AN ABSTRACT OF THE DISSERTATION OF

Daalkhaijav Damiran for the degree of Doctor of Philosophy in Animal Science
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Title: Influence of Previous Cattle and Elk Grazing on the Subsequent Diet Quality and Nutrient Intake Rate of Cattle, Deer, and Elk Grazing Late-Summer Mixed-Conifer Rangelands.

Abstract approved:

Timothy DelCurto

Four studies were conducted on late-summer diet quality and quantity of cattle (*Bos taurus*), mule deer (*Odocoileus hemionus hemionus*), and elk (*Cervus elaphus*) in response to prior grazing by cattle and elk on mixed-conifer rangelands and on related research techniques. In our first study we assessed a photographic technique to estimate shrub browse yield and utilization. Our results indicate the photographic method could be used to measure available browse yield and utilization of shrubs in a nondestructive way. In our second study we compared DMD and NDF digestibility (NDFD) estimates of in vivo digestibility using the following techniques: 1) Tilley and Terry two-stage in vitro, 2) Daisy^{II} in vitro, and 3) filter bag in situ preceded by 48 h acid-pepsin treatment. In most cases, the Daisy^{II} and in situ techniques overestimate both DM and NDF digestibility compared to the in vivo and two-stage in vitro techniques. We compared the bite-count technique (BC) of estimating diet intake and synthesized diet quality to direct estimates of diet quality using rumen evacuation technique (RE) in our third study. In summary, although the BC technique has the advantage of not requiring rumen fistulated animals, for some variables, it did not yield results that were comparable to RE technique. In our fourth study determined late-summer diet quality and nutrient intake rates of cattle, deer, and elk in response to previous early-summer grazing by cattle and elk at moderate utilization level' (31.9 ± 2.7%) in northeast Oregon. Crude protein level of the animals' diets did not differ ($P > 0.10$) on the ungrazed paddock compared to cattle or elk grazed paddocks, however, it was higher ($P < 0.10$) on cattle grazed paddock than on elk grazed paddock. Cattle diets contained lower CP and IVDMD ($P < 0.10$) compared to deer or elk diets and relative to elk, deer consistently selected forages which contained higher CP ($P < 0.10$). Our study suggested that early-summer grazing by cattle or elk at moderate utilization has little effect on the subsequent nutrient intake rate of cattle, deer, and elk in mixed-conifer rangelands during the late-summer in northeast Oregon.

Key Words: *Bos taurus*, bite-count, *Cervus elaphus*, diet quality, nutrient intake, *Odocoilleus hemionus hemionus,* and resource partition

Influence of Previous Cattle and Elk Grazing on the Subsequent Diet Quality and Nutrient Intake Rate of Cattle, Deer, and Elk Grazing Late-Summer Mixed-Conifer Rangelands

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Daalkhaijav Damiran

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APPROVED:

Major Professor, representing Animal Science

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I understand that my dissertation will become part of the permanent collection of the Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Daalkhaijav Damiran, Author

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CONTRIBUTIONS OF AUTHORS

Dr. Scott Findholt assisted with the design and data collection, data interpretation, and manuscript preparation for Chapter 2, 3, 4, and 5. Dr. Douglas Johnson assisted with the design and data interpretation of Chapter 2. Dr. David Bohnert assisted with the design and manuscript preparation for Chapter 3. Dr. Bruce Johnson assisted with the design, data collection, and manuscript preparation for Chapter 2, 4, and 5.

DEDICATION

This dissertation is dedicated to my mother Devee Damdin, a woman who has given everything to me to become who I am.

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CHAPTER 1

INTRODUCTION

Mule deer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) herds have declined during the last three decades (Carpenter 1997; Cook et al. 2004). Cattle, deer and elk share more spring, summer, and fall range than any other combination of wild and domestic ungulates in National Forests of western United States (Wisdom and Thomas 1996). Potential competition between cattle, deer, and elk is an issue of intense controversy among rangeland users and may explain declines in deer and elk populations (Miller 2002; Beck et al. 2005; Vavra 2005). However, proof that competition for forage actually occurs under judicious, carefully managed livestock grazing programs is lacking.

According to Wiens (1989) the necessary conditions for interspecific competition are (1) populations of the different species must share resources, (2) these resources must be limited, and (3) the joint exploitation of those resources and/or interference interactions related to the resources must negatively affect the performance of either or both species. These effects have population consequences as well. In contrast, commensalism occurs when one species benefits from being associated with another species, while the other species is unaffected (Martin 1990).

Resource overlap, that is the combination of diet overlap and habitat overlap (Prins 2000), is the main indicator of resource sharing. Much of the literature on competition focuses on dietary overlap. Ellis et al. (1976) developed a conceptual model of diet selection. They state that much of the variation in diets can be accounted for by (1) consumer food requirements, (2) consumer food preference, (3) food availability and, (4) consumer selectivity. Consumer food requirements influence availability and are controlled by secondary variables such as size and metabolic rate of the consumer. Consumer preference is the measure of how well a consumer likes equally available foods. Food availability determines the extent that food can be selected in accordance with preference. Selectivity relates to hunger in that a consumer's preference tends to change as hunger is satiated. Degree of differences in diet selection by organisms influences overlap.

In general, during the summer, dietary overlap is high between cattle and elk, and low between cattle and deer (Kingery et al. 1996; Peek and Krausman 1996; Findholt et al. 2004). As others (Kingery et al. 1996; Nelson 1982) have suggested, the dietary choices of elk can overlap more with dietary selection by deer, making the two species potential competitors for available forage and vice versa. Changes in forage availability, however, often lead to increased dietary overlap as forage resources become less available (Schwartz and Ellis 1981). Conversely, increased dietary overlap has been reported between cattle and elk (Stevens 1966), deer and elk (Mower and Smith 1989), and deer and cattle (Bowyer and Bleich 1984, Findholt et al. 2004) when forage abundance and availability were reduced.

Nelson (1982) mentioned the strong diet overlap between livestock and wild ungulates as possible evidence of competition. Jenkins and Wright (1988) pointed out, however, that a high level of forage overlap does not necessarily mean that competition is occurring because it is the density of individuals relative to resource base that determines the strength of competitive interactions. Conversely, Willms et al. (1980) observed that 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. Thus, strength of flexibility in their diet could result in changes of overlap with elk or cattle in areas that have high ungulates or cattle densities or low forage production. Cattle, deer, and elk are capable of drastic shifts in their diets depending upon what is available and what is palatable (Findholt et al. 2004; DelCurto et al. 2005; Sandoval et al. 2005).

Stewart et al. (2002) and Coe et al. (2004) found significant overlap in habitat use among these three species of ungulates during late-summer in northeast Oregon. Also, in northeast Oregon, Skovlin et al. (1976) found that both elk and deer used pastures not grazed by cattle more than cattle grazed pastures, with use declining as cattle stocking rate increased indicating competitive displacement of deer and elk by cattle. Competition for space and other resources is assumed to be minimal among sympatric species of wild ungulates that have evolved together (McNaughton 1991). To mitigate competition between species and facilitate coexistence, they may spatially segregate, temporally avoid each other, and use different types of resources (Sheehy and Vavra 1996).

Diet shifting or spatial segregation, however, does not mean that competition exists if the animal’s diet selection and spatial distribution are results of the presence of competing species (Schoener 1983; Coe et al. 2004; Stewart et al. 2002). Nelson (1982) also believed that deer may leave or avoid areas of heavy use by elk, even if forage is abundant and dietary overlap with elk is low. Likewise, even though diet and habitat overlap are indicators of resource sharing, they do not equate to high or low levels of competition. Coe at al. (2004) hypothesized that elk could suffer nutritional deficits sooner than cattle, and deer sooner than elk in a foraging-limited situation in the Blue Mountains of northeast Oregon. Lack of direct, cause-effect evidence, however, limits firm conclusions.

Most aspects of the ecology of large mammals are influenced by density-dependent mechanisms (McCullough 1999). Hobbs et al. (1996) found that at high densities, elk were in direct competition with cattle, but at low densities, elk had a facilitative effect on cattle diets. Further, nutrition may be inadequate at low animal densities, simply because available forage, no matter how abundant, may not adequately satisfy requirements. Ruminants cannot be expected to compensate appreciably for poor forage quality simply by eating more; they instead eat less as quality declines (Minson and Wilson 1994). This density independent aspect of nutritional influences is rarely recognized but may be important in some ecosystems (Cook et al. 2004). Climate is typically identified as having a density independent effect on ungulates (Gaillard et al. 2000). Kie et al. (1991) concluded that competition between cattle and deer was highest during years of below average precipitation.

Maintaining a proper utilization level is one way to decrease resource limitation to wild ungulates due to livestock grazing in public shared grazing allotments. The concept of animal unit equivalents (AUE) evolved from general ecological impacts of livestock grazing on allotments to set stocking rates to equivalents based on body weights (Perrier 1996). Animal unit equivalents among these three species have been based on equivalent body mass (Jacoby 1989) whereby 1 cow is equivalent to 2.5 elk or 6 deer. The classic definition of AUE (Stoddart and Smith 1955) assumes direct competition exists for forage among elk, deer, and cattle when setting stocking rates. But, by and large, as Hobbs and Carpenter (1986), Scarnecchia (1986), and Perrier (1996) emphasize, this logic is flawed in spatially heterogeneous habitats. Stocking rates cannot be set by substitution to meet utilization standards without understanding the dietary differences between competing species and the spatial distributions of those animals. Perrier (1996) further suggests adopting a definition that incorporates an impact rate of one species on whatever ecological measurement is in question. Understanding interactions between forage quality and quantity and ruminant diets is essential in assessing carrying capacity of herbivores. Based on the review of Holechek et al. (2004), if little dietary overlap (less than 5%) occurs between two species of animals when grazing them on the same range, grazing capacity is considered additive; in contrast, if dietary overlap between the two species reaches a moderate level (30 % to 70%), grazing capacity is, in most cases, non-additive. Holechek et al. (2004) further postulated that when 2 species share 3 or more of the 5 primary forages in their diets, and dietary overlaps are 50% or more, grazing capacity is considered non-additive. However, limited data have been published regarding effects of cattle presence on deer and elk diet composition in forested rangelands (Stewart et al. 2002).

Competition between animals due to resource sharing is difficult to measure (Salter and Hudson 1980; Schoener 1983; Stewart et al. 2002). Over the near-term (1-10 year) and long term (> 10 year), as Prins (2000) stated, effects of competition have to be measured in terms of either yield per individual, fertility, natality and/or mortality. No studies have documented effects of summer resource sharing on population performance of deer or elk except Cook et al.s’ (2004) study which addressed the influence of late summer nutrition on cow elk nutritional condition and calf survival in northeast Oregon. Assessing nutritional condition of animals has been impractical in the field, inaccurate, or inadequately tested (Robbins 1993; Harder and Kirkpatrick 1994). Nelson (1982) implied this kind of study is probably impossible to conduct for large ungulates under free ranging conditions. Rate of forage intake by herbivores is also used for habitat evaluation (Wickstrom et al. 1984; Spalinger and Hobbs 1992; Parker et al. 1996). Rate of food intake exerts an important influence on many aspects of herbivore ecology, including diet and habitat choices, social organization, and predator avoidance (Shipley et al. 1994). The rate of forage intake by ungulates is controlled over several timescales. Over an animal's lifetime, nutrient intake is regulated to meet the costs of maintenance and production. On daily scales, intake rate is limited by digestion and excretion, by the amount of time an animal can invest in feeding, and by the short-term rate of consumption achieved while the animal feeds. On yet a finer scale, intake rate is limited by abundance and distribution of plants (Forbs 1988; Gross et al. 1993; Gong et al. 1996). Therefore, induced changes in short-term nutrient intake rate by wild ungulates in response to cattle grazing provide an initial indication of grazing interactions. Also, clearly identifying changes in diet composition induced by initial grazing treatments will help clarify an important aspect of competition. Furthermore, different species or combinations of herbivores can have dramatically different influences on the composition of forest understory, provided that foraging selectivity is accommodated (Riggs et al. 2004). However, less is known of how nutrient intake rate of diet composition of deer and elk respond to sharing rangelands with cattle. Diet studies of ungulates during different seasons, both with and without prior grazing, should help to establish competitive interactions.

Moreover, nutrition has largely been discounted in national forest models used to reconcile deer and elk habitat quality with other land management concerns (Edge et al. 1990). This reflects an apparent perception that nutrition is not a particularly important factor affecting most deer and elk herds. It may also reflect uncertainty regarding how to evaluate nutritional resources across large landscapes in a manner relevant to ungulate populations (Cook et al. 2004).

A controlled experiment examining the effects of cattle grazing on wild ungulate foraging dynamics holds the most promise for understanding and quantifying nutritional competition among large ungulates. Therefore, the primary objectives of our study are:

1. To determine if grazing by either cattle or elk at a moderate utilization level affects botanical composition, nutritional quality, and nutrient intake rate during subsequent grazing of cattle, deer, and elk. We chose study sites in previously logged grand fir (*Abies grandis* [Dougl. ex D. Don]) sites or mixed-conifer sites at the Starkey Experimental Forest and Range (Starkey) in the Blue Mountains of northeast Oregon. These sites were selected because spatial and temporal overlap of the three species occurs in this habitat (Coe et al. 2004). Moderate (30-40%) utilization 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 (Findholt et al. 2004). Timber harvest, livestock grazing, motorized traffic, hunting, camping, and other public uses at Starkey are managed like those on National Forests elsewhere in the western United States (Wisdom et al. 2004); thus, this research is designed to address the magnitude of competition between cattle, deer, and elk on shared rangelands in the Blue

Mountains of Oregon and Washington. This data should be applicable to other National Forests of the western United States. Another significant aspect of my study is data gathered on forage intake rate, forage biomass, and other foraging behavior factors can be incorporated into a forage allocation model for resource managers (Shipley and Spalinger 1995; Ager et al. 2004) at Starkey.

Estimating nutrient intake rate requires measurement of a variety of other foraging attributes, including bite weight; bite rates, diet intake rates, and dietary quality. The two most common approaches used by nutritional ecologists in recent years for estimating short term nutrient intake with large ungulates is to combine the bite-count (Free et al. 1971; Wickstrom et al. 1984; Canon et al. 1987) or fistulae technique (Stobbs 1973; Chacon and Stobbs 1976; Sidahmed et al. 1977) with in vitro digestibility (Tilley and Terry 1963). Both approaches can result in biased estimates that may not truly represent the actual diet free ranging animals are consuming. We chose the bite-count and in vitro digestibility techniques combination for our study because it has been equally useful for wild and domesticated ungulates (Wallis De Vries 1995). Also, field and laboratory techniques that cause even a small bias of in forage nutrient concentration might lead to important misinterpretations of nutritional adequacy. Therefore, when this technique is used the calibration or validation under experimental conditions is advisable, especially when using this technique in rangelands with heterogeneous vegetation. The bite-count technique can be evaluated by esophageal or rumen fistulation. As many researchers have reported, fistulated diet quantity and quality samples provide a better representation of what a grazing animal actually consumes (Bohman and Lesperance 1967; Holechek et al. 1982; Forbs 1988), but it is difficult to use with wild animals (Rice 1970). In addition, it is cost-intensive and requires considerable time.

Even though the two-stage technique for in vitro digestion of forages developed by Tilley and Terry (1963) is highly correlated with in vivo digestibility (Goldman et al. 1987; De Boever et al. 1988), this technique is time-consuming and labor intensive. Therefore, we used the newer Daisy^{II} technique (ANKOM Technology, Macedon, NY) for determination of in vitro digestibility. Compared to conventional methods, this technique simplifies the measurement of in vitro digestibility by eliminating the requirement for filtering samples after digestion, which is often one of the most labor intensive steps in the conventional procedure (Holden 1999). The incubation of several samples within a jar in the Daisy^{II} incubator also reduces the need for individual incubation of samples in tubes. Several studies have demonstrated the Daisy^{II} technique does have comparable digestibility values to traditional procedures for some feeds (Holden 1999; Mabjeesh et al. 2000; Wilman and Adesogan 2000); however, more research is needed before it is accepted as a tool for evaluation of diet quality.

Shrub utilization was measured by an environmentally friendly (Hyder et al. 2003), simple, fast, inexpensive, and recently developed method photographic technique (Reynolds 1999). It is based on photographing shrubs before and after grazing, downloading digital images into a computer, and then calculating the foliage removed for each plant. However, this technique needs to be tested for accuracy and repeatability for measuring changes in shrub biomass.

Other objectives were:

2. To validate the photographic technique for shrub utilization and the bite-count technique for estimating animal diet intake in the heterogeneous environmental condition at Starkey. In addition, we hope to validate the Daisy^{II} technique of estimating in vitro digestibility.

In the following chapters data will be presented to answer these two objectives. Chapter 2 contains the results of assessing a photographic technique to estimate shrub yield and utilization. Chapter 3 contains the results of comparison of techniques and grinding sizes to estimate digestibility of forage based ruminant diets. Chapter 4 addresses results of comparison of the bite-count and rumen evacuation techniques to estimate diet quantity and quality. Therefore, the studies presented in these 3 chapters were designed to be follow-up research which was to validate the techniques used in the main study. Finally, Chapter 5 evaluates the influence of previous cattle and elk grazing at the moderate utilization level on subsequent diet quality and quantity of diets for cattle, deer, and elk grazing late-summer mixed-conifer rangelands.

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CHAPTER 2

Estimating Shrub Forage Yield and Utilization Using a Photographic Technique

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ABSTRACT

We assessed a photographic technique to estimate shrub yield and utilization of common snowberry, snowbrush, and firmleaf willow found in mixed-conifer rangelands. We determined the correlation between green leaf area size (LA) and forage yield (Y) and compared plant utilization estimated by the photographic technique (ULA) to actual utilization (UY) values. Shrub forage yield and utilization were determined by hand plucking in five to eight increments. Before the first plucking, and after each subsequent plucking, we took two photos that were perpendicular to each other at the intersection of the shrub. Each photo was evaluated using image-processing software to produce red (R), green (G), and blue (B) color band images. Green leaf area was determined as follows: pixel = ([G - R] + [G - B]) / (G + R + G + B); Green leaf area, cm^2 = (Calibration [C], $\text{cm}^2 \cdot \text{pixel}^{-1}$) x (LA, pixel).

Green leaf area calculated from the photographic technique was strongly correlated ($r^2 = 0.83\text{-}0.94$, $P < 0.001$) with forage yield for all three shrubs. A strong correlation ($r^2 = 0.95$, $n = 142$) was detected between utilization values estimated through green leaf area size and actual values. Utilization estimated by LA did not differ ($P = 0.60$, $n = 142$) from actual utilization values. In summary, our results indicate the photographic technique could be used once calibration curves are developed to measure available browse yield and utilization of shrubs in a nondestructive approach.

Key Words: photography, shrub utilization, vegetation inventory

INTRODUCTION

Shrubs comprise a significant amount of total forage resources in rangelands; however, estimating browse yield and use is one of the most difficult vegetation characteristics to determine (Bonham 1989). The twig length measurement technique (Nelson 1930) is used to determine yield after completion of annual growth in particular shrubs. This technique gives good estimates of utilization but is only effective on shrubs that have a definitive growth period. The extensive browse technique (BLM 1996) is designed to provide data on age and form classes, utilization, species composition, availability, and hedging of the browse component. This technique is more rapid than technques requiring measurements but is less accurate because estimates are used. Basile and Hutchings (1966) and Lyon (1968) concluded that using length-diameter relationships was a promising technique of estimating utilization from post browsing diameter measurements. However, twig diameter measurement required a definitive period of growth and was not effective on shrubs that had indeterminate or opportunistic growth (Reynolds 1999).

This study was designed to determine the potential of a photographic technique in assessing shrub forage yield and its utilization. If practical, digital sampling of vegetation could prove to be efficient, economical, accurate, less subjective, and nondestructive.

MATERIALS AND METHODS

Study Area

Research was conducted on the USDA, Forest Service, Starkey Experimental Forest and Range (Starkey) in the Blue Mountains (45°15’N, 118°25’W) of northeast Oregon, which is approximately 35 km southwest of La Grande, Oregon. Vegetation characteristics of this area are described by Pickford and Reid (1948), Skovlin et al. (1976) and Holechek et al. (1982). Cattle (*Bos taurus*) graze seasonally, and mule deer (*Odocoileus hemionus hemionus*) or elk (*Cervus elaphus*) are sympatric with cattle at Starkey (Coe et al. 2001).

Shrub Selection

We selected three shrubs that represented variation in leaf area density, leaf orientation, and leaf shape, abundance on the landscape, and nutritive value for wild and domestic ungulates. We sampled common snowberry (*Symphoricarpos albus* [L.] Blake), snowbrush (*Ceanothus velutinus* Douglas ex Hook.) and firmleaf willow (*Salix rigida* Muhl.) found in mixed-conifer rangelands at Starkey. We sampled ten randomly chosen plants from each species on clear days on 27-29 June 2000 between 1000 and 1500 hours, using techniques generally similar to those as described by Reynolds (1999) and Hyder et al. (2003). Size of shrubs ranged from 35 to 96 cm tall and 15 to 180 cm wide. Shrubs were accessible to wildlife year round, but were not accessible to cattle for this growing season. Additionally, shrubs selected showed no sign of heavy utilization but evidence of light browsing was present on some individual plants of all three species selected.

Preparation of Plants for Photographing

Before taking photographs, excess herbaceous vegetation was cleared from around the shrubs to eliminate potential interference from leaf material on stems and background vegetation during later analysis. A backdrop was made of a white bed sheet supported on a plastic pipe frame measuring 1 x 1 m or 1.5 x 2.0 m, which was large enough to provide a background for the entire shrub. White sheets were also spread on the ground separating shrubs from ground vegetation. A meter board painted yellow and marked with 1-cm wide bands at 10-cm intervals was placed perpendicular to each photo point at the center of each shrub without interfering with the shrub image. A wooden stake was placed behind the meterboard to allow for relocation of the board placement in successive photos. The shrub identification, sample number, side of approach, and increment number of leaf removal was written on a dry-erase notepad and attached to the backdrop so it would appear in each photograph.

Photographing and Browsing

Shrubs were photographed using an “Olympus D-500L” digital camera. The camera was mounted on a tripod 50 cm above the ground and photos were taken at a distance of 1.5 or 3.0 m from the shrub depending on shrub size. We simulated browsing each shrub through hand plucking (Cook and Stubbendieck 1986) in five to eight increments until the shrubs were completely defoliated. Before the first plucking, and after each plucking, photos were taken from two horizontal directions perpendicular to each other.

The harvested plant material for each shrub and plucking event was placed in separate paper bags, dried in a forced air dryer at 50°C for 2 days, and weighed to obtain forage yield for each shrub and plucking event. Total forage yield (Y, g) of each shrub was determined by summing all dry weights from each plucking event for the shrub. Utilization (UY, %) for each plucking event was then calculated based on the total plant material removed from the shrub up to and including the current plucking event.

Image Processing

The images were downloaded to a computer and saved as JPEG files. Then images were imported into Corel Photo-Paint 8 (SYNEX Inc, Brooklyn, NY) software, cropped to show just the shrubs and meter board, and saved in a Windows Bitmap (BMP) file format for computer processing. The BMPs were imported into a software package “VegMeasure” (Johnson et al. 2003) to produce red (R), green (G), and blue (B) color band images. Each of these images was recombined using the image calculator function. Green leaf area size was determined as follows: pixel = ([G - R] + [G - B]) / (G + R + G + B) (Johnson et al. 2003). For each image, we then analyzed the meter board to determine the ratio between the metric height and pixel height to calculate a scaling factor for the size of each pixel (C $\mathrm{cm \cdot pixel^{-1}}$) to convert image’s pixel length to “metric” length. For each image, we then summed the number of green pixels to calculate green leaf area. We averaged the green leaf area from the two images made at perpendicular directions after each plucking event. Utilization estimated by green leaf area (ULA) size, was calculated, % = ([Before browsing leaf area size, cm^2 – After browsing leaf area, cm^2] / [Before browsing leaf area size, cm^2] x 100).

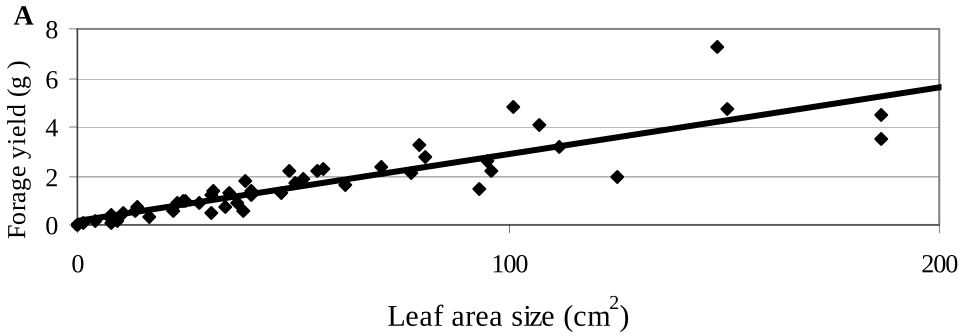
Statistical Analyses

Shrub green leaf area size was regressed against the corresponding forage yield using the REG procedure of SAS (SAS Institute, 2001). Utilization values analyzed as split-plot design with 3 (shrub species) x 2 (technique for estimate utilization) factorial arrangements of treatments using the DIFF option in the SAS/GLM LSMeans statement of SAS.

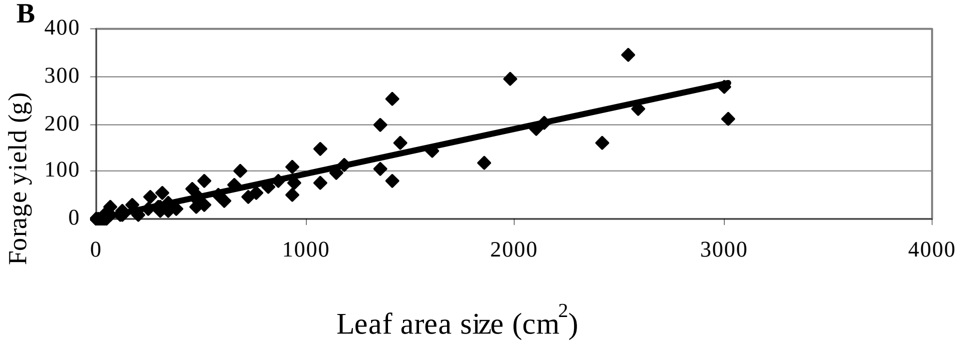
RESULTS AND DISCUSSION

Using the photographic technique the correlation (r^2) between green leaf area and forage yield was 0.81 ($n = 169$, $P < 0.001$) when data were pooled from all three shrubs. Both the slope and the Y-intercept of the regression model differed significantly ($P < 0.05$) among shrubs (Figure 2.1, 2.2).

