

The Role of Ungulate Herbivory and Management on Ecosystem Patterns and Processes: Future Direction of the Starkey Project

Martin Vavra

*U. S. Department of Agriculture, Forest Service,
Pacific Northwest Research Station
La Grande, Oregon*

Michael J. Wisdom

*U. S. Department of Agriculture, Forest Service,
Pacific Northwest Research Station
La Grande, Oregon*

John G. Kie

*U. S. Department of Agriculture, Forest Service,
Pacific Northwest Research Station
La Grande, Oregon*

John G. Cook

*National Council for Air and Stream Improvement
La Grande, Oregon*

Robert A. Riggs

*Boise Cascade Corporation
La Grande, Oregon*

Introduction

In the national forests of the Blue Mountains, a high percentage of commercial tree species, such as Douglas fir (*Pseudotsuga menziesii*) and true firs (*Abies* spp.), have died as a result of overcrowding on drier sites, drought and insects (Johnson et al. 1995, Quigley and Arbelbide 1997). These conditions are typical of forested land throughout the West (Covington and Moore 1994, Quigley and Arbelbide 1997). Traditional forest management practices (fire exclusion, harvest practices) (Johnson et al. 1995) and livestock grazing (Belsky and

Blumenthal 1997) have contributed substantially to the current situation (Hann et al. 1997). Because of these influences, trees in many stands exist at higher basal areas and higher densities (live and dead) than occurred historically, creating ladder fuels that have dramatically increased the risk of catastrophic wildfires covering very large acreages. In the coming years, it can be expected that fires will continue on forests where excessive fuel build-ups have occurred. And, extensive fuel reduction projects will be initiated to prevent them per the Healthy Forest Restoration Act of 2003.

Secondary succession of both understory and conifer components is initiated following either large fires or fuel reduction treatments. These areas often become focal points of ungulate herbivory for two reasons: (1) vegetation developing after disturbance is often more palatable to ungulates than that available on undisturbed sites (Asherin 1976), and (2) forage production in recently disturbed areas is often greater than in surrounding forest communities with dense canopies (McConnell and Smith 1970, Klinka et al. 1996). Large herbivores are attracted to areas that are characterized by relatively high biomass of palatable food resources; thus, they can be expected to focus foraging activity in recently disturbed areas.

Only rudimentary data exist (Riggs et al. 2000), but these data implicate ungulate herbivory as a significant agent in altering successional trajectories following disturbance (fire, logging, fuel reduction) in the Blue Mountains. Raedeke (1988) stated that selective feeding by forest animals can result in complete changes in the structure, composition and productivity of the forest. In general, plant communities within grazing exclosures are more diverse than the surrounding forest community subjected to continual herbivory (Raedeke 1988). Recent literature reviews (Hobbs 1996, Augustine and McNaughton 1998) clearly indicate the important role of herbivory not only in modifying the composition of plant communities but of ecosystems.

In the Blue Mountains, herbivory has long been recognized to be a competitive factor in ungulate relationships (Cliff 1939, Pickford and Reid 1943) and in suppressing the understory shrub component (Mitchell 1951). However, the role of herbivory as a major disturbance agent is not well recognized in the predominant management paradigms, both in the Blue Mountains and in all forest ecosystems of the western United States. Moreover, knowledge of herbivory effects is more anecdotal than predictive (Riggs et al. 2000).

In this paper, we briefly describe current knowledge regarding the effects of ungulate herbivory on ecosystem patterns and on processes in forests

of western North America. We then describe new research that is being initiated at the Starkey Experimental Forest and Range (Starkey) to understand ungulate herbivory effects. Finally, we identify some of the key policy implications associated with management of ungulate herbivory on national forests in the western United States.

Why Study and Manage Ungulate Herbivory?

