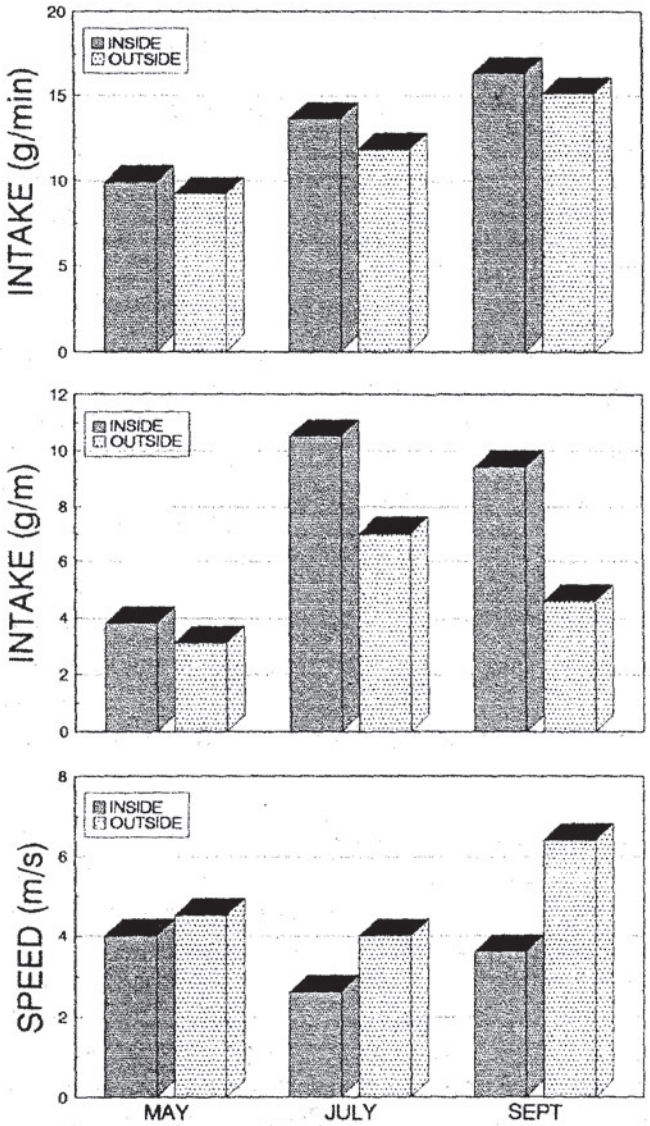

Figure 11. Foraging efficiency of two tame elk during summer 1992 in controlled grazing trials at four exclosures on elk summer range between Elgin and Troy, Oregon. Differences in forage intake per minute, forage intake per meter of travel, and rate of travel between treatments and among sampling dates are tested with multivariate repeated measures ANOVA.

Empirical data on forage quality and livestock nutritional status support a view that large herbivores subsist on suboptimal forage conditions most of the year in the Blue Mountains. Data from exclosures show that plant composition has changed substantially, particularly because of reduction in shrubs. Food habitats studies (Korfhage and others 1980) and tame-animal grazing experiments show elk prefer palatable shrubs. These studies support the premise that large herbivores are responsible for changes in plant species composition. Therefore, density-dependent negative feedback effects on productivity of large herbivores are highly probable in the Blue Mountains.

We have presented evidence of substantial growth of elk populations in the Blue Mountains over the last several decades. We also presented evidence that ungulates have altered the structure and composition of plant communities. These results predict that productivity of elk populations also has been altered, if ecological carrying capacity has been reduced and if ungulate densities remain high relative to carrying capacity. With this prediction in mind, we review evidence of density-dependent feedback mechanisms that may depress reproduction and recruitment of elk populations in the Blue Mountains Ecoregion.

Inverse relations between density and reproduction may be manifested in the reproductive rates for adults or yearling female elk (table 4). Little information has been published on the rate at which yearling elk breed successfully in teh Blue Mountains. Beuchner and Swanson (1955) noted, however, that the proportion of 2 1/2-year-old females that were lactating increased from 21 percent in 1952 to 58 percent in 1954. Those data suggested that an increasing proportion of yearling females was becoming pregnant because lactation in 2-year-old females indicates conception as 16-month yearlings.

