John G. Kie, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, Oregon 97850 email: jkie@fs.fed.us

and

John F. Lehmkuhl, Pacific Northwest Research Station, Forestry Sciences Laboratory, 1133 N. Western Avenue, Wenatchee, Washington 98801.

Herbivory by Wild and Domestic Ungulates in the Intermountain West

Abstract

Management of wild ungulates is seldom undertaken with a focus on the effects on forest health and productivity but rather focusing on populations of the ungulates and their habitat needs. Consequently, only limited research has examined grazing and browsing by ungulates in coniferous forests as a chronic disturbance factor affecting nutrient turnovers, competitive interactions among plant species, and rates and trajectories of successional pathways. Local effects are quite variable and depend on ecosystem productivity. Grazing can have mixed effects on species richness and the spread of exotic plants at the landscape scale. Grazing also can affect nitrogen fixation and rate of nitrogen mineralization. Ungulate density relative to carrying capacity of the site largely determines the effects of herbivory. High population densities of ungulates have been shown to change plant species composition, growth of trees, and to damage regeneration. Grazing also reduces accumulation of fine fuels on the forest floor, which formerly carried low-intensity, high-frequency ground fires. Effects of wild ungulates can be controlled by hunting regulations, and in some cases, by artificial contraception. Effects of grazing by livestock can be controlled through management actions such as changes in livestock numbers, changes in timing and duration of grazing, altering livestock distribution with fencing and placement of salt and supplemental feed, and specialized rotational grazing systems such as deferred and rest rotation.

Basic Knowledge

Ungulates are important components of healthy ecosystems and can serve as important ecological indicators (Hanley 1996). The biology of wild ungulates is well known compared to that of other species of wildlife, they have relatively large home ranges, and are often seasonally migratory, requiring resource managers to consider entire landscapes rather than isolated patches of habitat. They require temporally and spatially diverse habitat elements such as food and cover. Finally, ungulates can have significant effects on vegetation composition as well as basic ecosystem function thereby acting as keystone species (Hanley 1984, Hanley et al. 1989, Wallis de Vries 1995, Hanley 1996, Hobbs 1996, Kie et al. *In press*).

This review relies primarily on research conducted throughout the intermountain region of the western United States. The scope of this paper was expanded beyond just eastern Oregon and Washington because of the relative lack of geographic-specific research on ungulates, particularly at the watershed and higher spatial scales (see table on literature richness in this volume, Quigley et al. 2001). Applicable information only available from elsewhere, such as the Olympic Peninsula of western Washington or the deciduous forests of the eastern United States, is also mentioned briefly. Finally, no attempt is made to review the literature on the effects of grazing by domestic ungulates in riparian ecosystems; rather, the reader is referred to other papers in this volume (Wales 2001, Howell 2001).

Grazing and browsing by ungulates act more as chronic disturbance factors rather than as episodic disturbances. Although the presence of a large number of ungulates in a single herd at a specific location for a short period of time can have a profound effect on vegetation, ungulate herbivory more strongly affects ecosystems through modification of basic processes such as nutrient turnovers, competitive interactions among plant species, and rates and trajectories of successional pathways (Hobbs 1996, Rodgers 1996, Augustine and McNaughton 1998). Direct effects of herbivory, however, are often complex and may depend in part on interactions with other disturbance factors such as fire and logging (Hobbs et al. 1991, Bartos et al. 1994, Collins et al. 1998). More research on these interactions is needed.

Effects of Ungulates

Effects on Plant Species Diversity

Ungulate herbivory can enhance species diversity in plant communities by directly reducing the abundance of preferred species and indirectly influencing competitive interactions among plants. High densities of herbivores, however, can result in decreases in diversity of plant species (Olff and Richie 1998). These effects also depend, in part, on ecosystem productivity. A given level of herbivory may result in increases in plant species richness in nutrient-rich ecosystems but a decrease in plant species richness in nutrient-poor ecosystems (Proulx and Mazumder 1998). Bison (*Bos bison*) have been shown to increase plant species diversity in the tallgrass prairies of Kansas (Collins et al. 1998). Whether domestic cattle, however, are the functional equivalent of bison in such ecosystems has been debated and remains unclear (Kaiser 1998).