In the western United States, state and federal land management plans outside of national parks have not recognized the ecological effects of foraging by wild ungulates, as evidenced by the lack of its mention in land management plans. Aber et al. (2000) made no reference to ungulate herbivory, either wild or domestic, in their publication, *Applying Ecological Principles to Management of the U. S. National Forests*. In Europe, the effects of ungulate herbivory are better recognized but primarily for impacts on regeneration of conifers (Kräuchi et al. 2000). At the same time, livestock grazing has long been identified as a potent agent of change in the composition, structure and production of plant communities (Fleischner 1994), and management and research have attempted to address the potentially deleterious effects of this agent. Historically, however, native herbivores, such as deer and elk, usually were perceived as benign constituents of the environment. In this context, native herbivores are considered a product of management rather than a disturbance factor that might influence other resources and various ecological processes. More recently, empirical evidence increasingly indicates that ungulate herbivory, wild or domestic, can have dramatic effects on ecosystem structure and function (Hobbs 1996, Augustine and McNaughton 1998).

In the Blue Mountains, recent findings indicate that wild ungulates dramatically alter the successional pathways of forest understories following disturbance (Riggs et al. 2000) and impact grasslands (Johnson and Vavra 2001, but see Coughenour 1991, Singer 1995). This evidence largely refutes the notion that successional pathways can be predicted without regard to the herbivory regimes that may be expected and, thus, underscores the need to understand how interactions between herbivores and episodic disturbance function, in the context of both wild and domestic herbivory. We define ungulate herbivory as referring to both wild and domestic herbivores unless otherwise specified. Identifying how ungulate herbivory influences composition and structure of forest understories

following disturbance is critical to the success of forest planning over the next several years for several reasons.

Forest conditions in the western United States are such that major changes in management focus probably will occur in the next several years. Years of fire suppression, resulting from forest ingrowth, and tree mortality, caused by insect and disease outbreaks, have all contributed to the development of forests that exceed the natural range of variability and are susceptible to conflagrations (Quigley and Arbelbide 1997). For example, 17 percent of the Wallowa-Whitman National Forest has burned in the last 10 years. As a result, management actions are being planned to reduce tree density and fuels and to increase prescribed burning. Nevertheless, vast areas will probably remain untreated well into the future, so the risk of conflagrations will remain high in many areas. Management to restore more natural conditions and continued wildfire conflagrations both set in motion secondary plant successions that will be influenced by ungulate herbivory. The nature and extent of these herbivory effects are currently unknown, but sufficient evidence indicates the effects may be relevant and perhaps deleterious to other wildlife species, biodiversity and ecosystems processes in general. Additionally, herbivory-induced changes in understory may affect productivity of native ungulate herds via negative feedback (Irwin et al. 1994) and may increase the degree of interspecific competition among ungulates (Vavra and Riggs 2004).

New Research at Starkey: Effects of Ungulates on the Forest Ecosystem

Past research at Starkey focused on deer and elk responses to management (Wisdom et al. 2004). New research, however, also will focus on the effects of deer, elk and cattle as disturbance agents in the ecosystem. This new research will specifically measure effects of ungulate herbivory on plant succession and associated changes in nutrient cycling and biodiversity. Results are expected to provide insights to how herbivore regimes can be sustainably integrated with other disturbances in conifer-dominated ecosystems in the Blue Mountains.

The new herbivory research at Starkey specifically is designed to evaluate the effects of ungulate grazing, the interaction with episodic disturbances, the vegetation development and the development of a variety of

other vegetative resources (such as grand fir [*Abies grandis*]) and Douglas-fir forests) that are predominant across much of the interior western United States. Within this context, we will assess effects of herbivory by elk and by cattle, the two dominant ungulate species in these ecosystems, using a variety of response variables, including (a) understory forest development, (b) elk and cattle forage selection and digestibility, (c) nitrogen availability and availability of other key nutrients that affect forest productivity, (d) insect herbivory and biodiversity, and (e) small mammal herbivory and biodiversity.