Buechner and Swanson (1955) hypothesized that the increase in yearling breeding had resulted from a dramatic increase in the number of elk that were harvested in 1949 and 1950. They concluded that the increased harvest had reduced the density of elk, therby increasing the amount of food available to the remaining animals, enhancing their nutritional status and increasing the incidence of yearling reproduction in subsequent years. Their results were the first test density-depenclent effects on reproduction in a Blue Mountains elk herd, almost 40 years ago. Although their results are cited as a classic example of a density-dependent response (Fowles 1987), their conclusion was derived from post-hoc observations and was thus highly inferential. Experimental manipulation of selected elk populations would test the veracity of Buechner and Swanson's (1955) results.

Juvenile survival should be reduced if density-dependent mechanisms have influenced productivity of elk (table 4). Juvenile survival has not been monitored, but recruitment of calves into the yearling age-class has been monitored. Calf recruitment is a product of the birth rate and the juvenile survival rate. Thus, examining trends in calf recruitment could help clarify the potential for density depenent effects on juvenile survival.

Long-term data on calf recruitment have been recorded by ODFW since 1953 (fig. 12). Calf recruitment clearly declined over a widespread area as density increased (see fig. 5). Rates of decline between population units associated with extensive wilderness areas (for example, Minam) are interesting when compared to those of units in which the forest as been intensively managed for commercial timber production (for example, Sled Springs). Lack of substantial differences does not demonstrate density-dependence, but it does suggest a common underlying mechanism that may supersede the effects of local recruitment management practices. An ongoing analysis of unit-specific relations between density (fig. 5) and calf recruitment (fig. 12) suggests that calf recruitment declines are inversely correlated with elk densityin a large subset of Blue Mountains elk population units (Riggs, unpublished).

