

DIET COMPOSITION, DRY MATTER INTAKE, AND DIET OVERLAP OF MULE DEER, ELK,  
AND CATTLE

Scott L. Findholt  
Wildlife Research Biologist  
Oregon Department of Fish and Wildlife  
Forestry and Range Sciences Laboratory  
1401 Gekeler Lane, La Grande, Oregon 97850  
Phone (541-962-6538), fax (541-962-6504)  
Email [findhos@eou.edu](mailto:findhos@eou.edu)

Daalkhaijav Damiran  
Research Assistant  
Eastern Oregon Agricultural Research Center  
Oregon State University  
Union, Oregon 97883  
Phone (541-562-5129), fax (541-562-5348)  
Email [daal.damiran@orst.edu](mailto:daal.damiran@orst.edu)

Bruce K. Johnson  
Starkey Project Leader  
Oregon Department of Fish and Wildlife  
Forestry and Range Sciences Laboratory  
1401 Gekeler Lane, La Grande, Oregon 97850  
Phone (541-962-6556), fax (541-962-6504)  
Email [johnsobd@eou.edu](mailto:johnsobd@eou.edu)

Tim DelCurto  
Associate Professor  
Eastern Oregon Agricultural Research Center  
Oregon State University  
Union, Oregon 97883  
Phone (541-562-5129), fax (541-562-5348)  
Email [Tim.Delcurto@orst.edu](mailto:Tim.Delcurto@orst.edu)

John G. Kie  
Research Wildlife Biologist  
USDA Forest Service, Pacific Northwest Research Station  
Forestry and Range Sciences Laboratory  
1401 Gekeler Lane, La Grande, Oregon 97850  
Phone (541-962-6529), fax (541-962-6504)  
Email [jkie@fs.fed.us](mailto:jkie@fs.fed.us)

Suggested Citation:

Findholt, S. L., B. K. Johnson, D. Damiran, T. DelCurto, and J. G. Kie. 2004. Diet Composition, Dry Matter Intake, and Diet Overlap of Mule Deer, Elk, and Cattle. Transactions of the North American Wildlife and Natural Resource Conference 69: in press.

## Diet Composition, Dry Matter Intake, and Diet Overlap of Mule Deer, Elk, and Cattle

Scott L. Findholt  
*Oregon Department of Fish and Wildlife*  
*La Grande*

Bruce K. Johnson  
*Oregon Department of Fish and Wildlife*  
*La Grande*

Daalkhajjav Damiran  
*Eastern Oregon Agricultural Research Center*  
*Union*

Tim DelCurto  
*Eastern Oregon Agricultural Research Center*  
*Union*

John G. Kie  
*U.S. Department of Agriculture, Forest Service*  
*La Grande, Oregon*

Mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and cattle share rangelands throughout much of interior western North America. Considerable debate exists about the degree to which facilitation or competition occurs for forage between these three species (Nelson 1982, Wisdom and Thomas 1996, Miller 2002).

Prior cattle grazing can have beneficial effects on elk nutrition. The removal of forage by cattle can improve forage quality by enhancing regrowth of forage or by changing ratios of live to dead plant material (Cook 2002), and forage quality on elk winter ranges in the interior Northwest can be improved by cattle grazing in the spring (Anderson and Scherzinger 1975, Clark 1996). To date, however, studies have not shown enhancement of forage quality in the summer following late spring or early summer grazing by elk or cattle.

Competition for forage between mule deer, elk, and cattle is probably greatest on winter and spring/autumn ranges (Nelson 1982, Wisdom and Thomas 1996), and minimal between wild ungulates and cattle during summer (Miller 2002). Most summer ranges for mule deer and elk are on large areas of public land containing a diversity of habitats and high potential for forage production (Miller 2002). On some summer ranges, however, competition for forage may exist in late summer and early fall because forage quality can be poor and not meet nutritional requirements of wild ungulates and cattle (Torbit 1985, Hanley et al. 1989, Cook 2002). This is especially evident in regions where summer drought is the normal part of the climatic regime (Vavra and Phillips 1980, Svejcar and Vavra 1985).

On the Starkey Experimental Forest and Range (Starkey), northeast Oregon, competition for forage may occur in late summer among all three species, especially between elk and cattle (Coe et al. 2001, Stewart et al. 2002). Conditions at Starkey typify those on summer ranges shared by mule deer, elk, and cattle in forests of the interior western United States. Consequently, we conducted a manipulative experiment on Starkey summer range to evaluate the potential for competition or facilitation for forage among mule deer, elk, and cattle in grand fir (*Abies grandis*) forests. Our specific objectives were to determine diet composition, dry matter intake rates, and percent dietary overlap of all three species in response to prior grazing by elk and cattle. In this paper we focus on results obtained from the bite count data. A detailed analysis of the nutritional consequences of previous grazing by elk or cattle on subsequent diets of mule deer, elk, or cattle will be presented elsewhere (Damiran in prep.). Results from

our study could improve range management for mule deer, elk and cattle on public land, especially with regards to allocating forage among these three species when ranges are shared in forested habitats (Ager et al. 2004).

