

Herbivore Optimization by North American Elk: Consequences for Theory and Management

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ABSTRACT

Understanding herbivore optimization has implications for theories underpinning ecosystem processes, management of large herbivores, and the landscapes they inhabit. We designed an experiment to examine interactions related to density dependence of North American elk (*Cervus elaphus*) and resulting plant responses to herbivory in the Blue Mountains of Oregon, USA, from 1999 to 2001. We experimentally created high (20.1 elk/km²) and low (4.1 elk/km²) population densities of elk and built exclosures to examine effects of herbivory on productivity and species composition of plants. We hypothesized that if herbivore optimization occurred with increasing density of elk, there should be a concordant increase in plant production, followed by a decline in productivity as grazing intensity continued to increase (i.e., herbivore optimization). Net aboveground primary productivity (NAPP) increased from no herbivory to herbivory by elk at moderate density and then declined as herbivory by elk continued to increase in areas with high NAPP (mesic and logged forests) but not in areas with low NAPP (xeric forests and grasslands). Herbivore optimization occurred across all functional groups of plants, including graminoids, forbs, and shrubs for high-NAPP areas. Herbivore optimization may be difficult to detect in woody plants compared with graminoids because of their differing structure and growth forms. Although herbivore optimization previously has been reported in grasslands, our study documents this phenomenon in woody plant communities. We hypothesize that such subtle changes in NAPP from herbivory might be more common than previously thought; carefully designed experiments are required to detect those responses to herbivory by large herbivores. Apparent offtake of plants followed a similar pattern to NAPP and was greatest at intermediate levels of herbivory by elk, and then declined as NAPP approached zero. Quality of plants, as indexed by percent nitrogen (N), also exhibited a parabolic function with increasing density of elk. Nonetheless, we observed no changes in species composition or diversity of plants with our density manipulations of elk, probably because of the extensive history of grazing by native and domestic herbivores in the Blue Mountains, the resilience of the remaining plants to herbivory, and the short 3-year duration of our study. Likewise, we observed no increases in rates of nutrient cycling with changes in densities of elk, perhaps because areas where large amounts of elk urine and feces were concentrated (e.g., grazing lawns) did not occur in this ecosystem.

Herbivore optimization could have ramifications for population dynamics of ungulates. We argue that other processes, such as migration, predation, or harvest, might be necessary to maintain areas of increased NAPP because of strong density-dependent feedbacks and negative effects of ungulates on their food supply would not allow equilibrium between herbivores and their food supply at the low densities where we documented herbivore optimization. We also hypothesize that increased NAPP at low to moderate population densities of herbivores could lead to rapid population growth of these herbivores and help reduce density-dependent feedbacks and promote overshoots of carrying capacity. Our data do not support stocking large densities of ungulates on western rangelands to obtain peak production of NAPP. We recommend maintaining low to moderate densities of large herbivores in ecosystems if goals are to maximize NAPP and forage quality or to maximize body condition and reproduction of ungulates.

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KEY WORDS

Cervus elaphus, density dependence, herbivore optimization, herbivory, management, NAPP, North American elk, management, population density.

Optimización de Herbívoría por los Alces Norteamericanos: Consecuencias para la Teoría y el Manejo

RESUMEN

El entender la optimización de la herbivoría tiene implicaciones en las teorías que sostienen los procesos de los ecosistemas, el manejo de los herbívoros grandes y los lugares que habitan. Diseñamos un experimento para analizar las interacciones relacionadas a la denso-dependencia del wapiti de norte América (*Cervus elaphus*) y la respuesta de las plantas como resultado de la herbivoría en las montañas Azules de Oregón,

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USA, desde 1999 hasta el 2001. Creamos experimentalmente poblaciones de alta (20.1 alces/km^2) y baja (4.1 alces/km^2) densidad de wapiti y construimos áreas cercadas para examinar los efectos de la herbivoría en la productividad y composición de las especies de plantas. Nuestra hipótesis fue que si la optimización de herbivoría ocurría con el incremento en la densidad de los alces, debería haber un concordante incremento en la producción de plantas, seguido por una disminución en la producción de acuerdo al incremento en la intensidad de forrajeo (por ejemplo, optimización de la herbivoría). Incrementamos la producción primaria sobre el terreno neta (NAPP) desde no herbivoría hasta intensidad de forrajeo moderada, luego disminuimos a media que la intensidad de forrajeo aumentaba en áreas (hábitats) con alta NAPP (bosques talados y mésicos) pero no en áreas con bajo NAPP (bosques xéricos y pastizales). La optimización de la herbivoría ha sido previamente reportada en pastizales; nuestro estudio documenta este fenómeno en comunidades de plantas leñosas. Nuestra hipótesis es que estos cambios sutiles in NAPP de herbivoría pueden ser mas comunes de lo que previamente se ha sugerido, se requieren experimentos cuidadosamente diseñados para detectar tales respuestas a la herbivoría producida por los herbívoros grandes. El consumo aparente de plantas siguió un patrón similar, siendo mayor a niveles intermedios de intensidad de forrajeo, luego declina a medida que NAPP se aproxima a cero. La calidad de las plantas, detectada como un índice del porcentaje de nitrógeno (N) también tuvo una función parabólica con el incremento de la densidad de alces. Sin embargo, no observamos cambios en la composición de las especies ni en la diversidad con nuestra manipulación de densidad de alces, probablemente debido a la larga historia de pastoreo por parte de herbívoros nativos y domésticos en las montañas azules, la resistencia a la herbivoría de las plantas que han quedado en el área y la corta duración de este estudio (tres años). De la misma manera, no se observaron incrementos en el rango del ciclo de los nutrientes debido a cambios en las densidades de los alces, quizás debido a que las áreas donde se concentraron la mayor cantidad de orina y excrementos de los alces (por ejemplo en las áreas de pastoreo) no ocurrieron dentro de este ecosistema.

La optimización de la herbivoría puede tener ramificaciones en la dinámica de las poblaciones de ungulados. Nosotros discutimos que otros procesos como la migración, depredación o cosecha podrían ser necesarios para mantener los prados de pastoreo dada la fuerte retroalimentación denso-dependiente y los efectos negativos de los grandes herbívoros sobre su stock alimenticio. También ponemos a prueba nuestra hipótesis de que el incremento en NAPP a bajas y moderadas densidades poblacionales pueden conducir a un rápido incremento poblacional, ayudar a reducir la retroalimentación denso-dependiente y promover excesos en la capacidad de carga. Nuestros datos no soportan el colocar grandes densidades de ungulados en áreas de pastoreo del oeste para obtener un pico en la producción. Recomendamos mantener densidades bajas o moderadas de grandes herbívoros en ecosistemas si la meta es maximizar NAPP y calidad forrajeo o el mantener una máxima calidad del organismo y la reproducción de los ungulados.

Optimisation Herbivore par les Élans Nord-Américains: Conséquences pour la Théorie et la Gestion

RÉSUMÉ

La comprehension l'optimisation d'herbivore a les implications pour des theories soutenant les processus d'écosystème, et l'aménagement des grandes herbivores et leurs habitats. Nous avons effectué une expérience pour examiner les interactions reliées à la dépendance à la densité du wapiti (*Cervus elaphus*) et les réponses des plantes à l'herbivorie dans les Blue Mountains de l'Oregon, E.U.A. de 1999 à 2001. Nous avons créé expérimentalement des populations de wapiti de haute et de basse densité, et construit des exclos pour examiner les effets de l'herbivorie sur la productivité et la composition des espèces de plantes. Nous avons proposé l'hypothèse que si l'optimisation d'herbivore se réalise avec une augmentation de la densité de population de wapiti, il devrait y avoir un accroissement concordant de productivité des plantes, suivi par une baisse en productivité quand l'intensité de pâturage continue à augmenter (i.e., l'optimisation d'herbivore). La production primaire épigée nette (PPEN) a augmenté en absence d'herbivorie jusqu'à une intensité modérée de pâturage, puis a décliné avec une augmentation de l'intensité de pâturage dans les habitats avec une haute PPEN (forêts mésiques ou coupées). Cette relation n'a pas été observée dans les habitats de basse PPEN (forêts xériques ou prairies). L'optimisation d'herbivore s'est aussi réalisée pour les groupes fonctionnels de plantes, comprenant les graminées, les herbacées, et les arbustes dans les habitats de haute PPEN. Cette réponse est beaucoup plus difficile à remarquer chez les plantes ligneuses, comme les arbustes, à cause de leur structure et de leur forme de croissance en comparaison des plantes herbacées. Nos données ont démontré que l'optimisation d'herbivore n'était pas restreinte aux prairies. Nous suggérons que ces subtil changements en PPEN suite à l'herbivorie sont plus communs qu'accepté auparavant; des expériences soigneusement conçues sont requises pour découvrir ces réponses à l'herbivorie par les grands herbivores. Une réponse semblable était observé dans l'analyse de la différence entre la biomasse épigée à l'intérieur et à l'extérieur des exclos ("apparent offtake"); celle-ci était la plus grande au niveau intermédiaire de pâturage, et puis a diminué quand la PPEN a approché zéro. La qualité des plantes, indexé par % nitrógeno (N), avait aussi une relation parabolique avec la densité de wapiti. Nous n'avons pas observé de changements dans la composition d'espèces de plantes avec nos manipulations de la densité de wapitis. Ce résultat est probablement dû à une histoire de pâturage important par les herbivores natifs et domestiques dans les Blue Mountains, et à la résilience des plantes restantes à l'herbivorie. De même, nous n'avons pas trouvé de relation entre les taux de cyclage des nutriments et la densité de wapitis, probablement parce que nous n'avons pas pu identifier de sites pour échantillonner où il y avait des concentrations d'urine et de fèces, comme dans les pâtures.

L'optimisation d'herbivore peut avoir des ramifications pour la dynamique de la population des ongulés. Nous soutenons que d'autres processus, comme la migration, la prédation et la récolte peuvent être nécessaires pour maintenir des endroits de haute PPEN à cause des rétroactions fortes dépendantes de la densité et des effets negatifs des grandes herbivores sur leurs réserve de nourriture. Nous proposons aussi l'hypothèse qu'une forte PPEN à des densités de population basse à modérées peut mener une rapide expansion démographique et aider à réduire les rétroactions dépendantes de la densité qui peuvent promouvoir un dépassement de la capacité de support. Nos données ne soutiennent pas le stockage en haute densité des ongulés sur les pâtures occidentaux pour obtenir d'une PPEN maximale. Nous recommandons la maintenance des densités basse a intermédiaire des grands herbivores si les buts sont à maximiser la PPEN et la qualité de fourrage, ou à maximiser l'état physique et la reproduction des ongulés.

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INTRODUCTION

The herbivore optimization hypothesis (Fig. 1) predicts the increase of plant production with moderate levels of herbivory compared with ungrazed or heavily grazed areas (McNaughton 1979, 1983; Hilbert et al. 1981; Hik and Jefferies 1990; Dyer et al. 1993). Herbivores can influence or regulate forage quality and availability through changes in plant production, plant species composition, and rates and pathways of nutrient cycling (Coppock et al. 1983, Ruess et al. 1988, Hik and Jefferies 1990, Mulder and Ruess 1998, Person et al. 2003). This process is well-documented in field studies of large mammals (Pastor and Naiman 1992, Molvar et al. 1993, Frank et al. 1994, Augustine and Frank 2001, Frank et al. 2002), in clipping experiments (Seagle et al. 1992), and in theoretical ecosystem models (de Mazancourt et al. 1998, de Mazancourt and Loreau 2000). Grazing can increase palatability of forages by increasing nitrogen content of above-ground biomass or by shifting demographies of plants toward younger and more mitotically active individuals (Bryant et al. 1983, Bazely and Jefferies 1985, Kotanen and Jefferies 1987, Georgiadis et al. 1989, Ritchie et al. 1998). Intermediate levels of grazing by lesser snow geese (*Chen caerulescens caerulescens*) increased NAPP on grazing lawns relative to heavily grazed or ungrazed swards (Hik and Jefferies 1990). We define grazing lawns as vegetation swards dominated by high densities of grazing-tolerant plants with high nutrient concentrations that are maintained by herbivory (Person et al. 2003). Grazing lawns are influenced principally by herbivore species, herbivore densities, and landscape structure (Person et al. 2003), and can range from a few square meters (Person et al. 1998) to many square kilometers (McNaughton 1983, 1985). Evidence also exists of increases in NAPP and nutrient cycling in response to herbivory for other functional classes of vegetation, including shrubs (du Toit et al. 1990, Molvar et al. 1993).