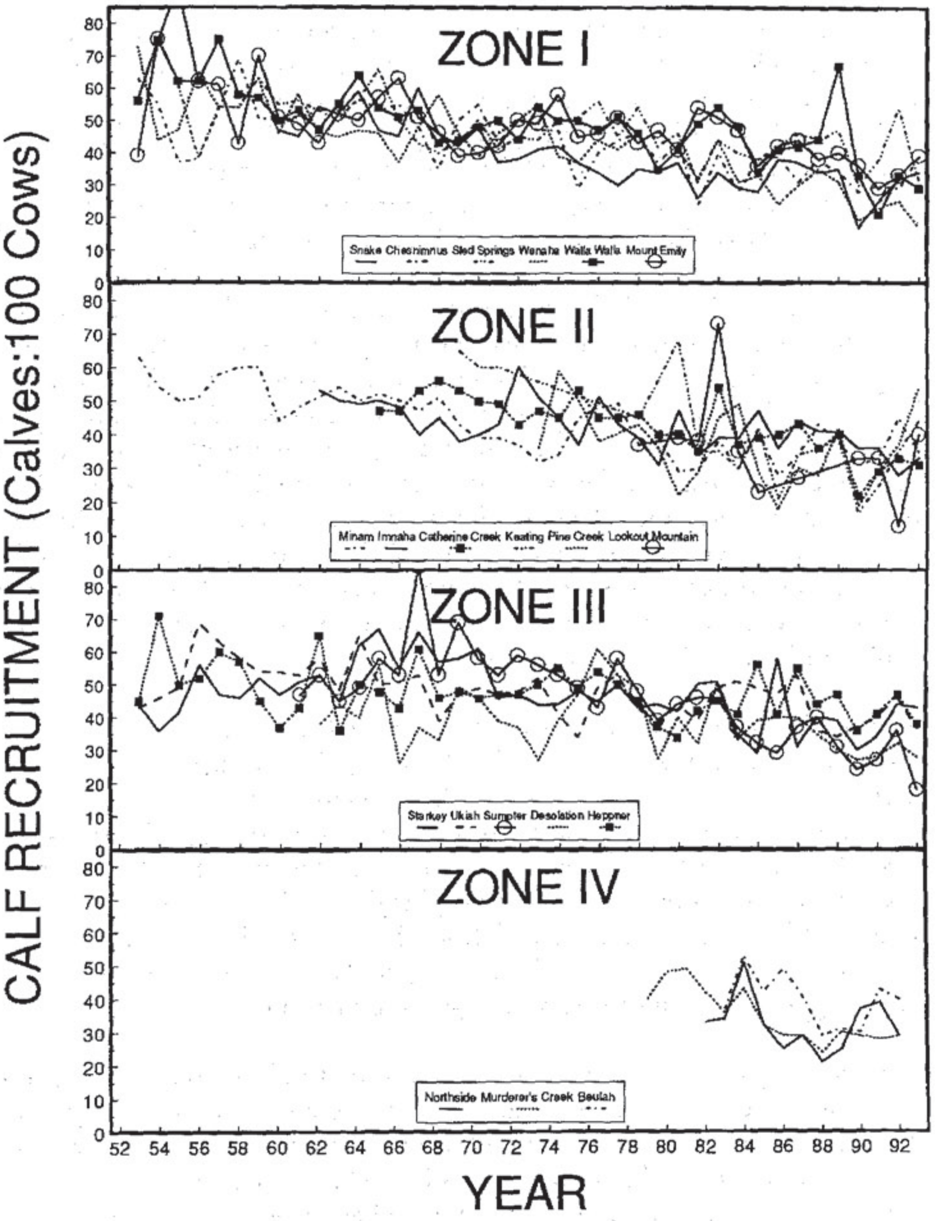

Figure 12. Annual elk calf recruitment estimates, by zone and unit, for the northeastern Oregon management area, 1953-92. Pre-1960 data points were derived by summing annual data for herd range samples that were nested within the boundaries of the current Game Management Units. Reprinted from Riggs (in prep.). Original data from Oregon Department of Fish and Wildlife annual reports, 1953-92.

DISCUSSION

Ungulate-vegetation interactions in the Blue Mountains are both complex and different from pre-settlement conditions. Vegetation composition, production, and diversity have been influenced by ungulates, fire control, insects and diseases, and historic logging regimes. Despite such complexity, evidence is clear that long-term herbivory by both wild and domestic ungulates has changed vegetation productivity in foothill winter ranges, montane grasslands, and understory vegetation in forest communities. Also, ungulates have facilitated dominance of annuals on some winter ranges (Vavra 1980). Forage quality in montane rangelands is below what is necessary for optimum growth of young deer, elk, and cattle. Tall shrubs have been reduced in clearcuts, selectively harvested stands, and unlogged timber stands.

Additional influences of herbivory on ecosystem processes are subtle. Ungulate grazing probably has altered nutrient cycling rates by transferring nutrients among forest and range communities, by volatilizing ammonia, and by reducing nitrogen-fixing shrubs. Herbivore-induced reductions in soil microbial populations and nutrient availability may have reduced growth rates of coniferous trees (Tiedemann and Berndt 1972). Also, ungulate grazing probably influenced the frequency of wildfire by removing fine fuels and shrubs, which affected the density of conifer regeneration, at least in the ponderosa pine and Douglas-fir zones. This reduced fire frequency could have acted to increase nutrient pools that might otherwise have been lower through heat-volatization or leaching.

Evidence also suggests that herbivore-induced vegetation changes have interacted with other factors to produce negative feedback effects on productivity of elk populations and cattle. Cattle do not achieve desirable weight gains in summer allotments. Data on elk populations provide evidence of long-term declines in calf survival, which may be a manifestation of density-dependent juvenile mortality related to summer dietary quality and winter forage availability (Riggs, unpublished).. Influences of poor summer dietary quality on elk calf survival may be exacerbated by low adult bull:cow ratios, which also cause delayed and lengthy birthing periods. The low bull:cow ratios resulted from high densities of elk hunters (Vales and others 1991) and increased vulnerability of bull elk to hunters after road building and alteration or reduction of cover from timber harvesting (Leckenby and others 1991). Quality of hiding cover for big game probably also has been reduced over time as shrubs were removed by ungulates browsing in timber stands (for example, see fig. 7, A-F).

Mule deer populations in the Blue Mountains Ecoregion were high in the 1960s (Schommer 1991b), similar to observations in other western States. The large populations may have been due to the increase in shrubs that resulted from cattle grazing in the 1930s and 1940s (Urness 1976). Mule deer populations currently are much lower than in the 1960s, and suffer from low fawn crops (Schommer 1991b). Those declines might have been associated with successional trends in forage, some of which may have been caused by the deer themselves, as reported elsewhere (Caughley 1970, Rasmussen 1941). Low fawn crops might also by caused by increased predator populations (Schommer 1991b), although density-dependent factors could predispose fawns to predation. Dense elk populations could preclude increases in mule deer herds, too, by reducing shrubs on mule deer winter and summer ranges.