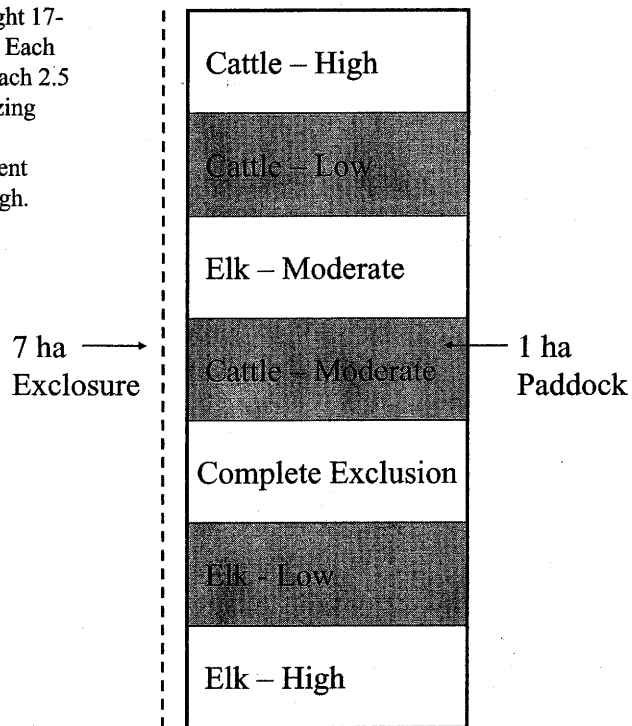
The research is designed to answer the following questions.

1. How does herbivory by elk and by cattle affect alien plant invasions and the composition, life forms, species richness, cover and structure of forest understories of grand fir and Douglas-fir forests?
2. How do effects of herbivory by elk and by cattle on vegetation development vary with low, moderate and high densities of each ungulate, in contrast to no herbivory by either ungulate?
3. How does nitrogen availability and that of other key nutrients change in relation to low, moderate and high densities of elk and cattle, and how might this affect vegetation development?
4. How does diet selection by elk and by cattle interact with herbivory effects on vegetation development under low, moderate and high ungulate densities?
5. How does diet selection by elk and by cattle and the resultant digestibility of forage consumed change over time in relation to low, moderate and high ungulate densities, as changes in forage biomass and quality occur?
6. What are the implications of question 5 on the long-term performance of elk and cattle populations?
7. How do herbivory effects by elk and by cattle change in relation to episodic disturbances of intensive timber harvest and prescribed fire, in contrast to effects with no harvest or fire?
8. How does herbivory by insects and by small mammals affect vegetation development as such forms of herbivory interact with ungulate herbivory?
9. Does biodiversity of insects and small mammals change in relation to ungulate herbivory?
10. How might conceptual models of ungulate herbivory-episodic disturbance interactions be refined and parameterized for stand-level

management of grand fir and Douglas-fir forests of the Interior Northwest?

These questions are being addressed with the use of 8 ungulate exclosures, each 17 acres (7 ha) that have been completed or are under construction at Starkey. Exclosure sites were selected within the strata of timber harvest and fire versus no timber harvest or fire. Each exclosure has been subdivided into 7 enclosed paddocks, each 2.5 acres (1 ha) for stocking density manipulation of ungulates (Figure 1).

Figure 1. Schematic of one of eight 17-acre (7-ha) exclosures at Starkey. Each exclosure contains 7 paddocks, each 2.5 acre (1 ha), within which the grazing trials for cattle and elk will be conducted. Each of seven treatment levels will be low, moderate or high.



Each of the 7 individual paddocks that compose a 17-acre (7-ha) exclosure (Figure 1) are randomly assigned 1 of 7 different treatment levels: 3 levels of grazing by tame elk, 3 levels of grazing by cattle (low, moderate or high density) and 1 level of total ungulate exclusion.

Construction of the eight exclosures began in summer of 2002 and will continue through 2004. Summer grazing trials will take place each July, using

tame elk and cattle at each stocking level in the paddocks. Over 40 response variables related to effects on plants, nutrients, ungulate diets, ungulate nutrition and insect and small mammal diversity will be measured over the life of the study, which is intended to last at least 10 years.

This new herbivory study will address effects of multiple densities of ungulates, of wild versus domestic ungulates, and of the interactions of herbivory with episodic disturbances of reduction in wood fuels and prescribed fire. These treatment effects have rarely been evaluated in past herbivory research, which typically compared complete exclusion versus extant herbivore use. There was little measurement of stocking levels and identification of herbivore species, and there was little consideration of interactions with other disturbances (Riggs et al. 2000, Wisdom et al. in review).