## **Study Area**

Starkey is located on the Wallowa-Whitman National Forest, 22 miles (35 km) southwest of La Grande, Union County, northeast Oregon. Vegetation is a mosaic of coniferous forests and open areas containing shrublands and grasslands. Forest stands are dominated by ponderosa pine (*Pinus ponderosa*), with grand fir, and Douglas fir (*Pseudotsuga menziesii*) occurring on northern aspects. Elevation ranges from 3,675 to 4,922 feet (1,120 to 1,500 m).

We conducted our research in four, 5.56 acre (2.25- ha) enclosures located in grand fir- forests logged 15-20 years ago. We chose the grand fir vegetation type because of its dominance on summer and fall ranges in the Blue Mountains and the interior western United States. Moreover, grand fir forests support a high level of forage production, particularly after logging or burning. In addition, other research at Starkey indicated that mule deer, elk, and cattle concentrated much of their foraging activity after mid-summer on early successional stages of logged grand fir vegetation types (Coe et al. 2001).

## **Methods**

### **Grazing Treatments**

Each enclosure contained three, 1.85 acre (0.75 ha) pastures ([Figure 1](#)). In 1998 and 1999, during late June and again in mid to late July, one pasture of each enclosure was grazed by four to five steers and another pasture was grazed by four elk. The remaining pasture of each enclosure was not grazed (control pasture). Our goal during grazing treatments was to have 40 percent of the current year's vegetation production utilized by elk and steers on each pasture. This is the standard used by the U.S. Department of Agriculture, Forest Service for cattle allotments on upland sites in good condition in northeast Oregon. Assignment of grazing treatments to pastures was done randomly, and remained the same in 1998 and 1999.

### **Feeding Trials**

After completion of the grazing treatments each 1.85 acre (0.75 ha) pasture was subdivided into three, 0.62 acre (0.25 ha) pastures. In August 1998 and 1999 we used bite-counts to obtain information on diet composition of tractable mule deer, elk, and cattle from each pasture as described by Wickstrom et al. (1984). Each 0.62 acre (0.25 ha) pasture was grazed by four mule deer, four elk, or four steers. The elk and steers were the same animals used during grazing treatments. We conducted four feeding trials with each animal in each 0.62 acre (0.25) ha pasture. This resulted in 16 feeding trials for each species in each treatment at the four enclosures, for a total of 192 feeding trials for each species each year.

During each 20 minute feeding trial we used a small hand-held tape recorder to record the number of bites of each plant species consumed. We randomly assigned animal species to pastures for the feeding trials at the start of each year.

### **Dry Matter Intake**

After feeding trials were completed in each 0.62 acre (0.25 ha) pasture, we clipped at least 25 samples of the most common plant species (greater than 5 percent of the diet) to simulate plant parts and sizes of bites recorded during feeding trials. Samples were oven-dried at 122° Fahrenheit (50° C) to constant weight. We calculated mean weights of bites of each plant species found in the diet in each 0.62

acre (0.25 ha) pasture. Mean weights were multiplied by the number of bites of each plant species to determine total dry matter intake.

### **Data Analysis**

Data were analyzed as a split-plot design with the Proc Mixed procedure in SAS (Littell et al. 1996) to determine whether diets of mule deer, elk, and cattle differed among pastures previously grazed by cattle or elk and control (ungrazed) pastures. We used the LS means procedure of SAS to determine if treatment means were different. Bite count data (bites/minute) were used to calculate percent overlap in diet. Percent overlap of major forage classes composing the diets of mule deer, elk, and steers was determined with Horn's Index of Similarity (Horn 1966).

## **Results**

### **Diet Composition and Bite Rates**

#### Cattle.

Total bites/minute of steers was less in pastures previously grazed by cattle in 1998 and 1999 compared to ungrazed pastures and pastures previously grazed by elk ( $P \leq 0.03$ ; [Figure 2](#)). Graminoids composed the bulk of the steer diets both years ([Figure 3](#)). Steers consumed less graminoids and more shrubs/trees in pastures previously grazed by cattle however, compared to ungrazed pastures or pastures previously grazed by elk in 1998 and 1999 ( $P \leq 0.04$ ). Also, steers consumed more forbs in pastures previously grazed by cattle in 1999 ( $P \leq 0.02$ ) but not in 1998 ( $P \geq 0.11$ ). Intake of major forage categories in steer diets did not change in response to prior elk grazing ( $P > 0.10$ ).

#### Elk.

Total bites/minute of elk was greater in pastures previously grazed by elk compared to ungrazed pastures in 1998 ( $P = 0.02$ ), but not in 1999 ( $P = 0.58$ ; [Figure 2](#)). Although elk consumed mostly forbs, graminoids, and shrubs/trees, lichens were also prevalent in their diets ([Figure 3](#)). Bites/minute of graminoids in elk diets was greater in pastures previously grazed by elk compared to pastures previously grazed by cattle during both years ( $P \leq 0.01$ ). Elk diets also contained more graminoids in pastures previously grazed by elk compared to control pastures in 1998 ( $P = 0.05$ ). Bites/minute of forbs was higher in pastures previously grazed by cattle compared to control pastures and pastures previously grazed by elk but less in pastures previously grazed by elk compared to control pastures ( $P \leq 0.03$ ). In 1998 bites/minute of elk did not vary with treatment ( $P \geq 0.43$ ). However, this same year elk consumed more shrubs/trees in pastures previously grazed by cattle compared to control pastures ( $P = 0.02$ ). In 1998 and 1999 elk consumed less lichen in pastures previously grazed by elk ( $P \leq 0.05$ ; [Figure 3](#)).