Reduced productivity of big game populations has led to restrictions on hunting (Leckenby and others 1991). The number of days that hunters spent hunting for deer and elk decreased by 350 percent and 210 percent, respectively, since 1973 on the Wallowa-Whitman National Forest (Schommer 1991a, 1991b). The opportunity costs of the reduced hunting were estimated at more than $10 million in lost revenues to the local economy in 1990 (Schommer 1991b), based on dollar values for a day of deer or elk hunting.

Elk use has increased on private lands along with increased elk densities and increased roading and recreational use of the National Forests (Gowan and others 1989, Vavra 1980). Such use has resulted in damage on private lands, particularly in spring. Livestock producers have complained that, although cattle were reduced when drought reduced forage production, the big game hunting permits were not increased (Vavra 1980). On the other hand, cattle use elk winter ranges in summer and fall. Forage allocation among livestock and big game is therefore an important topic, particularly from the perspective of an altered vegetation-herbivore system. Thus, researchers are examining forage resource partitioning among cattle and elk (Johnson and others 1991).

Is the current herbivore-vegetation interaction sustainable? Answering that question requires that we address two concepts: grazing systems and economic carrying capacity.

Elk and livestock grazing systems on National Forests differ in important ways. Cattle are fed hay or other rations in winter at lower elevations, and their calves generally are born in March. Elk migrate to lower elevations after snow buries forage; their forage supplies are low on many winter ranges. Elk benefit from early green growth in spring, and their calves are born on transition ranges. Livestock may remain for lengthy periods on some summer ranges, particularly riparian zones. Elk may move to new foraging sites when forage supplies are reduced, because forage intake rate declines with declining forage biomass (Wickstrom and others 1984). Elk use a broader variety of slopes and vegetation communities than do cattle (hackie 1970). Cattle numbers and distributions are controlled, but elk distributions vary with forage conditions, recreational use along roads, and perhaps social interactions with cattle.

The second concept requires that we determine whether long-term herbivory in the Blue Mountains Ecoregion has reduced economic carrying capacities. Big game and livestock populations might be sustainable at current densities, although productivity will continue to be low. Long-term trends in productivity might be masked by short-term fluctuations associated with variation in summer and winter precipitation. Also, the high mule deer populations of the 1960s are unlikely to return. Thus, the current plant-herbivore subsystem probably is not stable, and objectives should be evaluated carefully for densities of both domestic and wild herbivores.

We believe that the appropriate density of either elk or cattle is neither what is commensurate with wise land use, nor what is consistent with the continuing health of the forest. We believe so, because multiple solution-sets are possible for sustaining livestock and big game at differing rates of productivity. The appropriate densities should be specifiable-either indexed or measured-and vary with quality of diets (Hobbs and Swift 1985) that meet the long-term goals for the ecosystem (Caughley 1989). Informed choices can only be made by identifying options and assessing the social, economic, aesthetic, and environmental effects of each alternative.

Management programs will soon be developed to begin overcoming current forest-health problems. Prescribed burning, salvage timber harvests, insect control, adjustment of ungulate densities, and control of timber-stand densities and composition will probably be emphasized in the short term. The process of identifying optimal approaches for the long term will proceed faster by implementing more than one option and monitoring ecosystem responses (that is, ungulate and vegetation responses) in manipulative experiments (Irwin and Wigley 1993).

The recent practice of dispersing timber-harvest units and limiting their size was intended to optimize the arrangement of cover and open areas (Thomas and others 1979). Although such practices stem largely from social concerns for aesthetics, they also accord with elk/habitat models (for example, Thomas and others 1988b). The habitat recommendations maximize distributions of elk, which often feed in openings and rest in adjacent stands of timber (Irwin and Peek 1983, Skovlin and others 1989). This strategy probably maximized herbivory by both cattle and elk in harvested units and adjacent forest stands, thereby facilitating suppression of floral diversity and productivity in subsequent successional stages.