To complement this research, models will be developed to predict effects of varying densities of ungulates on plant succession and fire risk (Wisdom et al. in review). The new research at Starkey will be used to parameterize the models for integrated management of ungulate herbivory with episodic disturbances of timber harvest, fuels reduction and fire.

New Research at Starkey: Ungulate Response to Forest Management Practices

As a result of the recently passed Healthy Forests Restoration Act of 2003, efforts to reduce fuel loadings throughout eastern Oregon, eastern Washington and western Idaho will be intensified. These efforts will likely include mechanical treatments, prescribed burning and other techniques used in the past. One such project was recently completed on Starkey. In 1996 the Pacific Northwest Research Station and the Wallowa-Whitman National Forest began planning an Adaptive Resource Management (ARM) fuel reduction program. ARM projects offer unique opportunities for collaboration between research and management. Rarely do research stations have the funds, personnel and expertise to conduct land management activities at such a broad scale. Conversely, national forests lack personnel trained in experimental design and the infrastructure to conduct sound, scientific experiments. By combining the talents and resources of both the Pacific Northwest Research Station and the U. S. National Forest System in a collaborative ARM project, benefits accrue that would be impossible for either branch if operating independently. Many

professional, scientific organizations have identified the value of such adaptive, collaborative resource management efforts (Lancia et al. 1996).

The fuel reduction treatments began in spring 2001 and were completed in fall 2003. A total of 46 stands of true fir and Douglas-fir that had suffered substantial mortality during the spruce budworm outbreak in the late 1980s were chosen for treatment. A similar number of stands were left untreated as experimental controls. The treated stands totaled 1,999 acres (809 ha) (mean 34.6 acres [14 ha], range 2.8 to 114.0 acres [1.1–46 ha]). In many of those stands, fuel loadings exceeded 60 tons per acre. The objective of the treatments was to reduce fuel loadings to no more than about 15 to 20 tons per acre. All stands were mechanically thinned using a feller-buncher. About 75 percent of the treated stands were then either broadcast burned or piled and burned to achieve final fuel objectives.

On Starkey, we are using an automated radio telemetry system to track elk, mule deer and cattle to determine how they respond to fuel reduction treatments. Our goal is to determine how they respond to the fuel treatments at the landscape level. Some specific hypotheses we are testing include: (1) animals will be attracted to the treatment areas because of increased production of preferred forages, (2) elk and deer use of treatment areas will be influenced by the presence of roads and traffic levels, (3) spatial memory (remembering where the treatment areas are located and the amount of forage in each) and exploratory trips (to find newly treated patches) will influence the process by which animals use fuel treatment areas, and (4) the shape, size and spacing of treatment patches will affect their use by elk, mule deer and cattle. The automated telemetry system is critical to successfully testing these hypotheses.

This study will yield critically needed information about how overstory and understory vegetation responds once the fuel reduction treatments have been completed. The success of future fuel treatments, even the ability to complete such treatments, will be greatly enhanced if we understand the vegetation response to treatments. In addition, identification of cattle, deer and elk responses will be useful for future environmental assessments and planning efforts.

Similar future research is in the planning stages that will incorporate prescribed fire and, if needed, prior fuel reduction treatments in ponderosa pine (*Pinus ponderosa*) communities. The design of the experiment will be similar to that just described in that experimental protocols will be utilized, but the size of the treatments applied will be on a management scale.

Policy Implications

Herbivory exists as an unrecognized disturbance on landscapes in western North America. Extant plant communities may be influenced by herbivory and may be termed grazing disclimaxes (Riggs et al. 2000). However, the influence of herbivory to alter successional trajectories may be most critical following disturbance, such as fire or fuels reduction treatments. After disturbance, plants often reestablish either from rootstocks or seeds and are more susceptible to foraging by herbivores. Research results relating herbivory and disturbance from Starkey and from elsewhere in eastern Oregon are critically important as the new Healthy Forest Initiative is implemented.