In a comprehensive study using sites in Colorado, Wyoming, Montana, and South Dakota, Stohlgren et al. (1999:45) concluded that: (1) grazing probably has little effect on native species richness at landscape scales, (2) grazing probably has little effect on the accelerated spread of most exotic plant species at landscape scales, (3) grazing affects local plant species and life-form composition and cover, but spatial variation is considerable, (4) soil characteristics, climate, and disturbances may have a greater effect on plant species diversity than do current levels of grazing, and (5) few plant species show consistent, directional responses to grazing or cessation of grazing. Fleischner (1994), however, concluded that effects of livestock grazing can include loss of biodiversity, decreases in population densities of many plant taxa, and disruption of ecosystem function.

In contrast to these studies that dealt primarily with grassland ecosystems, research conducted in coniferous forests in Olympic National Park in western Washington suggested that herbivory primarily by elk (*Cervus elaphus*) reduced plant standing crop, increased species richness of forbs, and helped determine the distribution of several shrub species (Woodward et al. 1994, Schreiner et al. 1996). McShea and Rappole (2000) also found that herbivory by white-tailed deer (*Odocoileus virginianus*) decreased the density and diversity of understory vegetation in the eastern deciduous forests of Virginia.

Effects on Rates of Nutrient Cycling

Disturbances such as grazing can affect the ground-level microbial crust in arid ecosystems, and thereby decrease the rate at which nitrogen is fixed (Evans and Belnap 1999). In more mesic forest soils, rates of nitrogen mineralization are highly dependent on the amount and nitrogen content of plant litter deposited on the ground each year (Fan et al. 1998). Large herbivores can have short-term positive effects on rates of nitrogen mineralization through their consumption of palatable plant species and the subsequent fertilization effects of urine and feces deposition (McNaughton 1992, Seagle et al. 1992, Pastor and Cohen 1997). For example, moose (*Alces alces*) browsing on diamondleaf willow (*Salix planifolia pulchra*) in Alaska not only caused significant increases in the growth of willow stems and leaves, but also increased the rate of nitrogen turnover (Molvar et al. 1993). Grazing by large herds of migratory ungulates also increased the rates of nitrogen mineralization in soils in Yellowstone National Park (Frank et al. 1994, Frank and Evans 1997, Frank 1998, Frank and Groffman 1998, Singer et al. 1998a).

Long-term effects of ungulate herbivory may be different, however, when changes in plant species composition occur as a result of herbivory. In Michigan, where high population densities of moose have existed for long periods, forest composition has changed from deciduous woody species palatable to moose to stands dominated by conifer species that are less palatable. Conifer species produce less litter each year than do deciduous species, and that litter contains greater concentrations of compounds used by plants as defense mechanisms against herbivory, which is why conifers are less palatable in general than are deciduous species. Those same compounds, which act to inhibit microbial action in the ruminant digestive system, are also resistant to bacterial decomposition in forest soils. The results are decreases in rates of nitrogen mineralization (Pastor et al. 1988, Pastor and Naiman 1992, Pastor et al.1993, Pastor and Cohen 1997, Pastor et al. 1997, Pastor et al. 1998).

Effects on Plant Productivity

Where grazing and browsing by ungulates act to increase the cycling of a nutrient in limited supply, the result may be an overall increase in net primary productivity (Frank and Evans 1997, de Mazancourt et al. 1998). This most likely occurs in systems with large losses of the limiting nutrient during recycling of plant detritus (de Mazancourt et al. 1998). Increases in primary productivity resulting from herbivory have been well documented in the Serengeti grasslands of eastern Africa (McNaughton 1992, Seagle et al. 1992, Singer et al. 1998a).

Whether such herbivore optimization occurs in the forests of the western United States has been questioned in the past (Frank 1998), although much remains to be tested. In addition, predicting the effect of specific levels of grazing on plant productivity, however, may be difficult. There is evidence that two alternate stable states exist between population densities of white-tailed deer and the forb *Laportea canadensis* in deciduous forests in Minnesota, depending on initial forb abundance (Augustine et al. 1998).