In contrast, numerous studies have reported that effects of grazing were neutral or negative and questioned the validity of the

herbivore-optimization hypothesis (Belsky 1986, 1987; Painter and Belsky 1993). In a review based on 236 studies worldwide, effects of grazing on primary production was largely neutral or negative; only 17% of those studies reported increased production (Milchunas and Lauenroth 1993). Moreover, some of the methods used to determine grazing intensity are statistically autocorrelated with production (Mitchell and Wass 1996, Person

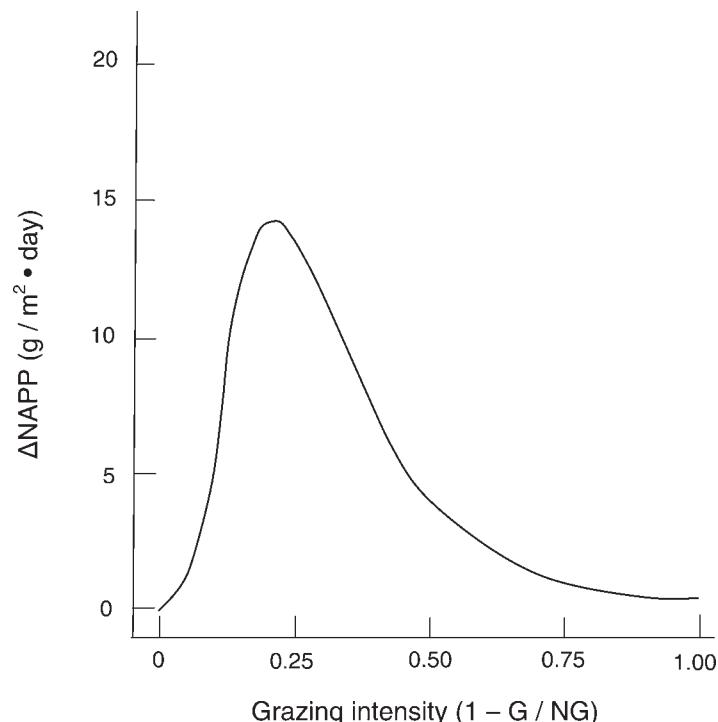


Figure 1. An example of a herbivore optimization curve, which illustrates the relationship between increase in grazing intensity and changes in net aboveground primary production (NAPP) in grasslands, where G = biomass in grazed areas, NG = biomass in ungrazed areas, and ΔNAPP = increase in productivity measured in $\text{g}/\text{m}^2/\text{day}$ (after McNaughton 1979, Kie et al. 2003).

et al. 1998). An independent measure of herbivory or documented use of those study sites by large herbivores is requisite to obtain a valid test of this hypothesis.

Nutrient and moisture availability is likely a major factor of plant responses to herbivory (McNaughton 1979, Coughenour et al. 1985, Belsky 1986, Chapin and McNaughton 1989); several studies reported compensation where soil was fertilized but no compensation occurred in unfertilized plots (Bryant et al. 1983, Ruess and McNaughton 1987, Georgiadis et al. 1989, Holland and Detling 1990). Moreover, the Serengeti savannas of East Africa, where the herbivore optimization was documented, are characterized by high soil fertility and soil moisture (Chapin and McNaughton 1989). In Yellowstone National Park, compensation to herbivory was more likely when nutrient availability was high (Maschinski and Whitham 1989).

Ungulate Population Density and Ecosystem Processes

Population densities of herbivores and intensity of their foraging can determine whether herbivory increases nutrient cycling and plant productivity (Molvar et al. 1993, Kielland et al. 1997), or affects plant communities by driving changes in successional pathways (Pastor and Cohen 1997, Jefferies and Rockwell 2002), decreasing nutrient cycling (Harrison and Bardgett 2004), and thereby influencing biodiversity of those communities (Augustine and McNaughton 1998, Olff and Ritchie 1998, Fletcher et al. 2001). At high population density, large herbivores exceed their available food resources, thereby intensifying density-dependent feedbacks on their physical condition and reproduction (McCullough 1979, Kie et al. 1983, Kie and White 1985, Bowyer et al. 1999, Gaillard et al. 2000, Stewart et al. 2005). There are likely strong interactions among density-dependent processes in large herbivores and effects of their foraging on plant productivity and nutrient cycling, but those interactions have not been studied with experimental manipulation for large, free-ranging mammals.

When herbivores exhibit density-dependent reductions in physical condition and fecundity with increasing population size (i.e., as the population nears carrying capacity [K]), a corresponding negative effect on the plant community is expected with reductions in plant productivity and nutrient cycling. Such effects drive changes in successional pathways or lead to degradation of plant communities (Ruess et al. 1998, Jefferies and Rockwell 2002, Person et al. 2003, Schoenecker et al. 2004). At sufficiently high densities, large herbivores can trample vegetation and compact soil (Packer 1953, 1963), denude vegetation (Jefferies and Rockwell 2002), lower species diversity of forage plants (Nicholson et al. 2006), and cause trophic cascades that result in “ecological meltdowns” (Terborgh et al. 2001, Coté et al. 2004, Bowyer et al. 2005, Hebblewhite et al. 2005, McShea 2005). Conversely, low or intermediate levels of herbivory, resulting from populations at low density, can initiate positive feedbacks on the plant community with increases in plant production and enhanced nutrient cycling (Hik and Jefferies 1990, Molvar et al. 1993, Frank et al. 1994). Large herbivores also can benefit some plants by dispersing their seeds (Vellend et al. 2003). Ungulates offer an unique opportunity to study interactions between density-dependent processes and ecosystem structure and function because these large mammals exhibit life-history characteristics that change markedly with

population density (McCullough 1979, 1999; Kie and Bowyer 1999; Kie et al. 2003; Reimers et al. 2005).

Although herbivore optimization is thought to occur primarily in grassland ecosystems, some studies have indicated that it might occur in other functional groups of plants (du Toit et al. 1990, Molvar et al. 1993, Kielland et al. 1997, McNeil and Cushman 2005). Herbivory by elk in Olympic National Park in western Washington, USA, reduced plant standing crop, increased species richness of forbs, and affected the distribution of several species of shrubs (Woodward et al. 1994, Schreiner et al. 1996). In addition, elk herbivory has been implicated both in increasing and decreasing rates of nutrient cycles in soils (Singer and Schoenecker 2003).

Elk are an especially good model for examining herbivore optimization in different functional groups of plants in montane ecosystems because they occur extensively across the intermountain west. Moreover, elk consume a variety of forages including forbs, shrubs, and graminoids (Stewart et al. 2002, 2003b). Consequently, several functional groups of plants can be examined for possible optimization following foraging by elk, in addition to examining density-dependent processes in elk populations on herbivore optimization.

Sexual Segregation and Optimization

Sexual segregation is pronounced among polygynous ruminants (Bowyer 2004), with resource partitioning between sexes typically occurring along habitat, dietary, and spatial niche axes (Bowyer and Kie 2004). Spatial differences between sexes often result in males occurring at low population density and females occupying areas of high density (Bowyer 1984, Bleich et al. 1997, Kie and Bowyer 1999, Stewart et al. 2003a). Further, males require absolutely more forage than females, but females require a diet with a higher nutrient content to support reproduction than do males (Barboza and Bowyer 2000, 2001). Consequently, the spatial distribution of sexes of cervids in general (Bowyer 1984, Kie and Bowyer 1999), and elk in particular (Peek and Lovaas 1968, Weckerly 1998), hold import for understanding the distribution of these animals across the landscape and their effects on ecosystem processes. Bowyer (2004) stated that the concept of sexual segregation must be integrated into the disciplines of range and wildlife management and become a standard consideration in designing research and implementing habitat manipulations. Moreover, understanding the distribution of ungulates across landscapes and the subsequent effects on ecosystem structure and function requires knowledge about how sexes partition space, habitat components, and forage (Bowyer 2004). Sexual segregation is prevalent in North American elk (Peek and Lovaas 1968, Weckerly 1998), and this phenomenon results in differences in density between sexes for much of the year. Sexual segregation must be addressed when examining effects of population densities of elk on ecosystem processes such as herbivore optimization. Our purpose was not to test for sexual segregation in our study; this phenomenon has been documented previously in this species (Peek and Lovaas 1968, Weckerly 1998). In our analyses, however, we account for males and females occurring at different densities and using habitats and forages differently across study areas.

Research Design and Hypotheses

Detecting herbivore optimization by large mammals is neither straightforward nor simple. Testing for herbivore optimization requires comprehensive data on the distribution and density of large herbivores and detailed information on species composition of plants, their productivity, and rates of nutrient cycling. In addition, obtaining an experimental test of herbivore optimization has yet to occur with a large, free-ranging mammal, in part because of the difficulty in manipulating these large, vagile herbivores (Stewart et al. 2002). Nonetheless, Stewart et al. (2005) completed a manipulative experiment that examined effects of density dependence in North American elk by creating free-ranging populations of elk at low ($4.1 \text{ elk}/\text{km}^2$) and high ($20.1 \text{ elk}/\text{km}^2$) densities during spring, summer, and autumn. Elk in the low-density population were in better physical condition and had higher rates of reproduction than those in the high-density population (Stewart et al. 2005). Concurrent with research on density dependence in elk, we studied effects of herbivore population density on NAPP and ecosystem processes.

Most studies investigating plant responses to herbivory are clipping experiments (Bergstrom and Danell 1987, Hjalten et al. 1993, Wardle et al. 2000, Leriche et al. 2003) or examine effects of free-ranging herbivores (du Toit et al. 1990, Hik and Jefferies 1990, McInnes et al. 1992, Molvar et al. 1993, Post and Klein 1996), including those involving elk (Cougenour 1991; Frank and McNaughton 1992; Augustine and Frank 2001; Peinetti et al. 2001, 2002). In our experiment, we manipulated population density on a large scale (1,452 ha) to account for effects of habitat selection (Stewart et al. 2002) on herbivory by a large herbivore. Few studies have been able to obtain data on NAPP and physical condition of individuals to couple and investigate interactions of density dependence with forage production and other ecosystem processes.

We investigated effects of density dependence of elk on NAPP at high and low population densities of elk. Accordingly, we tested hypotheses related to herbivore optimization, and how population densities of elk affected plant productivity. We hypothesized that there initially would be an increase in NAPP with an increasing population density of elk, followed by a decline in productivity as grazing and browsing intensity continued to increase. This parabolic relationship between density and plant productivity (Fig. 1) is requisite to postulate herbivore optimization. Following Hik and Jefferies (1990), we hypothesized that changes in NAPP and plant quality would be most prevalent during the spring growing season. We also postulated that rates of vegetation offtake (i.e., removal) by elk would increase concurrently with increasing productivity, and then decline as herbivory by elk continued to increase and NAPP declined. Furthermore, we tested the hypothesis that changes in plant productivity would result from changes in species composition of plants in the community. We hypothesized that rates of N mineralization and respiration in soils also would be highest at intermediate levels of herbivory. Finally, we link the role of herbivore optimization to the management and population dynamics of ungulates by relating this process to the life-history strategies of elk. Many studies have investigated effects of herbivores on plant production, but few have examined feedbacks on the herbivore population.

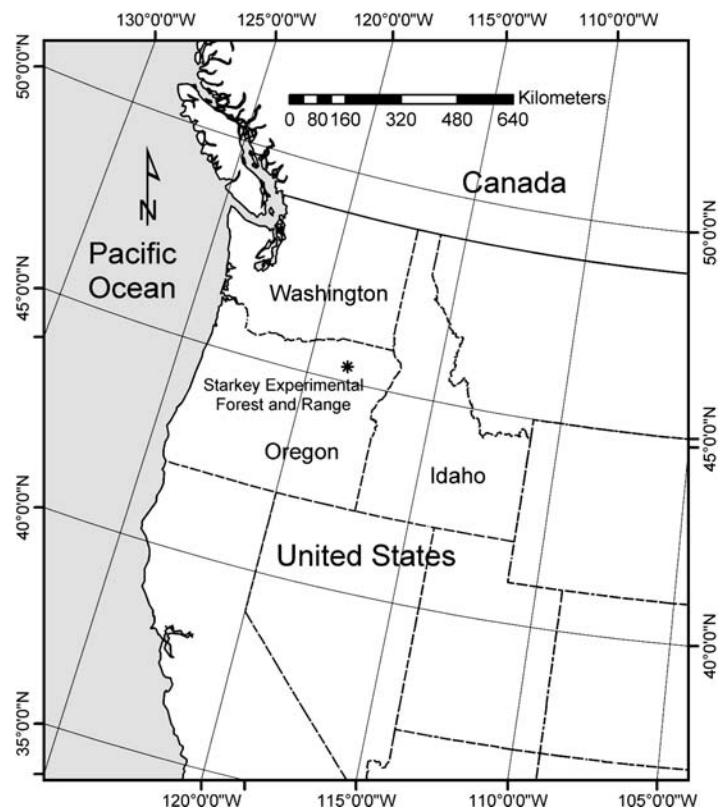


Figure 2. Location of the Starkey Experimental Forest and Range, Oregon, USA.

STUDY AREA

Location

We conducted research from 1999 through 2001 on the Starkey Experimental Forest and Range (hereafter Starkey) of the United States Forest Service. Starkey ($45^{\circ}12'N$, $118^{\circ}3'W$) is situated in the Blue Mountains of northeastern Oregon and southeastern Washington, and is located 35 km southwest of La Grande, Oregon, USA (Fig. 2). Elevations ranged from 1,120 to 1,500 m. This site supported a mosaic of forests and xeric grasslands, with moderately sloping uplands dissected by drainages, which are typical spring and summer ranges for elk (Rowland et al. 1997, Johnson et al. 2000). Starkey encompassed 10,125 ha and since 1987 has been surrounded by a 2.4-m fence that prevents immigration or emigration of large herbivores, including migration to traditional winter ranges (Rowland et al. 1997). We restricted our experiment to the northeast area on Starkey, which encompassed 1,452 ha, and was separated from the remainder of the study area by the same high fence (Stewart et al. 2002). The northeast area was divided into 2 study sites, east (842 ha) and west (610 ha), to accommodate experimental comparisons of population densities of elk. We divided the northeast area in a manner that resulted in plant communities being equal in proportions in eastern and western areas (Stewart et al. 2002; Fig. 2). Such study sites are sufficiently large to allow natural movements and other behaviors of large herbivores (Hirth 1977, McCullough 1979, Stewart et al. 2002). Fence-related effects on habitat selection and use by elk in the northeast study area were

not significant (Stewart et al. 2002). The high-density population was randomly assigned to the eastern study area.