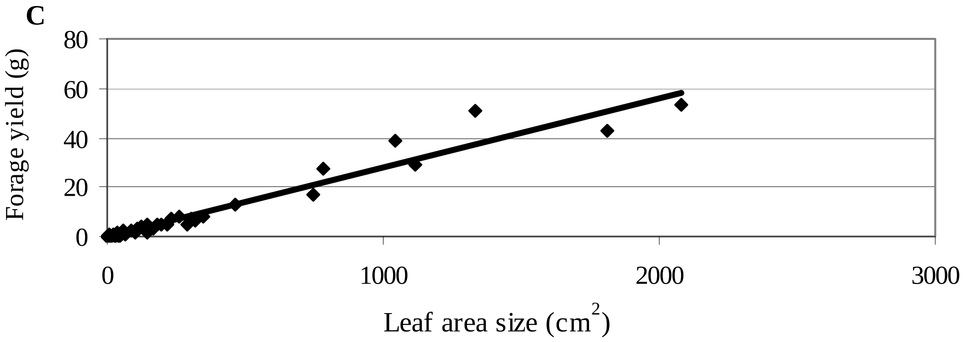
Utilization values using green leaf area size were strongly correlated with actual utilization values (Table 2.1). A shrub species x research technique interaction on utilization estimates was not detected ($P > 0.05$). Utilization values estimated through green leaf area were not different ($P = 0.60$, $n = 142$) from actual utilization values.



$Y = 0.174 + 0.027\ X\ (r^2 = 0.87,\ P < 0.01)$



$Y = 1.06 + 0.094X\ \ (r^2 = 0.84,\ P < 0.01)$



$Y = -\ 0.212 + 0.028X\ (r^2 = 0.94,\ P < 0.01)$

Figure 2.1. Regression equations for the linear model fit to the green leaf area size (X; cm^2) and predicted forage yield (Y; g, DM) of common snowberry (A), snowbrush (B), and firmleaf willow (C).

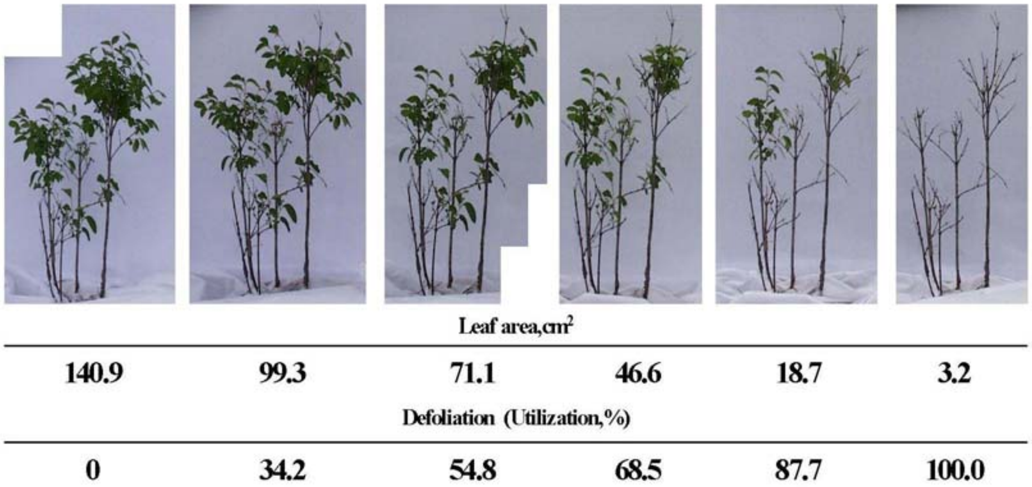


Figure 2.2. This common snowberry shrub simulated browsing in five increments until the shrub was completely defoliated. Before the first plucking, and after each subsequent plucking, photos were taken from two horizontal directions perpendicular to each other and averaged for estimation of leaf area sizes.

Table 2.1. Correlation coefficients (r^2), slope, Y-intercepts, *F*-value and number of observations (n) for the linear model fit to utilization (%) estimated by green leaf area size (X) and predicted actual (Y) values.

Shrubs	Y-intercept	Slope	r^2	*F*	n^1	*P*-value
Common snowberry	3.943	0.955	0.934	694	50	<0.001
Snowbrush	2.042	0.976	0.963	1454	57	<0.001
Firmleaf willow	8.913	0.932	0.962	869	35	<0.001

[1] *n* = number of data pairs used to develop a prediction equation.

To detect a difference of 20% of the mean forage yield with a probability of 80% and using a 5% significance level (Kuehl 2000), at least 25, 18, and 79 snowberry, snowbrush, and firmleaf willow plants, respectively, would be required. Likewise, to detect above-mentioned differences using a traditional technique (hand plucking) at least 21, 22, and 79 snowberry, snowbrush, and firmleaf willow plants would be required, respectively. This suggests the photographic technique has similar precision with the traditional technique. However, as image analysis technology improves, the applicability, accuracy, and precision of techniques, such as the photographic technique will improve.

Our results suggest that digital images and an algorithm based on color theory can provide good estimates of shrub forage yield in mixed-conifer rangelands. However, the technique requires a proper calibration based on double sampling, harvesting forage yield, and taking photos of shrub species at a particular stage of growth. Consequently shrub utilization can be assessed through direct comparison of green leaf area size estimated from images taken before and after browsing.

Care should be taken to minimize shadows that fall on shrubs photographed. Shadows make it more difficult, but not impossible, to separate leaves from woody material and background in photographs. Consequently, cloudy days may reduce shadows and be better than bright sunny days for this technique. If the shrubs' twigs and stems contain high chlorophyll pigment, the available forage yield and utilization value may be overestimated. This technique will be difficult to use on large shrubs due to the limitations of harvesting the entire plant which is necessary for creating regression equations. Raindrops, or early morning dew, and windy days also may affect green leaf area size. If during browsing, natural /climatic events occurred (i.e., frost, insect damage, or disease), utilization values may also be biased. To avoid bias caused by utilization during the growing season, some shrubs should be protected with wire cages which would be inaccessible to browsing animals. Protected shrubs would serve as a control to adjust growth or senescing rate and loss caused by reasons other than browsing. To determine proper calibration, photographs of protected shrubs should be taken before and after utilization photos. The use of readily available computer technology and photographic equipment will decrease the subjectivity and increase the accuracy of field measurement of plant geometry and associated losses due to herbivory or other factors (Hyder et al. 2003).

MANAGEMENT IMPLICATIONS

This study demonstrated that the photographic technique has a very high probability of improving shrub yield and utilization estimates in range conditions in terms of economic and research accuracy. Unlike many of the traditional utilization techniques, this technique is non-destructive.

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CHAPTER 3

Comparison of Techniques and Grinding Sizes to Estimate Digestibility of Forage Based Ruminant Diets

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ABSTRACT

We compared dry matter (DMD) and neutral detergent fiber (NDFD) digestibility estimates of in vivo digestibility using the following techniques: 1) Tilley and Terry two-stage in vitro (conventional in vitro or IVDMD), 2) Daisy^{II} in vitro (Daisy^{II}), and 3) filter bag in situ preceded by 48 h acid-pepsin treatment. In addition, we also evaluated the effects due to sampling size (0.25 vs. 0.50 g) and Wiley Mill grinding size (1-mm vs. 2-mm). In Experiment 1, fifteen forage species from mixed-conifer rangelands were used to evaluate digestion estimation techniques. Compared to IVDMD, Daisy^{II} and in situ techniques overestimated ($P < 0.01$) DMD. In Experiment 2, we used meadow hay samples to compare the above techniques to in vivo DMD. In situ DMD, Daisy^{II} DMD, and IVDMD were greater ($P < 0.01$) than in vivo DMD. In contrast, in situ NDFD did not differ ($P = 0.13$) from in vivo NDFD for sheep. In Experiment 3, we used grasses, forbs, shrubs, and lichen in separate analyses to evaluate the interaction of Wiley Mill grinding size (1-mm vs. 2-mm) and digestibility technique. For grass hay, Daisy^{II} and in situ DMD increased ($P < 0.05$), but IVDMD decreased ($P < 0.05$) compared to in vivo DMD. Daisy^{II} and in situ NDFD decreased ($P < 0.05$) compared to in vivo NDFD. In contrast, straw IVDMD, Daisy^{II} and in situ DM, and NDF digestibility decreased ($P < 0.01$) compared to in vivo DM and NDF digestibility. Daisy^{II} and in situ digestibility estimates were greater ($P < 0.01$) for grass hay milled at 1-mm vs. 2-mm, while all digestibility estimates were higher ($P < 0.01$) for straw ground at 1-mm. For the Daisy^{II} and in situ techniques, a 0.25 g sample resulted in greater ($P < 0.05$) estimates of digestibility than a 0.5 g sample. The coefficients of variation were slightly higher with the filter bag based techniques than with the conventional in vitro technique; of fifty-five coefficients of variation calculated for each technique, means were 4.26%, 4.69%, and 4.65% for conventional in vitro, Daisy$^{\mathrm{II}}$, and in situ techniques, respectively.

Digestibility values estimated by Daisy$^{\mathrm{II}}$ and in situ techniques were correlated (r^2 = 0.58–0.88) with values estimated by conventional in vitro and in vivo techniques, although in most cases Daisy$^{\mathrm{II}}$ and in situ techniques overestimated DM and NDF digestibility. The sieving off of different size particles in the ground forage sample, correcting for the fine particle losses from the filter bag during digestion, washing, and/or grouping the feeds into categories based on cell wall structure, and applying a corresponding correction factor may increase predictability and accuracy of Daisy$^{\mathrm{II}}$ technique.

Key Words: digestion techniques, filter bags, grinding size, in vitro digestibility

INTRODUCTION

The two-stage technique (conventional in vitro or IVDMD) for in vitro digestion of forages developed by Tilley and Terry (1963) has been widely used because of its convenience and high degree of correlation to in vivo digestibility and accuracy (Tilley and Terry 1963; Goldman et al. 1987; De Boever et al. 1988). However, the technique is time-consuming and labor intensive. Recently, a filter bag technique (Daisy^{II}) for analyzing forage in vitro dry matter (DM) and neutral detergent fiber (NDF) digestibility was developed by ANKOM Technology Corporation (Fairport, NY). The technique entails digesting several forage samples in bags within glass jars which are rotated in an insulated chamber. This new approach must be validated on a wide variety of forages before becoming generally accepted.

Holden (1999) conducted an experiment with 10 feeds which were digested by the conventional in vitro technique or the Daisy^{II} technique and concluded that the Daisy^{II} technique can be used to improve labor efficiency in estimating DM digestibility. Vogel et al. (1999) recorded conflicting results when they used three different forages for comparing the conventional in vitro technique with the Daisy^{II} technique; with switchgrass (*Panicum virgatum* L.) and forage sorghum (*Sorghum bicolor* L.) both techniques resulted in similar dry matter digestibility (DMD) estimates, but with smooth bromegrass (*Bromus inermis* Leyss.) the Daisy^{II} technique increased DMD compared with conventional IVDMD.

Wilman and Adesogan (2000) compared conventional IVDMD estimates of 72 forage samples from two forage species (Italian ryegrass [*Lolium multiflorum* Lam.]

and alfalfa [*Medicago sativa* L.]) to DMD estimates using the Daisy^{II} technique. They found that the conventional in vitro technique is likely to give more precise results than the Daisy^{II}. However, they also postulated that use of the Daisy^{II}, rather than conventional in vitro technique, gave acceptable digestibility estimates for forage when the emphasis was on saving labor. Furthermore, Adesogon (2002) noted that the digestibility results obtained by the Daisy^{II} technique can be affected by sample size and processing method, the proximity of the incubation jars to the heat source, and the extent to which individual bags are submerged throughout incubation. There is an absence of in vivo data against which the Daisy^{II} technique can be validated.

Our objectives were to 1) compare digestibility estimates for forage based ruminant diets using the Daisy^{II} technique, filter bag in situ DMD, and NDF digestibility (NDFD) to in vivo and conventional in vitro DM and NDF digestibility, 2) evaluate effects of sample size and grinding size on digestibility estimates, and 3) determine whether it is possible to predict conventional in vitro/in vivo digestibility with Daisy^{II} or filter bag in situ technique.

MATERIALS AND METHODS

Experimental Design and Data Collection

We conducted three experiments to evaluate some common techniques used to estimate forage digestibility of grazing ruminants using 150 samples from cool-season (C_3) forage species or types. Plant nomenclature throughout paper follows the recommendations of the USDA Natural Resources Conservation Service (USDA, NRCS 2005).

Experiment 1

One hundred forage samples including five grasses (California brome [*Bromus carinatus* H. & A], elk sedge [*Carex geyeri* Boott], pinegrass [*Calamagrostis rubescens* Bukl.], orchardgrass [*Dactylis glomerate* L.], and western fescue [*Festuca occidentalis* Walt.]); five forbs (western yarrow [*Achillea millefolium lanulosa* L.], tall annual willowherb [*Epilobium paniculatum* Nutt.], strawberry [*Fragaria* spp.], white hawkweed [*Hieracium albiflorum* Hook.], and lupine [*Lupinus* spp.]); four shrubs (low oregongrape [*Berberis repens* Lindl.], shinyleaf spirea [*Spiraea betulifolia lucida* Pall.], common snowberry [*Symphoricarpos albus* {L.} Blake], and big huckleberry [*Vaccinium membranaceum* Hook.]); and one lichen (tree hair lichen [*Bryoria fremontii* Tuck.]) species from a mixed-conifer rangeland were used to evaluate digestion estimation techniques.

We collected samples in late August, stored them in labeled paper bags in the field, and oven-dried them at 50ºC for 48 h. Dried samples were ground through a Wiley Mill (Model #2, Arthur H. Thomas Co, Philadelphia, PA) to pass a 1-mm screen. Techniques used to compare digestibility estimates were the conventional in vitro (Tilley and Terry 1963), filter bag in vitro (Daisy^{II}), and filter bag in situ (in situ). In this study, each sample was replicated twice for each of the techniques evaluated. If the coefficient of variation within replicates for each technique of each sample mean was > 4.0%, results were rejected and analyses reapplied to samples.

Experiment 2

Meadow hay samples from previously conducted in vivo digestibility trials were used to compare the conventional in vitro, Daisy^{II}, and in situ techniques. Low-quality meadow hay was harvested from native flood meadows consisting of approximately 82% meadow foxtail (*Alopecurus pratensis* L.) with the majority of the remaining vegetation consisting of rushes (*Juncus* spp.), sedges (*Carex* spp.), and blue wild rye (*Elymus triticoides* Buckl.; Wenick 2000). We obtained in vivo apparent digestibility estimates from four wether sheep (Bohnert et al. 2002a) with an average body weight (BW) of 36 ± 1 kg and four steers (Bohnert et al. 2002b) with an average BW of 264 ± 8 kg, that consumed meadow hay without supplementation. Dried hay, ort, and fecal samples were ground in a Wiley Mill (1-mm screen size).

Experiment 3

We used meadow hay and fine fescue (*Festuca* spp.) straw samples from previously conducted (White 2003) digestibility trials to compare the conventional in vitro, Daisy^{II}, and in situ techniques. In vivo apparent digestibility data were from three unsupplemented steers (BW = 456 ± 6 kg) that had consumed each type of harvested forage. Samples were ground through either a 1- or 2-mm screen in a Wiley Mill to evaluate the effect of grinding size on digestibility estimates. Also, two forbs (western yarrow and strawberry), two shrubs (red alder [*Alnus rubra* Bong.] and firmleaf willow [*Salix rigida* Muhl.]), and tree hair lichen were ground through a 1- or 2-mm screen and subjected to ten consecutive conventional in vitro, Daisy^{II}, and in situ runs for DMD and NDF digestibility estimates. In addition, for the Daisy^{II} and in situ techniques, two sampling sizes (0.25 or 0.5 g) were used for the meadow hay and firmleaf willow to evaluate effects of sampling size on digestibility estimates.

Study Techniques

Conventional in vitro

The technique for determination of conventional in vitro digestibility complied with the Galyean (1997) modification of the Tilley and Terry (1963) two-stage procedure. Twenty-four 50-mL Nalgene tubes were placed in a rack. Subsequently, 0.5 g of experimental samples were added to each of 20 tubes, 0.5 g samples from laboratory standards (grass hay) were added to 2 tubes, and other 2 tubes were used as blanks for experiments. In each tube, 35 mL of a buffer-inoculum mixture as described by Marten and Barnes (1980) was added under purging with CO_2 and caped tightly with a rubber stopper/gas-release port (Galyean 1997). Samples were incubated for 48 h in a water bath at 39ºC, followed by further digestion in an acid-pepsin solution containing 0.1% pepsin (Catalog # P53-500, Fisher Scientific, Pittsburgh, PA) and 10% 1 N HCL (35 mL of acid-pepsin solution was added to each tube) for 48 h in water bath at 39ºC. All tubes were mixed by swirling (Vortex Genie-2 Mixer, VWR Scientific, West Chester, PA) them at 2, 4, 20, and 28 h after adding the buffer-inoculum and at 2, 4, and 6 h after adding acid-pepsin. After completion of the digestion, contents were filtered into pre-weighed standard coarse fritted disk gooch crucibles under mild vacuum, dried at 100ºC for 12 h, weighed for determination of DM, placed in a muffle furnace at 525ºC for at least 12 h, and re-weighed for complete calculation.

Daisy^{II} in vitro

For the Daisy^{II} technique, Ankom filter bags (F57, 5.0 x 5.5 cm; ANKOM Technology Corporation, Fairport, NY) and an incubator (Daisy^{II}; ANKOM Technology Corporation, Fairport, NY) were utilized. The incubator consisted of a constant temperature cabinet that contains four glass fermentation jars that are placed on rotation racks in the cabinet (Vogel et al. 1999). Sample sizes used were either 0.25 g (only for sample size trials of Experiment 3) or 0.5 g (for Experiments 1, 2, and 3) per bag with 24 bags per incubation jar. Each run contained one replicate of the experimental forage samples (20 samples) as well as two standards and two blank bags. Samples were heat sealed (Heat sealer #1915; ANKOM Technology

Corporation, Fairport, NY) in filter bags, placed in jars, and incubated for 48 h at 39ºC in a buffer-inoculum solution using techniques similar to those described in detail by Vogel et al. (1999) and Holden (1999). Briefly, buffer solution (1 600 mL) and rumen inoculum (400 mL) were added to each jar, the jars purged with CO_2, and lids with gas relief valves were placed on the jars. After incubation, the buffer-inoculum was drained from the jars and the filter bags were gently squeezed against the sides of the jar to remove the gas trapped in the inflated bags. The bags were rinsed in jars with three changes of warm tap water (Holden 1999) and then removed and boiled in a neutral detergent solution (Van Soest et al. 1991) for 80 min using an Ankom^{200} fiber analyzer (ANKOM Technology Corporation, Fairport, NY). After the boiling period, NDF solution was drained from the reaction vessel and the reaction vessel was filled with 2 L of 95ºC distilled water. The top was left open and the samples were agitated for 5 min. The hot water rinse was repeated five times. Four mL of Ankom heat stable α-amylase (ANKOM Technology FAA) with activity level of 340-374MWU·mL^{-1} was added to each of the first three rinses. Subsequently, filter bags were removed from jars and soaked in acetone for 5 min, air-dried, then stored at least 12 h in a 100ºC oven, cooled in a desiccator, and weighed.

Filter bag in situ

Samples were weighed (0.25 g or 0.5 g; sample weight : bag surface area ratio was 8 and 16mg·cm^{-2} for the 0.25 g and 0.5 g samples, respectively) into acetone pre-rinsed, pre-weighed, and numbered Ankom filter bags (F57; ANKOM Technology Corporation, Fairport, NY). Twenty-four sample bags (20 for samples, consisting of

10 from each sample size, 2 standards, and 2 blanks) were placed in each jar in a Daisy^{II} incubator. The sample bags were incubated for 48 h at 39ºC in an acid-pepsin solution (same solution as described in the conventional in vitro technique section) using a Daisy^{II} incubator. Sample bags were then removed, rinsed with warm tap water, placed in a polyester mesh bag (36 x 42 cm), inserted into the rumen of two cannulated steers, and incubated for 48 h. The cord length between cannula cap and anchor weight was 80 cm. After incubation, sample bags were removed and rinsed with tap water (39ºC) until the rinse water was clear. Subsequently, excess water was removed by gently pressuring and samples analyzed for NDF as described in the Daisy^{II} in vitro section.

Preparation of the rumen inoculum

Ruminal inoculum was obtained from two rumen cannulated steers consuming a moderate quality (8.6% CP, 69.0% NDF; DM) meadow hay diet. Meadow hay was provided once daily. Ruminal contents were obtained approximately 30 minutes after feeding. Steers in this study were cared for in accordance with guidelines established by the Institutional Animal Care and Use Committee at the Oregon State University. We collected approximately 4 L of rumen contents from each steer into an 8 L pre-warmed (39ºC) container. Ruminal contents were brought into the laboratory, immediately strained through four layers of cheesecloth into two 4 L conical flasks, and placed in a 39ºC water bath. In addition, approximately 1 L of rumen contents were blended (Waring blender; Waring Products, New Hartford, CT) at high speed for 30 seconds, strained through four layers of cheesecloth, and added to the conical flasks containing rumen inoculum. The blending action serves to dislodge particulate associated microbes and assures a representative microbial population for the in vitro fermentation (Holden 1999). Under constant purging with CO_2 and mixing, rumen inoculum was divided into two pre-warmed flasks; the one was used for the conventional in vitro and the second was used for Daisy^{II} techniques.

Control of study accuracy and calculation

Control and corrections of results

Each rack, jar, and mesh bag/rumen was considered as a run for the conventional in vitro, Daisy^{II}, and filter bag in situ techniques, respectively. As described above, each run was comprised of 20 experimental samples, two standards (hay sample, with a digestibility value pre-determined), and two blanks (empty bags). Blank bags and blank tubes were used to correct for bacterial contamination (Robertson et al. 1972). Each sample for Experiments 2 and 3 was analyzed with ten replicates (n = 10) in a separate run for each of the techniques evaluated. For estimating mean values, we selected only those values that were within two standard deviations (error term between batch runs); otherwise the data were rejected and repeated analysis was undertaken. We expected that coefficients of variation of the means for standard samples would be at an acceptable level (CV < 4.0%). If means were outside two standard deviations of pre-determined values for standard samples in a particular run, all data from that particular run were discarded. However, this situation did not occur during the current study.

Calculation of dry matter and neutral detergent fiber digestibility

Conventional in vitro digestibility (IVDMD, % DM) was calculated as follows: (1 – ([{DM residue – Ash residue} – {blank_{DM} –Ash $\text{residue}_{\text{blank}}$] / DM original)) x 100, where DM residue is the DM recovered after incubation, blank_{DM} is the DM recovered in the corresponding blank after the same fermentation time, ash residue is the residue after combustion in a muffle furnace, and DM original is the DM of the substrate placed in the tube.

Daisy^{II} and in situ dry matter digestibility values (%, DM) were calculated as follows: 100 – (([W_3 – {W_1 x C_1}] x 100) / [W_2 x DM]), where W_1 is the filter bag weight, W_2 is the sample weight, W_3 is the final weight after in vitro or in situ and sequential NDF determination, C_1 is the blank bag correction (final oven-dried weight/original blank weight.), and DM is the dry matter content of samples.

Neutral detergent fiber digestibility (NDFD) was calculated using the following equation: NDFD, % DM = (1 – [{100 – DMD, % DM}/ NDF, % DM]) x100. In vivo digestibility estimates of forage DM and NDF digestibility (%, DM) were calculated using the following equation: DMD or NDFD = ([total forage offered x percentage forage DM or NDF digestibility] – [total orts collected x percentage orts DM or NDF digestibility]) divided by ([total forage of NDF offered - total orts or NDF collected] x 100).

Variation within and between runs

The same technician performed all three experiments; therefore, technician bias was assumed to be only a minor source of variation of DM and NDF digestibility estimates across the techniques tested. To evaluate precision of technique or to estimate coefficient of variation (CV, %) between runs, all raw values of tested forages obtained during Experiment 2 and 3 were utilized.

Laboratory methods

The samples were analyzed according to AOAC (1990) for dry matter (DM; method ID 934.01) and crude protein (CP; method ID 942.01) content was determined by the Kjeldahl procedure (method ID 954.01; AOAC, 1990) using a Kjeltec Auto System (Kjeltec Auto System, Büchi, Flawil, Switzerland). Acid detergent fiber (ADF; Goering and Van Soest 1970) and NDF (Van Soest et al. 1991) were determined using procedures modified for use in an Ankom^{200} fiber analyzer (ANKOM Technology Corporation, Fairport, NY). Sodium sulfite (Na_2SO_3) was included, but decalin ($C_{10}H_{18}$) was excluded for preparation of NDF and ADF detergent solutions, respectively. Analyses were conducted with two replicates and acceptable coefficients of variation of analyses' means were < 0.5%, < 2.0%, < 3.0%, and < 3.0% for DM, CP, ADF, and NDF, respectively. Chemical content and digestibility was determined on a DM basis and expressed as percentage of forage sample (%, DM).

Statistical Analyses

Experiment 1

Analysis of variance was performed on data using the General Linear Model (GLM) procedure of SAS (SAS 2001) as a split plot design: $Y_{ijr} = \alpha_i + e_{ir}$; Y_{ijr} is the variable studied (DMD, NDFD), α_i is the technique effect, and e_{jr} is the residual standard deviation used as the error term. Means were separated using preplanned pair-wise comparisons of LSMeans generated with the PDIFF and STDERR functions of SAS. Replicates of each forage type were considered the experimental units. Laboratory analyses' replicates within each sample were considered the observational units.

Experiment 2

Dry matter and NDF digestibility estimates were analyzed using the GLM procedure of SAS (2001) appropriate for a split plot design: $Y_{ijr} = \alpha_i + \beta j + e_{ijr}$; where Y_{ijr} is the variable studied, α_i is the animal effect, βj is the technique effect, and e_{ijr} is the residual standard deviation used as the error term. LSMeans were separated using pre-planned orthogonal contrasts for a 2 x 4 (DMD) or a 2 x 3 (NDFD) factorial design. Each trial or run was considered the experimental unit.

Experiment 3

Results were subjected to a 2-way analysis of variance (sampling/grinding size and technique) with GLM procedures of SAS (2001) as a split-plot design: the whole-plot experimental unit was grinding screen (1-mm and 2-mm) or sampling (0.25 g and 0.5 g) sizes and the sub-subplot experimental unit was research technique within the grinding screen/sampling sizes. The model used was: $Y_{ijr} = \alpha_i + \beta j + e_{ijr}$; where Y_{ijr} is the variable studied, α_i is the grinding/sampling sizes, βj is the technique effect, and e_{ijr} is the residual standard deviation used as the error term.

Each trial was considered as the experimental unit; therefore in vivo estimates included four replicates (*n* = 4), whereas conventional in vitro, Daisy^{II}, and in situ techniques included ten (*n* = 10) replicates per treatment combination. LSMeans were calculated and separated using selected pre-planned orthogonal contrast statements, depending on the response variable being evaluated. The results were considered significant at the $P < 0.05$ level for all three experiments of this study. All data are presented as LSMeans ± SEM. For estimating coefficients of variation (CV, %) within runs, rack (conventional in vitro), jar (Daisy^{II}), and mesh bag (in situ) was considered the experimental unit. For estimates of precision or for estimates of coefficients of variation (CV, %) between replicates, sample/forage species was considered the experimental unit.