#### Mule deer.

Total bites/minute of mule deer did not vary with treatment either year ( $P > 0.10$ ; [Figure 2](#)). Mule deer consumed mostly forbs and shrubs/trees ([Figure 3](#)). Intake of graminoids, forbs, shrubs/trees, and other food did not differ in those pastures previously grazed by cattle or elk compared to control pastures ([Figure 3](#)).

## **Dry Matter Intake**

In 1998 and 1999 total dry matter intake (grams/minute) of steers was less in pastures previously grazed by cattle compared to pastures previously grazed by elk or ungrazed pastures ( $P \leq 0.03$ ; [Figure 4](#)). Total dry matter intake (grams/minute) did not vary among treatments either year for elk or mule deer ( $P \geq 0.26$ ; [Figure 4](#)).

## **Percent Diet Overlap**

Mean diet overlap of major forage classes in control pastures (ungrazed pastures) was 49 percent between cattle and elk, 59 percent between mule deer and elk, but only 19 percent between cattle and deer when data from 1998 and 1999 were combined ([Figure 5](#)). During both years, diet overlap between cattle and deer increased in pastures previously grazed by cattle ( $P \leq 0.01$ ), but not in pastures previously grazed by elk ( $P \geq 0.67$ ). Percent diet overlap between cattle and elk was higher in pastures previously grazed by elk compared to control pastures both years ( $P \leq 0.006$ ) and also higher in pastures previously grazed by cattle in 1999 ( $P \leq 0.001$ ). Percent diet overlap between mule deer and elk did not vary with treatment either year ( $P \geq 0.17$ ).

## **Discussion**

Numerous studies have evaluated the food habits of mule deer, elk, and cattle (Kufeld 1973, Kufeld et al. 1973, Holechek 1979, Cook 2002). These studies show large variation by year of study, location, specific herbivore, and research technique. Thus, in this discussion we focus on the results of our study in relation to other studies in northeast Oregon where habitats are generally similar to those in our study area.

Forage intake estimated from clipping or handpicking simulated bites that represent bites ingested can be biased, especially with wild ungulates (Parker et al. 1993). In our study, results from bite counts (bites/minute) and dry matter intake rates (grams/minute) showed similar effects of previous grazing by cattle or elk. This similarity suggests that both methods can be used to estimate diet composition and evaluate the potential for competition for forage among mule deer, elk, and cattle.

Holechek et al. (1982) found that cattle grazed mostly on grasses, but also consumed large quantities of forbs and shrubs in ponderosa pine or Douglas fir forest types on Starkey in late summer. In our study, cattle also consumed mostly grasses and sedges. In response to previous cattle grazing, however, cattle reduced their consumption of graminoids and increased their use of forbs and shrubs. The potential for competition for forage between cattle and elk and cattle and mule deer increased when cattle changed their diets as preferred cattle forage was consumed. Holechek et al. (1982) and Miller and Vavra (1981) also reported that cattle readily switch their diets from one forage type to another. Elk are an intermediate feeder compared to mule deer or cattle (Kufeld 1973, Hofmann 1988). Edgerton and Smith (1971) found that elk and mule deer diets consisted of 58 percent grasses and sedges, 27 percent forbs, and 15 percent shrubs during summer at Starkey. In their study it was not possible to separate elk from mule deer diets because forage production and utilization were estimated on summer range shared by the two species. Korfhage (1974) and Korfhage et al. (1980) found that elk diets in the Blue Mountains, northeast Oregon were evenly balanced among all major vegetative components but forbs and shrubs were more important dietary components than graminoids during late summer. In our study, elk diets consisted of a more even percentage of all major forage classes in contrast to the more concentrated diets of mule deer and cattle. Interestingly, elk consumed a substantially higher percentage of lichens, with no consumption of this forage by cattle, and only a minor percentage consumed by mule deer. Like cattle, elk also switched their diets in response to previous grazing. The most dramatic change in elk diets was in pastures previously grazed by elk. Elk appeared to increase their consumption of graminoids in response to a decline of available lichens. This increased the potential for competition between cattle and elk.

Other research at Starkey suggests that competition may exist between cattle and elk during late summer. In ponderosa pine- bunchgrass summer range at Starkey, Skovlin et al. (1968) found that elk use decreased as rate of cattle stocking increased. In a more recent study at Starkey, Coe et al. (2001) discovered that when cattle were present, elk use of the same pastures decreased and use of the ponderosa pine/ Douglas fir plant community in the same pasture increased in late summer. In Colorado, however, Hobbs et al. (1996) found that at high densities, elk were in direct competition with cattle, but at low density, elk had a facilitative effect on cattle diets.

Because of their anatomical and digestive attributes, mule deer were expected to have a more selective diet and choose higher quality forages than elk or cattle (Hofmann 1988). Mule deer switched their diet the least of the three herbivores in response to previous grazing by cattle or elk. This lack of flexibility in their diet could result in increased competition with elk or cattle in areas that have high ungulate or cattle densities or low forage production. Kie et al. (1991) concluded that competition between cattle and mule deer was highest during years of below-average precipitation. Austin and Urness (1986), however, concluded that deer and cattle did not compete for forage in their study area as deer use increased.