Other Large Mammals

Mule deer (*Odocoileus hemionus*) also were present in eastern and western study areas at low population densities. Mean (\pm SE) population density of mule deer was 3.2 (\pm 0.71) deer/km² in the west and 2.1 (\pm 0.64) deer/km² in the east study sites (Oregon Department of Fish and Wildlife annual helicopter survey 1997–2001). Because this study focused on population density of elk, and deer were present in low densities, no attempt was made to manipulate or further evaluate populations of mule deer for this study. Cattle were removed from our study areas during 1997 and remained absent during our experiment.

Eastern Oregon is host to a suite of large predators, including black bears (*Ursus americanus*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*; Virts and Carraway 1998). These predators occasionally occur on Starkey, but we made no effort to enumerate or manipulate predators on our study areas. There were no confirmed mortalities of radiocollared elk during the duration of our study (1998–2001); thus, few differences in predation levels between the 2 study areas were likely. Animals selected and used habitats and forages in this study as they would in any area where predators were present, which likely provides a more realistic reflection of habitat selection and use by free-ranging animals than in area where predators were absent or controlled (sensu Berger et al. 2001).

Climate

We defined seasons by months with similar ranges of temperature and precipitation, which reflected changes in plant phenology (Stewart et al. 2002). Spring occurred from April through June and exhibited relatively high precipitation (62.1 \pm 4.27 mm) and warm (9.1 \pm 3.2 °C) air temperatures (Stewart et al. 2002). Summer (Jul–Sep) had relatively high temperatures (16.0 \pm 1.8 °C) and low precipitation (22.2 \pm 6.2 mm). Autumn (October) was transitional with respect to temperatures (7.3 °C) and precipitation (39.5 mm), and winter (Nov–Mar) had relatively low temperatures (−0.7 \pm 2.2 °C) and high precipitation (60.5 \pm 12.7 mm).

Plant Communities and Soils

The northeast area consisted of 4 major plant communities: (1) mesic forest, (2) xeric forest, (3) xeric grassland, and (4) logged forest (Stewart et al. 2002; Fig. 3). Plant nomenclature follows Hitchcock and Cronquist (1996). Mesic forest occurs on north-facing slopes with overstory composition dominated by grand fir (*Abies grandis*). Plants in the understory consisted primarily of forbs and shrubs with a few grasses, including pinegrass (*Calamagrostis rubescens*). Forbs included golden pea (*Thermopsis montana*) and strawberry (*Fragaria* spp.); common shrubs included serviceberry (*Amelanchier alnifolia*) and rose (*Rosa* spp.; Stewart 2004). Soils, consisting primarily of volcanic ash and loess derived from basalt, were well drained and deep with an effective rooting depth \geq 150 cm; available water capacity was 38–60 cm (Dyksterhuis and High 1978).

Xeric forests generally occur on south- and east-facing slopes. Tree composition consisted primarily of ponderosa pine (*Pinus*

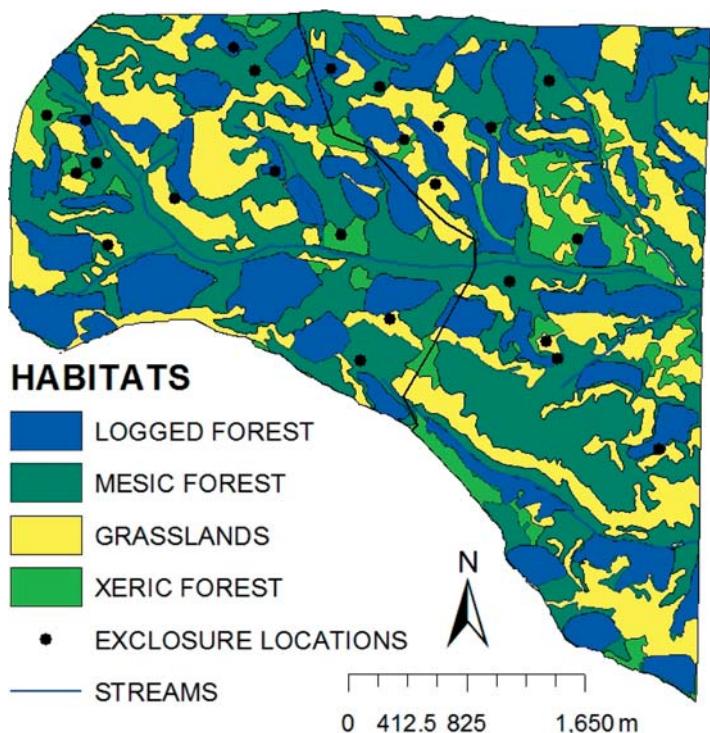


Figure 3. The northeast study area with east and west areas for manipulation of population density of North American elk on the Starkey Experimental Forest and Range, Oregon, USA. Four major plant communities are indicated with corresponding locations of herbivore exclosures.

ponderosa). Plants in the understory were dominated by elk sedge (*Carex geyeri*; Stewart 2004). Soils in xeric forests consisted of colluvium and residuum, derived from basalt, and were dark reddish-brown and very stony, silty loams (Dyksterhuis and High 1978). Depth to bedrock in xeric forest was 20–50 cm; available water capacity was 2.5–5.0 cm (Dyksterhuis and High 1978).

Xeric grasslands occur primarily on south- and east-facing slopes; this plant community was dominated by a few grasses and forbs. Grasses consisted of onespike oatgrass (*Danthonia unispicata*), Idaho fescue (*Festuca idahoensis*), and bluebunch wheatgrass (*Agropyron spicatum*), and forbs included low gumweed (*Grindelia nana*; Stewart 2004). Grassland soils were similar to those in xeric forests and consisted of colluvium and residuum; soils were shallow and extremely stony. Production of vegetation was limited by stony substrates, shallow depth to bedrock, and low available water capacity (1.0–2.5 cm; Dyksterhuis and High 1978).

Logged-forest communities were areas where timber was harvested during 1991–1992. Grand fir on Starkey suffered widespread mortality (>90%) from spruce budworm (*Choristoneura occidentalis*) during the late 1980s and timber was harvested in areas where most trees were killed (Rowland et al. 1997, Stewart et al. 2002). Following removal of trees, those areas were seeded with several species of grasses including orchardgrass (*Dactylis glomerata*) and bluegrass (*Poa* spp.; Stewart 2004). Mesic and logged forests had similar soil types because those plant communities were similar prior to harvest (Rowland et al. 1997, Stewart et al. 2002). Soils, consisting primarily of volcanic ash and loess derived from basalt, were well-drained and deep with an

effective rooting depth >150 cm; available water capacity was 38–60 cm (Dyksterhuis and High 1978).

METHODS

Experimental Design

During 1999, we began an experiment to examine effects of elk population density on plant productivity and offtake of plant biomass by elk. We assessed vegetation responses to herbivory by examining elk populations at high (20.1 elk/km^2) and low (4.1 elk/km^2) densities. We were able to account for habitat use by elk when examining effects of population density on NAPP because of our ability to manipulate populations of elk on Starkey and use of radiotelemetry to determine precise animal locations. Moreover, exclosures were replicated within plant communities and density treatments. We assumed the size of our study areas (842 ha and 610 ha) were adequate to test our hypotheses. Indeed, the size of each of our study areas was as large as The George Reserve, Michigan, USA, where extensive research was conducted on density dependence in white-tailed deer (*Odocoileus virginianus*; McCullough 1979).

We selected low and high densities based on earlier research conducted on Starkey (Rowland et al. 1997). Our high-density population (20.1 elk/km^2) represented a high concentration of animals; however, unhunted populations of elk attain densities as high as 33 elk/km^2 (Houston 1982, Hobbs et al. 1996, Stewart et al. 2005). The high-density treatment in an experiment examining resource competition between domestic cattle and elk was 31 elk/km^2 (Hobbs et al. 1996).

Our experiment began May 1999. During that first month, however, a gate was inadvertently left open between study areas, resulting in movement of elk from the high- to the low-density population (Stewart et al. 2005). Thus, our low-density population for that year was 6.6 elk/km^2 , and the high-density population 10.8 elk/km^2 . Although not part of our original design, the resulting array of animal densities across years fortuitously allowed us to examine low, moderate, and high densities of elk in our treatment areas. During the final 2 yr of the study, we maintained a high-density population at 20.1 elk/km^2 and low-density population of 4.1 elk/km^2 .

Elk no longer migrate from the study area to traditional winter ranges because of the fence; consequently, animals were maintained throughout winter in a holding area where they were fed a maintenance diet of alfalfa hay (Rowland et al. 1997). Elk were concentrated and contained within a winter feeding ground from early December to late April. Few elk remained on the

northeast study area during winter; consequently, herbivory by elk was constrained primarily to spring, summer, and autumn (Stewart et al. 2002). Detailed studies of winter foraging by elk and their effects on plants and ecosystem processes, however, are available elsewhere (Hobbs et al. 1982; Coughenour 1991; Peinetti et al. 2001, 2002; Zeigenfuss et al. 2002).

During 1998, we placed permanent exclosures in each of 3 major plant communities (mesic forest, xeric forest, and logged forest), with 3 replications per community for each high and low-density treatment. We constructed grassland exclosures during 1999. We placed 6 $32 \times 32 \text{ m}$ exclosures each in mesic, logged, and xeric forests. In xeric grasslands, however, the exclosures were $12 \times 12 \text{ m}$ to accommodate plant communities that occurred in smaller patches (Fig. 3). We used permanent exclosures in vegetation associations (24 total) in combination with moveable exclusion cages (1 m^2) to estimate seasonal NAPP in the presence and absence of herbivores, and offtake of vegetation by large mammals. Herbivory by elk was inferred from locations of elk during periods of activity and densities tabulated via telemetry locations (Stewart et al. 2002).

Animal Movements and Population Density

We equipped a subset of animals in each study area with radio transmitters (Table 1). We attached radiocollars to males and females because elk sexually segregate outside the mating season and we needed to account for areas predominately used by males or females. Adult sex ratios in ungulates often favor females (Bowyer 1991, Berger and Gompper 1999), and males typically occur at low densities when segregated compared with females (Bowyer et al. 1997; Barboza and Bowyer 2000, 2001). Indeed, in each of our study areas, we used an adult sex ratio of about 20 adult males to 100 adult females; thus, we equipped 4 males and 8 females with radiocollars in each study area during each year (Table 1).

Locations of radiocollared elk were obtained with a rebroadcast civilian long range navigation (LORAN-C) system from 1999 to 2001 (Findholt et al. 1996). Mean location error of this telemetry system was $52.8 \pm 5.87 \text{ m}$ (Findholt et al. 1996). This automated telemetry system located each radiocollared animal approximately every 1.5 hours throughout a diel cycle from May to early November each year (Rowland et al. 1997). We restricted our analyses to locations occurring during crepuscular periods for 3 hours ($\pm 1.5 \text{ hr}$ before and after sunrise and sunset), because we were interested in periods when animals were actively foraging. Major peaks of foraging activity for cervids tend to occur during

Table 1. Sample sizes and correction factors for number of adult female and male elk at each radiotelemetry location used to calculate population density of elk in 2.25-ha spatial window on Starkey Experimental Forest, northeastern Oregon, USA, 1999–2001.