Risk, Susceptibility, and Hazard

Kienast et al. (1999) conducted an ecological risk assessment of the effects of red deer (*Cervus elaphus*, called elk in North America), roe deer (*Capreolus capreolus*), and chamois (*Rupicapra rupicapra*) on stand dynamics in xeric forests of central Europe. The analysis was based on a forest-succession model supplemented by an empirically based browsing subroutine for both coniferous and deciduous plant species. The model indicated that browsing below critical mean intensities had limited effects on long-term total woody biomass and successional pathways (Kienast et al. 1999). Critical levels of mean browsing intensity ranged from 30% to 50% depending on tree species. Forest structure was affected, however, with heavily browsed forests tending to be more open with trees reaching intermediate and adult sizes more quickly (Kienast et al. 1999).

In another study conducted in central Europe, Reimoser and Gossow (1996) concluded that damage to regenerating forests depends in part on the silvicultural system. They concluded that open clear-cuts tend to attract red deer, roe deer, and chamois, exacerbating damage problems. Natural regeneration in a shelterwood silvicultural system, however, usually results in less damage to developing stands (Reimoser and Gossow 1996).

In the western Untied States, the effects of herbivory on willows (*Salix* spp.) by elk was found to differ between two locations. Willows in Rocky Mountain National Park produced up to 2.5 times the amount of annual growth of those in Yellowstone National Park (Singer et al. 1998b). Growth conditions for willows were better in Rocky Mountain National Park; annual precipitation was higher and there were more beaver (*Castor canadensis*) ponds. Use by elk was similar in both locations, however, with elk removing about 26-28% of the annual growth of willow. As a result, elk had greater negative effects on willows in Yellowstone National Park (Singer et al. 1998b).

Effects of Management

Efforts at managing populations of wild ungulates are often directed at providing recreational hunting opportunities or controlling nuisance animals. Immunocontraception in wild ungulates has also been suggested as a method to control population densities (DeNicola et al. 1997, Muller et al. 1997). Management options for domestic ungulates include: changes in livestock numbers, changes in timing and duration of grazing, altering livestock distribution with fencing and placement of salt and supplemental feed, and specialized rotational grazing systems such as deferred and rest rotation (Kie et al. 1994).

The effects on vegetation of long-term grazing and browsing pressure by wild and domestic ungulates, however, is often dramatic. The exclusion of elk, mule deer (*Odocoileus hemionus*), and cattle from exclosures in the northern Blue Mountains of Oregon for 30 years following tree harvest has resulted in striking results (Weigand et al. 1993, Riggs et al. 2000). Forests stands subjected to grazing are more open and lack a diverse mid-story component (Figure 1). Where wild and domestic ungulates have been excluded, there is a denser mid-story consisting of woody plant species that are palatable to ungulates and which are not otherwise abundant (Figure 2).

During the 18th century, red deer were reported as scarce near Braemar in Scotland (Watson 1983). The Earl of Fife, subsequently took actions to reduce poaching of red deer, and populations