In our study we determined the crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), and in vitro dry matter digestibility (IVDMD) of plant samples collected that represented those parts of species common in the diets of mule deer, elk, and cattle (Damiran et al. 2003). The most dramatic effect of prior grazing on subsequent diets of mule deer, elk, or cattle was the influence of previous cattle grazing on diets of steers. Grams/minute of CP and IVDMD consumed by cattle in pastures previously grazed by cattle was 32.4 and 43.0 percent less respectively, compared to control (ungrazed) pastures. This suggests that the potential for intraspecific competition among cattle in secondary succession grand fir vegetation types is high during late summer.

Our results support Holechek's et al. (1981) findings that, overall, the diets of cattle at Starkey did not meet the NRC standard for nutrient (CP and digestible energy (DE)) requirements during late summer. By contrast, nutrient intake of mule deer and elk did not change in response to previous grazing by cattle or elk (Damiran et al 2003).

One measure of the potential for competition between species is the amount of dietary overlap. Diet overlap or lack of diet overlap, however, does not necessarily equate to high or low levels of competition. One would expect that the distinct differences in ruminant physiology among mule deer, elk, and cattle would result in low dietary overlap, especially between mule deer and cattle (Hanley 1982, Baker and Hobbs 1987, Hofmann 1988). Willms et al. (1980) observed that mule deer diets in British Columbia changed in response to varying levels of forage utilization by cattle. When forages were abundant, cattle and deer diets were similar, but as forage utilization increased, diet overlap decreased, with deer preferring shrubs and cattle preferring grasses. In our study diet overlap was the lowest between cattle and mule deer in ungrazed pastures. The potential for competition between these two species, however, increased greatly in response to previous cattle grazing. Steers consumed less graminoids and more forbs and shrubs in response to prior cattle grazing. This switching of cattle diets from graminoids to forbs and shrubs nearly doubled the dietary overlap between cattle and deer. By contrast, Damiran et al. (2003) found that intake of CP and IVDMD for mule deer did not change in response to prior grazing by cattle or elk, suggesting that competition was not occurring at the grazing intensity in our study even though diet overlap increased.

The greatest potential for competition in ungrazed secondary succession grand fir was between mule deer and elk. Mule deer and elk consumed many of the same forbs and shrubs. Dietary overlap of mule deer with elk, however, did not change in response to previous grazing by cattle or elk. Coe et al. (2001) found that mule deer use of pastures at Starkey declined when elk were present which suggests that interference competition may be occurring between these two species.

Dietary overlap was also high between cattle and elk, especially in pastures previously grazed by steers or elk. As others have suggested, the dietary choices of elk can overlap closely with dietary selection by cattle, making the two species potential competitors for available forage. Based on interactions between cattle and elk at Starkey Coe et al. (2001) concluded that dietary competition for

forage could occur between elk and cattle in late summer. At the level of grazing in our study, CP and IVDMD in elk diets were not affected by previous grazing but these two nutrients declined in steer diets (Damiran et al. 2003). As mentioned previously, however, the decline in CP and IVDMD in cattle diets was a result of intraspecific competition for forage among cattle, not interspecific competition with elk.

In contrast to results from our study, Stewart et al. (2003) determined diet composition of free-ranging mule deer, elk, and cattle at Starkey using microhistological analyses of fecal samples and found little overlap in dietary niche among these three herbivores. This study was conducted later in the summer during July and August however, and on free-ranging animals with access to a variety of habitat types. Also, cattle feces were collected from the main study area and feces from mule deer and elk were collected from the northeast study area where cattle were not present. Finally, results from microhistological analyses of fecal samples are not comparable to bite count data because of inherent biases associated with fecal samples that cannot control for different rates of digestion of different forage classes (McInnis et al. 1983).

Our results suggest that inter- and intraspecific competition for forage may exist among all three species during summer in previously logged grand fir forests. However, realization of competition depends on the densities of the various herbivores and annual net primary production, and on diet overlap resulting in negative nutritional consequences. The probability of competition would be increased during years of low forage production, heavy herbivore stocking, or both. Moreover, demonstration of true competition between two or more species requires a documented reduction in animal or population performance by one species as a result of sharing a limited resource with the other species (Wisdom and Thomas 1996).

### **Policy Implications**

1. Our results suggest that intra- and interspecific dietary competition may exist among mule deer, elk and cattle during the summer in secondary succession grand fir vegetation types. Consequently, it is important for managers to monitor the forage base in this habitat type and if necessary, reduce livestock use to maintain plant vigor and leave adequate forage for mule deer and elk. Or, alternatively, it may be necessary to reduce densities of mule deer and elk to maintain adequate nutrition for cattle. Which approach is taken (reduction of livestock or wild ungulate use) depends on the multi-species objectives set for the allotment, as evaluated from analyses of the trade-offs of varying stocking rates among the species (Wisdom and Thomas 1996). Although the fitness of mule deer and elk may not be affected during the summer, their ability to survive severe winters and reproduce may be negatively affected by poor summer nutrition (Cook et al. 2004).
2. We found no strong evidence that previous elk or cattle grazing improved forage quality of mule deer, elk or cattle that grazed the same pastures later that year. During the summer in secondary succession grand fir it appears that prior grazing by cattle or elk does not improve the forage quality for those herbivores that subsequently graze the same pastures. In our study, however, forage quality did not improve subsequent to cattle and elk grazing because soil moisture may not have been adequate in late June and July for vegetation regrowth. The potential for prescribed cattle grazing, however, as a management tool to maintain or improve mule deer and elk forage during late summer needs more exploration.
3. High diet similarity among these three species and an increase in dietary overlap in response to previous grazing by cattle and elk indicate that cattle and elk readily shift their diets during late summer. This knowledge will help managers optimize use of grand fir vegetation types for grazing by wild ungulates and livestock.