Regression analysis

The regressions between forage ADF and digestibility or between each pair of DM and NDF digestibility values from the different techniques were obtained using the REG procedure of SAS (2001). Based on data obtained from Experiment 2 and 3, we also estimated correlations between in vivo DMD and DMD estimated by the conventional in vitro, Daisy^{II}, and in situ techniques. In addition, since our study covers a diverse range of forage samples, Spearman rank correlation (Altman 1991) was used to determine if the techniques ranked the forage species/types samples in a similar order.

RESULTS

Experiment 1

Chemical composition and digestibility estimates of forage species by all tested techniques in Experiment 1 are presented in Table 3.1. Grasses contained lower ($P < 0.001$) CP than lichens, forbs, and shrubs, which did not differ ($P > 0.10$) from each other. Acid detergent fiber composition was higher ($P < 0.001$) for grasses compared to lichen with forbs and shrubs being intermediate. Across the forage species, ADF content ranged from 8.7% to 48.5% which indicated that our samples are diverse in terms of cell wall content. Compared to conventional in vitro, Daisy^{II} and the in situ techniques overestimated ($P < 0.05$) DMD. In addition, the difference in digestibility estimates between the techniques appeared to be greatest with forbs, shrub, and lichen. In particular, incredibly high estimates of DMD were obtained on tree hair lichen using the Daisy^{II} (93.5%) and in situ (86.3%) techniques. Mean values were overestimated by 23.6 and 16.4 percent unit, respectively compared to the conventional in vitro technique. The conventional in vitro and in situ techniques were similar ($P > 0.05$) for two (California brome and elk sedge) of the five grass species, whereas the Daisy^{II} technique differed from conventional in vitro estimates for all forage species ($P < 0.05$).

Table 3.1. Chemical composition (LSMeans ± standard error), conventional in vitro, Daisy^{II}, and filter bag in situ dry matter digestibility (DMD), and Daisy^{II}, filter bag in situ neutral detergent fiber digestibility (NDFD) for clipped forage samples (%, DM) from mixed-conifer rangelands in Experiment 1.

		Composition			DMD				NDFD		
Forages	*n*	CP	ADF	NDF	In vitro	Daisy^{II}	In situ	SEM[1]	Daisy^{II}	In situ	SEM
Grasses											
California brome	8	6.0 ± 0.9	47.9 ± 1.6	66.5 ± 2.6	54.1^{a}	62.1^{b}	56.6^{a}	2.4	43.4^{a}	33.2^{b}	1.7
Elk sedge	7	6.4 ± 0.4	40.7 ± 1.3	62.4 ± 1.1	57.1^{a}	79.5^{b}	59.3^{a}	1.6	66.3^{a}	33.3^{b}	2.5
Orchardgrass	7	7.9 ± 0.6	38.0 ± 1.1	55.0 ± 0.7	63.7^{a}	78.5^{b}	72.9^{c}	1.5	60.8^{a}	49.4^{b}	2.8
Pinegrass	7	7.4 ± 0.2	43.5 ± 0.5	58.7 ± 0.7	55.2^{a}	79.3^{b}	64.8^{c}	0.8	63.9^{a}	38.6^{a}	1.5
Western fescue	7	4.3 ± 0.8	48.5 ± 1.5	71.0 ± 3.0	42.5^{a}	52.6^{b}	49.5^{c}	1.9	33.1^{a}	27.7^{b}	1.0
Forbs											
Annual willowherb	5	9.1 ± 0.7	34.8 ± 2.1	45.6 ± 2.6	50.9^{a}	69.9^{b}	66.4^{b}	2.3	33.0^{a}	24.4^{b}	2.4
Lupine	6	10.7 ± 0.1	28.8 ± 3.2	38.8 ± 4.0	75.2^{a}	83.2^{b}	77.7^{a}	3.6	57.4^{a}	42.5^{b}	6.1
Strawberry	7	9.3 ± 0.3	17.7 ± 0.7	30.6 ± 1.7	56.6^{a}	90.9^{b}	87.0^{c}	0.9	68.0^{a}	54.6^{b}	2.8
Western yarrow	4	9.2 ± 0.9	35.3 ± 2.3	38.3 ± 1.8	69.5^{a}	80.5^{b}	74.9^{c}	1.3	48.3^{a}	33.3^{b}	2.2
White hawkweed	6	7.3 ± 0.6	35.1 ± 2.3	45.2 ± 2.3	64.0^{a}	74.3^{b}	70.5^{c}	1.8	42.3^{a}	33.5^{b}	1.4
Shrubs											
Big huckleberry	7	8.8 ± 0.2	27.6 ± 1.4	32.1 ± 1.0	58.5^{a}	77.5^{b}	76.5^{b}	1.2	29.1^{a}	24.7^{b}	1.4
Low oregongrape	6	10.6 ± 0.2	29.5 ± 7.9	39.9 ± 1.3	65.0^{a}	74.9^{b}	72.1^{b}	1.0	37.2^{a}	28.0^{b}	1.9
Shinyleaf spirea	8	8.3 ± 0.2	27.8 ± 1.5	36.3 ± 1.3	55.8^{a}	76.3^{b}	74.7^{b}	1.8	35.0^{a}	29.9^{b}	2.5
Snowberry	10	8.1 ± 0.2	26.3 ± 1.6	31.6 ± 1.3	66.1^{a}	79.9^{b}	78.9^{b}	1.5	36.7^{a}	32.2^{b}	2.4
Lichen											
Tree hair lichen	5	10.1 ± 0.5	8.7 ± 1.1	36.0 ± 1.9	69.9^{a}	93.5^{b}	86.3^{c}	1.1	79.6^{a}	59.1^{b}	3.6

[abc] LSMeans in the same row for either DMD or NDFD with different superscripts differ ($P < 0.05$).

[1] Standard error of the LSMeans.

Experiment 2

Chemical composition of forages and digestibility estimates for this experiment are shown in Table 3.2. Sheep and steer in vivo DMD were overestimated ($P < 0.05$) by the conventional in vitro, Daisy^{II}, and in situ techniques. In turn, Daisy^{II} DMD estimates were greater ($P < 0.05$) than all other estimates of digestibility. In vivo DMD differed ($P < 0.05$) between animal species, but the differences in techniques were not different ($P > 0.05$) consistently across animal species. Daisy^{II} and in situ NDF digestibility did not differ ($P > 0.05$) from in vivo NDF digestibility for wether diets. Although, for steer diets, both the Daisy^{II} and in situ techniques were greater ($P < 0.05$) than in vivo NDF digestibility estimates. No statistical difference ($P > 0.05$) was detected with the Daisy^{II} technique between NDF digestibility of diets of sheep and steers. However, in situ and in vivo techniques were decreased ($P < 0.01$) in steer diets as compared to sheep.

Experiment 3

Chemical composition and digestibility estimates for forages in this study are presented in Tables 3.3 and 3.4. For grass hay, Daisy^{II} and in situ DMD estimates were higher ($P < 0.05$) than in vivo and conventional in vitro DMD. In addition, IVDMD was lower ($P < 0.05$) than in vivo estimates. In contrast, for grass straw, IVDMD, Daisy^{II} DMD, and in situ DMD were lower ($P < 0.01$) compared to in vivo DMD. For grass hay and straw hay diets, NDF digestibility was underestimated ($P <$

Table 3.2. Chemical composition, in vivo, conventional in vitro, Daisy^{II}, and filter bag in situ dry matter digestibility (DMD), and in vivo, Daisy^{II}, and filter bag in situ neutral detergent fiber digestibility (NDFD) of meadow hay (%, DM) in Experiment 2.

	Composition			DMD				NDFD		
Animals	CP	ADF	NDF	In vivo	In vitro	Daisy^{II}	In situ	In vivo	Daisy^{II}	In situ
Wether	5.2	31.4	60.4	50.8^{a}	58.0^{b}	68.4^{c}	65.6^{d}	48.0^{a}	48.5^{a}	47.4^{a}
Steer	5.3	30.3	59.0	49.2^{a}	58.6^{b}	69.4^{c}	65.0^{d}	41.3^{a}	48.1^{b}	43.5^{c}
SEM[1]	0	0.6	0.1	0.5	0.5	0.5	0.5	0.7	0.7	0.8
P[2]	0.46	0.27	0.15	0.05	0.49	0.25	0.45	<0.01	0.65	<0.01

[a,b,c,d] LSMeans in the same row for either DMD or NDFD with different superscripts differ ($P < 0.05$).

[1] Standard error of LSMeans; $n = 4$ for CP, ADF, NDF, in vivo DMD, and in vivo NDF; $n = 10$ for in vitro, Daisy^{II}, and in situ DMD and in vitro, Daisy^{II}, filter bag in situ NDFD.

[2] Probability of F-test contrasts wether vs. steer.

Table 3.3. Chemical composition, in vivo, conventional in vitro, Daisy^{II}, and filter bag in situ dry matter digestibility (DMD), and in vivo, Daisy^{II}, and filter bag in situ neutral detergent fiber digestibility (NDFD) of two harvested forages (%, DM) at two different grinding sizes in Experiment 3.

		Composition			DMD					NDFD			
Forages	Size^{1}	CP	ADF	NDF	In vivo	In vitro	Daisy^{II}	In situ	SEM^{3}	In vivo	Daisy^{II}	In situ	SEM
Grass hay		8.6							6				11
	1		34.5	58.3	62.4^{a}	53.3^{b}	70.8^{c}	72.8^{d}		56.2^{a}	51.9^{b}	52.1^{b}	
	2		35.6	61.5	62.4^{a}	51.9^{b}	66.7^{c}	69.8^{d}		58.1^{a}	47.9^{b}	49.8^{b}	
P^{2}					0.973	0.148	<0.001	0.003		0.059	0.001	0.019	
Grass straw		3.6							7				8
	1		50.5	80.4	50.0^{a}	34.2^{b}	42.5^{c}	43.3^{c}		57.2^{a}	29.5^{b}	30.4^{b}	
	2		51.5	81.4	50.1^{a}	30.6^{b}	38.4^{c}	38.5^{c}		57.7^{a}	26.9^{b}	24.6^{c}	
P^{2}					0.863	0.002	<0.001	<0.001		0.610	0.021	<0.001	

[a,b,c,d] LSMeans in the same row for either DMD or NDFD with different superscripts differ ($P < 0.05$).

[1] Grinding screen size, diameter; 1 = 1-mm, 2 = 2-mm.

[2] Probability of F-test contrasts sample grinding size 1-mm vs. 2-mm in the same forage species.

[3] Standard error of the least squares means; $n = 4$ for in vivo DMD, in vivo NDF; $n = 10$ for in vitro, Daisy^{II}, in situ DMD; and Daisy^{II}, filter bag in situ NDFD.

Table 3.4. Chemical composition, conventional in vitro, Daisy^{II}, and filter bag in situ dry matter digestibility (DMD), and Daisy^{II}, filter bag in situ neutral detergent fiber digestibility (NDFD) of five clipped forage samples (%, DM) at two different grinding sizes in Experiment 3.

		Composition			DMD				NDFD		
Forages	Size[1]	CP	ADF	NDF	In vitro	Daisy^{II}	In situ	SEM[3]	Daisy^{II}	*In situ*	SEM
Strawberry		9.1						8			12
	1		24.6	28.6	59.0[a]	77.9[b]	81.6[c]		30.5[a]	38.8[b]	
	2				54.1[a]	76.1[b]	81.1[c]		20.0[a]	35.6[b]	
P[2]					<0.001	0.118	0.707		<0.001	0.007	
Western yarrow		9.9						6			10
	1		43.9	50.5	53.2[a]	63.9[b]	62.4[b]		28.5[a]	26.1[b]	
	2		43.2	48.7	54.6[a]	62.8[b]	64.1[c]		27.9[a]	27.4[a]	
P[2]					0.241	0.329	0.134		0.680	0.293	
Red alder		10.3						6			11
	1		26.9	36.4	54.7[a]	82.7[b]	82.1[b]		52.9[a]	48.6[b]	
	2		23.1	28.8	54.7[a]	83.7[b]	83.9[b]		43.9[a]	42.9[b]	
P[2]					0.987	0.403	0.109		<0.001	<0.001	
Firmleaf willow		7.5						6			14
	1		30.8	25.6	61.6[a]	86.5[b]	82.4[c]		47.9[a]	30.6[b]	
	2		29.8	24.3	61.2[a]	85.8[b]	82.5[c]		42.6[a]	32.6[b]	
P[2]					0.731	0.572	0.917		<0.001	0.222	
Tree hair lichen		13.8						7			17
	1		11.4	31.9	66.6[a]	85.2[b]	86.6[b]		56.3[a]	59.1[b]	
	2		11.3	33.7	67.9[a]	86.7[b]	87.8[b]		60.7[a]	63.8[b]	
P[2]					0.274	0.192	0.333		0.003	<0.001	

[a,b,c,d] LSMeans in the same row for either DM or NDF digestibility with different superscripts differ ($P < 0.05$). [1] Grinding screen size, diameter; 1 = 1-mm, 2 = 2-mm. [2] Probability of F-test contrasts sample grinding size 1-mm vs. 2-mm in the same forage species. [3] Standard error of LSMeans ($n = 10$).

0.05) by both Daisy^{II} and in situ techniques compared to in vivo estimates of digestibility.

Dry matter digestibility for the Daisy^{II} and in situ techniques were greater ($P < 0.01$) for grass hay milled at 1-mm vs. 2-mm. For grass straw, DMD estimates from the conventional in vitro, Daisy^{II}, and in situ techniques were greater ($P < 0.01$) for 1-mm compared to 2-mm milling. In addition, NDF digestibility was higher ($P < 0.05$) for 1-mm milled samples of the two forage types using the Daisy^{II} and in situ techniques.

Daisy^{II} and in situ estimates were higher ($P < 0.05$) than IVDMD for all clipped forage species (Table 3.4). Grinding diameter only influenced digestibility estimates for one forage species (strawberry) and that was only with the conventional in vitro technique.

Effects of sample mass on digestibility estimates are presented in Table 3.5. For grass hay, DM and NDF digestibility estimates increased ($P < 0.05$) when sample mass was reduced from 0.5 to 0.25 g in both the Daisy^{II} and in situ techniques. Likewise, for firmleaf willow, reducing sample mass increased ($P < 0.05$) DMD estimates for the Daisy^{II} technique and NDF digestibility estimates for both techniques.

Table 3.5. Comparison of Daisy^{II}, filter bag in situ dry matter digestibility (DMD) and Daisy^{II}, filter bag in situ neutral detergent fiber digestibility (NDFD) estimates[1] of meadow hay and firmleaf willow (%, DM) using two different sample sizes.

		DMD			NDFD		
	Size[2]	Daisy^{II}	In situ	SEM[4]	Daisy^{II}	In situ	SEM
Meadow hay				6			10
	1	69.2^{a}	70.0^{a}		50.2^{a}	51.6^{a}	
	2	63.5^{a}	65.1^{a}		42.0^{a}	45.8^{a}	
P^3		<0.001	<0.001		<0.001	<0.001	
Firmleaf willow				4			11
	1	86.7^{a}	84.4^{a}		50.0^{a}	42.9^{a}	
	2	81.5^{a}	83.0^{a}		37.0^{a}	38.3^{a}	
P^3		<0.001	0.112		<0.001	<0.001	

[a,b] LSMeans in the same row for either DMD or NDFD with different superscripts differ ($P < 0.05$).

[1] Estimates of in vivo digestibility of meadow hay were 49.2 and 41.3% DM for DMD and NDFD, respectively.

[2] Sample size; 1 = 0.25g, 2 = 0.5g.

[3] Probability of *F*-test contrasts sample size 0.25 vs. 0.5g in the same forage species.

[4] Standard error of LSMeans ($n = 10$).

The Relationships between Digestibility Values Estimated by Different Techniques

Summarizing all three experiments, DM digestibility estimated by Daisy^{II} (IVDMD, % DM = 10.1 + 0.641 x Daisy^{II} DMD, % DM; $r^2 = 0.63$, $n = 115$, $P < 0.001$) and by the in situ technique (IVDMD, % DM = 14.9 + 0.614 x in situ DMD, % DM; $r^2 = 0.58$, $n = 115$, $P < 0.001$) was not much accurate but was correlated with IVDMD (Figure 3.1). The Daisy^{II} technique gave the best prediction for in situ DMD (in situ DMD, % DM = 2.7 + 0.904 x Daisy^{II} DMD, % DM; $r^2 = 0.81$, $n = 115$, $P < 0.001$). The Spearman rank correlation coefficients (r^2) for all forage species/types (*n*

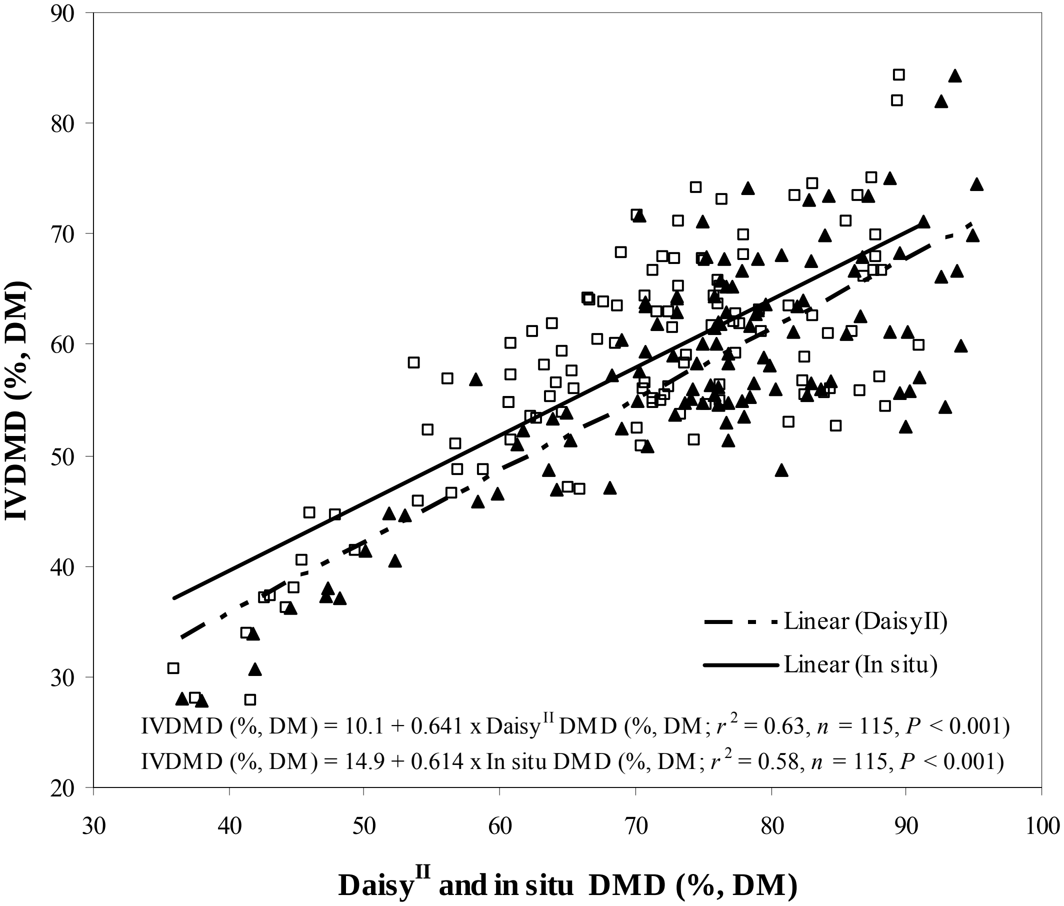

Figure 3.1. The relationship between digestibility of dry matter (DMD) estimated by conventional in vitro (IVDMD, Y) on DMD estimated by Daisy^{II} (▲) and filter bag in situ (□) techniques (X).

Table 3.6. Ranking order for forages based on dry matter digestibility (DMD) and neutral detergent fiber digestibility (NDFD) values determined by the conventional in vitro, Daisy^{II}, and in situ techniques.

Forages	Rank[1]				
	DMD			NDFD	
	IVDMD	Daisy^{II}	In situ	Daisy^{II}	In situ
Grasses					
California brome	16	18	18	12	12
Elk sedge	11	8	17	3	10
Grass hay	17	17	12	7	3
Grass straw	20	20	20	20	18
Meadow hay	10	16	15	10	6
Orchardgrass	7	10	10	5	4
Pinegrass	14	9	16	4	8
Western fescue	19	19	19	17	17
Forbs					
Lupine	1	5	6	6	7
Strawberry	12	2	1	2	2
Western yarrow	3	6	8	9	11
White hawkweed	6	14	13	13	9
Shrubs					
Annual willowherb	18	15	14	18	20
Big huckleberry	9	11	7	19	19
Firmleaf willow	8	3	4	11	14
Low oregongrape	5	13	11	14	16
Red alder	15	4	3	8	5
Shinyleaf spirea	13	12	9	16	15
Snowberry	4	7	5	15	13
Lichen					
Tree hair lichen	2	1	2	1	1

[1] Ranking is achieved by giving the ranking ‘1’ to the biggest digestibility value, ‘2’ to the second biggest value so on. The smallest digestibility value will get the lowest ranking in the column.

= 20) were 0.62 ($P < 0.01$), 0.58 ($P < 0.05$), and 0.85 ($P < 0.001$) for IVDMD vs. Daisy^{II}, IVDMD vs. in situ, and Daisy^{II} vs. in situ digestibility “paired” estimates, respectively, which indicated that these techniques ranked the samples in a relatively similar order (Table 3.6). Likewise, greater Spearman correlation coefficients were detected for NDF digestibility estimates ($r^2 = 0.88$, $n = 20$, $P < 0.001$) between the Daisy^{II} and in situ techniques. Overall, regressions were highly significant using different samples in terms of both botanical classification and chemical composition but the relationship between digestibility values estimated by the conventional in vitro vs. the Daisy^{II} or in situ technique was not good enough to be used interchangeably for analysis of forage samples from mixed-conifer rangelands.

Based on the three test diets (meadow hay, moderate quality hay, and grass straw), the correlations between in vivo and Daisy^{II} (in vivo DMD, % DM = 33.5 + 0.402 x Daisy^{II} DMD, % DM; $r^2 = 0.85$, $n = 24$, $P < 0.001$) or in vivo and in situ (in vivo DMD, % DM = 35.2 + 0.373 x in situ DMD, % DM; $r^2 = 0.80$, $n = 24$, $P < 0.001$) were slightly better than that between in vivo and IVDMD (in vivo DMD, % DM = 33.0 + 0.542 x IVDMD, % DM; $r^2 = 0.78$, $n = 24$, $P < 0.001$). In similar fashion, other studies (Khazaal et al. 1993; Huntington and Givens 1995; Ferret et al.1997) have also documented that the in situ technique predicted in vivo digestibility with greater accuracy (higher r^2) than the in vitro techniques.

Based on the results of all three experiments, it is clear that compared to IVDMD (IVDMD, % DM = 77.9 – 0.589 x ADF, % DM; $r^2 = 0.45$, $n = 115$, $P < 0.001$), Daisy^{II} (Daisy^{II} DMD, % DM = 105.4 – 0.912 x ADF, % DM; $r^2 = 0.71$, $n = 115$, $P < 0.001$) and in situ (in situ DMD, % DM = 104.2 – 1.01 x ADF % DM; $r^2 =$

0.86, $n = 115$, $P < 0.001$) DMD were more negatively correlated with forage ADF content (Figure 3.2). The differences between Daisy^{II} DMD and IVDMD (Daisy^{II} DMD – IVDMD, % DM = 27.5 – 0.323 x ADF, % DM; $r^2 = 0.24$, $n = 115$, $P < 0.001$) and between in situ DMD and IVDMD (in situ DMD – IVDMD, % DM = 26.3 – 0.420 x ADF, % DM; $r^2 = 0.35$, $n = 115$, $P < 0.001$) were significantly correlated with forage ADF content, though power (r^2) was low.

Variations Within and Between Runs

According to data from experiment 2 and 3, the average CV's of each run (within run, $n = 26$ for each technique) for DMD were 9.7%, 14.8%, and 14.9% for the conventional in vitro, Daisy^{II}, and in situ techniques, respectively. In our experiment, CV's of digestibility values estimated by the conventional in vitro technique were lower ($P < 0.05$) compared to CV's of digestibility values estimated by the other techniques. Neutral detergent fiber digestibility CV's estimated by the Daisy^{II} (23.6%) and in situ techniques (23.1%) were not significantly different ($P > 0.05$).

Using the pooled results of Experiment 2 and 3, the mean CV's of 55 DM digestibility samples across different runs (run-to-run fluctuations within each sample); ($n = 10$ for each CV) were 4.3%, 4.7%, and 4.7% for the conventional in vitro, Daisy^{II}, and in situ techniques, respectively. The CV's of NDF digestibility were 12.4% and 12.2% for the Daisy^{II} and in situ techniques, respectively. Differences in the coefficient of variation of DMD or NDFD were not detected ($P > 0.05$) across the techniques. One criterion of an approach that has not been generally

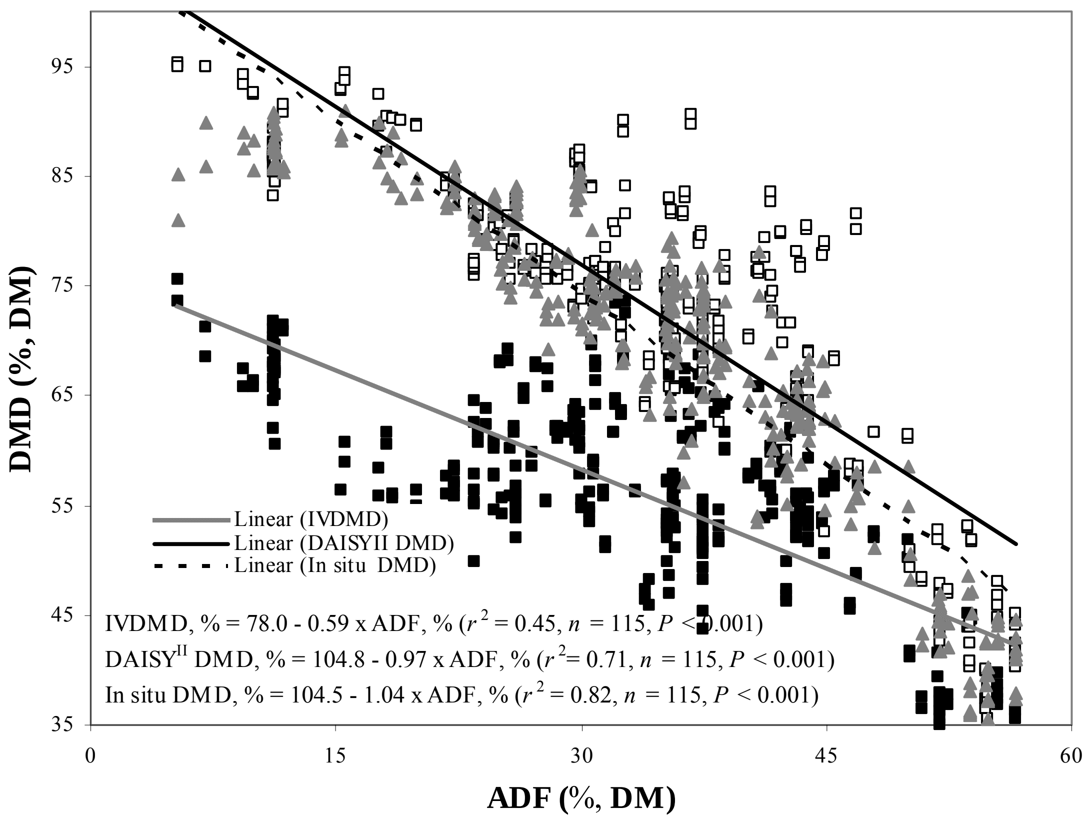

Figure 3.2. The relationship between digestibility of dry matter (DMD) estimated by conventional in vitro (IVDMD, ■), Daisy$^{\text{II}}$ (□), and filter bag in situ (▲) techniques (Y) on acid detergent fiber (ADF, X) of forages.

accepted is to minimize the required replicate number of samples without damaging the precision and accuracy of the results. We have estimated that in order to be within 10 units of mean digestibility values with 90% power at the 5% significance level (Kuehl 2000), it would require a minimum of 4(2-10), 4 (1-13), 6 (1-9), 29 (5-165), and 34 (16-189) replicates per sample for DM conventional in vitro, DM Daisy^{II}, DM in situ, NDF Daisy^{II}, and NDF in situ digestibility techniques, respectively.