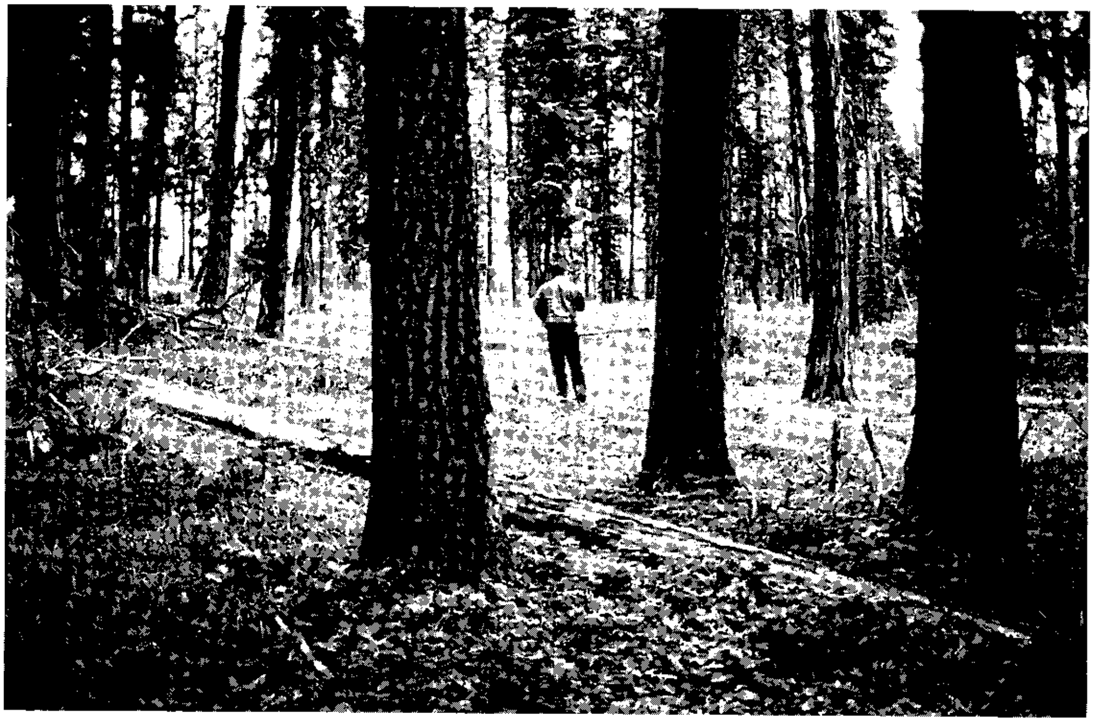

Figure 1. Example of a forest stand at Hoodoo in the Blue Mountains of northeastern Oregon that has been available to both wild and domestic ungulates, including elk, mule deer, and cattle (Riggs et al. 2000).

Figure 2. Example of a forest stand at Hodoo in the Blue Mountains of northeastern Oregon that has been fenced to exclude ungulates since 1965 (Riggs et al. 2000).

increased accordingly. Many of the trees currently alive regenerated prior to that time when deer densities were low, with deer preventing regeneration since (Watson 1983). Other ecosystems in Europe have also responded similarly to reductions in deer numbers (Rose and Platt 1987).

Tilghman (1989) reported that population densities of white-tailed deer above about 7 deer per 100 hectares adversely affected tree regeneration and species composition in northeastern Pennsylvania. Tree growth was reduced, species diversity of tree seedlings, and fern cover increased at higher densities of deer. Similar effects have been found elsewhere (Anderson and Katz 1993). High population densities of white-tailed deer have also been shown to have cascading effects throughout ecosystems in the northeastern United States, adversely affecting other species groups such as songbirds (deCalesta 1994).

Belsky and Blumenthal (1997:315) have hypothesized that long-term grazing by domestic ungulates in western forests has resulted in: (1) reduced biomass and density of understory grasses and sedges that otherwise compete with conifer seedlings and prevent dense recruitment of trees, and (2) reduced abundance of fine fuels, which formerly carried low-intensity, high-frequency ground fires. Similar interactions were discussed by Hobbs (1996).

In forests throughout the western United States, herbivory by domestic ungulates is a function of timing, duration, and intensity of grazing, all of which are factors under direct control of resource managers and grazing permittees. Similarly, population densities of wild ungulates, and hence their impact on forested landscapes, can be influenced by the numbers that hunters are allowed to remove each year. Although these concepts are relatively easily to apply from a technical concept, decisions regarding them are often very sensitive from a political standpoint, and require that managers consider not only the biological aspects of such actions, but the economic and social ramifications surrounding them.

Decision-Support Tools and Thresholds

DeCalesta and Stout (1997) have proposed a framework for using relative deer density, defined as the absolute population density relative to their ecological carrying capacity for managing white-tailed deer as one of multiple components of forested ecosystems. Population densities of ungulates *per se* are not the critical factor determining their effects on other ecosystem values, but rather population densities with respect to the carrying capacity of the landscape. McShea and Rappole (2000) also suggested that manipulating population densities of ungulates such as white-tailed deer may be a valuable tool in influencing the abundance and diversity of breeding birds.