- Important management and policy implications are relevant to herbivory.
- Ungulates act as keystone species that control ecosystem function and properties. These effects have substantial ecological, economic and social consequences that deserve increased focus in forest research and management. Improved understanding of the effects of wild and domestic ungulates, under varying population densities, is a critical need for improved management of ungulate herbivory.
- Structure and composition of vegetation can change dramatically in relation to the intensity of ungulate herbivory, and it can have significant impacts on biodiversity. Biodiversity responses to varying levels of ungulate herbivory are not well documented and deserve high priority in research.
- Marked changes in structure and composition of vegetation due to herbivory may increase error associated with identification of vegetative communities (Riggs et al. 2000) in the context of potential natural vegetation, reducing the accuracy and the value of the predominant vegetative and land classification systems currently used by federal management agencies throughout the Northwest (e. g., see Henderson et al. 1992).
- Ungulate herbivory can negatively affect ungulate productivity through negative feedback mechanisms mediated through suppression of food resources. Declining biomass of forage is likely to increase the intensity of ungulate herbivory. In turn, the increased herbivory may not allow preferred forage plants to establish, recover and persist unless disturbances, such as fire or timber harvest, occur across spatial extents

sufficient to providing a forage biomass far in excess of what can be utilized by ungulates. On the other hand, where disturbance is not sufficient, ungulate populations will have to be reduced to avoid degradation. In any event, managers and policy makers might consider how the balance between landscape disturbance and herbivore population management influences long-term carrying capacity and ecosystem stability. These relations deserve attention in future ungulate-landscape research.

- Ungulate herbivory may contribute to conifer ingrowth in forest understories, particularly when high levels of herbivory are combined with fire suppression, resulting in substantially higher risk of stand-replacement fires than existed historically.
- When considering forest management practices, such as timber harvest, fuels reduction and prescribed burning, the size and number of treated areas will affect the recovery of those areas, with smaller treatments likely to attract intensive herbivory and associated changes in vegetation development and other ecosystem processes.

Reference List

- Aber, J., N. Christensen, I. Fernandez, J. Franklin, L. Hiding, M. Hunter, J. MacMahon, D. Mladenoff, J. Pastor, D. Perry, R. Slangen, H. van Miegroet. 2000. Applying ecological principles to management of the U. S. National Forests. *Issues in Ecology*. 6:1–20.
- Asherin, D. A. 1976. Changes in elk use and available browse production on north Idaho winter ranges following prescribed burning. In *Proceedings of the elk-logging-roads symposium*, ed. S. R. Hieb, 122–34. Moscow, Idaho: Forest, Wildlife, and Range Experiment Station, University of Idaho.
- 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*. 62:1,165–83.
- 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*. 11:315–27.

- Cliff, E. P. 1939. Relationship between elk and mule deer in the Blue Mountains of Oregon. In *4th North American wildlife conference*. Portland, Oregon: U. S. Department of Agriculture, Forest Service.
- Cook, J. G., L. Irwin, L. Bender, B. Johnson, and D. Boyce. 1999. *Declining elk herd productivity: Assessing habitat's role in the Pacific and inland Northwest—A Proposal*. unpublished.
- Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *Journal of Applied Ecology*. 28:71–82.
- Covington, W. W., and M. Moore. 1994. Southwestern Ponderosa forest structure, changes since Euro-American settlement. *Journal of Forestry*. 92:39–47.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology*. 8:629–44.
- Hann, W. J., J. L. Jones, M. G. Karl, P. F. Hessburg, R. E. Keane, D. G. Long, J. P. Menakis, C. H. McNicoll, S. G. Leonard, R. A. Gravenmier, and B. G. Smith. 1997. Landscape dynamics of the basin. In *An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins, general technical report PNW-GTR-405*, eds. T. M. Quigley, and S. J. Arbelbide. Portland, Oregon: U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Henderson, J. A., R. D. Leshner, D. H. Peter, and D. C. Shaw. 1992. *Field guide to the forested plant associations of the Mt. Baker-Snoqualmie National Forest, technical paper R6 ECOL TP 028–91*. Portland, Oregon: U. S. Department of Agriculture, Forest Service.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management*. 60:695–713.
- Irwin, L. L., J. G. Cook, R. A. Riggs, and J. M. Skovlin. 1994. *Effects of long-term grazing by big game and livestock in the Blue Mountains forest ecosystem, general technical report PNW-GTR-325*. Portland, Oregon: U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Johnson, K. N., J. Agee, R. Beschta, J. Beuter, S. Gregory, L. Kellogg, W. McComb, J. Sedell, T. Schowalter, and S. Tesch. 1995. *Forest health*