Variable	1999				2000				2001			
	West study area		East study area		West study area		East study area		West study area		East study area	
	Ad M	Ad F										
Population density (elk/km^2)	6.56		10.79		4.10		20.07		4.01		20.07	
No. elk	5	22	11	63	5	16	17	105	5	17	20	116
No. radio collars	4	8	4	8	4	8	4	8	4	8	4	8
Correction factor (no. elk/collar)	1	3	1	8	1	2	5	14	1	3	5	15

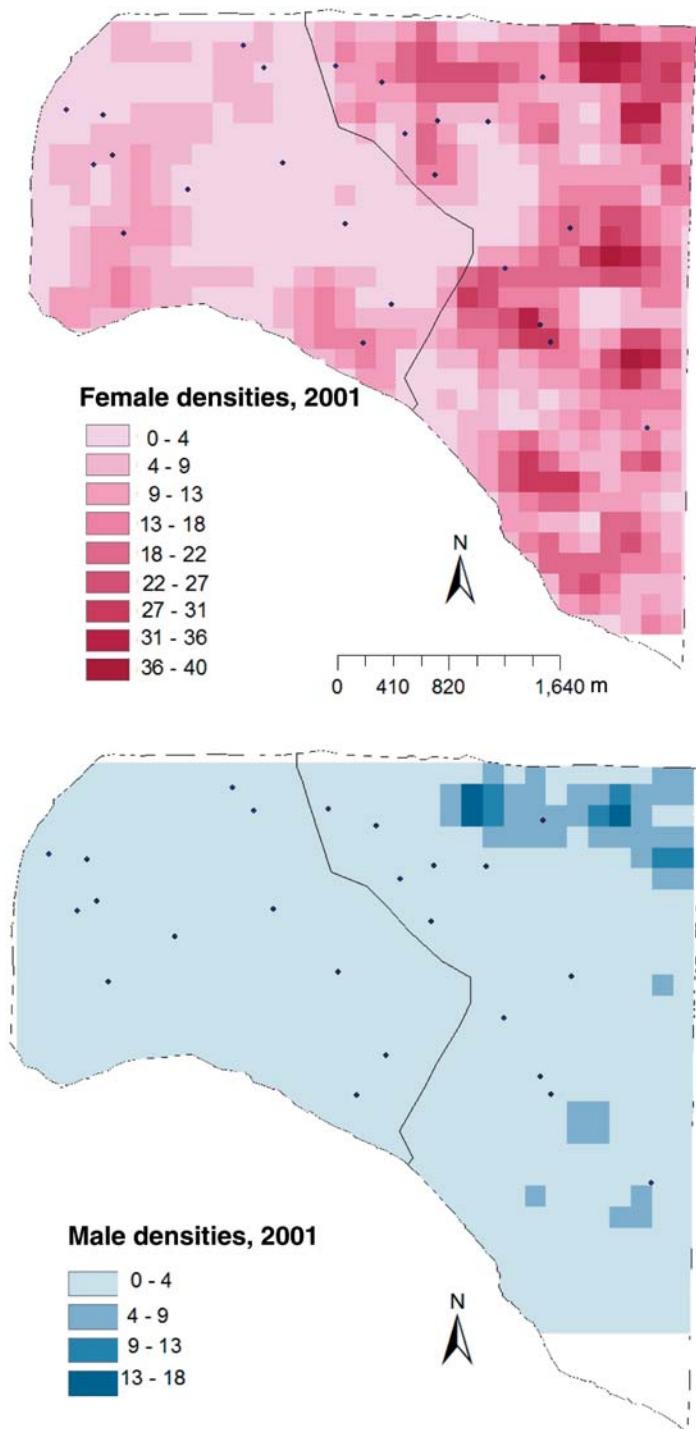


Figure 4. Example of density maps for female (above) and male (below) North American elk indicating cumulative elk population density for spring and summer (May–Sep) 2001 on the Starkey Experimental Forest and Range, Oregon, USA.

crepuscular periods (Bowyer 1981, Stewart et al. 2000, Ager et al. 2003, Kie et al. 2005) and activity peaks of elk on Starkey are consistent with those observations (Ager et al. 2003, Preisler et al. 2004).

Ungulates do not use their habitats uniformly (Fretwell 1972, Fryxell 1991, Kie et al. 2003); thus, the overall population density for the entire study area was inappropriate for estimating grazing

intensity at each enclosure. Accordingly, we estimated density of elk at enclosures from telemetry locations. Forage abundance at relatively small spatial scales was important in determining movements of elk (Anderson et al. 2005). Consequently, data for telemetry locations were determined on a 30 m²-pixel basis from raster-based Geographic Information System (GIS) maps maintained by the Oregon Department of Fish and Wildlife and the United States Forest Service (Rowland et al. 1998).

Our telemetry system exhibited differences in location rates of animals, which varied spatially across the study area (Johnson et al. 1998). Thus, each animal location was weighted by the inverse of the correction factor developed for Starkey in each year to mitigate effects of telemetry error in our analyses. We also weighted each animal location by the number of adult females or males that each radio collar represented for each study area and year (Table 1). We weighted locations differently for males and females because the sexes occurred at different densities. A spatial window of 25 pixels (5 × 5 pixels; 2.25 ha) was used to calculate density of animals (Stewart et al. 2002). We used ArcGIS Spatial Analyst to calculate density of male and female elk for each spatial window of 2.25 ha across the entire study area.

We used multiresponse permutation procedures (MRPP) to determine if spatial distributions of males and females differed across the study areas (Sluson et al. 1991). MRPP are distribution-free statistics that rely on permutations of data based on randomization theory, and use simple Euclidean distances rather than squared deviations (variances) common to most other inferential statistics (Sluson et al. 1991, Pierce et al. 2000). These tests offer a powerful method to assess the distributions of mammals even when sample sizes are small (Nicholson et al. 1997; Pierce et al. 2000).

Results from MRPP indicated that spatial distributions of males and female densities differed in our study areas ($P < 0.0001$); consequently, we created separate density maps for males and females for each year (Fig. 4). Although spatial distributions of males and females differed, both sexes used the entire study areas. Males and females were sexually segregated outside the mating season, but they often used the same plant communities and habitats in each of the study areas at different times. Therefore when calculating densities of elk at each of the enclosure sites, we accounted for the presence of both males and females, which occurred at different densities and had different weighting factors for the number of animals. Consequently, density maps for females and males were overlaid and density of sexes summed to maintain the weighting factors for both sexes and to determine final densities for each treatment area. By summing density maps for the sexes we maintain the weighting factors, which differed for males and females, and we account for use of treatment areas by both sexes at different times. Thus, our final densities reported for each enclosure location account for locations of both males and females.

We then smoothed data on density of elk, obtained from the summed maps of males and females, using kriging with spherical semivariance models using ArcGIS Geostatistical Analyst for spring and summer within years to test hypotheses of effects of elk on plant growth and productivity specifically related to season (Johnston et al. 2001; Fig. 5). We also used kriging to model

population density of elk across the northeast study area for each year for both sexes. Based on kriged values, we obtained an estimate for population density of elk at each enclosure site, which we used to index to herbivory or intensity of grazing at each enclosure location. Thus, our index for intensity of herbivory was calculated independently from vegetation data sampled to estimate NAPP and offtake by elk. Population-density estimates around each enclosure were based on radiotelemetry locations obtained throughout that year or season, and represented a density estimate for that time interval rather than any specific moment in time. Because we limited the timing of animal locations to periods when animals were active, we assume that those elk were predominately foraging during the intervals of time that we sampled. Consequently, those kriged values allowed us to obtain annual and seasonal estimates of population density that were specific to the area immediately surrounding each enclosure.

Vegetation Sampling

We sampled vegetation inside and outside of each permanent enclosure to estimate NAPP and plant species composition. Our replications consisted of permanent enclosure locations (inside and outside), 3 enclosures per plant community per treatment (24 total). We sampled vegetation with 10 1-m² moveable enclosures located outside permanent enclosures in mesic forest, logged forest, and xeric forest, and 5 moveable enclosures in grassland communities. We clipped 0.25-m² quadrats inside and outside moveable enclosures 1 time/month during spring and summer to assess seasonal productivity of vegetation. We sampled permanent enclosures with 0.25-m² quadrats at the beginning and end of each season to examine NAPP in the absence of herbivory by large mammals and to compare with areas grazed by elk. We sorted vegetation into forage classes: forbs, graminoids, shrubs, and standing dead. We dried all samples to a constant mass at 45 °C to prevent binding of proteins for future nutrient analyses (Robbins 1993) and weighed each to the nearest 0.01 g. We estimated NAPP as the difference between biomass within short-term enclosures and unenclosed biomass sampled at the time enclosures were established, divided by interval in days (McNaughton et al. 1996, Person et al. 2003). We included negative estimates of NAPP because eliminating them would overestimate NAPP (Person et al. 1998). During 1999, we clipped quadrats inside and outside all moveable and permanent enclosures; because of limited personnel during 2000 and 2001, however, we used double sampling of vegetation (Ahmed and Bonham 1982, Bonham 1989) and clipped a subsample of 3 moveable enclosures (inside and out) and 3 quadrats within enclosures. We estimated biomass of forage categories, including forbs, graminoids, and shrubs for the other 7 cages (Ahmed and Bonham 1982, Ahmed et al. 1983, Bonham 1989, Barten et al. 2001). We defined offtake following Person et al. (1998) as apparent offtake, because an assumption of the experiment is that grazing influences the rate of growth for vegetation. Consequently, apparent offtake might over- or underestimate true offtake, and is also subject to measurement error. We estimated amount of NAPP consumed by summing apparent offtake across periods divided by the interval in days (Person et al. 1998).

During June 2000 and 2001, we quantified species composition of vegetation using step-point transects inside and outside each

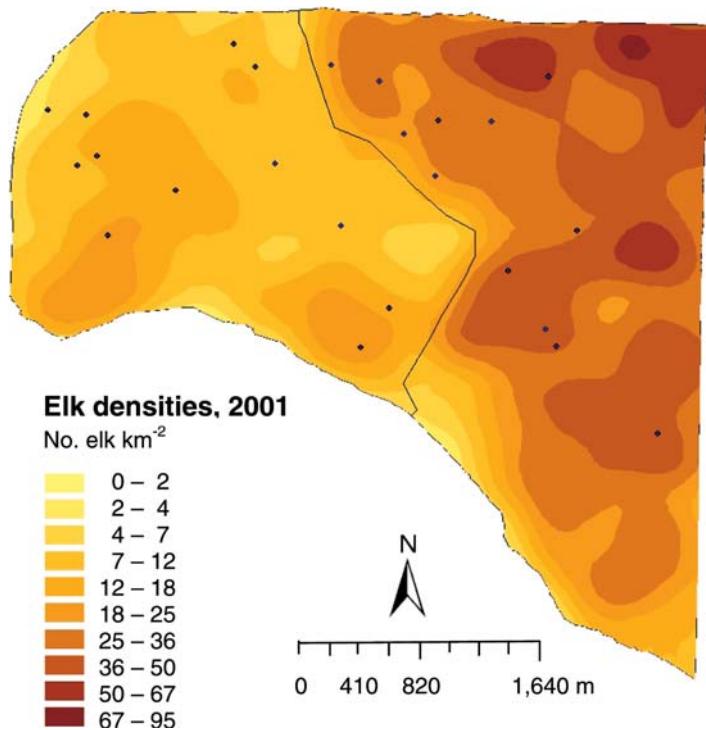


Figure 5. Example of kriged contours indicating cumulative population density of North American elk for spring and summer (May–Sep) 2001 on the Starkey Experimental Forest and Range, Oregon, USA.

permanent enclosure (Bowyer and Bleich 1984, Bleich et al. 1997). We recorded a cover hit if the point (≤ 1 mm in diameter) fell within the canopy of a shrub or on a stem or leaf of a plant. Points not recorded as cover for plants were litter or bare ground. Each random transect contained approximately 200 step-points outside the enclosure and 100 step-points inside the enclosure, primarily because of limited space within enclosures. Adequate sample size was determined by plotting the number of species against cumulative number of points sampled (Kershaw 1964, Geysel and Lyon 1980, Stewart et al. 2000). We used the Shannon–Weiner index to estimate species diversity of plants inside and outside each enclosure (Krebs 1999). Finally, we used Morisita's Index of Similarity (Morisita 1959, Krebs 1999) to compare species composition inside and outside each enclosure; we based Morisita's Index on functional groups of plants rather than individual species to broaden our area of inference. We then used regression to compare the similarity index to population density (from kriging) to determine if species composition changed outside enclosures with areas of changing population density.

Vegetation Quality

We analyzed subsamples from clipped vegetation from each sampling site for forage quality, including percent nitrogen (N), percent in vitro dry matter digestibility (IVDMD; Tilley and Terry 1963), and Van Soest fiber analysis (Van Soest 1994). Neutral detergent fiber (NDF), which consists of cell wall contents, cellulose, hemicellulose, and lignin, was determined from the Van Soest fiber analysis (Van Soest 1994). All analyses for forage quality were conducted by the Chemical Nutrition Laboratory at the Institute of Arctic Biology at the University of Alaska

Fairbanks (UAF). Subsamples of at least 50 g from each vegetation category inside and outside permanent exclosures were ground in a Wiley mill to pass a 20-mesh screen (1 mm). Ground material was thoroughly mixed before weighing samples for analysis. In vitro dry matter digestibility was conducted with reindeer from the Robert G. White Large Animal Research Station at UAF; fistulated reindeer (*Rangifer tarandus*) were pre-innucleated with vegetation from our study area for 5 days during summer to acclimate rumen flora.

Soil Analyses

Changes in N cycling and soil respiration in response to herbivory have been well-documented and might have cascading effects on plant production (Ruess and McNaughton 1987, Hik and Jefferies 1990, Ruess et al. 1998). Consequently, we sampled soils in and out of each exclosure to examine effects of herbivory on soil respiration and N mineralization. We collected 10 soil samples (5 inside and 5 outside each exclosure) with a 5-cm diameter by 10-cm height soil corer during spring 1999 (inside exclosures only), 2000, and 2001. Soil samples were frozen and stored in 1-ml plastic bags prior to analyses. Water-holding capacity was measured on a subset of samples collected in 1999 for each soil type represented in the study (Dyksterhuis and High 1978). Water-holding capacity was defined as the gravimetric water content of sieved soils (2-mm mesh) that were wet to saturation and allowed to drain for approximately 12 hours in filter funnels (Paul et al. 1999).

We thawed frozen soil samples at room temperature and pre-incubated them for approximately 11 days to allow microbial populations to stabilize. Soils were then analyzed for potential rates of net N mineralization and soil respiration. We calculated rates of net N mineralization from 12 g of soil placed in separate 150 ml specimen cups. Each pair of cups was placed in an approximately 1-L mason jar in an incubator, and held in aerobic microcosms at 60% water-holding capacity and 22 °C for 20 days (Robertson et al. 1999). We extracted N with K₂SO₄ under a vacuum. Solution NH₄⁺-N and NO₂/NO₃-N were then analyzed colorimetrically on a modified Technicon AutoAnalyzer (Technicon, Tarrytown, New York). We calculated net N mineralization potentials as the difference in extractable N (NH₄-N + NO₃-N) between the end and beginning of the incubation period (Molvar et al. 1993, Robertson et al. 1999).