Conclusions

Wild and domestic ungulates play important roles in coniferous forests throughout the Intermountain West. Wild ungulates require temporally and spatially diverse habitat elements such as food and cover, and these life-history characteristics require consideration of entire landscapes rather than isolated patches of habitat for purposes of conservation and management. These large mammals also can have significant effects on vegetation composition and basic ecosystem processes such as nutrient cycling, thereby acting as keystone species (Kie et al. *In press*). Domestic livestock also have significant effects on the structure and composition of vegetation, and in combination with wild ungulates, help shape vegetation communities at multiple spatial scales. In summary, wild and domestic ungulates are conspicuous and important ecosystem components in eastern Oregon and Washington, and throughout the Intermountain West.

Literature Cited

Anderson, R.C., and A.J. Katz. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer (*Odocoileus virginianus*, Zimmerman) browsing pressure. Biological Conservation 63:203-208.

Augustine, D.J., L.E. Frelich, and P.A. Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecological Applications 8:1260-1269.

Augustine, D.J., and S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165-1183.

Bartos, D.L., J.K. Brown, and G.D. Booth. 1994. Twelve years' biomass response in aspen communities following fire. Journal of Range Management 47:79-83.

Belsky, A.J., and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. Conservation Biology 11:315-327.

Collins, S.L., A.K. Knapp, J.M. Briggs, J.M. Blair, and E.M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745-747.

deCalesta, D.S. 1994. Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management 58:711-718.

deCalesta, D.S., and S.L. Stout. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildlife Society Bulletin 25:252-258.

de Mazancourt, C., M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? Ecology 79:2242-2252.

DeNicola, A.J., S.J. Weber, C.A. Bridges, and J.L. Stokes. 1997. Nontraditional techniques for management of overabundant deer populations. Wildlife Society Bulletin 25:496-499.

Evans, R.D., and J. Belnap. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. Ecology 80:150-160.

Fan, W., J.C. Randolph, and J.L. Ehman. 1998. Regional estimation of nitrogen mineralization in forest ecosystems using geographic information systems. Ecological Applications 8:734-747.

Fleischner, T.L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629-644.

Frank, D.A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. Wildlife Society Bulletin 26:410-418.

Frank, D.A., and R.D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78:2238-2248.

Frank, D.A., and P.M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229-2241.

Frank, D.A., R.S. Inouye, N. Huntly, G.W. Minshall, and J.E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry 10:163-180.

Hanley, T.A. 1984. Relationships between black-tailed deer and their habitat. USDA Forest Service General Technical Report PNW-GTR-168. Pacific Northwest Research Station, Portland, Oregon. 21 p.

Hanley, T.A. 1996. Potential role of deer (Cervidae) as ecological indicators of forest management. Forest Ecology and Management 88:199-204.

Hanley, T.A., C.T. Robbins, and D.E. Spalinger. 1989. Forest habitats and the nutritional ecology of Sitka black-tailed deer: a research synthesis with implications for forest management. USDA Forest Service General Technical Report PNW-GTR-230. Pacific Northwest Research Station, Portland, Oregon. 52 p.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695-713.

Hobbs, N.T., D.S. Schimel, C.E. Owensby, and D.S. Ojima. 1991. Fire and grazing in the tall grass prairie: contingent effects on nitrogen budgets. Ecology 72:1374-1382.

Howell, P.J. 2001. Effects of disturbance and management of forest health on fish and fish habitat in eastern Oregon and Washington. Northwest Science 75 (Special Issue): 157-165.

Kaiser, J. 1998. Bison prime prairie productivity. Science 280:677.

Kie, J.G., V.C. Bleich, A.L. Medina, J.D. Yoakim, and J.W. Thomas. 1994. Managing rangelands for wildlife. Pages 663-688 *In* T.A. Bookhout (editor), Research and Management Techniques for Wildlife and Habitats. The Wildlife Society, Bethesda, Maryland.

Kie, J.G., R.T. Bowyer, and K.M. Stewart. *In press.* Ungulates in western coniferous forests: habitat relationships, population dynamics, and ecosystem processes. *In* C. Zabel and R. Anthony (editors), Mammal Community Dynamics in Western Coniferous Forests: Management and Conservation for the New Millennium. Cambridge University Press.

Kienast, F., J. Fritschi, M. Bissegger, and W. Abderhalden. 1999. Modeling successional patterns of high-elevation forests under changing herbivore pressure—response at the landscape level. Forest Ecology and Management 120:35-46.