4. Overall, based on our findings and research by others (Holechek et al. 1981), the diets of cattle may not meet the NRC standard for nutrient (CP and DE) requirements during summer in forested vegetation types at Starkey. This finding further suggests that competition for forage is more likely during summer, and deserves careful consideration in allotment management planning for areas with similar environmental conditions as Starkey.
5. Our project and other studies indicate a need for additional research on inter- and intraspecific competition for forage among mule deer, elk, and cattle. More questions remain on how the timing and intensity of grazing affects the nutritional condition and fitness of all three species. Likewise, it would be helpful to have more information on their habitat selection and distributional overlap. This will insure the continuation of the multiple use concept mandated on public lands and guarantee proper management of the forage resource.

### Acknowledgments

Our study was funded under provisions of the Federal Aid in Wildlife Restoration Act (Pittman-Robertson Act), administered by the Oregon Department of Fish and Wildlife. Funding was also provided by the Eastern Oregon Agricultural Research Center, Rocky Mountain Elk Foundation, and the U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. We thank P. Coe, J. Noyes, J. Paustian, and R. Stussy for assistance with conducting feeding trials. J. Kern provided statistical advice. Reviews by R. Stussy, M. Vavra, and M. Wisdom improved this paper. Research on elk and mule deer at Starkey is in accordance with approved animal welfare protocols (Wisdom et al. 1993).

### References

- Ager, A. A., B. K. Johnson, M. J. Wisdom, and P. K. Coe. 2004. A management model to simulate forage utilization by elk, mule deer, and cattle on summer range. *Transactions of the North American Wildlife and Natural Resource Conference* 69: in press.
- Anderson, E. W. and R. J. Scherzinger. 1975. Improving quality of winter forage for elk by cattle grazing. *Journal of Range Management* 28: 120-125.
- Austin, D. D., and P. J. Urness. 1986. Effects of cattle grazing on mule deer diet and area selection. *Journal of Range Management* 39:18-21.
- Baker, D. L., and N. T. Hobbs. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. *Canadian Journal of Zoology* 65:1978-1984.
- Clark, P. E. 1996. Use of livestock to improve the quality of elk winter range forage in northeastern Oregon. Ph.D. dissertation, Oregon State University, Corvallis.
- Coe, P. K., B. K. Johnson, J. W. Kern, S. L. Findholt, J. G. Kie, M. J. Wisdom. 2001. Responses of elk and mule deer to cattle in summer. *Journal of Range Management* 54:A51-A76.
- Cook, J. G. 2002. Nutrition and food. In *North American elk: ecology and management*, eds. D. E. Toweill and J. W. Thomas, 259-349. Washington and London: Smithsonian Institution Press.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. DelCurto, L. D. Bryant, L. L. Erwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monograph* 155:1-61.
- Damiran, D., T. DelCurto, S. L. Findholt, G. D. Pulsipher, B. K. Johnson. 2003. Influence of previous cattle and elk grazing on the subsequent quality and quantity of diets for cattle, deer, and elk grazing late-summer mixed-conifer rangelands. In *Proceedings, Western Section, American Society of Animal Science* 54: 320-324.
- Damiran, D. (In prep.) Inter- and intraspecific summer foraging dynamics of mule deer, elk, and cattle. Ph.D. dissertation, Oregon State University, Corvallis.