We determined soil respiration rate by dividing the headspace CO₂ concentration, sampled at 5 and 15 days, by the duration of the incubation. We assumed that the initial headspace CO₂ concentration at T₀ was at 500 ppm, and subtracted this value from calculations (Robertson et al. 1999).

Statistical Analyses

We used regression analysis to compare vegetation, forage quality, and soil data with population density of elk (e.g., our index of foraging by elk) at each exclosure site. We tested for a parabolic relationship consistent with the shape of the herbivore optimization curve. We evaluated regression with an adjusted multiple coefficient of determination (R^2_a), Mallow's Cp statistic, probability values, and Akiike's Information Criterion (AIC; Zar 1999). All criteria selected the same models, but we present only R^2_a and P values, because AIC is not appropriate for situations

where hypotheses are being tested (Anderson et al. 2001:375). Data on vegetation included annual NAPP, rate of vegetation offtake by herbivores, Shannon-Weiner Index, and Morisita's Similarity Index (exclosure compared with outside). Analysis of forage quality included percent N, percent IVDMD, and Van Soest fiber analysis (percent NDF). Data on soils included potential rates of soil respiration and N mineralization. We used multivariate analysis of variance (MANOVA; Johnson and Wichern 1992) to compare our index of similarity (inside to outside exclosures at each site) to the high- and low-population density treatments (main effects).

Because of the highly variable nature of plant communities (Barten et al. 2001, Lenart et al. 2002), we designed our experiment to cover a range of areas with large number of replications among plant communities so that effects of treatments could be detected. The patchy nature of habitats and vegetation communities across the study areas (Fig. 1) required that we account for use of plant communities because they were not used uniformly by elk. Further, elk selected some plant communities differently (Stewart et al. 2002), which affected their diets (Stewart et al. 2003a). The automated telemetry system allowed us to index intensity of herbivory by elk at each exclosure site across both study areas to gain a better understanding of effects of population densities of herbivores on plant communities.

RESULTS

Net Aboveground Primary Production

We tested for differences in NAPP among plant communities to determine if those areas should be combined. Significant differences in NAPP occurred among communities ($P < 0.001$; Fig. 6), and for a plant community by population density interaction ($P < 0.001$). Mesic and logged forests differed from xeric forests and grasslands in NAPP; we observed that same pattern when we examined functional groups of plants separately (Fig. 6). Mesic and logged forests were categorized as high NAPP, and xeric forest and grasslands were grouped as low NAPP communities (Fig. 6). Accordingly, high and low NAPP communities were examined separately in further analyses.

Elk Density, NAPP, and Forage Quality

We observed a curvilinear relationship consistent with herbivore optimization between NAPP and population density of elk annually for the high NAPP communities of mesic and logged forests (Table 2). This same pattern held when we examined those regressions annually for each plant functional group, although that relationship was not significant for shrubs (Table 2). Conversely, parabolic relationships did not hold in the low NAPP communities of xeric forests and grasslands (Table 2). No relationship existed between NAPP and population density of elk when all functional groups of plants were combined in low-NAPP communities (Table 2).

When we examined seasonal effects of herbivory on NAPP, we observed significant influences of elk density on NAPP during spring in high NAPP communities (Fig. 7) for combined functional groups of plants and when forbs, graminoids, and shrubs were examined separately (Fig. 8)—no significant relationships existed in low NAPP communities (Table 2). Those relationships were not significant during summer in high- or low-

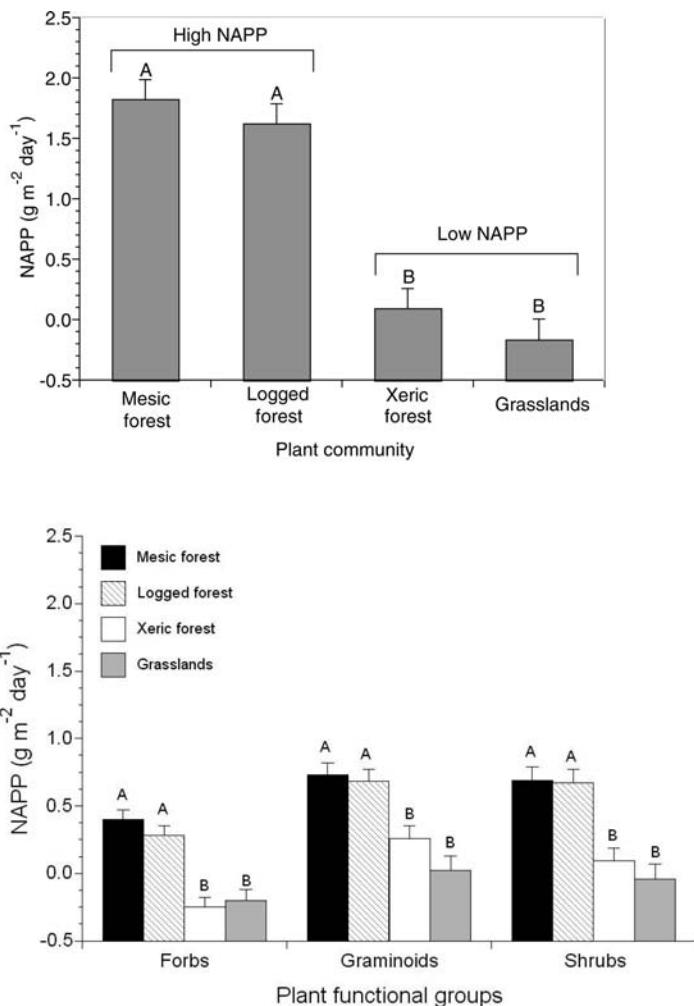


Figure 6. (top) Mean (\pm SE) net aboveground primary productivity (NAPP) for 4 major plant communities in the northeastern study area on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Letters over bars indicate results of comparisons following significant analysis of variance ($F_{3,124} = 36.62, P < 0.001$), in which different letters indicate significant differences ($P < 0.001$). (bottom) Mean (\pm SE) NAPP for each functional group of plants among 4 plant communities on the Starkey Experimental Forest and Range. Letters over bars indicate results of comparisons following significant multivariate analysis of variance (Wilks $\lambda F_{9,273} = 11.88, P < 0.001$).

NAPP communities (Table 2). Plant communities that were more productive responded to changes in herbivore density in a fashion consistent with herbivore optimization (i.e., a parabolic relationship; Figs. 7, 8), but less-productive communities did not respond with that characteristic parabolic relationship (Table 2).

A curvilinear relationship between rate of vegetation offtake by herbivores and population density of elk also occurred for both high- and low-NAPP communities (Fig. 9). Those relationships were similar for functional groups of plants in high-NAPP communities (Fig. 10) and for graminoids in low-NAPP communities (Fig. 10); no relationship existed between offtake and population density of elk for forbs ($R_a^2 < 0.001, P = 0.442$) or shrubs ($R_a^2 < 0.001, P = 0.658$) in low-NAPP communities. Annual NAPP and apparent offtake peaked at similar levels of population density: NAPP = 18 elk/km², and apparent offtake = 23 elk/km². NAPP was zero at approximately 42 elk/km²; that

observation was concordant with apparent offtake, which was zero at about 43 elk/km². Offtake of forage by elk tracked its production in high- and low-NAPP communities (Figs. 9, 10).

We examined changes in forage quality with elk density (Table 3). In high-NAPP communities, graminoids exhibited a parabolic relationship in percent N with population density of elk similar to that predicted by herbivore optimization; percent N increased at low elk density and then declined as elk density increased (Fig. 11). Those graminoids in high-NAPP communities exhibited a convex relationship in percent NDF (e.g., indigestible cell walls of plants), in which percent NDF declined slightly at low densities of elk and then increased with increasing elk density (Fig. 11). Thus, graminoids in high-NAPP communities increased in quality (percent N) at low densities of elk and then decreased in digestible components (percent N) at low density and exhibited lower quality (percent NDF) as population density and, concordantly, elk herbivory increased (Fig. 11). Forbs in low-NAPP communities exhibited a parabolic relationship with digestibility (percent IVDMD); at low density forbs were more digestible than those at higher densities in low-NAPP communities (Fig. 11). Although most regressions examining forage quality with increasing elk density were not significant (Table 3), graminoids in high-NAPP communities (percent N) and forbs in low-NAPP communities (percent IVDMD) exhibited a parabolic relationship in forage quality with increasing elk density and consequently responses were consistent with the herbivore-optimization hypothesis (Table 3, Fig. 11).

Plant Species Composition and Soil Processes

We estimated species composition within and outside exclosures in each of the 4 plant communities (Stewart [2004] provides lists of plant species). We observed no relationship between plant species diversity (Shannon–Weiner index) and population density of elk in high- ($\hat{Y} = 15.54 + 0.01x + 0.001x^2, R_a^2 = 0, P = 0.393$) or low- ($\hat{Y} = 10.24 + 0.05x + 0.000006x^2, R_a^2 = 0, P = 0.717$) NAPP communities. Likewise, we observed no significant relationships in high- ($\hat{Y} = 0.97 - 0.004x + 0.00007x^2, R_a^2 = 0.014, P = 0.302$) or low- ($\hat{Y} = 0.58 + 0.007x - 0.0002x^2, R_a^2 = -0.06, P = 0.815$) NAPP plant communities between probabilities from Morisita's Index of Similarity based on functional groups of plants inside versus outside exclosures with variation in population density of elk. Results from Morisita's Index indicate little change in species composition of plants with herbivore density in either high- ($\bar{X} = 0.96, SE = 0.010, n = 36$) or low- ($\bar{X} = 0.61, SE = 0.07, n = 30$; no data for xeric grasslands in 1999) NAPP communities.

We estimated soil respiration and N mineralization for exclosures, low-density, and high-density treatments in high- and low-NAPP plant communities (Table 4). No relationship existed between population density of elk and potential rates of soil respiration ($R_a^2 = -0.016, P = 0.952$) for all plant communities or when they were combined into high- ($R_a^2 = -0.032, P = 0.952$) or low- ($R_a^2 = -0.029, P = 0.833$) NAPP areas. Similarly, N mineralization exhibited no detectable relationship with elk population density ($R_a^2 = 0.004, P = 0.294$) for all plant communities combined or for those in high- ($R_a^2 = -0.017, P = 0.585$) or low- ($R_a^2 = 0.018, P = 0.224$) NAPP communities. The hypothesis that nutrient cycling would

Table 2. Results of regressions to examine annual and seasonal net aboveground primary production (NAPP, \hat{Y}) versus population density (x) of elk on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Plant communities were divided into those with high NAPP (mesic and logged forest) and low NAPP (xeric forest and grasslands) based on analysis of variance.

NAPP	Equation	R _a ²	P value
Annual			
High NAPP communities			
All functional groups	$\hat{Y} = 1.79 + 0.14x - 0.003x^2$	0.143	0.002
Forbs	$\hat{Y} = 0.26 + 0.03x - 0.002x^2$	0.100	0.010
Graminoids	$\hat{Y} = 0.35 + 0.09x - 0.002x^2$	0.174	<0.001
Shrubs	$\hat{Y} = 0.58 + 0.02x - 0.0004x^2$	0.013	0.647
Low NAPP communities			
All functional groups	$\hat{Y} = -0.13 + 0.04x - 0.002x^2$	0.037	0.115
Spring			
High NAPP communities			
All functional groups	$\hat{Y} = 1.32 + 0.28x - 0.011x^2$	0.267	<0.001
Forbs	$\hat{Y} = 0.43 + 0.11x - 0.004x^2$	0.229	<0.001
Graminoids	$\hat{Y} = 0.46 + 0.10x - 0.003x^2$	0.132	0.003
Shrubs	$\hat{Y} = 0.43 + 0.07x - 0.003x^2$	0.136	0.002
Low NAPP communities			
All functional groups	$\hat{Y} = 0.116 + 0.083x - 0.005x^2$	0.032	0.134
Summer			
High NAPP communities			
All functional groups	$\hat{Y} = -0.076 - 0.152s + 0.007x^2$	0.034	0.112
Low NAPP communities			
All functional groups	$\hat{Y} = -0.313 - 0.019x + 0.001x^2$	-0.027	0.865

exhibit a herbivore-optimization response in this ecosystem was rejected.

DISCUSSION

Elk Density, NAPP, and Forage Quality

Net aboveground primary production and apparent offtake of plants increased at low to intermediate levels of herbivory and then

declined with increasing levels of herbivory in high-NAPP communities, which supported the herbivore optimization hypothesis. At low levels of herbivory, removal of vegetation by herbivores increased outside the exclosures with increasing NAPP. Conversely, at high population densities, offtake by elk declined as forage availability decreased, because less forage was available for removal even though more elk were present. These results are consistent with a reduction in physical condition and pregnancy rates for these elk at high density (Stewart et al. 2005).

When our experiment began in 1999, animals moved between study areas after a gate was left open. Thus, the first year of our experiment resulted in moderate densities in both study areas: west = 6.6 elk/km² and east = 10.8 elk/km². This incident fortuitously resulted in our obtaining a broader range of elk densities to examine among years, rather than a clear high- and low-density comparison throughout the study (Stewart et al. 2005). Nonetheless, we observed very high and low densities of elk at our enclosure sites and observed strong changes in NAPP in response to herbivory.