When using 0.25 g sample for assay of digestibility estimation, to be within 10 units of mean digestibility with 90% power at the 5% significance level, the smallest required replicate numbers were 1, 4, 2, and 9 for Daisy^{II} DM, Daisy^{II} NDF, in situ DM, and in situ NDF digestibility, respectively. In contrast, when the sampling size was 0.5 g, these numbers reached 2, 10, 2, and 12 for Daisy^{II} DM, Daisy^{II} NDF, in situ DM, and in situ NDF digestibility, respectively, which is slightly higher than those with 0.25 g samples but is not considered to be of practical significance. However, as shown in Table 3.5, digestibility values obtained from a 0.5 g sample mass were closer to actual or in vivo DMD values, indicating that a 0.5 g sample mass may be more accurate.

DISCUSSION

Different values for the conventional in vitro and filter bag based (Daisy^{II} and filter bag in situ) techniques seem to be related to sample particle size and cell wall structure of forages (Adesogan 2004, 2002; Wilman and Adesogan 2000). The filter bag based techniques tended to overestimate digestibility when forage was more finely ground (1-mm) compared to 2-mm ground forage. This may be caused by agitation during incubation, boiling in neutral detergent solution, and through rinsing of the filter bags with water after 48 h incubation. During this procedure a proportion of non-digestible fine particles may have been removed, reducing the weight of residue and increasing the estimate of digestibility compared to the conventional in vitro technique in which microbial matter and fine particles are retained. The porosity of the F57 filter bag is 30 x 10^{-3} mm (ANKOM Technology Corporation 1997); therefore small particles of less than 30 x 10^{-3} mm in diameter can escape from the filter bag during processing of digestion. Further, Marinucci et al. (1992) speculated it is possible that relatively large particles can pass through the pores by exerting pressure on the loose fibers of the fabric. Adesogan (2005) also observed that predictions of in vivo digestibility from the filter bag technique were more accurate when forages were incubated in non-standard bags. However, when such non-standard bags are used results obtained will depend on pore size, seal treatment, and weave type.

In our study, digestion patterns of fine fescue grass straw (in which in vivo digestibility was higher compared to values estimated by the conventional in vitro technique) were similar to cereal straw digestion reported by Khazaal et al. (1993) and

Adesogan et al. (1998). Despite this, other workers (Kitessa et al. 1999) indicate the conventional in vitro technique, although accurate for fresh grasses, is not suited for predicting the digestibility value of feeds like straws, which are generally bulky and very low quality. They gave two reasons for this conclusion: (i) 48 h incubation may be insufficient for cereal straws, and (ii) rumen microbial population may gradually shift to highly fibrolytic species when animals are retained on straw diets, an opportunity that may be very limited under in vitro conditions. Since our rumen inoculum donor steers were fed moderate quality hay and incubation time was 48 h, both aforementioned possibilities may apply to the grass straw digestion values estimated by the different techniques.

In general, our data suggest that differences in digestion estimates between the conventional in vitro and filter bag based techniques decrease as forage fiber/ADF composition increase. In our study, the Daisy^{II} and in situ techniques estimated true digestibility while the conventional in vitro estimated apparent digestibility. Therefore, theoretically, IVDMD should be expected to have lower values. However, as documented by Wilman and Adesogan (2000), digestibility estimates using filter bags result in apparent and true digestibility differences that are very low. It is also possible to convert IVDMD values to "true" IVDMD values using Van Soest et al. (1966) equation (true IVDMD, % DM = 16.2 + 0.92 x IVDMD, % DM). Our results suggested that the difference in digestibility values estimated by the conventional in vitro and filter bag based techniques may vary among forages with different cell wall contents.

It should be also noted that when accuracy of the filter bag based technique is tested against the conventional in vitro technique, it is difficult to determine if a weaker correlation is due to problems with the Daisy^{II} or in situ technique (such as particle loss from the filter bag) or whether the conventional in vitro technique has a flaw. Ideally, results should be validated against in vivo measurements but these can also have methodological deficiencies (White and Ashes 1999).

The variation in coefficients of digestibility values between samples within runs should indicate possible associative effects (synergistic vs. antagonistic) between samples when they are incubated together (same jar or same mesh bag and rumen, for the Daisy^{II} and filter bag in situ techniques, respectively). Although some evidence exists that the microenvironment within bags can differ markedly from the environment of the incubation medium (Marinucci et al. 1992), the filter bag based technique is generally assumed to have conditions within bags similar to the conditions in the surrounding environment (Hvelplund and Weisbjerg 2000). In contrast, in the conventional in vitro technique, because each sample is incubated in separate tubes, values should have more independence compared to the other two techniques. In this study, within run CV of digestibility estimated by the conventional in vitro technique was lower ($P < 0.05$) compared to the CV of digestibility estimated by other techniques. Several possible explanations may exist for this. First, our results suggest that when incubating different forages in the same place, the microenvironment inside jars or mesh bags may create a more diverse microenvironment, resulting in varied, but mostly increased digestibility values. In other words, synergistic associative effects may have existed. As our study indicated, another effect of the filter bag based techniques maybe the interaction among forage types (data not shown), resulting in higher CV values estimated with these techniques. Animal to animal variation may add to the variability of the in situ technique (Mehrez and Orskov 1977). Since rumen fluid collected from animals is composited for the in vitro and Daisy^{II} techniques, this variation will not occur with conventional in vitro (Gulati et al. 1997) and Daisy^{II} techniques. Furthermore, the CV within runs did not differ between Daisy^{II} vs. in situ technique, which is suggesting that animal to animal variation was small.

The coefficient of variation for DM digestibility of each forage sample across different runs (run-to-run/replicate variation within each sample) can be used to estimate the precision of each digestion technique. Our results are similar to those obtained by Wilman and Adesogan (2000), who demonstrated that the conventional in vitro technique is preferred because of better repeatability. Also, the required replicate number appears to be more consistent within different forages than with other techniques tested in this study. A general trend was that both Daisy^{II} and in situ techniques demanded unusually low replicate number (in most cases $n = 1$) to determine DMD of forbs, shrubs, and lichen. In contrast, when using this result for NDF digestibility estimates, the required replicate number becomes much larger. This suggests that the Daisy^{II} and in situ techniques have some problems with estimation of NDF and DM digestibility for forbs, shrubs, and lichen. This may be because these techniques might not be sensitive enough to detect run-to-run variation for these kinds of forages, although based on mathematical calculation of required replicate number, it can be erroneously (committing Type II errors) assumed that Daisy^{II} technique is more precise. In particular, for low ADF forages, both Daisy^{II} and in situ techniques failed to accurately estimate NDF digestibility, and, as a result, required higher replicate numbers for sample accuracy. On the other hand, when determining forage NDF digestibility, taking isolated NDF as a sample instead of whole forage as a sample may increase magnitude of forage NDF digestibility and repeatability (Varel and Kreikemeier 1994; Kennedy et al. 1999). Therefore, for high quality forages Daisy^{II} and in situ techniques may not be the method of choice.

An unequal distribution of particles between different forages using the same grinding screen sizes may have contributed to forage type x research technique interactions (data not shown) in this study. Michalet-Doreau and Cerneau (1991) showed that plant material from different forage species ground through the same screen size could have a different distribution of particle sizes. This means that at the same screen size and at the same bag pore size, forages with different particle distribution after grinding will have different levels of mechanical loss of fine particles from filter bags (Kitessa et al. 1999). In addition, low ADF forages usually tend to get ground too much finer particles than high ADF forages (Mabjeesh et al. 2000).

Furthermore, according to Emanuele and Staples (1988), after grinding through a 2-mm screen, mean particle size of grass samples was greater than that of legume samples. Similarly, results from our study suggest digestion values for samples ground through 1- and 2-mm screens were similar for forbs, shrubs, and lichen, but different for grass.

When choosing the appropriate grinding size, sample size or appropriate technique for estimating DM and NDF digestibility, one should consider both precision and accuracy. Therefore, based on our data, a 0.5 g sample size seems more preferable than a 0.25 g sample size. We also felt that, when samples were 0.25 g, filter bag based techniques were not sensitive enough to estimate digestibility values accurately, particularly with low ADF forages. In order to explain why Daisy^{II} technique is getting more precise, but less accurate, when sampling size is decreased, in particular, with low fiber forages, further investigation is warranted.

Based on this research it could be stated that, in general, results from the Daisy^{II} technique were more similar to the in situ technique, therefore digestibility values estimated by the Daisy^{II} and in situ techniques might be interchangeable using general predictive equations generated across different forages. Sieving off different size particles (Huntington and Givens 1997) of the ground forage sample, correcting for the fine particle losses (Dhanoa et al. 1999) from the filter bag during digestion and washing, grouping the feeds into categories based on fiber fractions (summative and single fractions), applying a corresponding correction factor, and standardizing laboratory procedures may increase predictability and accuracy of the Daisy^{II} and in situ techniques.

MANAGEMENT IMPLICATIONS

Although IVDMD estimates are different than in vivo estimates of DMD, they are, generally, in closer agreement than the newer techniques. Sample size and grind size appear to have a large effect on filter bag based techniques, with larger sample size and greater grinding size lowering digestibility estimates. Daisy^{II} is an easier and less time-consuming in vitro technique of measuring forage digestibility than the conventional in vitro technique. However, for research involving wide ranges of forage quality and diverse forage species/types, some adjustments are necessary to ensure that estimates of digestibility are more biologically accurate. It appears that, to someone who has access to fistulated animals and is comfortable working with these animals, choosing the filter bag in situ technique may be a better choice. Because this technique requires less labor and equipment, and can process a large number of samples in a short time, plus predictions of in vivo digestibility from this technique were more accurate than from the conventional in vitro and Daisy^{II} techniques.

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CHAPTER 4

Comparison of Bite-Count and Rumen Evacuation Techniques to Estimate Diet Quantity and Quality in Grazing Cattle

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ABSTRACT

We conducted a study to compare the bite-count (BC) technique of estimating forage intake and synthesized diet quality to direct estimates of diet quantity and quality using the rumen evacuation (RE) technique. We used four rumen-fistulated steers to evaluate both techniques over a three-week period in August 1998. Four enclosures in a mixed-conifer rangeland were used. Each enclosure contained two 0.25 ha paddocks that were either ungrazed (UN) or grazed (GR) by cattle to remove approximately 40% (32.3 ± 4.4%) of forage biomass to create a more diverse test of diet quantity and quality techniques. We recorded bite-count data during 20 minutes feeding bouts for each steer in each enclosure, following each feeding bout we removed all rumen contents. Previous grazing resulted in reduced ($P < 0.05$) quantity of forage consumed during the bout regardless of technique. Bite-count and RE techniques gave similar ($P > 0.10$) results on diet intake and digestibility. However, bite-count derived estimates for crude protein (CP), acid detergent fiber (ADF), ash, and neutral detergent fiber (NDF) were lower ($P < 0.05$) than that derived from the ruminal evacuation. In summary, although the BC technique has the advantage of not requiring rumen fistulated animals, it did not yield results that were comparable to RE technique in range conditions with dense and diverse vegetation.

Key Words: *Abies grandis,* chemical composition, diet selection, forage intake, sampling

INTRODUCTION

The rumen evacuation technique (Lesperance et al. 1960) is widely used to assess foraging efficiency, botanical composition (Holechek et al. 1982; McInnis et al. 1983), and quality of grazing animals' diets (Beverlin et al. 1989; Olson 1991; Dubbs et al. 2003). However, disadvantages of this technique include increased time and labor to evacuate and clean the rumen, depressed digestibility if evacuations are repeated twice or more weekly, unsuitability for cold, open, winter range, and adaptability only to large animals (Van Dyne and Torell 1964; Holechek et al. 1982; Olson 1991). From a practical standpoint, the rumen evacuation technique is very useful in the short term, but is of less practical use for extended periods in the field because of the animal's care and attention required. The bite-count technique (Reppert 1960; Bjugstad et al. 1970; Free et al. 1971) can be used as an alternative to the rumen evacuation technique when investigating diet selection, diet intake, and diet quality. This technique is nonobtrusive (Parker and Gillingham 1993) and often is the only feasible approach to investigate the diet of free-ranging or wild ungulates in heterogeneous environments (Wallis De Vries 1995).

The bite-count technique has been proven useful for estimating diets of tame white-tailed deer (*Odocoileus virginianus* Boddaert; Bryant et al. 1979; Thill and Martin 1989) and mule deer (*Odocoileus hemionus* Rafinesques; Olson-Rutz and Urness 1987). Free et al. (1971), working in a semiarid Colorado environment, found that bite-count and esophageal-fistula techniques gave similar estimates of cattle diets. However, Ortega et al. (1995) reported that in diverse and rich vegetation types such as those found in the Texas Coastal Bend, the bite-count technique was not as reliable a method as using esophageal fistula. Likewise, Sanders et al. (1980) found that the bite-count technique and fecal analyses gave similar results for estimating major components of cattle diets in north-central Texas, but the bite-count technique could not be used on large, brush-infested pastures with rough terrain. Previous studies demonstrated that the accuracy of the bite-count technique is variable from region to region and may vary within a region depending on vegetation diversity and availability. In addition, information on comparison of the bite-count technique directly to the rumen evacuation technique is limited for estimating diet quality for free-grazing cattle.

Therefore, the objective of this study was to compare the bite-count technique of estimating diet quantity and quality to rumen evacuation derived forage intake and diet quality in diverse mixed-conifer rangelands with and without prior grazing.

MATERIALS AND METHODS

Study Area

The study was conducted on the Starkey Experimental Forest and Range (Starkey), which is located in the Wallowa-Whitman National Forest of the Blue Mountains (45°15′N, 118°25′ W), approximately 35 km southwest of La Grande, Oregon. Annual precipitation averages about 500 mm, two-thirds of which accumulates as winter snow (Skovlin et al. 1976). Elevations of the study area ranged from 1 120 m to 1 500 m. Vegetation characteristics of Starkey are described in detail by Miller and Krueger

(1976), Skovlin et al. (1976), and Holechek (1980). Pinegrass (*Calamagrostis rubescens* Buckl.), mountain brome (*Bromus carinatus* H. & A), western fescue (*Festuca occidentalis* Walt.), Kentucky bluegrass (*Poa pratensis* L.), Idaho fescue (*Festuca idahoensis* Elmer), and elk sedge (*Carex geyeri* Boott) are the dominant forage species for cattle. Several forb species are present and utilized including western yarrow (*Achillea millefolium lanulosa* L.), strawberry (*Fragaria* spp.), hawkweed (*Hieracium* spp.), lupine (*Lupinus* spp.), and tall annual willowherb (*Epilobium paniculatum* Nutt.). Common snowberry (*Symphoricarpos albus* [L.] Blake), big huckleberry (*Vaccinium membranaceum* Hook.), grouse huckleberry (*Vaccinium scoparium* Leib.), shinyleaf spiraea (*Spiraea betulifolia lucida* Pall.), and twinflower (*Linnaea borealis* L.) are the primary shrub species consumed by cattle. A more prevalent shrub, although minimally utilized by cattle, is bearberry (*Arctostaphylos uva-ursi* L.).

Experimental Pasture and Grazing Treatment

Four enclosures (Elk Dodo, Scotty's Gate, Bally Mountain, and Half Moon) were built in previously logged (15-20 years post harvest) grand fir (*Abies grandis* Lindl.) rangelands. Each enclosure was divided into two 0.25 ha paddocks. We selected paddocks at random as either ungrazed (UN) or grazed (GR). Paddock forage biomass and utilization were determined using the cage comparison method (Cook and Stubbendieck 1986). For paddocks that were allotted to grazing treatments, we clipped thirty 0.25-m^2 plots, from which ten plots were protected with wire cages (caged plot) before grazing treatment and twenty plots were not protected (uncaged plot). In ungrazed paddocks, we clipped twenty 0.25-m^2 plots in each paddock. Grazed paddocks were grazed by cattle in mid-June and mid-July 1998 to remove approximately 40% of forage biomass. Within 2-3 days before feeding bouts, we cropped clipped herbaceous vegetation in all plots to ground level. Browse was plucked by plant species to determine forage biomass and utilization. The biomass of each plot was calculated on a $kg \cdot ha^{-1}$ basis. Plant nomenclature throughout this paper follows the recommendations of the USDA Natural Resources Conservation Service (USDA, NRCS 2005).

Feeding Bouts

Feeding bouts were conducted 7-30 August 1998. Four rumen-fistulated crossbred steers (same steers used for grazing treatments) were used to evaluate both the bite-count (BC) and rumen evacuation (RE) techniques. Steer research protocol and use was approved by the Oregon State University Animal Care and Use Committee. We measured diet quantity and quality using a bite-count technique similar to that described by Wickstrom et al. (1984) and Canon et al. (1987). We conducted our bouts using two steers at a time, with one technician assigned to each steer. The two steers were selected at random: for morning (0800-1200) or afternoon (1300-1600) feeding bouts in each paddock. Food was not offered to steers each morning and between feeding bouts to ensure reasonable and similar appetites each day. Prior to bouts, steers were restrained and subjected to total ruminal evacuation. Reticulo-Rumen contents were physically removed from each animal and stored for later replacement after the feeding bouts. The rumen was then triple rinsed with water to assure complete removal of contents. During each feeding bout, steers were allowed to roam free in one of the paddocks for 20 minutes while two trained technicians followed steers and recorded bites by forage species. At the end of each bout, the entire ruminal masticate was collected and the steer was immediately taken to the alternate paddock where the second trial was completed. Ruminal masticate was cooled on ice for transport to the laboratory, then placed on aluminum trays, labeled, and put in a forced air oven at 50°C. After seven days of drying in the oven, rumen masticate was weighed (rumen evacuation DM intake [RE-DMI], $g{\cdot}20\text{-min}^{-1}$), sub-sampled, and stored for further laboratory analysis.

Samples of forages selected by steers during the feeding bouts were collected by hand clipping and plucking (Cook and Stubbendieck 1986). Variation in bite sizes due to different quantities of forage available or different forage species were accounted for by simulating bite sizes when samples were collected. Typically, we collected 100-200 simulated bites of each forage species per bout. Samples were placed in paper bags, dried in a forced air oven at 50°C for 2 days, and weighed to calculate BC bite size (BCBS, g = sample weight, $g{\cdot}\text{simulated bite number}^{-1}$).

Laboratory Analyses

Ruminal masticate and forage samples were ground in a Wiley Mill (Model #2, Arthur H. Thomas Co, Philadelphia, PA) to pass a 1-mm screen, analyzed in duplicate according to AOAC (1990) for DM, ash, organic matter (OM) and crude protein (CP). Crude protein was determined using the Kjeltec Auto System (Kjeltec Auto System, Büchi, Flawil, Switzerland). Acid detergent fiber (ADF) and neutral detergent fiber

(NDF) were determined by Ankom^{200} fiber analyzer (ANKOM Technology Corporation, Fairport, NY) using the procedures described by Komarek (1993) and Vogel et al. (1999). In vitro organic matter digestibility (IVOMD) was estimated by techniques similar to those described in detail by Vogel et al. (1999) and Holden (1999) using Daisy^{II} incubator (ANKOM Technology Corporation, Fairport, NY). Diet quantity and quality was determined on an OM basis.

Calculation and Statistical Analyses

Steer bite-count derived DM intake (BC-DMI) was determined as follows: $g \cdot min^{-1} = ([I_1 + I_2 + I_3 + \ldots + I_n] / 20)$ where I_n is the DMI for each forage species during a 20 minute feeding trial. It equals the bite number, $n \cdot 20\text{-}min^{-1}$ x bite-count bite size, g for a particular forage species. An average BC derived bite size corresponding to each feeding trial was calculated by a weighted mean of simulated bite sizes for the different forage species in accordance to their proportion in the bite count.

Bite-count derived organic matter intake (BC-OMI) was calculated as follows: $g \cdot min^{-1} = ([I_1OM_1 + I_2OM_2 + I_3OM_3 + \ldots + I_nOM_n] / 100)$; where OM_n is simulated sample's OM content (%) for each forage species. Bite count derived OM (BC-OM) content was determined as follows: $\% = ([I_1OM_1 + I_2OM_2 + I_3OM_3 + \ldots + I_nOM_n] / \text{BC-DMI}, g \cdot min^{-1})$; where OM_n is the bite-count derived OM content (%) for each forage species.

Bite-count derived estimates for CP (BC-CP), ADF (BC-ADF) and NDF (BC-NDF) were obtained in a similar manner to BC-OM content estimation. Rumen evacuated bite size was estimated by dividing ruminal masticate to total bite number for each trial.

Forage biomass by classes was analyzed as a completely randomized block design using the mixed model procedure of SAS (2001). The block (enclosure) and block x grazing treatment were included as random effects. Grazing treatment, forage classes, and their interaction were included as a fixed effect using Satterwaite degrees of freedom approximation techniques (Littell et al. 1999). The paddocks served as experimental units and plots served as observational units. Treatment means were separated using the DIFF option of the LSMeans statement in PROC MIXED of SAS. Diet quantity and quality data were analyzed as a split-plot in a randomized complete block design using the mixed procedure of SAS (2001). The random effect was block and its interaction with grazing treatment; grazing treatment, research technique and their interaction were included as a fixed effect using Satterwaite degrees of freedom approximation techniques. Treatment means were separated using the DIFF option of the LSMeans statement in PROC MIXED of SAS.

Results were considered significant at $P < 0.10$. Probability values of $P > 0.10$ and $P < 0.20$ were considered trends and probability value of $P > 0.20$ was considered not significant.

RESULTS

Biomass and Utilization of Forage

Forage biomass of study enclosures with and without prior grazing was presented in Table 4.1. Averaged across all 4 enclosures, forage biomass in previously ungrazed paddocks was comprised of 42.0 ± 3.4% grasses, 33.7 ± 2.8% forbs, with the remainder being shrubs (24.3 ± 3.3%). Thirteen species of grass (including sedges) plants contributed (data not shown) to the total grass yield, with the most prevalent species being mountain brome (avg 158.8-kg·ha^{-1} or 35.6%), western fescue (avg 106.2-kg·ha^{-1} or 23.8%), elk sedge (avg 69.8-kg·ha^{-1} or 15.7%), and pinegrass (avg 53.0-kg·ha^{-1} or 11.9%). Nineteen species of forbs were present within the enclosures. Willow-herb (avg 64.1-kg·ha^{-1} or 15.5%), lupine (avg 52.1-kg·ha^{-1} or 12.6%), and western yarrow (avg 38.2-kg·ha^{-1} or 9.2%) were the most common forbs. Bearberry (avg 322.7-kg·ha^{-1} or 98.1% of total shrubs) was the key shrub species in the ungrazed paddocks.

Utilization of forage in previously grazed paddock was 31 ± 13.9%, 21.4 ± 9.7%, and 39.5 ± 11.8% (n = 4) for grasses, forbs, and shrubs, respectively. Grasses, forbs and shrubs contributed 29.4 ± 2.4%, 36.3 ± 2.9%, and 29.5 ± 2.7% to the total biomass, respectively. As expected, biomass of highly preferred grasses tended to be less (P < 0.20) in grazed paddocks compared to caged plots. Biomass of orchard grass (*Dactylis glomerata* L.), northwestern sedge (*Carex concinnoides* Mack.), western fescue, elk sedge, and tall trisetum (*Trisetum canescens* Pers.) decreased by 3.7 (9.5 vs. 2.6-kg·ha^{-1}, P = 0.84), 4.52 (84.5 vs. 18.7-kg·ha^{-1}, P = 0.07), 1.4 (44.4 vs.

31.9-kg·ha^{-1}, $P = 0.72$), 1.8 (74.7 vs. 40.7-kg·ha^{-1}, $P = 0.33$), and 2.5 (17.4 vs. 7.0-kg·ha^{-1}, $P = 0.77$) times, respectively. Overall, grass was greater (data not shown) in ungrazed paddocks ($P < 0.10$), whereas, forbs, shrubs, and the total forage biomass did not differ ($P > 0.10$) between ungrazed and grazed paddocks.

Table 4.1. Forage biomass of mixed-conifer study sites with and without prior grazing. Study sites were located in previously logged grand fir (*Abies grandis* [Dougl.]) rangelands at Starkey Experimental Forest and Range, northeast Oregon.

Treatments	Forage biomass (Avg ± SE[3], kg·ha^{-1})		
	Grasses	Forbs	Shrubs
Elk Dodo enclosure			
Ungrazed paddock[1]	540 ± 75	184 ± 35	167 ± 62
Grazed paddock			
Caged[2] plots	594 ± 410	224 ± 47	741 ± 235
Uncaged[1] plots	211 ± 27	213 ± 34	531 ± 150
Scotty's Gate enclosure			
Ungrazed paddock	224 ± 66	259 ± 38	516 ± 125
Grazed paddock			
Caged plots	286 ± 80	444 ± 98	601 ± 152
Uncaged plots	183 ± 32	268 ± 56	520 ± 118
Bally Mountain enclosure			
Ungrazed paddock	393 ± 53	621 ± 150	116 ± 50
Grazed paddock			
Caged plots	288 ± 52	476 ± 155	466 ± 210
Uncaged plots	298 ± 51	500 ± 150	151 ± 76
Half Moon enclosure			
Ungrazed paddock	472 ± 104	455 ± 65	405 ± 129
Grazed paddock			
Caged plots	212 ± 50	411 ± 102	782 ± 167
Uncaged plots	148 ± 20	282 ± 36	404 ± 116

[1][2] $n = 20$ and 10 total clipped plots (0.25 m^2), respectively.

[3] Stardard error.

Quantity and Quality of Steer Diet

During the feeding trials, steers selected 13 species of grasses, 8 species of forbs, and 11 species of shrubs. In ungrazed paddocks, steer selected their diet mainly from grasses, while in previously grazed paddocks their diet became more diverse. Overall, steers took more ($P < 0.01$) bites in ungrazed paddocks compared to grazed paddocks (28 ± 2 vs. 21 ± 2 bites·min^{-1}). Also, steers took more ($P < 0.01$) bites from shrubs (3.5 ± 0.8 vs. 0.8 ± 0.2 bites·min^{-1}) and forbs (3.5 ± 0.5 vs. 1.9 ± 0.3 bites·min^{-1}), but took fewer ($P < 0.01$) bites from grasses (13.9 ± 1.9 vs. 25.5 ± 1.3 bites·min^{-1}) in grazed paddocks compared to ungrazed paddocks (Figure 4.1).