- Edgerton, P. J. and J. G. Smith. 1971. *Seasonal forage use by deer and elk on the Starkey Experimental Forest and Range, Oregon*. U.S. Department of Agriculture, Forest Service, Research Paper PNW-RP-112, Portland, Oregon.
- Hanley, T. A. 1982. The nutritional basis for food selection by ungulates. *Journal of Range Management* 35:146-149.
- 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*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-230, Portland, Oregon.
- Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: mechanisms of resource competition. *Ecological Applications* 6:200-217.
- Hofmann, R. R. 1988. Anatomy of the gastro-intestinal tract. In *The ruminant animal digestive physiology and nutrition*, ed. D.C. Church, 14-43. New Jersey: Prentice Hall, Englewood Cliffs.
- Holechek, J. L. 1979. The effects of vegetation type and grazing systems on the performance, diet and intake of yearling cattle. Ph.D. thesis, Oregon State University, Corvallis.
- Holechek, J. L., M. Vavra, and J. Skovlin. 1981. Diet quality and performance of cattle on forest and grassland range. *Journal of Animal Science* 53: 291-298.
- Holechek, J. L., M. Vavra, J. Skovlin and W. C. Krueger. 1982. Cattle diets in the Blue Mountains of Oregon II. Forests. *Journal of Range Management* 35:239-242.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *American Naturalist* 100:419-424.
- Kie, J. G., C. J. Evns, E. R. Loft, and J. W. Menke. 1991. Foraging behavior by mule deer- the influence of cattle grazing. *Journal of Wildlife Management* 55:665-674.
- Korfhage, R. C. 1974. Summer food habits of elk in the Blue Mountains of northeastern Oregon based on fecal analysis. M.S. thesis, Washington State University, Pullman.
- Korfhage, R. C., J. R. Nelson, and J. M. Skovlin. 1980. Summer diets of Rocky Mountain elk in Northeastern Oregon. *Journal of Wildlife Management* 44:746-750.
- Kufeld, R. C. 1973. Foods eaten by the Rocky Mountain elk. *Journal of Range Management* 26:106-113.
- Kufeld, R. C., O. C. Wallmo, and C. Feddema. 1973. *Foods of the Rocky Mountain mule deer*. U.S. Department of Agriculture, Forest Service, Research Paper RM-RP-111.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. Cary, North Carolina: SAS Institute Inc.
- McInnis, M. L., M. Vavra, and W. C. Krueger. 1983. A comparison of four methods used to determine the diets of large herbivores. *Journal of Range Management* 36:302-307.
- Miller, W. 2002. Elk interactions with other ungulates. In *North American elk: ecology and management*, eds. D. E. Toweill and J. W. Thomas, 435-447. Washington and London: Smithsonian Institution Press.
- Nelson, J. R. 1982. Relationships of elk and other large herbivores. In *Elk of North America, ecology and management*, eds. J. W. Thomas and D. E. Toweill, 415-441. Harrisburg, Penn: Stackpole Books.
- Parker, K. L., M. P. Gillingham, and T. A. Hanley. 1993. An accurate technique for estimating forage intake of tractable animals. *Canadian Journal of Zoology* 71: 1462-1465.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* 83:229-244.
- Stewart, K. M., R. T. Bowyer, J. G. Kie, B. L. Dick and M. Ben-David. 2003. Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? *Ecoscience* 10:297-302.
- Svejcar, T., and M. Vavra. 1985. The influence of several range improvements on estimated carrying capacity and potential beef production. *Journal of Range Management* 38:395-399.
- Vavra, M. and R. L. Phillips. 1980. Drought effects on cattle performance. In *Proceedings, Western Section, American Society of Animal Science* 31:157-160.

- Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1980. Deer and cattle diets on summer range in British Columbia. *Journal of Range Management* 33:55-59.
- Wisdom, M. J. and J. W. Thomas. 1996. Elk. In *Rangeland Wildlife*, ed. P. R. Krausman, 157-182. Denver, CO: Society of Range Management.
- Wisdom, M. J., J. G. Cook, M. M. Rowland, and J. H. Noyes. 1993. *Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-311, Portland, Oregon.

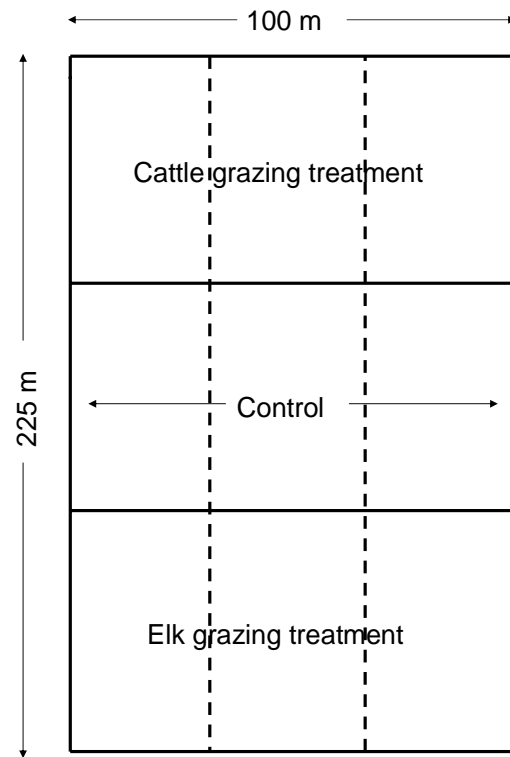


Figure 1. Layout of pastures used to determine diet composition, bite rates, dry matter intake, and diet overlap among cattle, elk, and mule deer in response to previous grazing by cattle or elk on the Starkey Experimental Forest and Range, northeast Oregon.