Some values of productivity in both high- and low-NAPP plant communities had negative values, although these occurred primarily in low-NAPP communities (Figs. 7, 8), where measured effects of herbivory were nil. We included negative estimates of NAPP because eliminating them would overestimate NAPP (Person et al. 1998). Those negative values might have resulted from sampling error as well as temporal changes in plant phenology within functional groups, which changed rapidly in low-NAPP communities.

We observed changes in forage quality that also were consistent with the hypothesis of herbivore optimization. Graminoids in high-NAPP habitats and forbs in low-NAPP habitats exhibited a parabolic relationship with percent N (graminoids) and percent IVDMD (forbs) indicating that some forages increased in quality at low to moderate densities of elk even in low-NAPP communities

Figure 7. Results of regression analysis examining net aboveground primary production (NAPP) for all functional groups of plants versus cumulative population density of North American elk for spring (May–Jun) as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Habitats were divided into high NAPP (mesic and logged forests) and low NAPP (xeric forest and grasslands) based on analysis of variance ($P < 0.001$). No herbivory was measured inside exclosures, low-density treatment was west study area (4.1 elk/km²) and high-density treatment was east study area (20.1 elk/km²). Regression was significant for all functional groups ($\hat{Y} = 1.32 + 0.28x - 0.01x^2$).

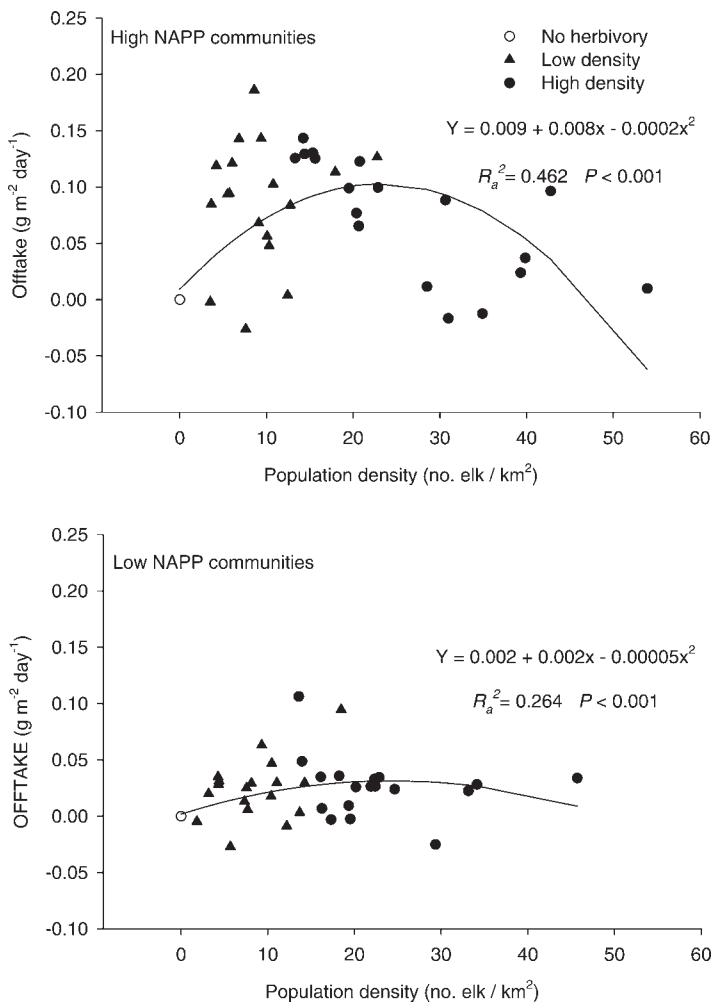
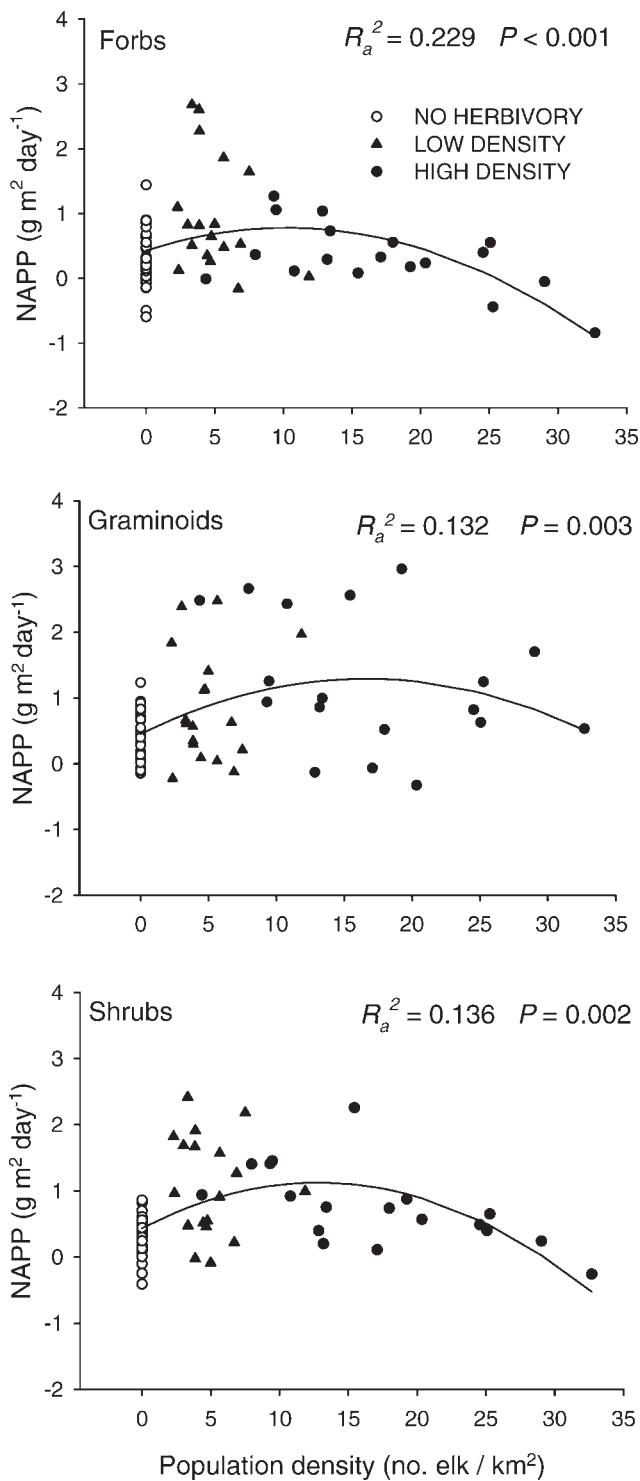


Figure 9. Results of regression analysis examining rates of apparent offtake versus cumulative population density of elk (May–Sep) as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Plant communities were divided into high net aboveground primary production (NAPP; mesic and logged forests) and low NAPP (xeric forest and grasslands) based on analysis of variance. No herbivory was measured inside exclosures; the low-density treatment was the west study area ($4.1 \text{ elk}/\text{km}^2$), and high-density treatment was east study area ($20.1 \text{ elk}/\text{km}^2$). Note: point representing zero apparent offtake by large herbivores represents 36 samples each for good and poor quality habitats.

(Fig. 11). Indigestible components of graminoids (percent NDF), cellulose, some hemicellulose, and lignin in high-NAPP communities exhibited the opposite response, and the indigestible components of graminoids were lowest when quality (percent N) was highest (Fig. 11). As the quality of forage increased, the fiber or indigestible portions declined and then increased with elk herbivory as forage quality declined. Thus, both digestible and indigestible components of plants were complementary and supported the hypothesis of herbivore optimization, in which forage quality was highest with low levels of herbivory by elk.

Changes in NAPP that we observed were not likely a result of differences in species composition within plant communities because we failed to observe changes in plant species diversity with changing elk density. In addition, we observed no changes in Morisita's Index of Similarity between grazing treatments and

Figure 8. Results of regression analysis examining net aboveground primary production (NAPP) by functional groups of plants versus cumulative population density of North American elk for spring (May–Jun) as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Habitats were divided into high NAPP (mesic and logged forest) and low NAPP (xeric forest and grasslands) based on analysis of variance. No herbivory is measured inside herbivory exclosures; low-density treatment was west study area ($4.1 \text{ elk}/\text{km}^2$) and high-density treatment was east study area ($20.1 \text{ elk}/\text{km}^2$). Regressions were significant for forbs ($\hat{Y} = 0.43 + 0.11x - 0.004x^2$), graminoids ($\hat{Y} = 0.46 + 0.10x - 0.003x^2$), and shrubs ($\hat{Y} = 0.43 + 0.07x - 0.003x^2$).

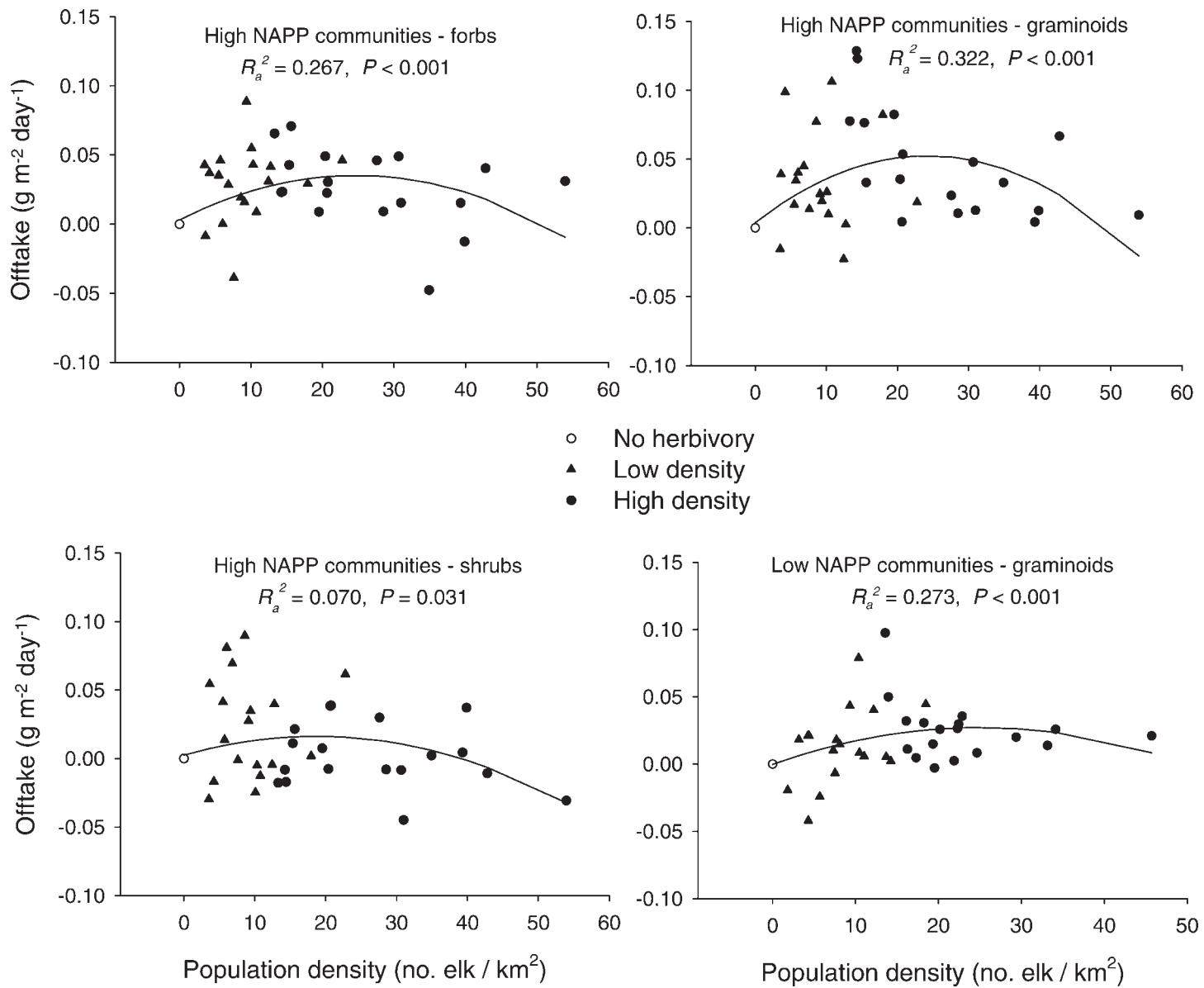


Figure 10. Results of regression analysis examining rates of apparent offtake by functional groups of plants versus cumulative population density of elk (May–Sep) as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Habitats were divided into high net aboveground primary production (NAPP; mesic and logged forest) and low NAPP (xeric forest and grasslands) based on analysis of variance. No herbivory is measured inside herbivory exclosures; low-density treatment was west study area (4.1 elk/km²) and high-density treatment was east study area (20.1 elk/km²). Regressions were significant for forbs ($\hat{Y} = 0.003 + 0.002x - 0.00005x^2$), graminoids ($\hat{Y} = 0.004 + 0.004x - 0.00008x^2$), and shrubs ($\hat{Y} = 0.003 + 0.001 - 0.00004x^2$) in high NAPP plant communities and for graminoids ($\hat{Y} = -0.0003 + 0.002x - 0.00004x^2$) in low NAPP communities. Note: point representing zero apparent offtake by large herbivores represents 36 samples each for high and low NAPP plant communities.

exclosures in response to population density of elk. The Blue Mountains in eastern Oregon have an extensive history of grazing by high-density populations of native and domestic herbivores (Skovlin 1991). The extensive grazing history on Starkey likely reduced the number of plant species that were sensitive to foraging by large herbivores. Those plants remaining on the study area probably were tolerant to foraging by elk and possessed defenses to reduce herbivory; such defenses, however, do not guarantee reduced consumption because of the complex nature of plant-animal interactions (Belovsky and Schmitz 1994). Fuhlendorf et al. (2001) reported that herbivory established long-term directions of plant composition and structure, and that over time, grazing

exerted a continuous selective influence on individual plant species or functional groups. Thus, plant communities on Starkey likely were resistant to changes in species composition from herbivory because most sensitive plant species ostensibly were removed previously from that ecosystem. Nonetheless, we cannot rule out the possibility that plant species composition might change over longer periods (>3 yr) or that there were changes in rare plant species that we failed to detect. Increased prevalence of grazing-sensitive species might result from maintaining long-term exclosures or low densities of large herbivores, provided that root stock or seed banks remained viable in the soil (Putman et al. 1989, Riggs et al. 2000, Coomes et al. 2003).