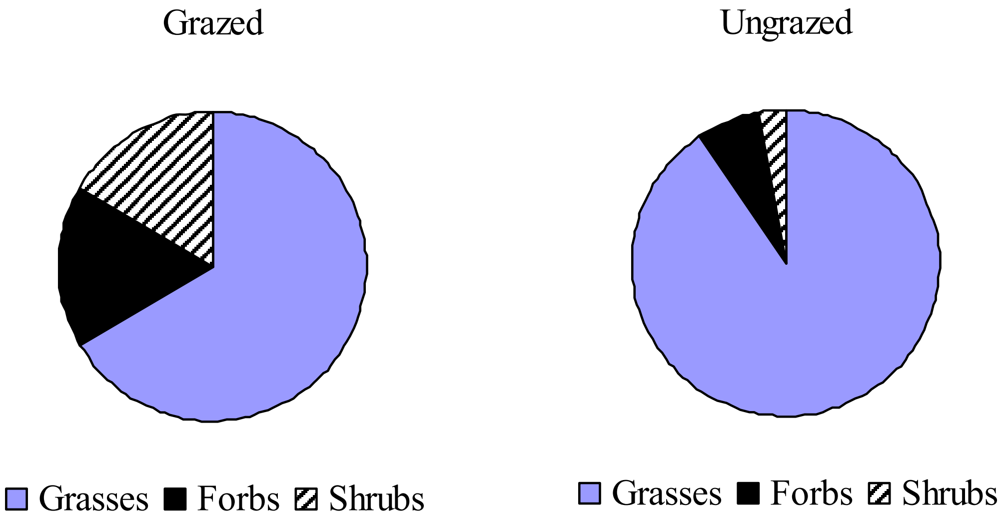

Figure 4.1. Diet composition (%) of steers grazing mixed-conifer rangelands with and without prior grazing.

Bite size was not different (*P* > 0.2) among grazing treatments, research techniques, and grazing treatment x research technique (Table 4.2). Previous grazing reduced (*P* < 0.05) diet quantity during the feeding trial regardless of technique used; however, BC and RE techniques gave similar (*P* > 0.10) results on diet quantity.

Ash content of BC derived diets was less (*P* < 0.01) compared to RE diets ash content. Previous grazing treatment did not have an effect (*P* > 0.20) on steer diet ash content.

Table 4.2. LSMeans of bite-count simulated (BC) vs. rumen evacuation (RE) derived steer diet quantity and quality in mixed-conifer rangelands, northeast Oregon.

	Ungrazed		Grazed			*P*-values		
	RE	BC	RE	BC	SE[1]	graze[a]	tech[b]	graze x tech
Bite (mg, DM)	661	677	615	421	123	0.27	0.49	0.42
OMI ($g \cdot min^{-1}$)	17.9	18.7	13.1	8.7	3.5	0.04	0.59	0.44
Ash (%, DM)	16.0	12.2	17.3	11.6	1.3	0.82	0.001	0.16
CP (%, OM)	9.8	6.6	10.5	8.3	0.8	0.16	0.006	0.45
ADF (%, OM)	47.2	41.5	50.0	39.3	1.3	0.75	0.001	0.02
NDF (%, OM)	70.4	66.3	66.1	57.1	2.0	0.03	0.001	0.06
IVOMD (%)	67.0	64.3	63.8	68.3	2.2	0.83	0.66	0.111

[a] Ungrazed paddock vs. grazed paddock

[b] Bite-count vs. rumen evacuation.

[2] Pooled standard error of LSMeans (*n* = 4).

The mean of BC derived CP (7.5 ± 0.7%) was lower (*P* = 0.006) compared to the mean of RE derived CP (10.2 ± 0.7%). Steer diet CP content tended (*P* < 0.2) to be higher in previously grazed paddocks compared to ungrazed paddocks.

A two-way interaction between grazing treatment and research technique was detected (*P* < 0.05) for diet ADF. Acid detergent fiber content of steer diets was higher in RE diets compared to BC derived diets in both ungrazed and grazed paddocks, and the magnitude of difference was greatest in the previously grazed paddocks.

An interaction existed ($P < 0.10$) between grazing treatment and research technique for NDF. The nature of the interaction suggest that the BC technique underestimates NDF content of diet and, similar to ADF, the magnitude of difference is greatest on previously grazed paddocks.

In vitro organic matter digestibility was not influenced by grazing treatment or research technique ($P > 0.20$). However, BC derived estimates for IVOMD tended to be lower in ungrazed paddocks and higher in grazed paddocks as compared to RE values ($P < 0.20$).

The present study showed that chemical composition and digestibility of rumen evacuated diets was more consistent than that estimated through BC technique, and steer diet content was more consistent in ungrazed paddocks regardless of techniques being used.

DISCUSSION

There are several possible reasons that may explain the differences found between the research techniques used to estimate nutritive quality and quantity of steer diets. Compared to actual diet composition, RE samples may have inflated ADF and NDF concentrations, and slightly lowered IVOMD due to soluble mineral contributions from saliva, and possible absorption through the rumen wall of soluble carbohydrates of ingesta. Salivary mineral contamination has been well documented with rumen collections (Lesperance et al. 1960; Bohman and Lesperance 1967). The magnitude of the increase in ash from salivary contamination is usually from 1 to 4% (Lesperance et al.1974) in masticate samples. Olson (1991) indicated that salivary ash contamination depressed OM and elevated nitrogen in rumen samples after evacuation compared to the feed offered.

Besides salivary contamination, bacterial contamination and direct infusion of urea from blood to the rumen are also potential factors that can raise RE-CP (Church 1976). Since essentially all the rumen bacteria were removed with the rumen contents prior to each feeding trial, contamination from bacteria had likely little effect in our experiments. Another possible consideration is that blood urea diffuses rapidly into the rumen as ammonia at a rate of diffusion directly related to the gradient (Church 1976).

In our trial, saliva and N diffusion could have added some nitrogen to rumen evacuation samples, but since collection periods were relatively short, this addition of nitrogen or absorption through the rumen wall of soluble carbohydrates of ingesta should probably be slight. Other studies (Little 1972; Holechek et al. 1982; Pinchak et al. 1990) also showed that nitrogen contents are altered by salivary contamination but do not differ on an organic matter basis. Furthermore, salivary contamination has very little influence on the CP contents of a wide variety of consumed forages (Harris et al. 1967; Galt and Theurer 1976; Hart 1983). Olson (1991) found that ADF, NDF, and cellulose content were not affected by rumen evacuation technique. Therefore, in the present study, the main reason for the differences detected between the two techniques was most likely our inability to properly estimate the bite size and bite number of the diverse species of grasses, forbs, and shrubs, especially in the enclosures with limited forage biomass.

Foraging behavior of cattle can explain potential problems when using the bite-count technique to estimate foraging efficiency and diet quality. The wide mouths and sweeping prehensile movements of their tongues makes accurate observation of the plant species being eaten difficult in dense vegetation as parts of several plant species can be consumed in one bite. In addition, grasses are more easily distinguished compared to forbs or browse; therefore, chances of underestimating forbs and browse is higher compared to grasses. Ortega et al. (1995) found that compared to the esophageal–fistula technique, the bite-count technique overestimated grasses and underestimated forbs. Since CP of grasses was lower than forbs in our study, the bite-count derived synthesized diet quality was expected to be lower compared to direct estimates of diet quality and quantity using the rumen evacuation technique.

We speculated that bite size has the greatest influence on diet intake and diet quality. As mentioned above, we simulated bite sizes on 32 forage species consumed by steers to estimate diet quality and quantity. In temperate grass swards, leaf surface height appears to be a dominant influence on bite size (Forbs 1988). When we simulated samples from grasses with high sward height and/or less bulk density, we obtained a bigger bite size, similar to Forbs' (1988) observations. Consequently, we probably collected samples with lower quality. In contrast, when forage yield was low we may have simulated smaller bite sizes compared to steers' actual bite sizes. Simulating the portion of the shrub being utilized by grazing steers is more difficult. Steers are able to strip the leaves and stems from woody stems of shrubs. Attempting to duplicate this action by hand is tedious and time-consuming. The technique we used for hand-plucking shrubs was that the samples were plucked between the thumb and a backward-bent forefinger. We wore gloves for own protection and to exert more force to simulate the steers' browsing as closely as possible. Nevertheless, we suspected that we were able to include fewer portions of the twigs and stems with the majority of their leaves compared to actual browsing. In previously grazed paddocks which, in turn, had higher proportions of shrubs in the steer diets, BC derived estimates of digestibility tended to be higher than diets from rumen extrusa. If we pooled chemical composition data by classes of forage consumed by steers (data not shown), the lowest ($P < 0.05$) CP was assessed in grasses (7.0%) compared to forbs (9.5%) and shrubs (9.3%). Lower ($P < 0.001$) IVOMD was also detected for grasses (64.7%) compared to forbs (76.5%) and shrubs (71.9%). Previous grazing causes changes in the composition of forages for subsequent grazers. The observed interaction between diet technique and previous grazing is likely related to the changes in forage availability and the nutritive variation in forage classes (DelCurto et al. 2005). At the time of our experiment dominant grass species like mountain brome, pinegrass, western fescue, Kentucky bluegrass, and Idaho fescue were beginning to senesce. Therefore, nutrients are being transferred to the root system which is likely to cause a wide variation in nutrient content for almost every leaf and stem, thereby making it difficult to simulate diet samples accurately.

In summary, the bite-count technique underestimated the protein content of the diet compared to rumen extrusa samples. In contrast, forage fiber constituents were lower with BC estimates compared to rumen extrusa values. Our findings were similar to Langlands (1974) who evaluated the bite-count technique in sheep. Forbs (1988) noted that it is often difficult to obtain suitable homogeneous study sites to minimize differences among replicates, which allows replication to be dropped from the analysis. However, but if the replication effect is larger than the treatment effect, the analyses are essentially separate, unreplicated trials. This happened in our study area. To obtain statistically analyzable data, it may be convenient to choose fewer pastures but more animals for an experiment with animals as blocks if resources are limited.

MANAGEMENT IMPLICATIONS

Our results suggest that the bite-count technique does not yield results that are identical to the RE technique in range conditions with dense and diverse vegetation. The BC technique has the advantage of not requiring rumen-fistulated animals and produces results that are not confounded by digestive contaminants. Both techniques, however, require tractable animals developed through repeated and continual human contact. In addition, fistulated animals require surgery and long-term care. The accuracy of the bite-count technique depends on the botanical composition of the pasture, the growth stage of the major forage species being grazed, forage biomass, previous utilization level, cattle bite rate during the feeding trial, and observer’s experience.

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CHAPTER 5

Influence of Previous Cattle and Elk Grazing on the Subsequent Diet Quality, and Nutrient Intake Rate of Cattle, Deer, and Elk Grazing Late-Summer Mixed-Conifer Rangelands

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ABSTRACT

A study was conducted to determine diet quality and nutrient intake rates of cattle (*Bos taurus*), mule deer (*Odocoileus hemionus hemionus*), and elk (*Cervus elaphus*) in response to previous grazing by elk and cattle. Four 2.3 ha enclosures, in previously logged grand fir (*Abies grandis* [Dougl. ex D. Don]) rangelands, were chosen and within each enclosure, three 0.75 ha paddocks were either: 1) ungrazed, 2) grazed by cattle, or 3) grazed by elk in early-summer (in mid-June and mid-July) at a moderate utilization level (31.9 ± 2.7). After grazing treatments, each paddock was subdivided into three 0.25 ha sub-paddocks and sixteen (4 animals per each species and 4 feeding bouts/animal) 20-minute feeding bouts were conducted during late-summer (August) of 1998 and 1999 for each sub-paddock.

Ten (6 grasses, 2 forbs, and 2 shrubs), 12 (6 forbs, 5 shrubs, and a lichen), and 12 (5 grasses, 2 forbs, 4 shrubs, and a lichen) principal forage species (≥ 5% of diet) contributed 79.8%-93.8%, 72.6%-76.7%, and 75.6%-86.5% of cattle, deer, and elk diets, respectively. Crude protein (CP) level of the animals' diets did not differ ($P >$ 0.10) on ungrazed paddocks compared to cattle or elk grazed paddocks, however, CP of diets was higher ($P < 0.10$) on cattle grazed paddocks than on elk grazed paddocks. In vitro dry matter digestibility (IVDMD) was lowest ($P < 0.10$) on prior elk grazed paddocks. Cattle diets contained lower CP and IVDMD ($P < 0.10$) compared to deer or elk diets, and, relative to elk, deer consistently selected forages which contained higher CP ($P < 0.10$). Means of diet metabolizable energy (ME) were 7.82 $kJ \cdot g^{-1}$, 8.20 $kJ \cdot g^{-1}$, and 8.19 $kJ \cdot g^{-1}$ ($n = 12$, SE = 0.13) for cattle, deer, and elk, respectively. In response to prior grazing, intake rate of DM (DMI), CP (CPI), and ME (MEI) did not change significantly ($P > 0.10$) for all three animal species; however, means of CPI were 23, 8, and 11 $\mathrm{mg \cdot kg^{0.75} \cdot min^{-1}}$ (SE = 1) and of MEI were 1 379, 757, 1 212 $\mathrm{J \cdot kg^{0.75}}$ $\mathrm{min^{-1}}$ (SE = 113) for cattle, deer, and elk, respectively.

In summary, our study suggests that early-summer grazing by cattle or elk a moderate utilization level has little effect on the subsequent nutrient intake rate of cattle, deer, and elk; however, diets of all ungulates may have been deficient of energy during the late-summer.

Key Words: *Bos taurus*, bite-count, *Cervus elaphus*, competition, resource partitioning, *Odocoileus hemionus hemionus*

INTRODUCTION

Cattle grazing is common on National Forests in the western United States with allowable use standards set for all grazing allotments. National Forests support over 90% of the elk (*Cervus elaphus*) and most mule deer populations (*Odocoileus hemionus hemionus*) during summer in the United States (Wisdom and Thomas 1996). Limited information is available, however, regarding the proper timing and level of use of forested areas by cattle, as well as the interaction and consequences on the following seasons' forage resources. Stewart et al. (2002) and Coe et al. (2004)

concluded that competition for forage could occur between elk and cattle in late-summer and species interactions may be stronger between elk and cattle compared to cattle and deer. Furthermore, the response of elk and/or deer to cattle grazing may vary seasonally depending on forage availability and quality (Peek and Krausman 1996; Wisdom and Thomas 1996). In fall, winter, and spring, elk preferred forage that cattle had lightly or moderately grazed the preceding summer (Crane et al. 2001). Also, 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). Late-summer and early fall forage quality and quantity can be critical for the nutritional well-being of livestock and wild ungulates because late-summer nutritional deficiencies are common in regions where summer drought is a normal part of the climatic season (Vavra and Phillips 1980; Svejcar and Vavra 1985; Cook et al. 2004). Foraging behavior of free ranging ungulates on large landscapes over time is a complex process that can only be approximated with models (Ager et al. 2004). Unfortunately, controlled replicated experiments are lacking on effects of early-summer elk and cattle grazing on subsequent late-summer foraging dynamics of cattle, deer, and elk.

The objectives of this study were to investigate late-summer diet quality and nutrient intake rate of cattle, deer, and elk in response to prior grazing by elk and cattle on mixed-conifer rangelands.

In a companion study, a detailed analysis of effects of previous grazing by elk or cattle on subsequent diet composition and diet overlap of cattle, deer, and elk is presented (Findholt et al. 2004).

MATERIALS AND METHODS

Study Area

The study was conducted on the Starkey Experimental Forest and Range, located in the Wallowa-Whitman National Forest in the Blue Mountains of northeast Oregon (45°15′ N, 118°25′ W), approximately 35 km southwest of La Grande, Oregon. Elevation of the experimental site ranged between 1 120 m to 1 500 m and total annual precipitation for the study years was 614 mm in 1998 and 449 mm in 1999, which was 12.2% above and 17.9% below average, respectively (Figure 5.1; weather records on file at PNW research laboratory in La Grande, Oregon). The growing season lasts about 120 days, but no months are considered frost-free (Skovlin et al. 1976).

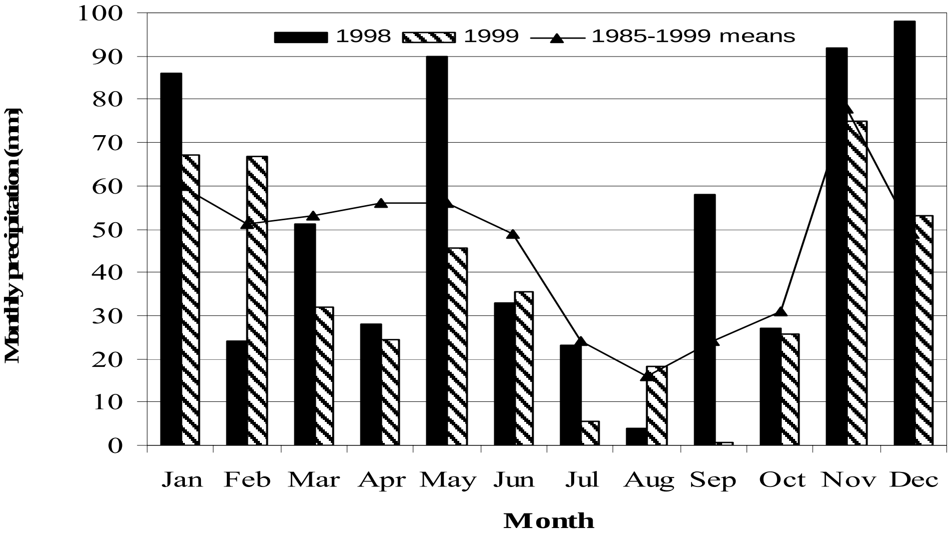

Figure 5.1. Monthly precipitation for 1998-1999 and long term (1985-1999) mean monthly precipitation for Starkey Experimental Forest and Range, northeast Oregon.

Pinegrass (*Calamagrostis rubescens* Buckl.), California brome (*Bromus carinatus* H. & A), western fescue (*Festuca occidentalis* Walt.), Kentucky bluegrass (*Poa pratensis* L.), Idaho fescue (*Festuca idahoensis* Elmer), and elk sedge (*Carex geyeri* Boott) are the dominant forage species in terms of availability. Several forb species are present including western yarrow (*Achillea millefolium lanulosa* L.), strawberries (*Fragaria vesca* L. and *Fragaria virginiana* Duchesne.), hawkweed (*Hieracium* spp.), lupine (*Lupinus* spp.), and tall annual willowherb (*Epilobium paniculatum* Nutt.). While common snowberry (*Symphoricarpos albus* [L.] Blake), big huckleberry (*Vaccinium membranaceum* Hook.), grouse huckleberry (*Vaccinium scoparium* Leib.), shinyleaf spiraea (*Spiraea betulifolia lucida* Pall.), twinflower (*Linnaea borealis* L.), and bearberry (*Arctostaphylos uva-ursi* L.) are the primary shrub species consumed by cattle, deer, and elk in the Blue Mountain region.

Experimental Design and Grazing Treatment

Four enclosures were placed in previously logged grand fir or mixed-conifer rangelands (15-20 years post harvest) and within each enclosure, three 0.75 ha pastures were either: 1) ungrazed, 2) grazed by cattle, or 3) grazed by elk in early-summer (mid-June and mid-July) to remove total forage biomass at a moderate utilization level (31.9 ± 2.7%). This level of rangeland utilization falls within the standard used by the U.S. Department of Agriculture, Forest Service for cattle allotments on upland sites in good condition in northeast Oregon (Findholt et al. 2004). We picked these previously logged, grand fir rangeland sites, because spatial and temporal overlap of all three species occurred in late-summer in this habitat (Coe et al. 2004). Forage in this habitat is most palatable and nutritious in early-summer (Holechek et al. 1982; Coe et al. 2004) with a decline in quality in late-summer due to advancing phenologic maturity and/or drought.

Forage biomass and utilization were determined using the cage plot comparison method (Cook and Stubbendieck 1986). In paddocks chosen at random for elk or cattle grazing treatments, ninety 0.25-m^2 plots were located, from which thirty plots were protected with wire cages (caged plot) and sixty plots were not protected (uncaged plot). In ungrazed paddocks, sixty 0.25-m^2 plots were placed randomly; the paddocks were not utilized during the current year. After grazing treatment and within 2-3 days before feeding trials, we clipped herbaceous vegetation in all plots to ground level and browse was plucked by plant species to determine biomass and utilization. Biomass of each plot was calculated on a $kg \cdot ha^{-1}$ basis.

We selected common snowberry as a key shrub species for estimating utilization level of early-summer grazing by cattle and elk because snowberry is considered valuable forage for cattle (Holechek et al. 1982), deer (Peek and Krausman 1996), and elk (Cook 2002). Shrub utilization was evaluated by the photographic technique (Damiran et al. 2006 in press; see also Chapter 2). Fifteen individual shrubs of common snowberry were selected randomly on each paddock, each year. Photos of shrubs were taken immediately before and after grazing with a digital camera and images were evaluated using image processing software. Shrub utilization was estimated based on leaf area reduction due to grazing treatment.

Feeding Bouts

After grazing treatments, each paddock within an enclosure was subdivided into three 0.25 ha sub-paddocks and 16 (4 animals and 4 feeding trials/animal/year) 20-minute feeding bouts were conducted in each paddock using four steers (BW = 454 kg), four tame mule deer (BW = 54 kg), or four tame elk (BW = 227 kg) during late-summer (August) of 1998 and 1999. Two feeding bouts were conducted in the morning (0800-1200) and another two were conducted in the afternoon (1300-1600) for each animal in each paddock. Dietary composition and forage intake of experimental animals were measured using bite-count technique similar to that described by Wickstrom et al. (1984) and Canon et al. (1987). Food was not offered to animals each morning and between feeding bouts to ensure reasonable and similar appetites each day. Thus, animals were fasted 7 to 10 h prior to bouts. Chacon and Stobbs (1977) found that bite size and diet quality were influenced more by stage of defoliation and individual animal variability than by fasting or diurnal variation in time of sampling, as long as fasting was less than 12 h. Therefore, by keeping fasting periods relatively short, we assumed there would be no measurable effects on our experimental results. During each feeding trial, animals were allowed to roam free in one of the paddocks for 20 minutes and trained observers followed each animal and recorded the number of bites of each forage species consumed using a small hand-held tape recorder. Bites were counted while the observer was close (1-2 m) to the animal, thereby assuring accurate identification of the consumed forage. All plants eaten were identified to species and later grouped into four forage classes: grasses (grasses, sedges, and rushes), forbs, shrubs (including tree species), and lichens.

After completion of feeding bouts each day, animals were fed alfalfa hay at 1.5% of body weight and held overnight in corrals for the next days' feeding trials. Cattle research protocol and use approved by the Oregon State University Animal Care and Use Committee and research on deer and elk at Starkey was in accordance with approved animal welfare protocols (Wisdom et al. 1993). Plant nomenclature throughout this paper follows the recommendations of the USDA Natural Resources Conservation Service (USDA, NRCS 2005).

Diet Sampling

Samples of plants selected by animals during feeding bouts in each treatment were collected through hand clipping and plucking (Cook and Stubbendieck 1986). Variation in plant parts and bite sizes due to different quantities of plants available or different plant forms were accounted for by simulating bite sizes when samples were collected. Typically, 100 to 200 simulated bites of each plant species were collected per feeding bout, placed in paper bags, dried in a forced air oven at 50°C, and weights were determined by dividing the total dry weight of the collected sample by the number of bites collected. An average bite size corresponding to each feeding bout was calculated by a weighted mean of simulated bite size for the different forage species in accordance to the bite number.

Diet Quality Analyses

Simulated forage samples were ground in a Wiley Mill (Model #2, Arthur H. Thomas Co, Philadelphia, PA) to pass a 1-mm screen, analyzed in duplicate according to

AOAC (1990) for DM, and crude protein (CP). Crude protein was determined using the Kjeltec Auto System (Kjeltec Auto System, Büchi, Flawil, Switzerland). Acid detergent fiber (ADF) and neutral detergent fiber (NDF) were determined by Ankom^{200} fiber analyzer (ANKOM Technology Corporation, Fairport, NY) using the procedures described by Vogel et al. (1999).

In vitro dry matter digestibility (IVDMD) was determined by techniques similar to those described by Vogel et al. (1999) and Holden (1999) using a Daisy^{II} incubator (ANKOM Technology Corporation, Fairport, NY). However, because this technique does not yield results that are comparable to conventional techniques, in particular, with forbs, shrubs, and lichens, or forages which contain low cell-wall carbohydrates, regression equations for each forage species were developed (Damiran et al. 2002) and used to convert filter bag digestibility estimates to values comparable to the two-stage IVDMD technique (Tilley and Terry 1963). Rumen ingesta was obtained from two steers and used for cattle, deer, and elk diet digestibility analysis.

We converted IVDMD to digestible energy (DE) with the formula of Rittenhouse et al. (1971): $\text{DE (kJ}\cdot\text{kg}^{-1}) = ([0.38 \times \text{IVDMD} (\%) + 0.18] \times 4.18 \times 1000)$, and for cattle and elk, DE was converted to metabolizable energy (ME) using the relationship provided by NRC (1984): $\text{ME (kJ}\cdot\text{kg}^{-1}) = \text{DE} \times 0.82$. In contrast, apparent metabolizable energy coefficients for deer were derived from Robbins (1993) and were: 0.818 for forbs and grasses; 0.806 for shrubs, and 0.764 for conifers.

Calculations and Statistical Analysis

Bite-count derived DM intake rate (DMI) was determined as follows: DMI ($g \cdot min^{-1}$) = $\sum N_iBS_i$; Nutrient intake rate N_i (g and $kJ \cdot g^{-1}$ for CP and ME, respectively) = $\sum N_iBS_i DQ_i$ and diet quality was calculated as: DQ (%) = $\sum(N_iBS_iDQ_i)/\sum N_iBS_i$, where: N_i is the number of bites of forage species during feeding trial ($n \cdot min^{-1}$), BS_i = bite size of forage species i (estimated through hand plucking sample, g), DQ_i = nutritive quality (CP, ADF, NDF, IVDMD; %, DM) or ME ($kJ \cdot g^{-1}$) of forage species i (%, DM). Crude protein and ME intake rates were expressed per metabolic weight ($kg^{0.75}$).

Forage biomass, as well as biomass summed by forage class data, was analyzed as a completely randomized block design with 4 blocks (enclosures) per grazing treatment. Diet quality and nutrient intake rate data were analyzed as split-plots with 4 blocks per treatment combination in a completely randomized block design with grazing treatment (three levels) as the main effects, and animal type (three levels) and grazing treatment x animal type interactions as sub-plot effects using the mixed model procedure of SAS (2001). Assignment of grazing treatments to paddocks was done randomly, and remained the same in 1998 and 1999. Therefore, data were averaged over 1998 and 1999. When a significant *F*-value was found ($P < 0.10$), then a Tukey-Kramer post-test (SAS 2001) was performed. LSMeans were computed and statistically separated with the PDIFF option of SAS. Results were considered significant at $P < 0.10$. Significance levels from $P \geq 0.10$ to $P \leq 0.20$ were recognized as tendencies and probability value of $P > 0.20$ was considered not significant.