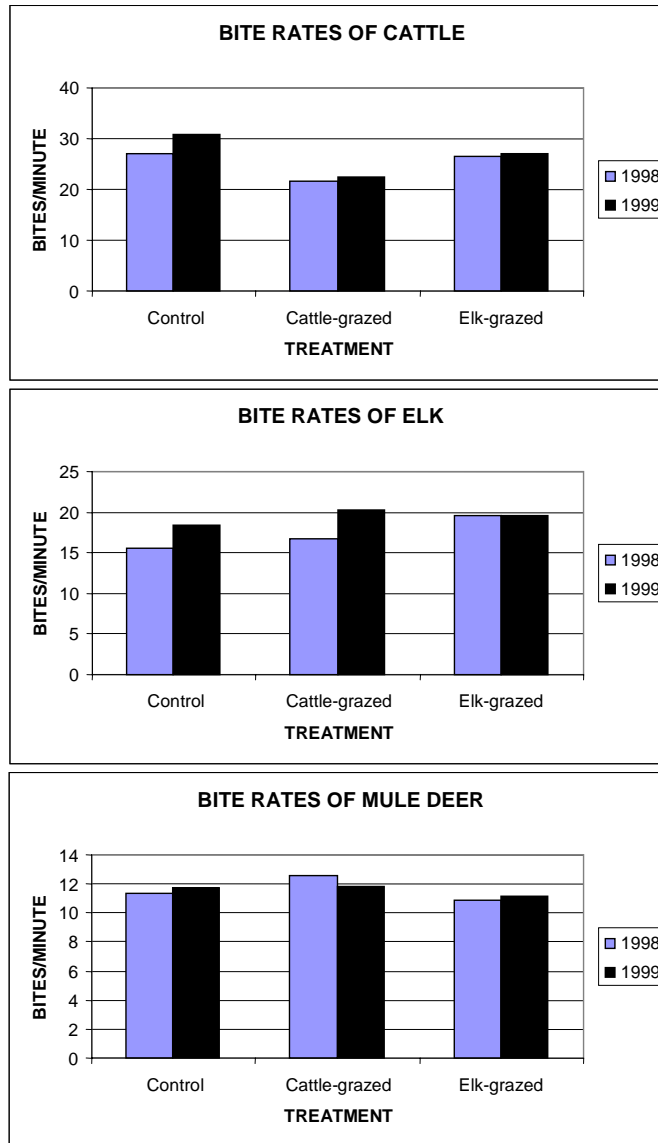


Figure 2. Bites/minute of cattle, elk, and mule deer in response to previous grazing by cattle or elk on the Starkey Experimental Forest and Range, northeast Oregon.

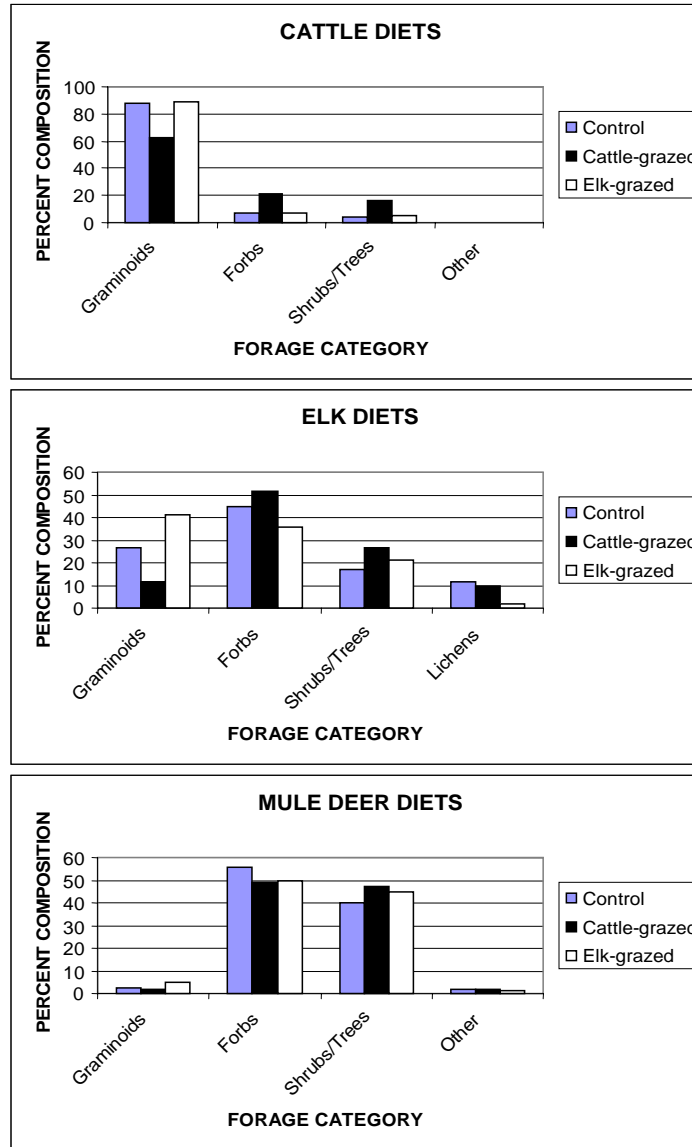


Figure 3. Diet composition of cattle, elk, and mule deer by major forage category on the Starkey Experimental Forest and Range, northeast Oregon. Diet composition was derived from bite count data.