If timber harvest units were larger, their centers would be less used by elk (Thomas and others 1979), increasing the probability that seral shrubs in treated areas would escape intense browsing. Treating large blocks of damaged forests to allow for greater expression of understory vegetation might improve the quality of hiding cover in future stands, if such treatment blocks are at least the size recommended by Lyon and Canfield (1991). The harvested units could be managed for a few years by light or moderate grazing by livestock to reduce the effects of herbaceous vegetation on regenerating conifers (Krueger and Winward 1976, Zimmerman and Neuenschwander 1984).

Both prescribed burning and timber harvesting can stimulate soil-nitrogen mineralization (for example, Hobbs and Spowart 1984), which likely would improve the nutritional status of ungulates over the short term. Expression of potential benefits, however, depends on the scale of treatment relative to the ungulate densities. Further, intense and recurrent burning could result in increased loss of nutrient capital over time (Boyer 1987), resulting in a reduction in ecological carrying capacity. Large timber-salvage operations might help maintain current forage production, or even increase it, but bull elk escapement will continue to be a concern (Leckenby and others 1991). Closing roads in areas larger than 20 to 30 square miles (Irwin and Peek 1979) might increase escapement of bull elk during hunting seasons.

Our review has implications for the use of elk/habitat models in land-use planning. Habitat-effectiveness models (for example, Thomas and others 1988a, 1988b) probably should be modified to account for density-dependent effects on elk productivity. Such models should probably also consider long-term ecosystem changes caused by high densities of ungulates. Such models might also be modified to include vulnerability to mortality from hunting, as indicated by Christensen and others (1991) and Vales and others (1991).

High ungulate densities may prevent reaching objectives for elk calf recruitment, mule deer populations, and may conflict with goals for vegetation management on the Forests. We suggest a careful evaluation of the relative potentials for improving calf recruitment by enhancing winter ranges and reducing densities of cattle or female elk, or both. Although predators and low buii:cow elk ratios may play a role, altering the ungulate density-vegetation relation might facilitate achieving long-term goals for the Blue Mountains Ecoregion.

We have provided vignettes of the interactions between long-term grazing by large herbivores and forest ecosystem dynamics, but we cannot specify the magnitude of the potential effects on biodiversity, nutrient cycling, and other ecosystem processes. Although we have identified reasonable relationships that are supported by ecological literature and data, our emphasis on elk and cattle may oversimplify an exceedingly complex herbivore-vegetation-management system that includes multiple interacting factors. Examples include the extent that fire suppression and long-term grazing by domestic sheep have modified plant-herbivore relationships and the degree to which hunting has influenced elk-calf recruitment through reducing adult bull:cow ratios. Moreover, the compensatory influences of other forms of mortality, including predation and diseases are largely unexplored. Ultimately, linkages between scientists and those that monitor the effects of management should clarify these relationships. We provide the following philosophical overview that may lead toward an appropriate path for managers and researchers to follow.

Cattle could be used as a tool to modify condition of elk winter ranges (Anderson and Scherzinger 1975, Pitt 1986). For example, elk move to areas that are rested or deferred from livestock grazing (Skovlin and others 1976). Most elk winter ranges lie on private lands (Vavra 1980), so using cattle to improve them might require innovative economic incentives for private landowners. Public managers might consider improving transition ranges that lie on the Forest. Using well-executed cattle grazing to do so may help mule deer because of the evidence that periodic cattle grazing can improve quality and availability of forage for mule deer (Urness 1976).

Below, we list several topics that may identify potential options and provide for assessments by linking monitoring programs with research. In so doing, we advocate use of adaptive management experiments (Waiters 1986), which imply simultaneously implementing several management options under rigorous experimental design (Irwin and Wigley 1993). We suggest that the Forest Service solicit proposals from qualified scientists to address the following questions:

- To what extent have plant composition and productivity of eastside forests been changed by persistent grazing by large ungulates?

- What are the relative contributions by domestic and wild herbivores to these changes?

- To what extent have ungulate-induced changes in plant communities altered the seasonal nutritional status and productivity of ungulate populations?

- To what extent do various management strategies for large herbivores affect long-term productivity of forest sites?

- How do frequency and intensity of prescribed fire and silviculture interact with ungulate grazing to influence soil-nutrient capital, plant community composition, site productivity, and associated productivity of large-mammal populations over time?

- What are the relative effects of density-dependent mortality and density-independent factors in regulating production and yield of big game populations in managed ecosystems?