RESULTS

Grazing Treatments

Grazing treatment, as well as grazing treatment x cage interactions, did not differ ($P > 0.20$) for forage biomass in experimental paddocks. However, mean of forage biomass (1 216 kg·ha^{-1}, $n = 4$, SE = 58) in ungrazed (caged) plots was higher ($P < 0.10$) than that in grazed (uncaged) plots (888 kg·ha^{-1}, $n = 4$, SE = 58). LSMeans of prior grazing utilization of were 32.6% and 31.2% for cattle and elk grazed paddocks, respectively ($P > 0.10$, $n = 4$, SEM = 3.0). Forage class (grasses, forbs, and shrubs), as well as grazing treatment x forage class interactions, did not reach significant levels ($P > 0.10$) for utilization. In ungrazed paddocks, forage biomass averaged 332 ± 43 kg·ha^{-1}, 335 ± 28 kg·ha^{-1}, and 550 ± 83 kg·ha^{-1} ($n = 8$) for grasses, forbs, and shrubs, respectively. Utilization level of grasses, forbs, and shrubs was 38.8%, 27.3%, and 30.4% in cattle grazed paddocks and 27.0%, 22.2%, and 28.5% for elk grazed paddocks, respectively ($n = 4$, SE = 6.2). In addition, no visible initiation of plant regrowth by early-summer grazing was detected. Elk consistently ate more ($P < 0.05$) snowberry than cattle in early-summer (Table 5.1).

Chemical Composition of Major Forage Species

Thirty four individual forage species (9 grasses, 13 forbs, 11 shrubs/trees, and a lichen) were collected for nutritional analysis during the two year study period yielding a total of 462 samples. Chemical composition of individual species differed dramatically ($P < 0.01$, Table 5.2), of which California brome, elk sedge, intermediate wheatgrass (*Agropyron intermedium* [Host] Beauv.), Kentucky bluegrass, northwestern sedge (*Carex concinnoides* Mackenzie), timothy (*Phleum pratense* L.), pinegrass (*Calamagrostis rubescens* Buckl.), western fescue, heartleaf arnica (*Arnica cordifolia* Hook.), sticky geranium (*Geranium viscosissimum* Fisch. & C.A. Mey. ex C.A. Mey.), western hawkweed (*Hieracium albertinum* Farr), yellow salsify (*Tragopogon dubius* Scop.), twinflower, and bearberry contained < 7.5% CP. Acid detergent fiber level ranged from 12.1 ± 1.4% to 46.3 ± 1.1% and NDF ranged from 22 ± 4.8 % to 67.3 ± 1.1% across forage species. The variability of IVDMD in forage species was considerable. Snowbrush (*Ceanothus velutinus* Dougl. ex Hook.) was the highest in metabolizable energy (10.0 ± 0.4 kJ$\cdot$g^{-1}), whereas western fescue and ponderosa pine were the lowest (6.7 ± 0.4 and 5.9 ± 0.4 kJ$\cdot$g^{-1}, respectively).

Table 5.1. Common snowberry utilization (LSMeans) during early-summer cattle and elk grazing on mixed-conifer rangelands of northeast Oregon.

Paddock	Green Leaf Area (pixel)		Utilization (%)	P^1
	Before grazing^2	After grazing		
Cattle grazed	14239	7641	46.3^a	0.008
Elk grazed	15599	5961	61.8^b	0.000

[1] Probability of *F*-test contrasts before vs. after grazing green leaf area for the same row (*n* = 6; SEM = 570).

[2] Leaf area size adjusted by shrub growth rate (1.51, between beginning of June and end of July) during grazing treatment.

[ab] Column values with different superscripts differ ($P < 0.05$, $n = 6$; SEM = 8.5).

Overall, pooled by forage classes, the lowest mean ($P < 0.01$) CP level was obtained in grasses (6.2 ± 0.7%), while forbs (9.6 ± 0.6%), shrubs (9.2 ± 0.6%), and

Table 5.2. Percentage (means ± SEM) of crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), in vitro dry matter digestibility (IVDMD) and metabolizable energy (ME) of the major forage species for cattle, deer and elk grazing late-summer mixed-conifer rangelands on the Starkey Experimental Forest and Range, northeast Oregon for 1998 and 1999.

Forage Species		Chemical Composition (% DM basis)				
	n	CP	ADF	NDF	IVDMD	ME[1]
Grasses						
California brome	29	6.6 ± 0.2	44.2 ± 0.9	63.1 ± 0.9	59.0 ± 0.8	8.4 ± 0.1
Elk sedge	31	6.1 ± 0.2	41.6 ± 0.8	62.2 ± 0.9	55.6 ± 0.8	7.9 ± 0.1
Intermediate wheatgrass	2	6.0 ± 0.9	41.1 ± 3.3	61.3 ± 3.4	56.1 ± 3.2	7.9 ± 0.4
Kentucky bluegrass	12	5.1 ± 0.4	43.9 ± 1.3	64.2 ± 1.4	54.0 ± 1.3	7.5 ± 0.1
Northwestern sedge	3	5.9 ± 0.7	40.4 ± 2.7	62.3 ± 2.8	56.5 ± 2.6	7.9 ± 0.4
Orchardgrass	19	8.3 ± 0.3	36.9 ± 1.1	54.1± 1.1	63.6 ± 1.0	8.8 ± 0.2
Pinegrass	36	7.5 ± 0.2	45.4 ± 0.8	58.7 ± 0.8	51.7 ± 0.7	7.5 ± 0.0
Timothy	4	5.5 ± 0.6	39.1 ± 2.3	63.2 ± 2.4	51.2 ± 2.2	7.1 ± 0.4
Western fescue	18	4.9 ± 0.3	46.3 ± 1.1	67.3 ± 1.1	47.0 ± 1.1	6.7 ± 0.1
Forbs						
Autumn willowweed	13	8.6 ± 0.4	35.8 ± 1.3	44.0 ± 1.3	49.8 ± 1.2	7.1 ± 0.3
Beauty cinquefoil	3	9.6 ± 0.7	22.2 ± 2.7	29.0 ± 2.8	64.1 ± 2.6	8.4 ± 0.4
Bull thistle	7	9.2 ± 0.5	30.1 ± 1.8	32.6 ± 1.8	63.7 ± 1.7	8.8 ± 0.4
Fireweed	3	11.7 ± 0.7	23.3 ± 2.7	24.1 ± 2.8	64.2 ± 2.6	8.8 ± 0.4
Heartleaf arnica	4	6.7 ± 0.6	24.5 ± 2.3	28.3± 2.4	64.6 ± 2.2	9.2 ± 0.5
Mountain thermopsis	1	14.2 ± 1.3	19.1 ± 4.7	22.0 ± 4.8	65.4 ± 4.5	8.8 ± 0.4
Spur lupine	19	11.5 ± 0.3	32.4 ± 1.1	41.4 ± 1.1	72.0 ± 1.0	8.8 ± 0.4
Stickystem penstemon	1	7.3 ± 1.3	38.0 ± 4.7	40.8 ± 4.8	60.8 ± 4.5	9.2 ± 0.4
Strawberry	39	9.6 ± 0.2	19.9 ± 0.7	26.9 ± 0.8	56.2 ± 0.7	7.9 ± 0.1
Western hawkweed	10	7.3 ± 0.4	37.1 ± 1.5	44.9 ± 1.5	63.1 ± 1.4	8.8 ± 0.2
White clover	2	14.0 ± 0.9	35.3 ± 3.3	38.7 ± 3.4	61.9 ± 3.2	7.1 ± 0.2

Table 5.2. Percentage (means ± SEM) of crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), in vitro dry matter digestibility (IVDMD) and metabolizable energy (ME) of the major forage species for cattle, deer and elk grazing late-summer mixed-conifer rangelands on the Starkey Experimental Forest and Range, northeast Oregon for 1998 and 1999 (Continued).

Forage Species		Chemical Composition (% DM basis)				
	n	CP	ADF	NDF	IVDMD	ME [1]
Forbs						
Western yarrow	9	9.4 ± 0.4	35.6 ± 1.6	37.5± 1.6	69.5 ± 1.5	9.6 ± 0.2
Yellow salsify	1	4.9 ± 1.3	37.3 ± 4.7	46.6 ± 4.8	58.4 ± 4.5	8.8 ± 0.5
Shrubs & Trees						
Baldhip rose	23	8.8 ± 0.3	21.4 ± 1.0	27.7 ± 1.0	67.5 ± 0.9	9.6 ± 0.2
Bearberry	28	5.9 ± 0.2	37.5 ± 0.9	36.0 ± 0.9	49.7 ± 0.8	8.8 ± 0.5
Big huckleberry	26	8.9 ± 0.3	27.2 ± 0.9	31.4 ± 0.9	58.3 ± 0.9	8.4 ± 0.1
Common snowberry	25	8.3 ± 0.3	24.2 ± 0.9	29.9 ± 1.0	68.8 ± 0.9	9.6 ± 0.3
Grouse huckleberry	8	8.2 ± 0.5	38.3 ± 1.6	40.3 ±1.7	52.6 ± 1.6	7.5 ± 0.2
Low oregongrape	14	10.5 ± 0.3	31.3 ± 1.2	41.9 ± 1.3	63.9 ± 1.2	8.4 ± 0.2
Ponderosa pine	2	9.0 ± 0.9	38.1 ± 3.3	47.0 ± 3.4	41.2 ± 3.2	5.8 ± 0.4
Saskatoon serviceberry	6	10.9 ± 0.5	26.2 ± 1.9	36.5 ± 2.0	63.3 ± 1.8	8.8 ± 0.0
Shinyleaf spirea	29	8.5 ± 0.2	28.1 ± 0.9	35.5 ± 0.9	56.4 ± 0.8	7.9 ± 0.0
Snowbrush	7	12.8 ± 0.5	26.8 ± 1.8	26.8 ± 1.8	62.1 ± 1.7	10.0 ± 0.0
Twinflower	9	6.8 ± 0.4	35.9 ± 1.6	40.9 ± 1.6	58.1 ± 1.5	8.4 ± 0.4
Lichen						
Tree hair lichen	11	9.6 ± 0.4	12.1 ± 1.4	38.1 ± 1.5	65.9 ± 1.3	9.2 ± 0.3

[1] ME calculated using the relationship provided by NRC (1984): ME (kJ g^{-1}) = DE (kJ g^{-1}) x 0.82. Digestible Energy (DE) was calculated with the formula from Rittenhouse et al. (1971): DE (kJ g^{-1}) = (0.38 x IVDMD (%) + 0.18.) x 4.18

lichen's (9.6 ± 2.2%) did not differ ($P > 0.20$). Moreover, higher ($P < 0.01$) ADF (42.1 ± 2.0%) and NDF (61.8 ± 2.2%) were detected for grasses.

We detected no differences ($P > 0.20$) between forbs and shrubs for ADF (30.0 ± 1.6 and 30.3 ± 1.7%, respectively) or NDF (35.1 ± 1.9 and 35.2 ± 2.0%, respectively). Grasses' ME level (7.9 ± 0.4 $\mathrm{kJ \cdot g^{-1}}$) was lower ($P < 0.01$) than those of forbs (8.8 ± 0.3 $\mathrm{kJ \cdot g^{-1}}$) and lichen (9.2 ± 0.8 $\mathrm{kJ \cdot g^{-1}}$), but did not differ ($P > 0.20$) with shrubs' ME (8.4 ± 0.4 $\mathrm{kJ \cdot g^{-1}}$). Mean digestibility was 55.1 ± 0.6%, 61.3 ± 0.7%, 59.7 ± 0.6%, and 65.9 ± 2.3% for grasses, forbs, shrubs, and lichen, respectively.

Diet Quality and Quantity

For animal diet quality, grazing treatment x animal species interactions were not significant ($P > 0.20$) indicating that the main effects functioned independently. In contrast, grazing treatment and animal species effects were noted ($P < 0.10$) for diet quality (Table 5.3).

Crude protein level of animal diets were higher ($P < 0.10$) on the prior cattle grazed paddocks compared to the prior elk grazed paddocks. However, CP levels of animal diets were not different ($P > 0.20$) on prior cattle or elk grazed paddocks compared to ungrazed paddocks.

Acid detergent fiber of animal diets was the greatest ($P < 0.10$), while IVDMD was the lowest ($P < 0.10$) on prior elk grazed paddocks. Metabolizable energy of animal diets was 8.15 $\mathrm{kJ \cdot g^{-1}}$, 8.19 $\mathrm{kJ \cdot g^{-1}}$, and 7.9 $\mathrm{kJ \cdot g^{-1}}$ for the ungrazed, cattle grazed, and elk grazed paddocks, respectively ($n = 12$, SE = 0.13).

Response of diet ADF under prior cattle and elk grazing varied. Under prior elk grazing, NDF level did not change ($P > 0.20$) relative to diets selected in ungrazed paddocks. In contrast, diet NDF level was lower ($P < 0.10$) on prior cattle grazed paddocks compared to ungrazed or prior elk grazed paddocks.

We found that cattle diets contained lower ($P < 0.10$) CP and DMD, but higher ADF and NDF compared to deer or elk diets. Relative to elk, deer consistently selected forages containing higher CP ($P < 0.10$), and lower ($P < 0.10$) ADF and NDF. In vitro DMD levels of deer and elk diets was similar ($P > 0.20$). Diet metabolizable energy was 7.81 $\text{kJ}\cdot\text{g}^{-1}$, 8.19 $\text{kJ}\cdot\text{g}^{-1}$, and 8.19 $\text{kJ}\cdot\text{g}^{-1}$ ($n = 12$, SE = 0.13) for cattle, deer, and elk diets, respectively. Grazing treatment x animal species x forage class interacted ($P < 0.01$) for CP (Figure 5.2) and ME (Figure 5.3).

Grazing treatment as well as grazing treatment x animal species interactions were not detected ($P > 0.20$) on nutrient intake rate (Table 5.4). Thus, the main effects did not influence ($P > 0.20$) animal CPI and MEI, but only DMI showed a slight decreasing trend ($P = 0.19$) in previously cattle grazed paddocks. Deer CPI, DMI, and MEI were lower ($P < 0.01$) than those of cattle and elk. Cattle and elk had similar ($P > 0.20$) nutrient intake rates. Grazing treatment x animal species interaction was not found ($P > 0.20$) for bite sizes. In addition, bite sizes tended to decline ($P = 0.16$) in prior cattle grazed paddocks. Animal species interacted ($P < 0.01$) with bite sizes. Bite size was 661, 160, and 471 mg (SE = 59) for cattle, deer, and elk, respectively.

Table 5.3. Diet quality (LSMeans) as affected by previous cattle and elk grazing on the Starkey Experimental Forest and Range, northeast Oregon (Data averaged over 1998 and 1999).

	Paddock[1]			Animal Species			
Diet Composition[2]	Ungrazed	Cattle Grazed	Elk Grazed	Cattle	Deer	Elk	SE[3]
CP (%, DM)	7.8^{ab}	8.3^{b}	7.6^{a}	6.8^{a}	9.0^{b}	7.9^{c}	0.3
ADF (%, DM)	33.8^{a}	31.8^{a}	37.5^{b}	41.5^{a}	29.0^{b}	32.6^{c}	0.8
NDF (%, DM)	46.3^{a}	42.2^{b}	48.1^{a}	57.2^{a}	35.0^{b}	44.3^{c}	1.2
IVDMD (%)	57.8^{a}	58.1^{a}	55.8^{b}	55.2^{a}	58.3^{b}	58.2^{b}	1.0

[1] No grazing treatment x animal species interaction ($P > 0.20$).

[abc] Row values within grazing treatment or animal species with different superscripts differ ($P < 0.10$, $n = 4$).

[2] Crude protein (CP), Acid detergent fiber (ADF), Neutral detergent fiber (NDF), and In vitro dry matter digestibility (IVDMD).

[3] Standard error of LSMeans.

Table 5.4. Cattle, deer and elk nutrient intake rate (LSMeans) during grazing in late-summer mixed-conifer rangelands on the Starkey Experimental Forest and Range, northeast Oregon (Data averaged over 1998 and 1999).

	Animal Species			
Nutrient Intake Rate[1]	Cattle	Deer	Elk	SEM[2]
CPI ($\text{g}\cdot\text{kg}^{0.75}\cdot\text{min}^{-1}$)	0.012^{a}	0.008^{b}	0.011^{a}	0.001
DMI ($\text{g}\cdot\text{kg}^{0.75}\cdot\text{min}^{-1}$)	0.179^{a}	0.093^{b}	0.148^{a}	0.015
MEI ($\text{kJ}\cdot\text{kg}^{0.75}\cdot\text{min}^{-1}$)	1.380^{a}	0.757^{b}	1.212^{a}	0.112

[abc] Row values with different superscripts differ ($P < 0.10$, $n = 4$).

[1] Crude protein intake (CPI), Dry matter intake (DMI), and metabolizable energy intake (MEI) rates. Metabolizable energy (ME) was calculated using the relationship provided by NRC (1984): ME ($\text{kJ}\cdot\text{g}^{-1}$) = DE ($\text{kJ}\cdot\text{g}^{-1}$) x 0.82. Digestible energy (DE) was calculated with the formula of Rittenhouse et al. (1971): DE ($\text{kJ}\cdot\text{g}^{-1}$) = (0.38 x IVDMD (%) + 0.18) x 4.18. But for deer the following apparent metabolizable energy coefficients (Robbins 1993) were used: 0.818 for forbs, grasses, and sedges; 0.806 for shrubs, and 0.764 for conifers.

[2] Standard error of LSMeans.

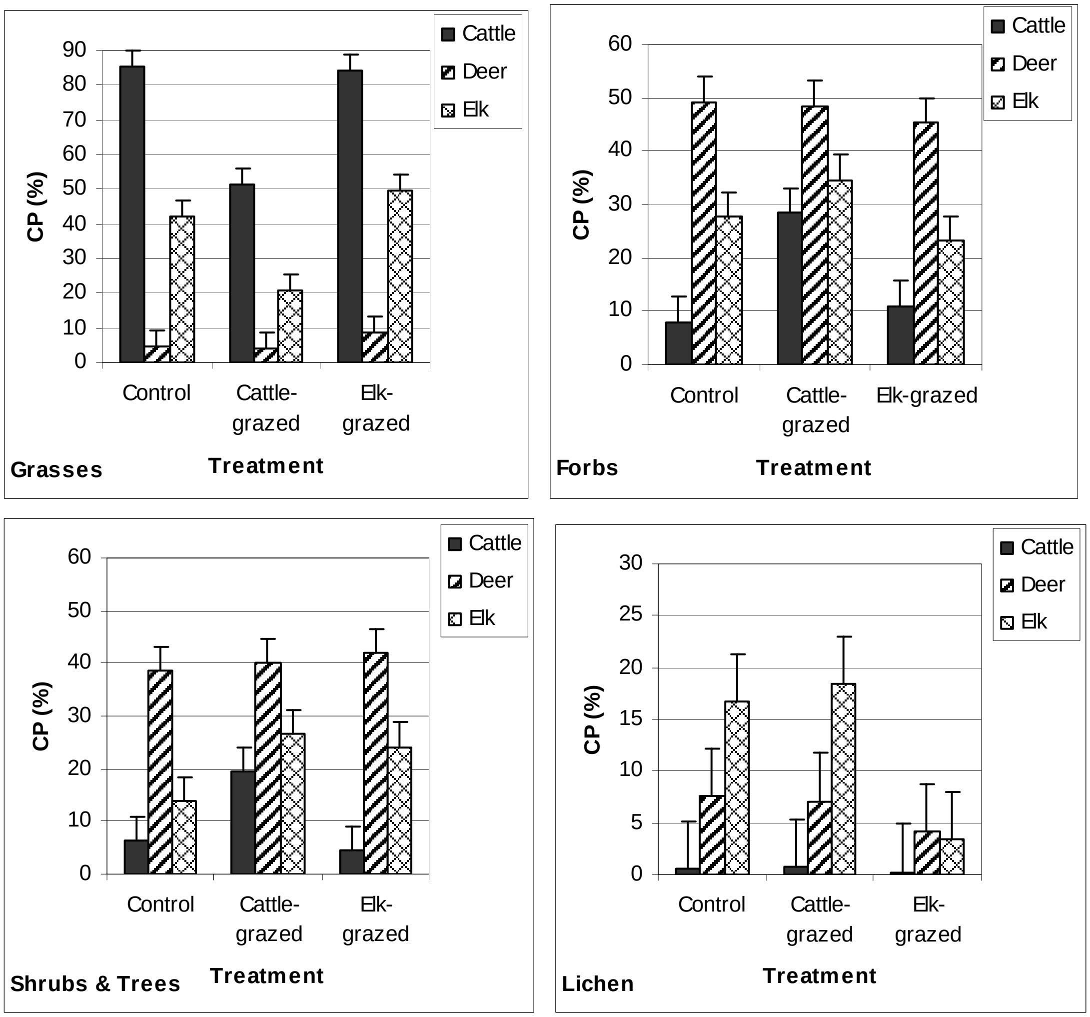

Figure 5.2. Influence of previous cattle and elk grazing to major forage contribution (%) on cattle, deer, and elk CP intake (LSMeans) in late-summer mixed-conifer rangelands on the Starkey Experimental Forest and Range, northeast Oregon (Data averaged over 1998 and 1999). Grazing treatment x animal species x forage class interactions are $P < 0.01$ and SEM = 4.26.

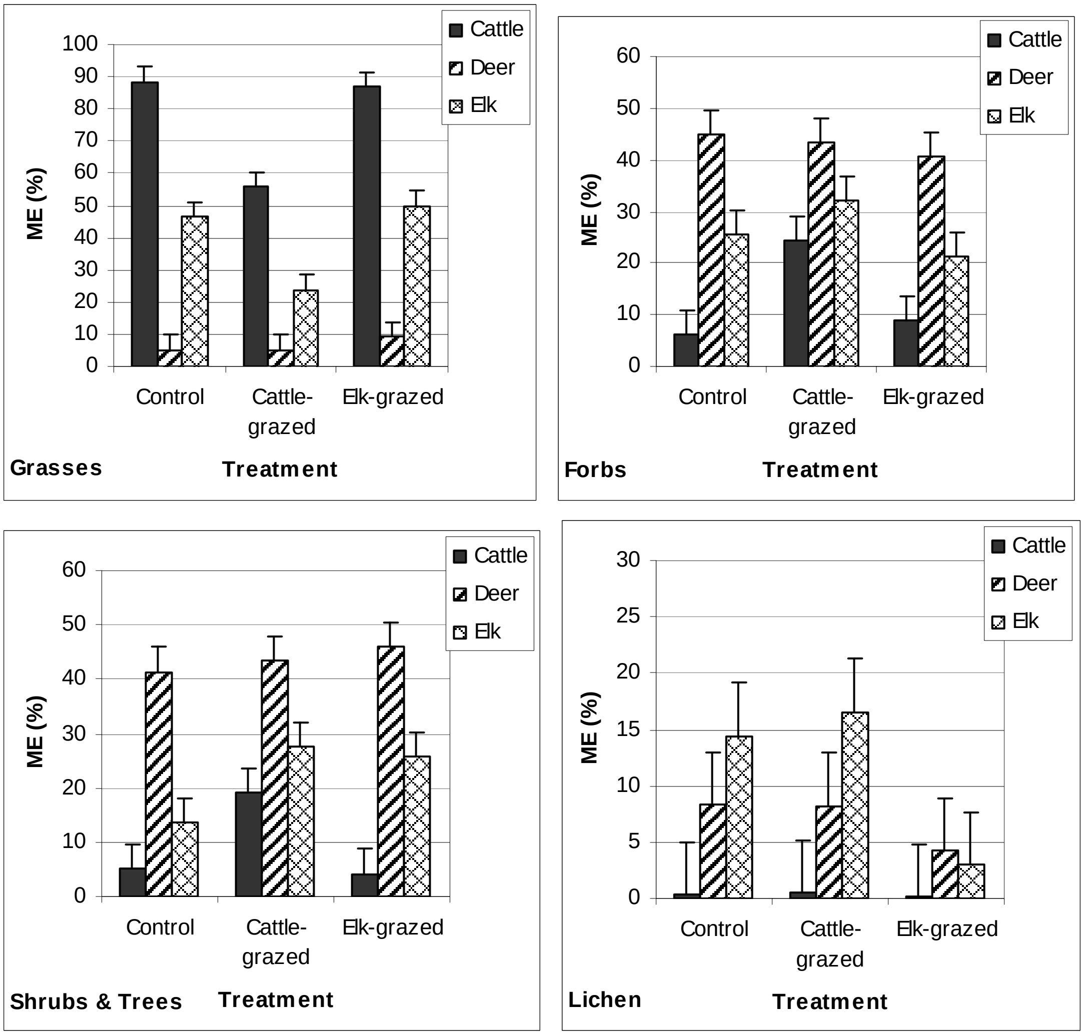

Figure 5.3. Influence of previous cattle and elk grazing to major forage contribution on cattle, deer, and elk ME intake (LSMeans) during in late summer in mixed-conifer rangelands on the Starkey Experimental Forest and Range, northeast Oregon (Data averaged over 1998 and 1999). Grazing treatment x animal species x forage class interactions are $P < 0.01$ and SEM = 4.64.

DISCUSSION

Diet Botanical Composition

Diet selection by free ranging ungulates is influenced by many plant and animal factors. The ability of animals to graze selectively depends on the structure and size of their jaws and teeth, and on their basic method of grazing (Arnold 1987). We observed > 68, > 84, and > 77 forage species in cattle, deer, and elk diets, respectively (Table A.5.1) and throughout feeding bouts 109 individual forage species were recorded in animal diets. However, only 20 species contributed > 5% to at least 1 animal species' diet, suggesting that animals selected a diversity of forages, but focused on few species during foraging. Table A.5.1 also shows 10 (6 grasses, 2 forbs, and 2 shrubs) principal forage species that accounted for 79.8%-93.8% of cattle diets, while 12 (6 forbs, 5 shrubs, and a lichen) species contributed 72.6%-76.7% to deer diets, and 12 forage species (5 grasses, 2 forbs, 4 shrubs, and a lichen) provided 75.6%-86.5% to elk diets in late-summer. Predictably, diets of deer and elk were more diverse than those of cattle in this study. Some plant species, as noted by Parker et al. (1999), are only tasted for palatability and eaten rarely by animals. In our study shrub and tree species like white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), grand fir, mallow ninebark (*Physocarpus malvaceus* [Greene] Kuntze), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), red raspberry (*Rubus idaeus* L.), and pacific yew (*Taxus brevifolia* Nutt.) were only consumed by deer in trace (< 0.1%) amounts.

Regardless of prior grazing treatment, California brome and Kentucky bluegrass dominated cattle diets, blueleaf strawberry (*Fragaria virginiana* Duchesne) and bearberry dominated deer diets, and orchardgrass (*Dactylis glomerata* L.) dominated elk diets. These species composed 5% or more of animal diets in each grazing treatment. The most consistently eaten forage species in this study, by both cattle and elk was pinegrass, whereas deer and elk preferred woods strawberry (*Fragaria vesca* L.) and tree hair lichen (*Bryoria fremontii* [Tuck.] Brodo & D. Hawksw.). Longspur lupine (*Lupinus laxiflorus* Dougl. ex Lindl.) M.E. Jones) was eaten frequently by all animal species in prior grazed paddocks, while orchardgrass was highly preferred by cattle when available.