Table 3. Results of regressions to examine forage quality (\hat{Y}), percent neutral detergent fiber (%NDF), nitrogen (%N), and in vitro dry matter disappearance (%IVDMD) versus population density (x) of elk on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Plant communities were divided into those with high net aboveground primary production (NAPP; mesic and logged forests) and low NAPP (xeric forest and grasslands) based on analysis of variance ($P < 0.001$). We did not have an a priori reason to test for a curvilinear relationship between forage quality and population density of elk for our forage quality analyses; therefore we have provided both the linear and quadratic regression equations.

Variable	Equation	R ²	P value
High NAPP communities			
Forbs			
%NDF	$\hat{Y} = 35.51 + 0.14x - 0.004x^2$	0.073	0.074
%N	$\hat{Y} = 1.64 + 0.007x - 0.0002x^2$	0.015	0.599
%IVDMD	$\hat{Y} = 69.21 - 0.14x + 0.005x^2$	0.060	0.117
Graminoids			
%NDF	$\hat{Y} = 61.31 - 0.09x + 0.004x^2$	0.097	0.030
%N	$\hat{Y} = 1.18 + 0.008x - 0.0002x^2$	0.093	0.035
%IVDMD	$\hat{Y} = 63.97 + 0.14x - 0.006x^2$	0.044	0.211
Shrubs			
%NDF	$\hat{Y} = 41.31 + 0.05x - 0.002x^2$	0.004	0.870
%N	$\hat{Y} = 1.20 + 0.01x - 0.0002x^2$	0.027	0.406
%IVDMD	$\hat{Y} = 59.13 + 0.04x - 0.002x^2$	0.006	0.823
Low NAPP communities			
Forbs			
%NDF	$\hat{Y} = 43.07 - 0.17x + 0.006x^2$	0.056	0.202
%N	$\hat{Y} = 1.19 + 0.02x - 0.003x^2$	0.099	0.054
%IVDMD	$\hat{Y} = 61.48 + 0.55x - 0.02x^2$	0.107	0.043
Graminoids			
%NDF	$\hat{Y} = 61.57 - 0.04x + 0.001x^2$	0.006	0.839
%N	$\hat{Y} = 1.08 + 0.01x - 0.0002x^2$	0.047	0.227
%IVDMD	$\hat{Y} = 64.21 + 0.14x - 0.002x^2$	0.026	0.444
Shrubs			
%NDF	$\hat{Y} = 40.01 + 0.35x - 0.01x^2$	0.143	0.583
%N	$\hat{Y} = 1.00 - 0.01x + 0.0004x^2$	0.308	0.276
%IVDMD	$\hat{Y} = 52.05 - 1.12x + 0.04x^2$	0.234	0.394

Some of the best examples of increasing NAPP and herbivore optimization with intermediate levels of herbivory occurred in ecosystems that supported high densities of highly migratory herbivores, which concentrate for relatively short time periods in localized areas, such as grasslands in African and North America (McNaughton 1979, 1985; Huntly 1991; Frank and McNaughton 1992; Frank and Groffman 1998) or subarctic salt marshes (Hik and Jefferies 1990), where graminoids were modified to prostrate, rapidly growing forms that were more nutritious and resilient to herbivory (McNaughton 1979, 1983; Day and Detling 1990; Hik and Jefferies 1990; Person et al. 2003). In those ecosystems that support large numbers of herbivores, increases in NAPP appear to occur with deposition of urine and feces that increase cycling of nutrients, particularly N (Ruess and McNaughton 1987, Hik and Jefferies 1990, Frank and Groffman 1998, Augustine and Frank 2001). Generally, NAPP in ecosystems dominated by graminoids is limited by N (Vitousek and Howarth 1991), which is a major determinate of plant-species composition (Frank and Groffman 1998). Indeed, feces from reindeer brought about shifts from mosses to grasses via effects on below-ground processes in a tundra ecosystem (Olofsson et al. 2004, van der Wal et al. 2004). Inputs of urine and feces could double available N and allow for increased between-site variation in productivity and species composition (Frank and McNaughton 1992, Frank and Groffman

1998). Although elk density varied across our study sites, these herbivores were distributed throughout the study areas and did not strongly concentrate in any localized areas. Thus, deposits of urine and feces were scattered throughout the study area and probably were not sufficiently concentrated so that we could detect concomitant increases in N cycling.

Stimulation of NAPP is not restricted to graminoid-dominated systems. African browsers stimulated shoot production and enhanced browse quality of *Acacia* species near watering holes (du Toit et al. 1990), and moose (*Alces alces*) in interior Alaska increased rates of N cycling and NAPP in a willow- (*Salix* spp.) dominated system (Molvar et al. 1993). Indeed, regrowth of previously browsed leaves and twigs typically is greater than on unbrowsed plants and herbivores selectively forage on regrowth from browsed twigs (Molvar et al. 1993, Bowyer and Bowyer 1997, Bergquist et al. 2001, Bowyer and Neville 2003). Large herbivores tend to return to areas where they have foraged previously (Fryxell 1991), offering opportunities for increased nutrient cycling.

Net aboveground primary production of forbs, shrubs, and graminoids increased at low to moderate population densities of elk in a forested ecosystem on Starkey. Indeed, we observed that increases in NAPP in response to intermediate levels of foraging occurred at lower levels of herbivory than exhibited in ecosystems dominated by graminoids. Most populations of moose in interior Alaska are held at relatively low population densities by predation (Gasaway et al. 1992, Bowyer et al. 1998), which likely prevents heavy browsing and allows for positive feedbacks in stimulating production of willows and cycling of N in areas where moose concentrate foraging (Molvar et al. 1993). Conversely, heavy browsing by high-population density of moose on the Tanana River floodplain of interior Alaska resulted in reduced aboveground and fine root growth and lower fine-root longevity (Kielland et al. 1997, Ruess et al. 1998).

One characteristic of those studies documenting increases in production or nutrient cycling are that those populations tend to be highly migratory and concentrated in relatively localized areas (McNaughton 1979, Hik and Jefferies 1990, Frank and Groffman 1998, Person et al. 2003, Jefferies et al. 2004). Grazing lawns in subarctic salt marshes are maintained by migratory populations of geese that generally are not in residence for extended periods. Grazing lawns used by ungulates on the Serengeti are maintained by both resident and highly migratory ungulates, although the migratory species likely had the greatest effects on vegetation (McNaughton 1985). Nonetheless, following the end of the wet season, when grasses dried out, those ungulates switched their diets to other graminoid species (McNaughton 1985). Although they do not produce grazing lawns, elk in Yellowstone are also migratory and tend to be concentrated in areas that allow for increased deposition of urine and feces (Houston 1982). Stimulation of N-cycling by moose in Alaska occurred in areas where herbivores were concentrated in relatively localized areas (Molvar et al. 1993).

Positive feedbacks associated with herbivory appear to be limited to populations at relatively low densities, as we observed at Starkey, and Molvar et al. (1993) observed in Alaska, or are highly migratory and concentrate foraging for short intervals and transfer

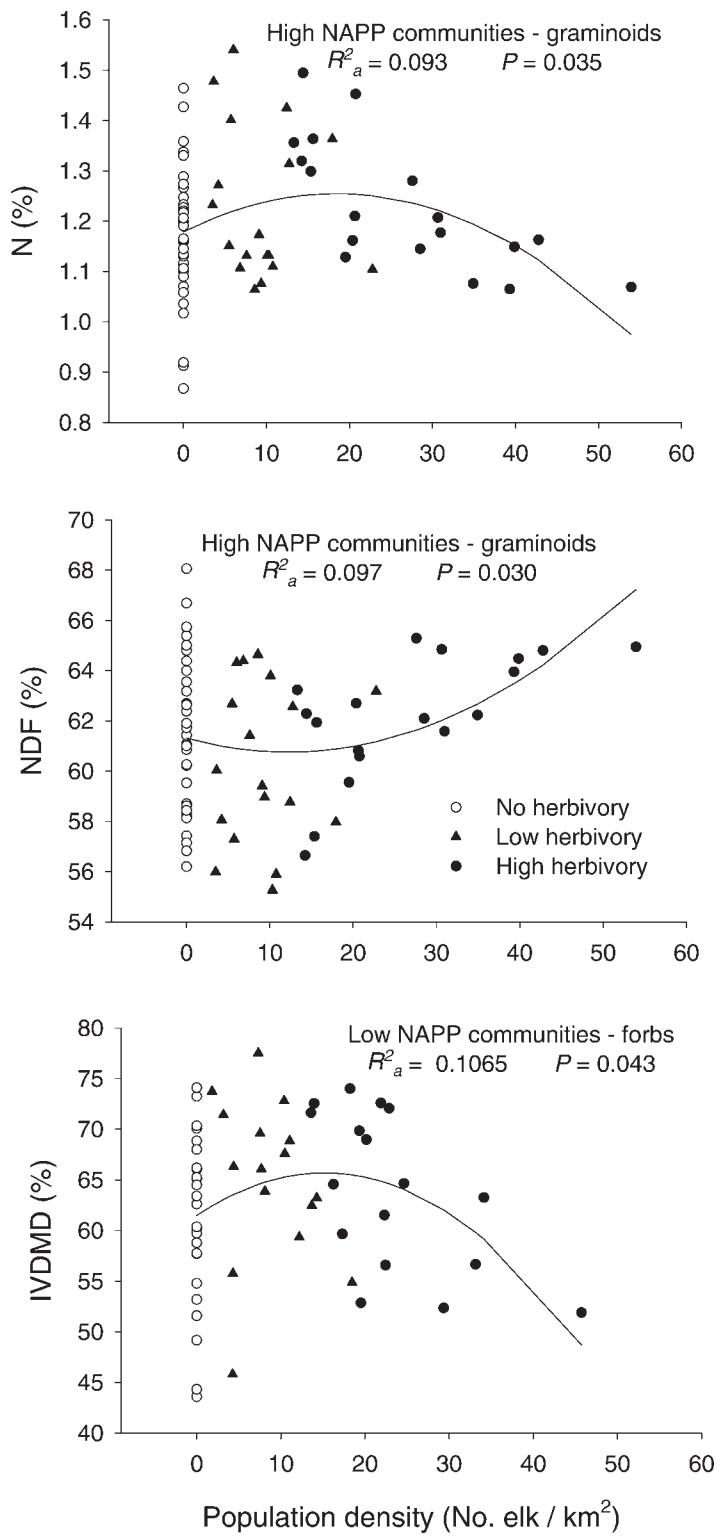


Figure 11. Results of regression analysis examining changes in plant quality versus population density of elk as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001. Habitats were divided into high net aboveground primary production (NAPP; mesic and logged forests) and low NAPP (xeric forest and grasslands) based on analysis of variance ($P < 0.001$). No herbivory was measured inside herbivory exclosures; low-density treatment was west study area (4.1 elk/km²) and high-density treatment was east study area (20.1 elk/km²). Regressions were significant in high NAPP communities for percent N ($\hat{Y} = 1.18 + 0.008x - 0.0002x^2$) and percent neutral detergent fiber (NDF; cell wall contents [e.g., cellulose, hemicellulose, and lignin]) content of graminoids ($\hat{Y} =$

nutrients via feces and urine from other areas (McNaughton 1979, Hik and Jefferies 1990). Conversely, foraging by moose at high density over long periods of time on Isle Royale, Michigan, resulted in strong negative feedbacks on nutrient cycling and changes in plant species composition (Pastor et al. 1993), an outcome consistent with herbivore optimization at high levels of herbivory (Fig. 1). Lesser snow geese in Canada have increased in population density and grazing intensity to the extent that the habitat is being degraded and density-dependence processes are evident (Jefferies and Rockwell 2002, Jefferies et al. 2004), a result that we also obtained for high densities of elk on Starkey (Figs. 7–11, Stewart et al. 2005).