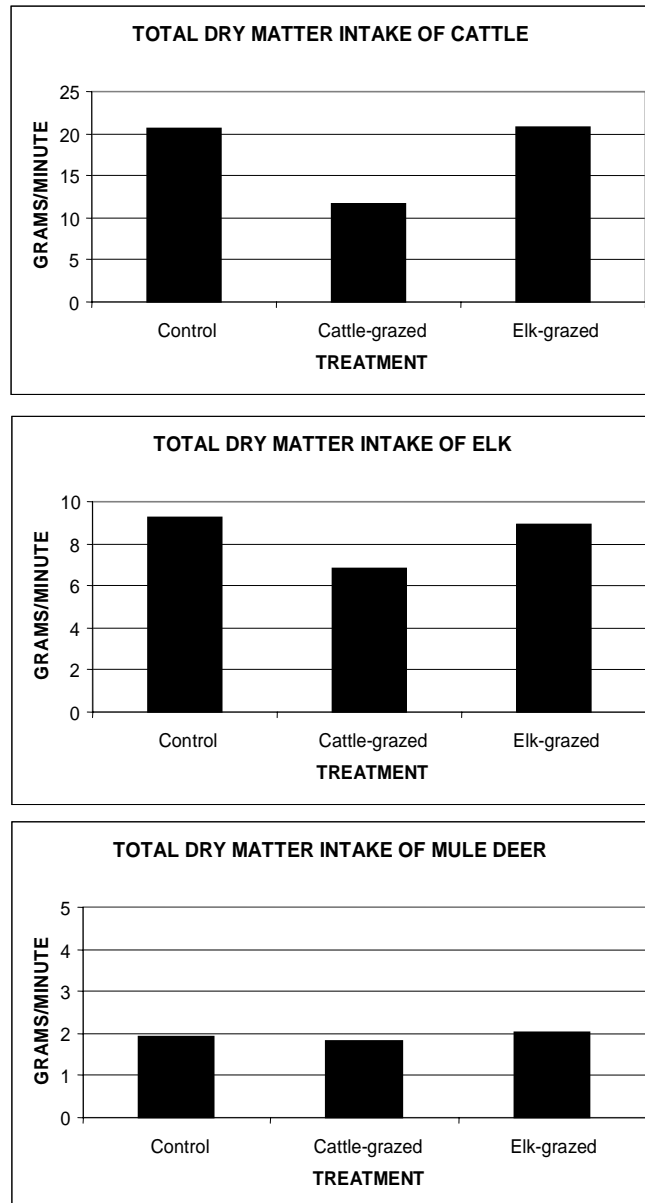


Figure 4. Total dry matter intake (grams/minute) of cattle, elk, and mule deer in response to previous grazing by cattle or elk on the Starkey Experimental Forest and Range, northeast Oregon.

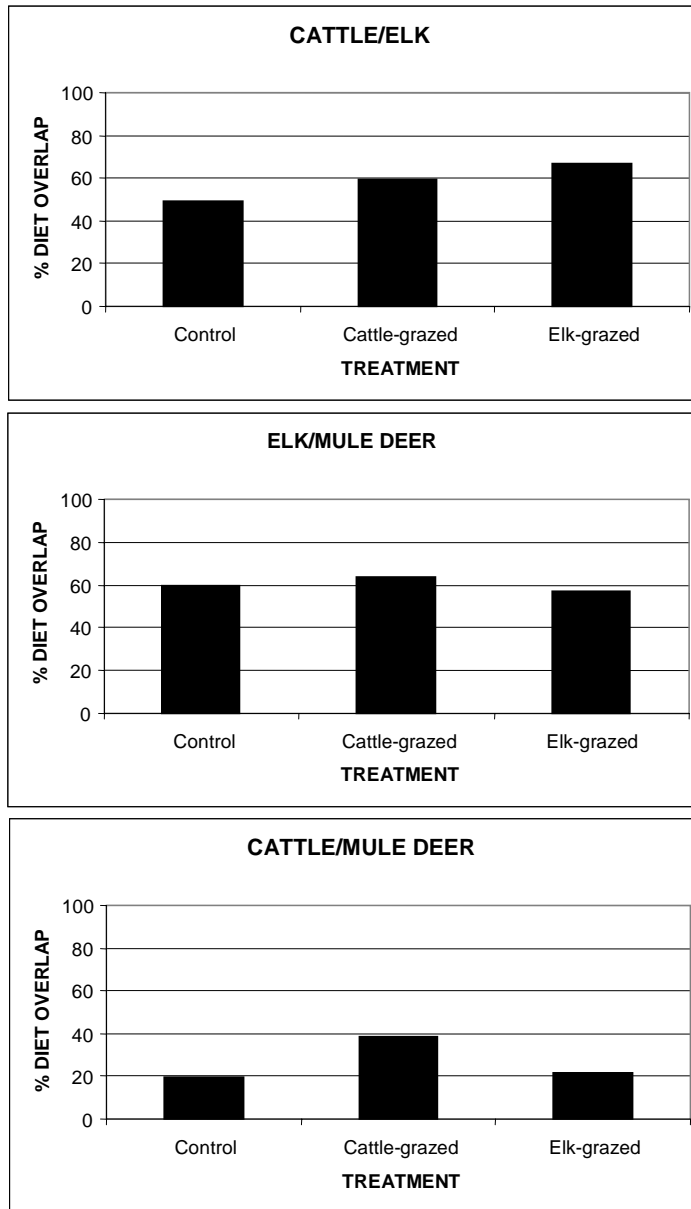


Figure 5. Percent diet overlap among mule deer, elk, and cattle by major forage category calculated with Horn's Index of Similarity at the Starkey Experimental Forest and Range, northeast Oregon. Bite count data were used to determine percent diet overlap.