In response to prior cattle or elk grazing, western fescue (*Festuca occidentalis* Hook.) and spur lupine became the principal forage species in cattle diets when orchardgrass declined. In prior cattle grazed paddocks, big huckleberry and scouler willow (*Salix scouleriana* Barratt ex Hook.) increased, while shinyleaf spirea decreased as principal species in deer diets. In prior elk grazed paddocks, tall annual willowherb, baldhip rose, and tree hair lichen decreased in deer diets, while spur lupine increased. In response to prior cattle grazing, spur lupine decreased, but bearberry and big huckleberry increased as principal forage species of elk. In response to prior elk grazing, California brome, western fescue, bearberry, and twinflower increased, as tree hair lichen decreased as principal species in elk diets.

In a companion study, Findholt et al. (2004) demonstrated mean diet overlap for forage classes in ungrazed paddock was 49% between cattle and elk, 59% between deer and elk, but only 19% between cattle and deer. Diet overlap between cattle and deer increased in paddocks previously grazed by cattle ($P < 0.10$), but not in paddocks grazed by elk ($P > 0.20$). Findholt et al. (2004) also found that percent diet overlap between cattle and elk was higher in paddocks previously grazed by elk, as compared to control paddocks ($P < 0.10$). Percent diet overlap between mule deer and elk did not vary with grazing treatments ($P > 0.10$).

Diet Quality

Hyder and Sneva (1963) first proposed spring grazing as a means to provide high-quality vegetation regrowth for fall use. Anderson and Scherzinger (1975) provide this hypothesis of grazing effects on nutritional quality of forage: properly timed grazing in the spring during the active growth stage of bunchgrasses delays reproductive effort and maturity of plants. Removing the current year's growth at or before the boot stage of phenology allows the plant to regrow.

Research verification of these applied practices has been mixed (Vavra and Sheehy 1996). Bryant (1993) and Westenskow-Wall et al. (1994) applied spring clipping to bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) during the preboot stage. Subsequent nutritive value and growth were not substantially enhanced in clipped plants compared to unclipped plants. Pitt (1986) reported an improvement in nutritive quality of clipped, boot-stage plants over those not clipped, but noted that forage quantity was compromised. Ganskopp (1998) periodically defoliated Thurber's needlegrass (*Stipa thurberiana* Piper) in southern Oregon, then observed subsequent biomass accumulation, and analyzed nutritive quality. Forage quality was improved by the regrowth subsequent to clipping, but as clipping date advanced, regrowth quantity diminished. He cautioned that the timing of grazing was critical to providing both adequate quality and quantity of regrowth. In dry years, regrowth forage production might be seriously curtailed (Vavra 2005). In our study, no strong evidence was found that previous elk or cattle grazing improved forage quantity and quality for deer, elk, and cattle that grazed the same pastures later that year. For conditions of our study, soil moisture may not have been adequate in late June and July for vegetation regrowth.

Nevertheless, compared to ungrazed paddocks, animal diet quality improved on prior cattle grazed paddocks and but declined on elk grazed paddocks, respectively. These contrasting findings on prior grazing effects are more likely explained by different foraging strategies of these two animal species. During grazing treatments, cattle (Hofmann 1989) primarily utilized grasses, therefore high quality forbs and shrubs still would be available over a longer period for later grazers if the utilization level was moderate (Skovlin et al. 1976). In contrast, elk are generalists (Hoffman 1989), therefore they select mostly high quality parts of forages more uniformly from all forage classes, and thus when paddocks are utilized by elk, forage nutritive value may decrease rapidly during a relatively short grazing period. In this regard, our study indicates that in prior elk grazed paddocks, by numerical comparison, mean yields of forages nutritionally valuable in that grazing period, like tall annual willowherb, hawkweed, baldhip rose, and big huckleberry were 1.5, 1.2, 1.3, and 6.7 times lower compared to those in prior cattle grazed paddocks.

The challenge of free-grazing animals is to meet nutritional requirements necessary to complete life processes by finding and ingesting scarce forage with nutrient concentrations higher than its requirement and mixing it with more abundant forages with lower nutrient concentrations (Rittenhouse 2000). As reported above, in our study, grasses contained lower CP and digestible DM, and higher cell wall carbohydrates (ADF and NDF) compared to forbs, shrubs, and lichen. These results concur with the existing literature (Huston et al. 1981; Holechek and Vavra 1983; and Darambazar 2003) which suggests shrubs retain more crude protein than mature grasses or forbs in late-summer. Our study and others (Miller and Vavra 1981; Holechek et al. 1982; DelCurto et al. 2005) suggest cattle and elk shift their diets to more forbs and shrubs to maintain their rate of intake when grass availability and/or palatability declines.

Because of their anatomical and digestive attributes, deer were expected to have a more selective diet and choose higher quality forages than elk or cattle (Hofmann 1989; Robbins 1993). Dietary CP of 7% is considered to be the minimum necessary for maintenance of a positive nitrogen balance (Murphy and Coates 1966) for adult female deer, while about 11% CP is adequate for yearling deer (Holter et al. 1979). Urness (1981) reported that important shrubs in mule deer diets contained CP levels ranging from 10 to 14%. Our study showed that several forage species may provide the required level of protein. Ammann et al. (1973) suggested that diet IVDMD should be $\geq 50\%$, while Ullrey et al. (1970) indicated diets that contain ME concentration of 9.45 $\mathrm{kJ \cdot g^{-1}}$ are considered adequate for deer. Therefore, we speculate that deer in our study probably would meet their CP requirement, whereas energy may have been limited.

Wakeling and Bender (2003) pointed out that if nutrient concentration (or density) is lower, nutritional limitation occurs when individual animals can eat to their maximum food processing ability, but still may not obtain an adequate amount of nutrients, such as energy. Cook et al. (2004) categorized late-summer-early autumn elk nutrition status based on diet ME as: 1) Excellent (> 9.95 kJ·g^{-1}), 2) Good (9.45-9.95 kJ·g^{-1}), 3) Marginal (8.23-9.45 kJ·g^{-1}), and 4) Poor (< 8.23 kJ·g^{-1}). Thus, elk in our study could fall in the last category.

Diet Quantity

Diet quantity and grazing treatment

Nutrient intake can be defined as the product of bite size, bite rate, and grazing time (Forbs 1988). Our study suggested that early-summer grazing by cattle or elk at the moderate utilization level has little effect on the subsequent late-summer nutrient intake rate of cattle, deer, and elk. This may be attributed to several factors including: pasture heterogeneity (Bailey et al. 1998), forage biomass (Wickstrom et al. 1984; Hobbs 1989), optimal utilization level (Johnson 1953; Holecheck 1988; Ganskopp et al. 1999), animal plasticity in diet selections (Miller and Vavra 1981; Holechek et al. 1982; DelCurto et al. 2005), and intake rate (Short et al. 1971; Wickstrom et al. 1984; Hobbs 1989).

In this study, the prior grazing treatment was at a moderate (Skovlin et al. 1976) level. Holecheck (1988) reported a proper use level being between 35 to 45% of the current year's growth of forage where precipitation is between 300 to 630 mm.

Similarly, both Johnson (1953) in Colorado and Skovlin et al. (1976) in Oregon reported that in mixed-conifer range, utilization levels of the primary forage grasses must be kept around 35% to prevent range degradation. Skovlin et al. (1976) also noted that moderate stocking maintained grazing capacity and provided acceptable cattle gains.

Range forage availability regulates instantaneous intake in a threshold fashion. Studies (Wickstrom et al. 1984; Hobbs 1989) indicated that deer eating rate declines when available forage biomass falls below 50 $kg \cdot ha^{-1}$. In contrast, Spalinger and Hobbs (1992) found that intake rate is poorly correlated with standing biomass for highly selective foragers like deer. Wickstrom et al. (1984) also determined that biomass of forage selected by elk in mixed-conifer rangelands ranged from 339 to 826 $kg \cdot ha^{-1}$.

It is often suggested that bovides are morphologically constrained to graze on short swards because they lack upper incisors (Illius and Gordon 1987). Results obtained from grazing trials on temperate grasses indicate that sward height is the dominant sward variable and bite size is the dominant animal variable that influences short-term herbage intake (Jamieson and Hodgson 1979a, 1979b; Hodgson 1981). Further studies of patch selection by cattle within grasslands suggested that cattle preferred vegetative patches (< 7-8 cm) even though they could have achieved greater intake rates on taller mature patches (Wallis De Vries and Daleboudt 1994; Ginane et al. 2003). Ganskopp et al. (1999) demonstrated that moderate, early-season cattle grazing improved both the height and volume of bitterbrush (*Purshia tridentata* Pursh DC.) plants compared with those in ungrazed pastures. Based on findings of aforementioned studies of forage yield, utilization, sward height, and their effects on animal foraging efficiency, we can assume that in our grazing treatment forage availability did not restrict intake rates.

In our study, dry matter intake was similar to that found in other studies conducted in similar environments. Intake estimates for grazing cattle have been highly variable, but most appear to be within a range of 40 to 90 g DM $kg^{0.75} \cdot day^{-1}$ (Cordova et al. 1978). Maximum diet intake rate reported for domestic livestock increased as a function of body weight and ranged from 4.8 $g \cdot min^{-1}$ in sheep to 18.0 $g \cdot min^{-1}$ in cattle (Allden and Whittaker 1970; Chacon and Stobbs 1976). Wickstrom et al. (1984), after conducting a field study on deer and elk, found that forage intake rates were 0.15 $g \cdot kg^{0.75} \cdot min^{-1}$ for deer and 0.31 $g \cdot kg^{0.75} \cdot min^{-1}$ for elk. Thus, deer consumed forage at a much slower rate (2.1 times lower) relative to their energy requirements than did elk. In our study, deer forage intake rate was also low (1.6 and 1.9 times lower compared to elk and cattle, respectively).

Bite size has the greatest influence on intake, with bite rate and grazing time being compensatory variables (Forbs 1988). In this study, mean values of bite size fell within the range of data reported in the literature for cattle (Free et al. 1971), deer (Deschamp 1977; Wickstrom et al. 1984; Parker et al. 1999), and elk (Collins et al. 1978; Wickstrom et al. 1984). Animals generally will attempt to compensate for reduction in bite size by increasing bite rate or grazing time (Forbs 1988). As part of this research project Findholt et al. (2004) found that on prior cattle grazed paddocks, bite rate declined and DMI tended to decline ($P < 0.20$), but was compensated by on elevated percentage of diet CP and ME. Whereas, in elk grazed paddocks, animal diets had slightly lower CP and ME, although numerically higher bite rate and size. Thus, animals apparently maintained nutrient intake rate consistently on all grazing treatments. As Senft et al. (1985) pointed out, for range animals both quantity and quality of forage is valuable to maintain their needs. The ability of animals to change diets in response to previous grazing was the key to the animal's ability to maintain nutrient intake rate.

Diet quantity and dietary condition of animals

To understand the influences of nutrition, knowledge of standard biological measurements and baseline nutritional requirements are necessary. Nutrient requirements for medium-frame yearling beef cattle, as outlined by NRC (1984), indicate that 453 kg beef cattle require 7.8% CP and 8.4 $MJ \cdot kg^{-1}$ ME (daily intake $\geq$ 82.5 MJ or 9.75 kg DM) of diet for a 0.45 $kg \cdot day^{-1}$ gain. Even though this study indicated that the average CP level in cattle diets was slightly below the recommended level, it will not be enough to conclude that cattle had diets deficient in CP in mixed-conifer rangelands in the late-summer grazing season, because our study (Damiran et al. 2000, see chapter 4) and others (Olson 1991; Ortega et al. 1995) have found, the bite-count technique underestimated diet CP. Although, due to higher NDF or gastrointestinal fill (Garcia et al. 2003), in our case, cattle should not exceed 9.52 kg DM. Consequently, their maximum consumption would not exceed 74.0 $MJ \cdot day^{-1}$ ME intake, and it barely meets a beef cattle 0.22 $g \cdot day^{-1}$ gain (NRC 1984) requirement. Therefore, gut fill is also a limiting factor for cattle in this grazing season. Furthermore, as Ganskopp and Bohnert (2001) indicated, CP of 7.5% has been considered a nutritional threshold for maintenance of wild and domestic herbivores, which we used as a benchmark for interpretation of our study results.

Among all three animal species, deer had the most consistent nutrient intake across experiments. The CP requirement for adult non-lactating deer is 4.8 $g \cdot kg^{0.75} \cdot day^{-1}$ (Holter et al. 1979), and deer ME requirement is 543 $kJ \cdot kg^{0.75} \cdot day^{-1}$ (McCall et al. 1997). Subsequently, if we assume our observations of foraging behavior were representative of foraging throughout the day based on the consumption rate we obtained in this study, then to meet their nutritional requirements deer needed to forage at least 10 and 12 h for CP and ME needs, respectively. In addition, daily forage intake, as a percentage of body weight would be equal to about 2.1% and 2.5%, if deer forage 10 and 12 h, respectively. Others (Parker et al. 1999) have postulated that deer daily intake of 2.5% of body weight or higher would be expected during summer when forage quality is normally high. Krysl and Hess (1993) in their study on foraging behavior, indicate that daily foraging time for cattle ranges from 6 to 13 $h \cdot day^{-1}$. Likewise, Parker et al. (1999) found that the average amount of time actually grazing by black-tailed deer on Channel Island averaged 11.5 h. In contrast, on summer range in the Sierra Nevada of California, female deer foraged 7.7 h (Kie et al. 1991). Nevertheless, as Canon et al. (1987) indicated, the upper limit of foraging time is about 13 h in ruminants.

Elk requirements for protein and energy have not been studied extensively. In late-summer, an adult non-lactating cow elk require 836 $kJ \cdot kg^{0.75} \cdot day^{-1}$ ME for live-weight maintenance (standard metabolic rate plus activity; Cook 2002). Also, females need an additional 92 $kJ \cdot kg^{0.75} \cdot day^{-1}$ or $230 \cdot kJ \cdot kg^{0.75} \cdot day^{-1}$ ME for 10% (mild winter) or 25% (harsh winter) of their body weight loss during winter, respectively, for replenishing winter-catabolized tissue (Jiang and Hudson 1992; Cook 2002). While, for daily minimum CP requirements elk would need 7.0 $g{\cdot}kg^{0.75}{\cdot}day^{-1}$ CP for live-weight maintenance and 0.72, and 1.81 $g{\cdot}kg^{0.75}{\cdot}day^{-1}$ CP, respectively in addition, for replacement of 10% and 25% winter catabolized body weight loss. Consequently, cow elk foraging with the same nutrient intake rate as in this study, would need a minimum of 12-13 and 13-15 h foraging time to cover daily CP and ME requirements, respectively. Thus, our study suggests that elk in mixed-conifer rangelands may be unable to meet their energy requirements in late-summer.

Chacon and Stobbs (1976) concluded that increases in bite rate or grazing time compensate for decreases in bite size as the sward is defoliated. If animals are not able to find enough high quality nutrients in the occupied pasture, rate of ingestion decreases, and they must graze longer to compensate (Demment et al. 1987; Kie 1996). Furthermore, Parker et al. (1996) concluded that the single most important factor determining foraging efficiency of deer was metabolizable energy intake per minute. In addition, foraging time and efficiency may be negatively influenced by human activities, such as road density and traffic related to logging, recreation (Rowland et al. 2004; Wisdom et al. 2004), and hunting pressure (Johnson et al. 2004).

In general, diet overlap between ungulates suggests potential for competition, but would likely only occur if forage resources are limiting (Voeten 1999; Prins 2000). Similarly, Hobbs et al. (1996) showed that competition was not evident above a certain threshold: if there is sufficient food, there is no competition. Even though short term nutrient intake, in our study, did not significantly change due to grazing treatment, since forage resources were low in energy density; animal temporal, spatial (Coe et al. 2004), and diet overlap and dietary shifts occurred (Findholt et al. 2004), which may suggest potential for competition between animals.

MANAGEMENT IMPLICATIONS

This study suggests that early-summer grazing by cattle or elk at the moderate utilization level has very little effect on the subsequent short-term nutrient intake rate of cattle, deer, and elk. However, assessment of long term effects of summer cattle grazing and use by wild ungulates on rangeland resources at different utilization levels is necessary. Monitoring productivity and use of key forage species, particularly in the allotments containing shrub communities, should also complement management objectives on shared mixed-conifer rangelands. Beef cattle, grazing in late-summer, were able to maintain dietary CP by increasing their shrub and forb consumption in response to previous grazing by cattle. This study further demonstrated that in late-summer on mixed-conifer rangelands ME is a limiting factor for all three animal species. Therefore, if the management goal is high productivity of ungulates, it may be necessary to implement supplemental feeding or use different pasture.

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CHAPTER 6

CONCLUSION

Estimating Shrub Forage Yield and Utilization Using a Photographic Technique

Techniques measuring shrub utilization have focused on the portion of forage or browse removed. Little progress has been made to establish a reliable technique. This study was designed to determine the potential of a photographic technique in assessing shrub forage yield and its utilization on common snowberry, snowbrush, and firmleaf willow found in mixed-conifer rangelands. Shrubs forage yield and utilization were determined by hand plucking in five to eight increments for each plant. Before the first plucking and after each subsequent plucking, we took two photos that were perpendicular to each other at the intersection of the shrub. Green leaf area size for each photo was estimated using image processing software.

Green leaf area size calculated from the photographic technique was strongly correlated with actual forage yield for all three species of shrubs. A strong correlation also existed between utilization values estimated through green leaf area size and actual values. Utilization estimated by green leaf area size did not differ from actual utilization values suggesting that shrub utilization can be assessed through direct comparison of green leaf area size estimated from images taken before and after browsing without calibration. Precision of the photographic technique was similar to the browsing technique with the optimal sample per plant is dependent on plant morphology. However, because of statistical assumptions of normality, we recommend no fewer than 30 plants.

The photographic technique tested in our study offers an objective and accurate method for measuring changes in shrub biomass with possible applications in ecology, botany, and range sciences. In particular, application of this technique for estimating shrub utilization may improve accuracy of estimates and thereby, improve range management practices. Unlike many of the traditional utilization techniques, this technique is non-destructive and requires little time.

Comparison of Techniques and Grinding Size to Estimate Digestibility of Ruminant Diets

We conducted this study to evaluate in vitro technique (Daisy^{II}) and to determine dry matter (DM) and neutral detergent fiber digestibilities in forage based ruminant diets. The results from Daisy^{II} were compared to those obtained by the conventional in vitro, filter bag in situ, and in vivo techniques. We also compared two sample sizes of sampling and two sizes of grinding.

In this study digestibility values measured by the Daisy^{II} technique and the in situ technique were consistently higher than those obtained with the conventional in vitro technique. In general, relative to conventional in vitro, the Daisy^{II} technique gave closer digestibility values for grasses and higher values for forbs, shrubs, and lichen. The higher values observed in the Daisy^{II} technique may relate mainly to the non-recovered material that escaped from the bag and was not digested by the conventional in vitro technique. Between the two filter-bag based techniques, Daisy^{II} tended to show higher digestibility values than in situ. The digestibility results obtained were also affected by sample size and sample grind size. The study also shows that regression analysis of the forages resulted in similar values, with Daisy^{II} and conventional in vitro techniques revealed that Daisy^{II} technique can be used to predict in vitro digestibility with relatively small variation. Further, Daisy^{II} technique gives more accurate predictions of filter bag in situ digestibility. It is interesting to note that a more precise, though less accurate, prediction of conventionally determined digestibility was obtained from Daisy^{II} and filter bag in situ techniques.

Digestibility values estimated by the Daisy^{II} or in situ technique might be interchangeable using general predictive equations generated across different forages. In addition, our study suggested that filter bag in situ is a good alternative to the Daisy^{II} technique especially to someone who has access to fistulated animals and is comfortable working with them. Sieving of different size particles of the ground forage sample, correcting for the fine particle losses from the filter bag during digestion and washing; and/or grouping the feeds into categories based on fiber fractions, applying a corresponding correction factor and standardizing sample processing may increase predictability and accuracy of the Daisy^{II} and filter bag in situ techniques. Because the difference between the techniques is mainly related to the particle size of the indigestible material in the feeds, Mabjeesh et al. (2000) suggest that these groups of feed be ground to a larger particle size, which may prevent the escape of indigestible particles from these components in the bags.

Overall, Daisy^{II} is an easier, less time-consuming technique of measuring in vitro digestibility of ruminant forage than the conventional in vitro technique. However, its use is currently limited to forages that do not contain a high level of small, indigestible derivatives that might escape from the bags during incubation.

Comparison of Bite-Count and Rumen Evacuation Techniques to Estimate Diet Quantity and Quality in Grazing Cattle

Five techniques have been used typically to quantify forage intake. They include the use of bite-count, biomass changes of feeding sites, fecal ratios, mass changes, and fistulated animals. The objective of this research was to compare the bite-count (BC) of estimating forage intake and diet quality to rumen evacuation (RE) derived forage intake and diet quality in diverse mixed-conifer rangelands with and without prior grazing. We used four rumen-fistulated steers to evaluate these techniques.

The BC and RE techniques gave similar results on bite size, total diet intake, and digestibility. The bite-count technique underestimated CP content of the diet compared to the RE technique. In contrast, forage fiber constituents were lower with the BC estimates compared to the RE values.

Our results suggest that the BC technique does not yield results that are identical to RE techniques in range conditions with dense and diverse vegetation. The BC technique has the advantage of not requiring rumen-fistulated animals and produces results that are not confounded by digestive contaminants. Our study and other studies show that the accuracy of BC technique depends on the botanical composition of the pasture, the growth stage of the major forage species being grazed, biomass, previous utilization level, animal related factors (species, age, sex, foraging behavior), animal foraging efficiency during the feeding bout, and mainly observer’s experience and skills.

Despite the importance of forage intake to ungulate ecology and management, accurately quantifying the daily diet intake and diet quality of ungulates in free-ranging condition remains difficult, largely because of methodological limitations. Nevertheless, understanding the inherited strengths and weaknesses of a research technique used on free-ranging ungulates is important for diet investigators to choose an appropriate technique for their study and consider it to make accurate inferences from their gathered data. Also, it is necessary whenever possible that investigators validate their choice of a research technique testing and adjusting it in the specific environmental condition to minimize biases.

Influence of Previous Cattle and Elk Grazing on the Subsequent Diet Quality and Nutrient Intake Rate of Diets for Cattle, Deer, and Elk Grazing Late-Summer Mixed-Conifer Rangelands

This research was designed to address intra- and interspecific competition between cattle, mule deer, and elk on shared rangelands in the Blue Mountains of Oregon and Washington. The main objective of this research was to document nutritional consequences of early summer grazing by either cattle or elk at the moderate utilization level on subsequent use by cattle, deer, and elk in late-summer. In a companion study, Findholt et al. (2004) presented a detailed analysis of the diet composition, and diet overlap of previous grazing by elk or cattle on subsequent diets of cattle, deer, and elk. On shared ranges the potential for competition for forage among these 3 species increases during summer, because nutritional requirements for these animals are appreciably elevated to support key summer-autumn life processes (Cook et al. 2004), but availability and quality of some forages decline, especially following the onset of prolonged seasonal drought. Consequently, the problem becomes managing grazing allotments to allocate forage among these species. Moderate (31.9 ± 2.7%) utilization 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 (Findholt et al. 2004). The primary factors evaluated in this study were simulated diet quality, and nutrient intake rate of 3 animal species, which provide direct estimates of the nutritional plan of animals on two grazing treatments.

Effects of grazing treatment and animal species were independent of nutritional quality of diets. Diet quality of cattle, deer, and elk slightly improved for prior cattle grazed paddocks, whereas, diet quality of all animal species declined in prior elk grazed paddocks. As we expected, cattle diet contained lower CP and digestible energy compared to deer or elk diet. In contrast, higher CP was measured in deer diets compared to elk diets. The rate of diet intake exerts an important influence on many aspects of herbivore ecology, including diet and habitat choices, social organization, and predator avoidance. Short term intake rate and diet selection provide direct estimates of the nutritional plane of animals (Shipley and Spalinger 1995). The rate of forage intake by ungulates is controlled by several timescales. On a finer scale, consumption rate is limited by abundance and distribution of plants. Therefore, induced changes in short-term nutrient intake rate of ungulates in response to prior grazing provide an initial indication of grazing interactions, particularly competitive interactions. In our study, early-summer grazing by cattle or elk at the moderate grazing intensity did not appear to subsequently change animal diet intake rate (DMI) and nutrient intake rate (CPI, MEI) for either species grazing late-summer. Several factors may attribute to this, including: vegetation heterogeneity, forage biomass, optimal prior utilization level, animal plasticity in diet selections, and (or) intake rate. Among deer, elk, and cattle; deer had the most consistent nutrient intake in both ungrazed and previously grazed paddocks.

While in grasslands, animals generally will attempt to compensate for reduction in bite size by increasing either bite rate, or grazing time, rarely both. In the heterogeneous environment in our study, where some forage is abundant but low in quality, or visa versa, animals tended to compensate through a decline in bite size and bite rate in response to previous grazing, primarily by the elevated quality of diets they selected. As a result, animals maintained a nutrient intake rate consistent in both grazing treatments. Furthermore, our study also demonstrated that diet quality is sufficient in late-summer to meet protein requirements; however, energy density of diet may limit elk and cattle productivity in mixed-conifer rangelands of northeast Oregon. This suggests that each animal species may not have been able to maintain animal performance level during this season. Thus, in late-summer at a moderate utilization level, density independent diet factors are likely to affect ungulate productivity more than density dependent diet factors.

A possible confounding feature of our study is that sample size was limited, which proved to be too small to provide much confidence in the data acquired. Diet selections, movement rates, and other mechanisms that occur at small scales can at least partially explain grazing patterns observed across landscapes and regions (Bailey et al. 1996). It is difficult to generalize about the competitive relationships among these animals. Several indicators of relationships between animals interact in different ways at different scales, making it difficult to make inferences. Even though short term nutrient intake rate was not affected much in response to prior grazing, other possible evidence existed that indicated effects of previous grazing. During our study, forage resources generally were lower in energy density. As a result, increased animal dietary overlap and diet shifting due to prior grazing occurred (Findholt et al. 2004), which suggests that potential competition between cattle, deer, and elk for forage is more likely during late-summer.

Despite a rich history of elk research over the last three decades, there has been little focus on influences of nutrition on elk herd abundance, productivity, and demographics, and on how management's influence on diet quality and quantity might affect these population attributes (Cook et al. 2004). Range forage availability regulates instantaneous intake in a threshold fashion (Wickstrom et al. 1984). As a result, further studies similar to this one but at different stocking rates and season of use will help us understand more and better establish grazing systems on forested rangelands.

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APPENDICES

Table A.4.1. Cattle bite-count derived diet intake and diet composition in mixed-conifer rangelands, northeast Oregon.