- and timber harvest on national forest in the Blue Mountains of Oregon. Corvallis, Oregon: Oregon State University.
- Johnson, C. G., and M. Vavra. 2001. Permanent monitoring points: An example of value and utility in the study of elk impacts on bunchgrass communities in Hells Canyon. *Abstracts Society for Range Management Annual Meeting*. February 2001.
- Klinka, K., H. Y. H. Chen, Q. Wang, and L. de Montigny. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on West Vancouver Island. *Northwest Science*. 70:193–200.
- Kräuchi, N., P. Brang, and W. Shönenberger. 2000. Forests of mountainous regions: Gaps in knowledge and research needs. *Forest Ecology and Management*. 132:78–82.
- Lancia, R. A., C. E. Braun, M. W. Collopy, R. D. Dueser, J. G. Kie, C. J. Martinka, J. D. Nichols, T. D. Nudds, W. R. Porath, and N. C. Tilghman. 1996. ARM For the future: Adaptive resource management in the wildlife profession. *Wildlife Society Bulletin*. 24:436–42.
- McConnell, B. R., and J. G. Smith. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. *Journal of Range Management*. 23:208–12.
- Mitchell, G. E. 1951. Status of browse on ranges of eastern Oregon and eastern Washington. *Journal of Range Management*. 4:249–53.
- Pickford, G., and E. Reid. 1943. Competition of elk and domestic livestock for summer range forage. *Journal of Wildlife Management*. 7:328–32.
- Quigley, T. M., and S. J. Arbelbide. 1997. *An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins, general technical report PNW-GTR-405*. Portland, Oregon: U. S. Department of Agriculture, Forest Service, Pacific Northwest Region and Bureau of Land Management.
- Raedeke, K. J. 1988. Forest management and wildlife in the Pacific Northwest. *Northwest Environmental Journal*. 4:263–78.
- Riggs, R. A., A. R. Tiedemann, J. G. Cook, T. M. 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, research paper PNW-RP-527*. La Grande, Oregon: U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

- Singer, F. J. 1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. *Northwest Science*. 69:191.
- U. S. Department of Agriculture and U. S. Forest Service. 2003. National Fire Plan. Wildland Fire Leadership Council. <http://www.fireplan.gov>.
- Vavra, M., and R. Riggs. 2004. Managing multiple herbivores across heterogeneous landscapes. In *Abstracts of 60th annual meeting of the Society of Range Management*. Salt Lake City, Utah: Society of Range Management.
- Wisdom, M. J., M. M. Rowland, B. K. Johnson, and B. L. Dick. 2004. Overview of the Starkey project: Mule deer and elk research for management benefits. *Transactions of the North American Wildlife and Natural Resources Conference*. 69:455-74.
- Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. In review. Understanding ungulate herbivory-episodic disturbance effects: knowledge gaps and research needs. *Wildlife Society Bulletin*.

**Transactions
of the
Sixty-ninth North American Wildlife
and Natural Resources Conference**

Conference Theme:
*Resource Stewardship in the 21st Century:
A Voyage of Rediscovery*

*March 16 to 20, 2004
DoubleTree Hotel and Spokane City Center
Spokane, Washington*

Edited by
Jennifer Rahm

Published by the
Wildlife Management Institute
Washington, DC
2004

Wildlife for Persons with Disabilities: Making the Outdoors Accessible through the Use of Motorized Vehicles.....	439
<i>Kirk Thomas and Illana Burkhart</i>	

Special Session Six. Policy Implications from Long-term Studies of Mule Deer and Elk: A Synthesis of the Starkey Project

The Starkey Project: Long-term Research for Long-term Management Solutions	443
<i>Thomas M. Quigley and Michael J. Wisdom</i>	

Overview of the Starkey Project: Mule Deer and Elk Research for Management Benefits.....	455
<i>Michael J. Wisdom, Mary M. Rowland, Bruce K. Johnson, and Brian L. Dick</i>	