McNaughton, S.J. 1992. The propagation of disturbance in savannas through food webs. Journal of Vegetation Science 3:301-314.

McShea, W.J., and J.H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology 14:1161-1170.

Molvar, E.M., R.T. Bowyer, and V. Van Ballenberghe. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472-479.

Muller L.L., R.J. Warren, and D.L. Evans. 1997. Theory and practice of immunocontraception in wild mammals. Wildlife Society Bulletin 25:504-514.

Olff, H., and M.E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 7:261-265.

Pastor, J., and Y. Cohen. 1997. Herbivores, the functional diversity of plants, and the cycling of nutrients in ecosystems. Theoretical Population Biology 51:165-179.

Pastor, J., B. Dewey, R. Moen, D.J. Mladenoff, M. White, and Y. Cohen. 1998. Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan. Ecological Applications 8:411-424.

Pastor, J., R. Moen, and Y. Cohen. 1997. Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. Journal of Mammalogy 78:1040-1052.

Pastor, J., and R.J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:691-705.

Pastor, J., R.J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. BioScience 38:770-777.

Pastor, J., R.J. Naiman, B. Dewey, P. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74:467-480.

Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79:2581-2592.

Quigley, T.M., J.L. Hayes, L. Starr, and G.E. Daterman. 2001. Improving forest health and productivity in eastern Oregon and Washington. Northwest Science 75 (Special Issue):234-251.

Reimoser, F., and H. Gossow. 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. Forest Ecology and Management 88:107-119.

Riggs, R.A., A.R. Tiedemann, J.G. Cook, T. Ballard, P.J. Edgerton, M. Vavra, W.C. Krueger, F.C. Hall, L.D. Bryant, L.L. Irwin, and T. DelCurto. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. USDA Forest Service Research Paper PNW-RP-527. Pacific Northwest Research Station, Portland, Oregon. 76 p.

Rodgers, P. 1996. Disturbance ecology and forest management: a review of the literature. USDA Forest Service General Technical Report INT-GTR-336. Intermountain Research Station, Ogden, Utah. 16 p.

Rose, A.B., and K.H. Platt. 1987. Recovery of northern fiordland alpine grasslands after reduction in the deer population. New Zealand Journal of Ecology 10:23-33.

Schreiner, E.G., K.A. Krueger, P.J. Happe, and D.B. Houston. 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Canadian Journal of Forest Research 26:255-265.

Seagle, S.W., S.J. McNaughton, and R.W. Ruess. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. Ecology 73:1105-1123.

Note

This special issue of *Northwest Science* is a set of papers reviewing the state of knowledge about disturbance processes in eastern Oregon and Washington, related management practices, and effects on key management issues.

Singer, F.J., D.M. Swift, M.B. Coughenour, and J.D. Varley. 1998a. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968-1993. Wildlife Society Bulletin 26:375-390.

Singer, F.J., L.C. Zeigenfuss, R.G. Gates, and D.T. Barnett. 1998b. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419-428.

Stohlgren, T.J., L.D. Schell, and B.V. Heuval. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45-64.

Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53:524-532.

Wallis de Vries, M.F. 1995. Large herbivores and the design of large-scale nature reserves in western Europe. Conservation Biology 9:25-33.

Wales, B.C. 2001. The management of insects, diseases, fire, and grazing, and implications for terrestrial vertebrates using riparian habitats in eastern Oregon and Washington. Northwest Science 75 (Special Issue):119-127.

Watson, A. 1983. Eighteenth century deer numbers and pine regeneration near Braemar, Scotland. Biological Conservation 25:289-305.

Weigand, J.F., R. Haynes, A.R. Tiedemann, R.A. Riggs, and T.M. Quigley. 1993. Ecological and economic impacts of ungulate herbivory on commercial stand development in forests of eastern Oregon and Washington. Forest Ecology and Management 61:137-155.

Woodward, A., E.G. Schreiner, D.B. Houston, and B.B. Moorhead. 1994. Ungulate-forest relationships on the Olympic Peninsula: retrospective exclosure studies. Northwest Science 68:97-110.