			Intake (g·20 min^{-1})		Composition (%, OM)			
Enclosures[1]	Paddocks[2]	Steer #	DMI	OMI	CP	ADF	NDF	IVOMD
1	1	7037	300.8	251.7	8.7	44.8	68.3	56.2
1	1	7045	376.7	329.8	7.1	47.6	69.1	55.0
1	1	7052	387.9	326.0	9.0	43.5	66.4	57.4
1	1	7192	213.8	183.2	8.1	46.0	67.6	56.1
1	2	7037	171.0	146.8	7.6	43.3	65.4	62.7
1	2	7045	175.2	157.2	9.1	39.7	49.6	71.1
1	2	7052	156.6	139.2	9.0	41.0	53.7	70.4
1	2	7192	191.4	168.2	8.7	42.6	55.2	67.9
2	1	7037	284.2	236.8	8.2	38.1	60.0	74.5
2	1	7045	168.1	140.9	7.8	38.8	61.5	70.9
2	1	7052	214.6	177.9	7.8	38.7	62.2	72.8
2	1	7192	277.3	235.4	8.4	37.1	58.2	75.0
2	2	7037	296.3	265.0	11.0	36.3	49.9	69.3
2	2	7045	183.0	161.8	10.2	35.3	48.2	70.3
2	2	7052	190.4	170.6	10.4	36.7	51.7	69.5
2	2	7192	235.7	208.1	10.9	37.1	54.7	70.3
3	1	7037	468.1	423.5	5.8	37.7	64.1	69.9
3	1	7045	435.0	393.9	5.4	41.5	67.0	62.6
3	1	7052	448.6	404.9	6.1	36.5	62.2	73.1
3	1	7192	453.1	413.3	4.9	39.2	67.6	62.8
3	2	7037	274.2	250.6	6.1	37.6	61.7	69.6

Table A.4.1 (Continued).

			Intake (g·20 min^{-1})		Composition (%, OM)			
Enclosures[1]	Paddocks[2]	Steer #	DMI	OMI	CP	ADF	NDF	IVOMD
3	2	7045	297.7	272.8	5.2	41.0	66.9	63.8
3	2	7052	305.3	273.6	6.0	39.8	64.2	66.2
3	2	7192	231.4	204.7	6.6	40.0	62.1	66.6
4	1	7037	801.7	737.7	5.0	42.0	69.4	62.2
4	1	7045	535.3	488.4	4.4	46.4	74.4	58.5
4	1	7052	765.9	702.3	4.6	43.9	72.0	60.8
4	1	7192	574.2	527.4	4.8	42.7	70.7	61.2
4	2	7037	166.0	150.6	6.4	40.6	57.5	63.9
4	2	7045	114.0	96.4	9.2	38.4	55.5	71.2
4	2	7052	89.7	80.6	8.3	39.3	53.5	66.6
4	2	7192	63.6	50.6	8.8	40.4	64.4	73.8

[1] Study enclosures: 1 - Elk Dodo; 2 - Scotty's Gate; 3 - Bally Mountain; 4 - Half Moon.

[2] Paddocks: 1 - Ungrazed paddocks; 2 - Grazed paddocks.

Table A.4.2. Cattle rumen evacuated diet intake and diet composition in mixed-conifer rangelands, northeast Oregon.

				Intake (g·20 min^{-1})		Composition (%, OM)			
Enclosure[1]	Paddocks[2]	Sample #	Steer #	DMI	OMI	CP	ADF	NDF	IVOMD
1	1	230	7037	199.6	162.4	9.9	47.1	72.7	70.0
1	1	231	7045	267.7	226.1	10.9	46.6	72.5	62.0
1	1	232	7052	189.5	157.4	9.2	49.2	73.7	67.2
1	1	233	7192	199.1	165.9	9.8	47.8	68.0	66.6
1	2	234	7037	121.0	96.3	11.4	53.6	72.5	60.7
1	2	235	7045	234.5	192.4	9.2	55.1	62.6	58.3
1	2	236	7052	107.5	87.9	10.6	54.7	69.6	56.2
1	2	237	7192	191.1	162.8	12.0	51.7	61.8	60.4
2	1	238	7037	592.1	501.2	11.6	47.6	67.1	65.7
2	1	239	7045	450.4	380.3	11.6	52.5	72.3	62.8
2	1	240	7052	470.2	383.4	11.4	42.7	58.4	69.0
2	1	241	7192	586.5	492.7	9.8	46.9	69.3	64.5
2	2	242	7037	413.6	346.1	10.1	50.4	60.7	64.5
2	2	243	7045	440.3	371.9	8.0	49.8	59.5	67.6
2	2	244	7052	261.6	216.5	9.3	48.0	66.1	58.9
2	2	245	7192	293.9	246.1	11.6	47.2	63.1	66.0
3	1	246	7037	605.7	499.4	7.7	46.6	70.8	69.8
3	1	247	7045	466.8	398.9	8.1	47.1	64.9	68.2
3	1	248	7052	606.4	497.8	10.9	44.4	71.4	66.1
3	1	249	7192	729.7	632.7	7.7	44.1	70.7	64.4
3	2	250	7037	522.0	454.0	9.9	48.1	67.6	66.4
3	2	251	7045	470.8	406.3	9.8	48.6	69.8	66.7

Table A.4.2 (Continued).

				Intake (g·20 min^{-1})		Composition (%, OM)			
Enclosure[1]	Paddocks[2]	Sample #	Steer #	DMI	OMI	CP	ADF	NDF	IVOMD
3	2	252	7052	441.6	378.6	8.5	47.5	69.8	69.0
3	2	253	7192	659.8	561.8	7.8	42.8	61.4	70.1
4	1	254	7037	391.8	337.8	8.7	48.8	75.5	67.1
4	1	255	7045	403.7	339.5	11.6	49.8	71.9	68.2
4	1	256	7052	332.4	281.0	9.2	48.6	76.4	71.8
4	1	257	7192	313.7	269.7	9.1	45.1	71.4	68.6
4	2	258	7037	228.8	200.0	11.3	50.6	62.3	62.3
4	2	259	7045	242.3	188.0	11.3	54.4	71.3	68.4
4	2	260	7052	134.5	93.7	18.6	44.4	65.3	52.4
4	2	262	7192	221.9	179.0	8.7	52.3	74.6	73.5

[1] Study enclosures: 1 - Elk Dodo; 2 - Scotty's Gate; 3 - Bally Mountain; 4 - Half Moon.

[2] Paddocks: 1 - Ungrazed paddocks; 2 - Grazed paddocks.

Table A.4.3. Cattle foraging efficiency in mixed-conifer rangelands.

			Bites (n·20 min^{-1})			
Enclosures[1]	Paddocks[2]	Steer #	Grasses	Forbs	Shrubs	Total
1	1	7037	593	44	7	644
1	1	7045	562	21	25	608
1	1	7052	729	73	22	824
1	1	7192	382	53	6	441
1	2	7037	195	46	18	259
1	2	7045	125	85	172	382
1	2	7052	192	66	42	300
1	2	7192	129	106	62	297
2	1	7037	604	40	3	647
2	1	7045	349	17	21	387
2	1	7052	489	23	11	523
2	1	7192	536	8	41	585
2	2	7037	276	73	158	507
2	2	7045	144	54	125	323
2	2	7052	224	39	107	370
2	2	7192	358	63	76	497
3	1	7037	520	48	19	587
3	1	7045	441	78	50	569
3	1	7052	526	52	7	585
3	1	7192	434	55	20	509
3	2	7037	550	78	28	656
3	2	7045	526	71	16	613
3	2	7052	529	125	7	661
3	2	7192	362	141	17	520
4	1	7037	581	17	0	598
4	1	7045	441	26	0	467
4	1	7052	572	24	0	596
4	1	7192	416	9	0	425
4	2	7037	234	67	160	461
4	2	7045	257	15	57	329
4	2	7052	120	71	54	245
4	2	7192	216	4	1	221

[1] Study enclosures: 1 - Elk Dodo; 2 - Scotty's Gate; 3 - Bally Mountain; 4 - Half Moon. [2] Paddocks: 1 - Ungrazed paddocks; 2 - Grazed paddocks.

Table A.4.4. Hand plucked cattle bite size in mixed-conifer rangelands.

Enclosures[1]	Paddocks[2]	Forages[3]	Forage Species[4]	Plucked bites	Bite Size (g·bite^{-1})
1	1	1	FEOC	100	0.280
1	1	1	CARU	100	0.501
1	1	1	BRCA	100	0.240
1	1	1	DAGL	75	0.488
1	1	2	CAGE	100	1.006
1	1	2	CACO	200	0.211
1	1	3	ACMIL	100	0.317
1	1	3	CIVU	50	0.516
1	1	3	HIAL	100	0.360
1	1	3	LUCA	25	1.805
1	1	3	*Fragaria* spp.	100	0.263
1	1	4	CEVE	60	0.731
1	1	4	SPBEL	100	0.254
1	1	4	SYAL	75	0.467
1	1	4	VAME	75	0.468
1	1	4	BERE	50	0.865
1	2	1	DAGL	125	0.181
1	2	1	BRCA	100	0.263
1	2	1	FEOC	100	0.250
1	2	1	CARU	75	0.921
1	2	2	CAGE	50	0.751
1	2	2	CACO	200	0.211
1	2	3	CIVU	50	0.516
1	2	3	ACMIL	100	0.317
1	2	3	HIAL	100	0.360
1	2	3	LUCA	25	1.805
1	2	3	*Fragaria* spp.	100	0.263
1	2	4	VAME	100	0.169
1	2	4	SYAL	100	0.246
1	2	4	SPBEL	50	0.544
1	2	4	CEVE	50	0.977
2	1	1	BRCA	100	0.305
2	1	1	CARU	100	0.618
2	1	1	POPR	100	1.045
2	1	1	AGIN	75	0.546

Table A.4.4 (Continued).

Enclosure[1]	Paddocks[2]	Forages[3]	Forage Species[4]	Plucked bites	Bite Size (g·bite^{-1})
2	1	1	DAGL	100	0.521
2	1	1	FEOC	100	0.255
2	1	2	CAGE	50	1.048
2	1	3	ACMIL	100	0.317
2	1	3	LUSE	50	1.234
2	1	3	CIVU	50	0.516
2	1	4	SPBEL	75	0.721
2	1	4	SYAL	50	0.737
2	1	4	BERE	50	0.865
2	1	4	VAME	50	0.575
2	2	1	BRIN	100	0.277
2	2	1	AGIN	75	0.546
2	2	1	BRCA	35	0.475
2	2	1	DAGL	100	0.203
2	2	1	CARU	75	0.673
2	2	1	FEOC	100	0.255
2	2	2	CACO	200	0.211
2	2	2	CAGE	50	1.048
2	2	3	ACMIL	100	0.317
2	2	3	CIVU	50	0.516
2	2	3	LUSE	50	1.574
2	2	3	HIAL	100	0.394
2	2	3	*Fragaria* spp.	100	0.263
2	2	3	PEGL	42	0.506
2	2	4	BERE	50	0.442
2	2	4	SYAL	50	0.793
2	2	4	VAME	50	0.575
2	2	4	SPBEL	60	0.661
3	1	1	FEOC	100	0.996
3	1	1	BRCA	100	0.749
3	1	1	CARU	75	0.673
3	1	1	POPR	100	1.045
3	1	1	PHPR	40	1.994
3	1	2	CAGE	60	0.786
3	1	3	ACMIL	100	0.317

Table A.4.4 (Continued).

Enclosures[1]	Paddocks[2]	Forages[3]	Forage Species[4]	Plucked bites	Bite Size (g·bite^{-1})
3	1	3	EPPA	100	0.457
3	1	3	CIVU	50	0.516
3	1	3	*Fragaria* spp.	100	0.263
3	1	3	PEGL	42	0.506
3	1	4	BERE	100	0.503
3	1	4	LIBO	75	0.773
3	1	4	SPBEL	60	0.661
3	1	4	SYAL	100	0.570
3	2	1	FEOC	100	0.920
3	2	1	POPR	100	0.478
3	2	1	BRCA	23	0.756
3	2	1	DAGL	100	0.203
3	2	1	CARU	75	0.673
3	2	2	CAGE	120	0.428
3	2	2	CACO	200	0.211
3	2	3	EPPA/EPMI	100	0.437
3	2	3	CIVU	100	0.256
3	2	3	*Fragaria* spp.	100	0.263
3	2	3	ACMIL	100	0.317
3	2	4	BERE	100	0.438
3	2	4	SYAL	55	0.417
4	1	1	FEOC	50	1.665
4	1	1	POPR	50	1.538
4	1	1	BRCA	65	1.156
4	1	1	CARU	120	0.283
4	1	1	PHPR	40	1.994
4	1	2	CAGE	80	1.012
4	1	3	ACMIL	100	0.317
4	1	3	LUSE	50	1.574
4	1	3	CIVU	50	0.516
4	1	3	*Fragaria* spp.	130	0.293
4	1	3	PEGL	42	0.506
4	1	4	LIBO	75	0.773

Table A.4.4 (Continued).

Enclosures[1]	Paddocks[2]	Forages[3]	Forage Species[4]	Plucked bites	Bite Size (g·bite^{-1})
4	2	1	FEOC	100	0.343
4	2	1	BRCA	50	0.287
4	2	1	PHPR	40	1.994
4	2	1	CARU	120	0.283
4	2	2	CACO	130	0.111
4	2	2	CAGE	40	0.192
4	2	3	CIVU	50	0.516
4	2	3	HIAL	100	0.394
4	2	3	EPPA/EPMI	100	0.437
4	2	3	ACMIL	80	0.228
4	2	3	*Fragaria* spp.	130	0.293
4	2	3	LUSE	50	1.574
4	2	4	BERE	100	0.438
4	2	4	SYAL	55	0.417
4	2	4	SPBEL	60	0.661
4	2	4	VASC	100	0.497
4	2	4	LIBO	100	0.445

[1] Study enclosures: 1 - Elk Dodo; 2 - Scotty's Gate; 3 - Bally Mountain; 4 - Half Moon.

[2] Paddocks: 1 - Ungrazed paddocks; 2 - Grazed paddocks.

[3] Forage classes: 1 - grasses; 2 - grasslikes; 3 - forbs; 4 - shrubs.

[4] Forage species alpha code follows the recommendations of the USDA Natural Resources Conservation Service (USDA, NRCS 2005).

Table A.5.1. Botanical composition (%) of diets consumed by cattle (C), deer (D), and elk (E) grazing late-summer mixed-conifer rangelands on the Starkey Experimental Forest and Range, northeast Oregon (Data averaged over 1998 and 1999) on prior ungrazed (UG), cattle grazed (CG), and elk grazed (EG) paddocks.

Alpha Code[1]	Forage Species[2] Scientific Name	Common Name	C			D			E		
			UG	CG	EG	UG	CG	EG	UG	CG	EG
	Grasses										
AGAL	*Agrostis alba*	Redtop	T[3]	T	T						
AGIN2	*Agropyron intermedium*	Intermediate wheatgrass	0.5	T	0.4	T	T	T	T	T	T
AGSP	*Agropyron spicatum*	Bluebunch wheatgrass	T	T	T				T	T	T
BRCA	*Bromus carinatus*	California brome	14.2	7.9	11.3	0.2	1.5	1.0	3.5	1.5	6.0
BRIN	*Bromus inermis*	Smooth brome	T	T	T	0.5	T	T			
BRTE	*Bromus tectorum*	Cheatgrass brome	T	T	T						
CACO	*Carex concinnoides*	Northwestern sedge	0.1	1.2	0.4	0.1	0.1	0.9	0.6	1.3	1.8
CAGE	*Carex geyeri*	Elk sedge	23.8	16.4	12.1	0.1	0.2	1.4	11.4	6.0	7.0
CARU	*Calamagrostis rubescens*	Pinegrass	19.8	18.3	35.9	1.1	0.1	1.5	11	7.9	20.0
DACA	*Danthonia californica*	California danthonia							T	T	T
DAGL	*Dactylis glomerata*	Orchardgrass	10.2	1.9	4.1	1.6	1.9	2.0	14.3	5.1	5.6
DECA	*Deschampsia caespitosa*	Tufted hairgrass	T	T	T						
ELGL	*Elymus glaucus*	Blue wildrye				T	T	T			
FEID	*Festuca idahoensis*	Idaho fescue	0.5	T	T	T	T	T			
FEOC	*Festuca occidentalis*	Western fescue	3.1	3.9	16.6	T	T	T	2.2	1.6	8.8
JUBA	*Juncus balticus*	Baltic rush	T	T	T				T	T	T
KOCR	*Koeleria cristata*	Prairie junegrass	0.2	T	T						
PHAL	*Phleum alpinum*	Alpine timothy				T	T	T			
PHPR	*Phleum pratense*	Timothy	2.0	0.4	0.4	0.2	T	T	2.8	0.2	T
POCO	*Poa compressa*	Canada bluegrass	T	T	T						
POGLG	*Poa glauca*	Glaucous bluegrass	T	T	T				0.6	0.6	T

Table A.5.1 (Continued).

Alpha Code[1]	Forage Species[2] Scientific Name	Common Name	C UG	C CG	C EG	D UG	D CG	D EG	E UG	E CG	E EG
	Grasses										
POPR	*Poa pratensis*	Kentucky bluegrass	13.7	5.3	5.1	T	0.8	2.1	0.4	T	0.4
STCON	*Stipa columbiana nelsoni*	Big columbia needlegrass	0.1	T	0.2	T	T	T			
	Forbs										
ACMI	*Achillea millefolium lanulosa*	Western yarrow	0.27	0.8	0.3	3.3	2.9	5.2	0.1	0.2	0.2
AGAU	*Agoseris aurantiaca*	Orange agoseris							T	T	T
AGGR	*Agoseris grandiflora*	Big-flowered agoseris							T	T	T
ANLU	*Antennaria luzuloides*	Woodrush pussytoes	T	0.6	T	0.2	T	0.1	0.1	1.0	1.0
ARAM2	*Arnica amplexicaulis Nutt.*	Clasping arnica	T	T	T				T	T	T
ARCO	*Arnica cordifolia*	Heartleaf arnica	0.2	0.3	0.1	0.4	0.6	0.3	0.5	0.2	0.2
ARMA3	*Arenaria macrophylla*	Bigleaf sandwort				T	T	T			
ASCO	*Aster conspicuus*	Showy aster	T	T	T	0.3	T	T	T	T	T
ASRE	*Astragalus reventus*	Longleaf milkvetch	T	T	T	T	T	T			
CAMI2	*Castilleja miniata*	Scarlet paintbrush							T	T	T
CIVU	*Cirsium vulgare*	Bull thistle	0.9	1.4	1.1	T	T	T	2.2	1.8	2.3
DELPH	*Delphinium* spp.	Larkspur				T	T	T			
EPAN	*Epilobium angustifolium*	Fireweed	T	T	T	1.4	3.2	0.5	1.0	3.6	0.1
EPMI	*Epilobium minutum*	Smallflower willowweed	0.3	0.6	T	2.5	2.0	1.7	0.8	1.0	1.0
EPPA	*Epilobium paniculatum*	Tall annual willowherb	T	T	T	5.1	7.4	4.4	0.8	1.7	0.4
ERAN	*Erigeron annuus*	Annual fleabane				T	T	T			

Table A.5.1 (Continued).

Alpha Code[1]	Forage Species[2] Scientific Name	Common Name	C UG	C CG	C EG	D UG	D CG	D EG	E UG	E CG	E EG
	Forbs										
ERCH	*Erigeron chrysopsidis*	Dwarf yellow fleabane	T	T	T	T	T	T	T	T	T
FRVE	*Fragaria vesca*	Woods strawberry	0.8	6.4	0.3	9.8	6.8	6.3	7.3	14.3	7.4
FRVI	*Fragaria virginiana*	Blueleaf strawberry	T	1.1	T	6.6	7.3	6.8	T	T	T
GABO	*Galium boreale*	Northern bedstraw							T	T	T
GATR	*Galium triflorum*	Sweetscented bedstraw				T	T	T	T	T	T
GEAL	*Geum aleppicum*	Yellow avens				T	T	T			
GESI	*Gentiana simplex*	One-flower gentian							T	T	T
GETR	*Geum triflorum*	Prairiesmoke avens				0.1	T	T			
GEVI	*Geranium viscosissimum*	Sticky geranium	T	T	T						
HIAL	*Hieracium albiflorum*	White hawkweed				T	T	T			
HIAL2	*Hieracium albertinum*	Western hawkweed	0.9	1.6	0.6	3.5	1.2	1.0	1.2	1.9	0.7
HYPE	*Hypericum perforatum*	Common St. johnswort				0.3	T	T			
IRMI	*Iris missouriensis*	Rockymountain iris							T	T	T
LALA3	*Lathyrus latifolius*	Perennial peavine	T	T	T				T	T	T
LASE	*Lactuca serriola*	Prickly lettuce				0.3	T	T			
LULA2	*Lupinus laxiflorus*	Longspur lupine	1.3	10.7	6.0	3.5	4.5	7.3	7.2	4.4	7.3
LUSE	*Lupinus sericeus*	Silky lupine				1.4	3.7	5.2	T	T	T
MIBR	*Mitella breweri*	Brewer miterwort							T	T	T
MIST2	*Mitella stauropetala*	Sideflower miterwort							T	T	T
PECO	*Penstemon confertus*	Yellow penstemon				T	T	0.1	T	T	T

Table A.5.1 (Continued).

Alpha Code[1]	Forage Species[2] Scientific Name	Common Name	C UG	C CG	C EG	D UG	D CG	D EG	E UG	E CG	E EG
	Forbs										
PEGL	*Penstemon glanulosus*	Stickystem penstemon	T	T	T				T	T	T
PERA	*Pedicularis racemosa*	Sickletop pedicularis	T	T	T						
PEVE	*Penstemon venustus*	Bluemountain penstemon	0.2	0.2	0.2	0.3	T	T	0.1	T	T
POGR	*Potentilla gracilis*	Beauty cinquefoil	T	T	T	2.2	2.0	0.2	0.4	0.9	T
POSA3	*Polygala sanguinea*	Purple milkwort	T	T	T						
PRVU	*Prunella vulgaris*	Common selfheal				T	T	T	0.2	T	T
PTAN	*Pterospora andromedea*	Woodland pinedrops				0.2	T	T	T	T	T
RUAC	*Rumex acetosella*	Sheep sorrel				T	0.6	0.1	T	T	T
SECA	*Senecio canus*	Woolly groundsel							T	T	T
SEST	*Sedum stenopetalum*	Wormleaf stonecrop				T	T	T			
SIOR	*Sidalcea oregana*	Oregon checkermallow				T	T	T			
STJA	*Stellaria jamesiana*	Sticky starwort	T	T	T	T	T	T	T	T	T
STLO	*Stellaria longipes*	Longstalk starwort				T	T	T			
TAOF	*Taraxacum officinale*	Common dandelion	T	T	T	0.2	T	T	0.2	T	T
THMO	*Thermopsis montana*	Mountain thermopsis	T	T	T	1.0	0.3	0.6	T	T	T
THOC	*Thalictrum occidentale*	Western meadowrue							T	T	T
TRDU	*Tragopogon dubius*	Yellow salsify	T	T	T	0.9	0.2	0.2	0.3	0.1	T
TROV	*Trillium ovatum*	White trillium				T	T	T			
TRRE	*Trifolium repens*	White clover	0.7	0.5	0.1	0.3	T	0.2	2.2	T	0.6
URDI	*Urtica dioica*	Stinging nettle	0.1	T	T	T	T	T	T	T	T

Table A.5.1 (Continued).

Alpha Code[1]	Forage Species[2] Scientific Name	Common Name	C			D			E		
			UG	CG	EG	UG	CG	EG	UG	CG	EG
	Forbs										
VECA	*Veratrum californicum*	California falsehellebore				T	T	T	T	T	T
VIAM	*Vicia americana*	American vetch	T	T	T	T	T	T	T	T	T
VIGL	*Viola glabella*	Pioneer violet	T	T	T	0.2	0.1	0.3	T	T	T
	Shrubs & Trees										
ABCO	*Abies concolor*	White fir				T	T	T			
ABGR	*Abies grandis*	Grand fir				T	T	T			
AMAL	*Amelanchier alnifolia*	Saskatoon serviceberry	T	T	T	1.7	1.9	0.7	0.1	0.1	0.1
ARUV	*Arctostaphylos uva-ursi*	Bearberry	T	1.6	0.2	11.6	11.7	24.4	2.0	6.0	10.1
BERE	*Berberis repens*	Low oregongrape	0.9	1.1	0.2	0.2	T	T	2.1	2.9	0.5
CEVE	*Ceanothus velutinus*	Snowbrush	T	0.4	0.1	0.3	0.6	2.6	0.1	0.2	0.2
CHUM	*Chimaphila umbellata*	Common pipsissewa	T	T	T	T	T	T			
LAOC	*Larix occidentalis*	Western larch				T	T	T	T	T	T
LIBO2	*Linnaea borealis*	Twinflower	0.2	4.8	1.3	T	T	0.3	0.7	1.9	8.5
LOIN	*Lonicera involucrata*	Bearberry honeysuckle	T	T	T	T	0.2	T	T	T	T
PHMA	*Physocarpus malvaceus*	Mallow ninebark				T	T	T			
PICO	*Pinus contorta*	Lodgepole pine				T	T	T			
PIPO	*Pinus ponderosa*	Ponderosa pine	T	T	T	0.9	1.4	1.1	T	T	T
PSME	*Pseudotsuga menziesii*	Douglass-fir interior				T	T	T	T	T	T
RICE	*Ribes cereum*	Wax currant	T	T	T	0.1	0.3	0.2	T	T	T
ROGY	*Rosa gymnocarpa*	Baldhip rose	0.1	0.5	T	9.8	10.0	4.1	2.3	3.3	0.8

Table A.5.1 (Continued).

Alpha Code[1]	Forage Species[2] Scientific Name	Common Name	C UG	C CG	C EG	D UG	D CG	D EG	E UG	E CG	E EG
	Shrubs & Trees										
RUID	*Rubus idaeus*	Red raspberry				T	T	T			
SACE	*Sambucus cerulea*	Blue elderberry							T	T	T
SASC	*Salix scouleriana*	Scouler willow	T	0.4	T	3.9	5.1	1.4	0.3	0.4	T
SHCA	*Shepherdia canadensis*	Russet buffaloberry				T	0.2	T	T	T	T
SPBE	*Spiraea betulifolia lucida*	Shinyleaf spirea	1.0	4.2	1.0	6.5	3.1	5.1	1.1	1.4	2.1
SYAL	*Symphoricarpos albus*	Common snowberry	1.5	3.4	1.1	3.2	2.5	2.2	2.8	4.9	2.2
TABR	*Taxus brevifolia*	Pacific yew				T	T	T			
VAME	*Vaccinium membranaceum*	Big huckleberry	1.3	2.1	0.1	2.6	5.7	2.2	1.8	5.3	0.6
VASC	*Vaccinium scoparium*	Grouse huckleberry	T	0.7	0.1	0.2	0.5	1.0	0.1	0.8	0.6
	Lichen										
BRFR	*Bryoria fremontii*	Tree hair lichen	0.4	0.6	0.2	8.6	8.3	4.4	14.5	16.6	3.0

[1] Forage species nomenclature follows the recommendations of the USDA Natural Resources Conservation Service (USDA, NRCS 2005).

[2] Contribution of each forage species to animal diet is expressed as a percentage of digestible dry matter intake (%, DDMI).

[3] T indicates trace (< 0.1%). Empty cells indicate that plants were not consumed by animals.