The Starkey Databases: Spatial-Environmental Relations of North American Elk, Mule Deer and Cattle at Starkey Experimental Forest and Range in Northeastern Oregon.....	475
<i>John G. Kie, Alan A. Ager, Norman J. Cimon, Michael J. Wisdom, Mary M. Rowland, Priscilla K. Coe, Scott L. Findholt, Bruce K. Johnson and Marvin Vavra</i>	

Effects of Roads on Elk: Implications for Management in Forested Ecosystems.....	491
<i>Mary M. Rowland, Michael J. Wisdom, Bruce K. Johnson and Mark A. Penninger</i>	

Spatial Partitioning by Mule Deer and Elk in Relation to Traffic.....	509
<i>Michael J. Wisdom, Norman J. Cimon, Bruce K. Johnson, Edward O. Garton and Jack Ward Thomas</i>	

Effects of Off-road Recreation on Mule Deer and Elk.....	531
<i>Michael J. Wisdom, Alan A. Ager, Haiganoush K. Preisler, Norman J. Cimon and Bruce K. Johnson</i>	

Issues of Elk Productivity for Research and Management.....	551
<i>Bruce K. Johnson, Michael J. Wisdom and John G. Cook</i>	
Influence of Age of Males and Nutritional Condition on Short- and Long-term Reproductive Success of Elk.....	572
<i>James H. Noyes, Bruce K. Johnson, Brian L. Dick and John G. Kie</i>	
Nutritional Condition Indices for Elk:	
The Good (and Less Good), the Bad and the Ugly.....	586
<i>Rachel C. Cook, John G. Cook, Dennis L. Murray, Pete Zager, Bruce K. Johnson and Michael W. Gratson</i>	
Nutrition and Parturition Date Effects on Elk:	
Potential Implications for Research and Management.....	604
<i>John G. Cook, Bruce K. Johnson, Rachel C. Cook, Robert A. Riggs, Tim DelCurto, Larry D. Bryant and Larry L. Irwin</i>	
Elk and Mule Deer Responses to Variation in Hunting Pressure.....	625
<i>Bruce K. Johnson, Alan A. Ager, James H. Noyes and Norm Cimon</i>	
Movements and Habitat Use of Rocky Mountain Elk and Mule Deer.....	641
<i>Alan A. Ager, Haiganoush K. Preisler, Bruce K. Johnson and John G. Kie</i>	
Spatial and Temporal Interactions of Elk, Mule Deer and Cattle.....	656
<i>Priscilla K. Coe, Bruce K. Johnson, Kelley M. Stewart and John G. Kie</i>	
Diet Composition, Dry Matter Intake and Diet Overlap of Mule Deer, Elk and Cattle.....	670
<i>Scott L. Findholt, Bruce K. Johnson, Daalkhaijav Damiran, Tim DelCurto and John G. Kie</i>	

Landscape Simulation of Foraging by Elk, Mule Deer and Cattle on Summer Range.....	687
<i>Alan A. Ager, Bruce K. Johnson, Priscilla K. Coe and Michael J. Wisdom</i>	
Thermal Cover Needs of Large Ungulates: A Review of Hypothesis Tests.....	708
<i>John C. Cook, Larry L. Irwin, Larry D. Bryant, Robert A. Riggs, Jack Ward Thomas</i>	
Cattle and Elk Responses to Intensive Timber Harvest.....	727
<i>Michael J. Wisdom, Bruce K. Johnson, Martin Vavra, Jennifer M. Boyd, Priscilla K. Coe, John G. Kie, Alan A. Ager and Norman J. Cimon</i>	
Management Implications of Ungulate Herbivory in Northwest Forest Ecosystems.....	759
<i>Robert A. Riggs, John G. Cook and Larry L. Irwin</i>	
The Role of Ungulate Herbivory and Management on Ecosystem Patterns and Processes: Future Direction of the Starkey Project.....	785
<i>Martin Vavra, Michael J. Wisdom, John G. Kie, John G. Cook and Robert A. Riggs</i>	
Has the Starkey Project Delivered on Its Commitments?.....	798
<i>Jack Ward Thomas and Michael J. Wisdom</i>	
Registered Attendance.....	813
2004 WMI Distinguished Service Award.....	823
2004 WMI Touchstone Award.....	825