- Can reduction in herbivore density reverse apparent declines in shrub production and juvenile recruitment to big game herds?

- What are the relevant scales and units of evaluation for integrating livestock and big game in ecosystem planning?

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APPENDIX A

List of Common and Scientific Names for Plants and Animals

Common Name	**Scientific Name**
Aspen	*Populus tremuloides* Michx.
Baldhip rose	*Rosa gymnocarpa* Nutt.
Balsam fir	*Abies balsamea* (L.) Mill.
Big huckleberry	*Vaccinium membranaceum* Dougl.
Bracken fern	*Pteridium aquilinum* (L.) Kuhn.
Canada yew	*Taxus canadensis* Marsh.
Cheatgrass	*Bromus tectorum* L.
Chokecherry	*Prunus virginianus* L.
Common snowberry	*Symphoricarpos albus* (L.) Blake
Elk	*Cervus elaphus* Linn.
Douglas-fir	*Pseudotsuga menziesii* (Mirb) Franco
Feral donkey	*Equus asinus*
Grand fir	*Abies grandis* (Dougl. ex D. Don) Lindl.
Mallow ninebark	*Physocarpus malvaceus* (Greene) Kuntze
Moose	*Alces alces* Gray
Mountain ash	*Sorbus americana* Marsh.
Mountain ash (west.)	*Sorbus sitchensis* Roen
Mountain maple	*Acer spicatum* Lam.
Mule deer	*Odocoileus hemionus* Rafinesque
Paper birch	*Betula papyrifera* Marsh.
Ponderosa pine	*Pinus ponderosa* Dougl. ex Laws.
Red pine	*Pinus resinosa* Ait.
Red deer	*Cervus elaphus* Linn.
Rocky Mountain maple	*Acer glabrum* Torr.

APPENDIX A (continued)

List of Common and Scientific Names for Plants and Animals

Common Name	Scientific Name
Rocky Mountain goat	*Oreamnos americanus* Rafinesque
Rose	*Rosa* species
Saskatoon serviceberry	*Amelanchier alnifolia* (Nutt.) Nutt.
Scouler's willow	*Salix scouleriana* Barrett ex Hook.
Snowbrush ceanothus	*Ceanothus velutinus* Dougl.
Spruce, black	*Picea mariana* (Mill.) B.S.P.
Spruce, white	*Picea glauca* (Moench) Voss
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.
Thimbleberry	*Rubus parviflorus* Nutt.
Utah honeysuckle	*Lonicera utahensis* Wats
Western coneflower	*Rudbeckia occidentalis* Nutt.
White pine, eastern	*Pinus strobus* L.
White-tailed deer	*Odocoileus virginianus* Rafinesque
Yellow pine	*Pinus ponderosa* Dougl. ex Laws.

GLOSSARY

Adaptive management-Implementing management decisions as experiments, whose results are used to modify management policy.

Allowable use-The degree of use considered desirable and attainable on various parts of a ranch or allotment, considering the present nature and condition of the resource, management objectives, and level of management.

Ammonia volatilization-During the fermentation process of digestion by hooved mammals, the release of ammonia as a gas.

Animal unit equivalent-An index that refers to the potential for forage removal by various classes of livestock; an animal unit equivalent = 1 horse, a domestic cow with her calf, or 5 domestic sheep.

Animal-unit month (AUM)-The quantity of forage required by an animal-unit or the equivalent for 1 month.

Animal-unit (stock unit)-Considered to be one mature (1000 pound) cow or the equivalent.

Bu11:Cow:Calf Ratio-The ratio used to monitor sex and age composition of a big game population.

Calf recruitment-The number of elk calves that survive their first year to enter the yearling age class, a product of the number of live births and the calf survival rate, and often expressed in terms of calves recruited per 100 cows.

Carrying capacity-A measure of the number of animals that can be maintained over a specified period on a specified amount of land; ecological carrying capacity refers to the number of animals that can be supported irrespective of how productive the animals are, and economic carrying capacity refers to the number of animals that can be supported at maximum rates of productivity.

Commensurability-A term used to describe a private ranching operation that has the capacity to provide for livestock when they are not grazed on public lands.

Deferred rotation grazing-A system of deferring the timing of livestock grazing on growing vegetation from year to year.

Density dependence-A term that suggests that factors that depress the growth rate of populations increase in effect as population density increases.

Density-dependent-The action of repressive environmental factors, on one or more aspects of population performance, which intensify as animal density increases and relax as animal density declines.

Dietary composition-The combination of items (plant species, for herbivores) present in an animal's diet.

Dynamic equilibrium-An interactive process whereby the growth rates of herbivores and vegetation are relatively stable.

Ecosystem-(1) An ecological community considered together with the nonliving factors of its environment taken as a unit; (2) any complex of living organisms taken together with all the other biotic and abiotic factors that affect them; a complete interacting system of organisms (that is, a community) considered together with its environment.

Either-sex hunt-A hunting season in which hunters are allowed to harvest either a male or female animal.

Fecundity-A specific statistic in population dynamics that refers to the average number of female offspring produced per reproducing female in a population.

General hunt-A hunting season in which the total number of hunters is not limited by administrative rules or regulation.

Herb-Nonwoody vegetation that includes both grasses and broad-leafed plants of low profile, known as forbs.

Limited-entry hunting-A system of controlling hunting permits through lottery drawings.

Limited-entry hunt-A hunting season in which the total number of hunters is limited by administrative rules or regulations.

Litter-Fallen leaves, twigs, woody debris, and other dead organic material.

Management objective-An administratively adopted target for size or sex and age composition of a big game population.

Metapopulation-A comprehensive term for a population that consists of several to many subpopulations.

Mineralizable nitrogen-A chemical state from which nitrogen may be released from combination with other elements.

Nutrient cycling-Process whereby elements move among animals, plants, and soils within an ecosystem.

Parturition-Birth.

Population management unit-An administrative area in which big game populations are managed according to administrative rules and regulations, and in which population status and production are monitored.

Proper use-A degree of use of current year’s growth which, if continued, will achieve management objectives and maintain or improve the long-term productivity of the site.

Range carrying capacity (grazing capacity)-The maximum stocking rate possible without inducing damage to vegetation or related resources.

Range condition-A generic term relating to present status of a unit of range in terms of specific values or potentials.

Rest-rotation-A grazing system that involves total removal of livestock grazing from year to year on a range.

Soil nutrient profile-Concentrations of nutrients at various depths in the soil.

Split-season hunt-A hunting season that is partitioned into two or more time segments, and during which hunters are allowed to hunt in only one segment.

Stability (ecological)-An ecological system may be termed stable during periods when no species becomes extinct (thereby creating a vacant niche) and none reaches plague proportions for long enough to destroy the niches of other species and cause them to become extinct; a stable ecosystem is one in which all niches are fully occupied by appropriate species; stability lies in the ability of species to bounce back, not in the ability to hold tenaciously to ground once taken or numbers once achieved.

Succession (ecological succession, ecosystem development)-An orderly process of biotic community development that involves changes in species, structure, and community processes with time; it is reasonably directional and, therefore, predictable.

Trend-The direction of change in ecological status or resource value rating observed over time.

Ungulates-Hooved mammals.

Vegetative composition-The set, or combination, of plant species present in a plant community.

Irwin, Larry L.; Cook John G.; Riggs, Robert A. Skovlin, Jon M. 1994 Effects of long-term grazing by big game and livestock in the blue Mountains forest ecosystems. Gen. Tech. Rep. PNW-GTR-325. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 49 p. (Everett, Richard L., assessment ream leader; Eastside forest ecosystem health assessment; Hessburg, Paul F., science team leader and tech. ed., Volume III: Assessment.)

The effects on eastside forest ecosystems from long-term grazing by large mammals are assessed, because long-term herbivory can reduce or increase ecosystem productivity. The assessment emphasizes elk and cattle in the blue Mountains of northeast Oregon and southeast Washington. Histories of populations of large mammals and their effects in the Blue Mountains are described. Long-term heavy use by domestic livestock, primarily cattle, and elk has changed ecosystem processes, and the changes in plant communities cause by the herbivores may have had negative feedback effects to productivity of both elk and cattle. The paper identifies adaptive management experiments that could identify options for clarifying the complex relationships between herbivores, vegetation, and ecosystem processes and identify management options for restoring forest health.

Keywords: Adaptive management, big game, Blue Mountains, cattle, density-dependence, ecosystem, elk, grazing, herbivory, livestock, nutrient cycling, ungulate

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