Soil Processes

We observed no differences in N mineralization across intensities of grazing, although the lack of observable changes does not preclude the possibility of some enhancement following deposition of urine and feces by elk. Changes in N cycling might have occurred in very small patches that we did not sample. Augustine and Frank (2001) noted very fine-grained variability in soil N and N-mineralization potential in grazed grasslands compared with ungrazed areas that exhibited no spatial structure in properties of soil N. Moreover, many of the plant species on Starkey fix N, which might have made changes in nutrient cycling difficult to detect. Binkley et al. (2003) likewise failed to find N enhancement in soil resulting from grazing and other activities by elk. Stimulation of NAPP without detectable increases in N cycling might occur if plants increase aboveground production at the expense of belowground production, thereby losing root biomass as shoot tissues are enhanced (Belsky 1986). We did not measure belowground biomass of plants, because foraging by elk occurs aboveground and large herbivores do not respond directly to belowground biomass. The link between foraging decisions made by large herbivores and changes in belowground biomass is in need of additional research.

Herbivore optimization might occur in numerous ecosystems, although probably at low population densities of herbivores and with small increases in NAPP that are difficult to detect. Only 17% of 236 studies that examined changes in NAPP in response to herbivory showed elevated NAPP in grazed areas relative to ungrazed sites (Milchunas and Lauenroth 1993). Many of the studies reviewed by Milchunas and Lauenroth (1993), however, examined effects of domestic herbivores—livestock grazing tends to be more intense and spatially constant than grazing by native herbivores (Hobbs 1996). Net aboveground primary production is predicted to occur at moderate levels of herbivory and studies of foraging by domestic herbivores might underestimate the prevalence of compensatory responses by plants (Hobbs 1996). The wide range of grazing intensities that we observed allowed us to detect those relatively subtle changes in NAPP in response to foraging by large herbivores, at least for high NAPP communities. Most studies that reported increases in NAPP in response to herbivory have been limited to areas with high nutrient and moisture availability (McNaughton 1979, 1985); the lack of a



61.3 – 0.09x + 0.004x²), and for in vitro dry matter digestibility of forbs in low NAPP plant communities ($\hat{Y} = 61.48 + 0.55x - 0.02x^2$).

Table 4. Descriptive statistics for soil data and treatments of no herbivory (inside exclosures), low-density treatment (west study area), and high-density treatment (east study area) by plant communities of high net aboveground primary production (NAPP; mesic and logged forests) and low NAPP (xeric forest and grasslands) on the Starkey Experimental Forest and Range, Oregon, USA, 1999–2001.

Soil variables	Population density								
	No herbivory			Low density (4.1 elk/km ²)			High density (20.1 elk/km ²)		
	n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE
High NAPP communities									
Soil respiration ($\mu\text{mol CO}_2/\text{g/day}$)	24	1.12	0.113	18	1.32	0.068	18	1.12	0.146
N mineralization ($\mu\text{g N/g/day}$)	23	0.23	0.494	15	0.15	0.069	18	0.28	0.057
Low NAPP communities									
Soil respiration ($\mu\text{mol CO}_2/\text{g/day}$)	24	1.19	0.133	18	1.09	0.127	18	1.14	0.150
N mineralization ($\mu\text{g N/g/day}$)	24	0.29	0.080	18	0.15	0.085	17	0.13	0.055

pronounced increase in NAPP in xeric forests or grassland (low-NAPP communities) is consistent with other studies in which herbivore optimization was not documented (Painter and Belsky 1993). Nonetheless, we observed changes in apparent offtake of all functional groups of plants and quality of forbs (percent IVDMD) in low-NAPP communities consistent with herbivore optimization, and we suspect that optimization of NAPP occurred in those areas but at low levels that we were unable to detect. Although we report high-population densities of elk across our enclosure sites, our density estimates reflect the cumulative density of elk over a season (e.g., spring or summer) or another time interval (May–Sep). Nevertheless, stimulation of NAPP occurred at low to moderate levels of herbivory and declined as population density increased, supporting the hypothesis of herbivore optimization in high-NAPP areas.

Linking NAPP with Density Dependence in Elk

Decreases in NAPP and forage quality that we observed at high population densities corresponded with density-dependent reductions in physical condition and reproduction of female elk in the high-density treatment (Stewart et al. 2005). Concurrent with this study, Stewart et al. (2005) examined physical condition and reproduction in elk in both study areas; females in the low density treatment (west study area) were in better physical condition and had higher pregnancy rates than those in the high density treatment (east study area). Such density-dependent responses are well documented for larger mammals (McCullough 1979, Fowler 1981, Skoglund 1985, Kie et al. 2003). Thus, stimulation of NAPP in areas with low levels of herbivory and low population density of elk on Starkey resulted in forage of better quality and increased reproduction and physical condition of female elk in those areas. In addition, females in the areas of decreased NAPP were in poorer physical condition and exhibited lower reproduction than those females in areas of increased NAPP. Declines in physical condition of maternal females also reduce survivorship of young (Singer et al. 1997, Keech et al. 2000). As we increased population density beyond moderate levels, NAPP and forage quality were reduced, and elk likely were forced to use less abundant and low-quality forage as those younger, actively growing shoots became less available. Conversely, in our low-density treatment, NAPP and forage quality of grazed plots were greater than areas without herbivory (e.g., inside permanent exclosures); elk were in better physical condition and exhibited

enhanced reproduction (Stewart et al. 2005). Thus, effects of herbivory on NAPP are strongly associated with density-dependent feedbacks to population dynamics of large herbivores and those processes should not be considered independently. Density-independent processes, such as rainfall and nutrient availability, also must be considered because enhancement of NAPP also is dependent upon high nutrient and moisture availability (Belsky 1986).

Although we did not observe changes in species composition, maintenance of high population densities of large herbivores often leads to reduction in palatable forages and increases in poor-quality forage over an extended time period. Indeed, we observed a parabolic effect of elk herbivory on plant quality and increases of less digestible forages with increases in population density. Herbivory from high-density populations of resident moose on Isle Royale, Michigan, changed successional pathways from deciduous species of willow, aspen (*Populus* spp.), and birch (*Betula* sp.) that were highly palatable and good-quality forage to forest composition dominated by poor-quality forage for large herbivores (Risenhoover and Maass 1987, Pastor et al. 1993, Pastor and Cohen 1997). Likewise, grazing by high densities of lesser snow geese in La Perouse Bay, Manitoba, Canada, produced a top-down cascade in the ecosystem that led to destruction of salt-marsh grazing lawns and exposure of intertidal sediments, resulting in reduced forage availability for geese (Jefferies 1988, Jefferies et al. 2004). Conversely, increases in mass of juvenile black brant (*Branta bernicla nigricans*) coincided with increases in surface area of grazing lawns in southwestern Alaska, where foraging by geese led to increases in the distribution of highly preferred grazing lawns (Person et al. 2003). Removing the effects of grazing altered the species composition and standing crop of plants in a salt-marsh community (Bazely 1986). Thus, at low levels of herbivory, herbivores improve quality and quantity of available forage as we observed in areas with low population densities of elk on Starkey.

Sexual Segregation

We did not directly test hypotheses concerning sexual segregation in North American elk (sensu Bowyer 2004). The occurrence of sexual segregation is nearly ubiquitous among polygynous ruminants (Bowyer 2004) and our results indicated that male and female elk used the study area differently. Nevertheless, areas that received the greatest use by males

generally also received high use by females, but some spatial separation was obvious within seasons. Bowyer et al. (1996, 2002) and Bowyer and Kie (2006) cautioned that temporal and spatial scales needed to assess sexual segregation could be difficult to ascertain. We suspect that combining seasons likely masked some of the spatial separation or that dietary niche partitioning, especially at high density, allowed greater spatial overlap between sexes (sensu Kie and Bowyer 1999, Bowyer and Kie 2004).

We calculated density maps separately for each of the sexes to account for the greater number of females and differences in foraging between sexes (Barboza and Bowyer 2000, 2001; Spaeth et al. 2004). We overlaid and added our density maps, prior to using kriging to smooth data across the study area, because of the differential nature of habitat use and foraging strategies by males and females (Fig. 4). Thus, both sexes were included in our estimates of elk density across the study area and at each enclosure site (Fig. 5). These procedures are essential for determining herbivore density in species that sexually segregate and for testing hypotheses concerning herbivore optimization. In other systems where males and females exhibit strong spatial separation such as mountain sheep (*Ovis canadensis*) that occur on different mountain ranges (Bleich et al. 1997), optimization can be effected to a greater extent by one sex or the other. Indeed, we hypothesize that during periods of sexual segregation, the process of optimization, especially peak NAPP and forage quality, might be effected more by males in high-density populations because of their lower density than females, and by females in low-density populations because of their higher density than males—ideas that require future tests. Clearly, sexual segregation must be considered when examining effects of optimization on NAPP for large herbivores, something that has seldom occurred. Several authors have contended that the sexes of sexually dimorphic ruminants are so different that they should be treated as if they were different species (Kie and Bowyer 1999, Bowyer et al. 2001b, Stewart et al. 2003b, Bowyer 2004, Bowyer and Kie 2004). Results supporting this view have ramifications for habitat manipulations but perhaps also for understanding the role of large mammals in affecting ecosystem structure and function.

Detecting Herbivore Optimization

In general, studies conducted on herbivore optimization in areas where grazing lawns occur have the advantage of specific habitat patches that are readily identifiable and therefore easy to concentrate sampling activities, such as on African grasslands (McNaughton 1979) or subarctic salt marshes (Ruess et al. 1989, Hik and Jefferies 1990, Person et al. 2003). Identifying changes in productivity and nutrient cycling in response to herbivory on grazing lawns or graminoid-dominated ecosystems is relatively easy compared with areas that lack visible patches of habitat consistently modified by herbivores or when plants exhibit multiple growth forms. Positive effects of herbivores on NAPP also are difficult to detect when plant responses to herbivory are subtle and occur at relatively low to moderate intensities of grazing or where there is an abundance of N-fixing plants.

Large herbivores in general, and elk in particular, do not use habitats uniformly (Fretwell 1972, Hobbs 1996, Boyce 1999, Fryxell et al. 2004); our experimental design allowed us to account for habitat selection by those large herbivores while simulta-

neously examining effects of population density on forage classes within plant communities. Elk selected logged-forest habitat and slightly avoided mesic forest and xeric grasslands during periods when they were actively foraging (Stewart et al. 2002). This experimental approach, combined with an independent measure of elk density to evaluate intensity of herbivory, permitted us to detect those subtle changes in NAPP within plant communities in response to varying levels of herbivory.

Clearly, functional classes of plants other than graminoids exhibited herbivore optimization in high-NAPP areas, an outcome that often has been overlooked in studies of ecosystem structure and function. Moreover, coupling changes in NAPP, species composition, apparent offtake of forage, and nutrient cycling in response to herbivory with density-dependent processes allows us to better understand, and thereby conserve and manage ecosystems with populations of large herbivores that change in size over time. Indeed, effects of herbivore optimization that we observed (Figs. 7–11) were directly related to density-dependent process involving reproduction in elk (Stewart et al. 2005).

Correlates and Potential Consequences of Herbivore Optimization

We demonstrated herbivore optimization in a montane ecosystem by varying population density of large herbivores and observing concomitant changes in NAPP for several functional groups of plants including graminoids, forbs, and shrubs. Stimulation of NAPP can occur when herbivores are at low density and populations are experiencing rapid growth (i.e., the exponential portion of the sigmoidal growth curve). If a population that is rapidly expanding is provided with a boost of additional high-quality forage, we hypothesize that expansion likely would be accelerated, potentially causing the population to be sling-shot beyond carrying capacity (K). Although poorly understood, irruptions of large herbivores play an important role in their population dynamics (Forsyth and Caley 2006). Whether herbivore optimization is involved in population irruptions and overshoots of K (Leopold 1943; Klein 1968; McCullough 1979, 1997; Mysterud 2006) is unclear and requires additional investigation. Moreover, measures of physical condition and reproduction (sensu Kie et al. 2003) or range condition, where herbivores had increased NAPP of shrubs, might not directly or immediately reflect such an irruption. In addition, where plants have had a long history of grazing and browsing, changes in species composition might not be evident, as we demonstrated in our experiment.

Diversity of the plant community in the Blue Mountains was resilient to foraging by high densities of elk during the 3 years of our study. A similar outcome was reported by Metzger et al. (2005) for grazers on the short-grass plains of Africa. Nevertheless, herbivores can have important effects on other taxa we did not investigate. For instance, changes in invertebrate communities were brought about following foraging by high-densities of lesser snow geese (Jefferies et al. 2004) and large mammals (Rambo and Faeth 1999; Suominen et al. 1999a,b; Gomez and Gonzalez-Megias 2002; Miyashita et al. 2004; Mysterud et al. 2005). Likewise, high densities of large herbivores have had deleterious affects on birds (de Calesta 1994, McShea and Rappole 2000, Berger et al. 2001) and small mammals (Flowerdew and Ellwood

2001, Keesing and Crawford 2001). Reptiles also might be adversely affected by activities of ungulates (Beever and Brussard 2004). We do not know if those taxa responded to herbivore optimization in our high NAPP communities or whether high densities of elk adversely affected them. This is an important area for future research. Conservation issues related to effects of grazing intensity on biodiversity are likely to become increasingly important in the management of large herbivores (Mysterud 2006). We recommend that the modeling approach to population management for ungulates advocated by Weisberg et al. (2002) be extended to other taxa of animals that are influenced by herbivory.

We also caution that population density per se might not be as critical in understanding herbivore optimization as is population size in relation to K (Kie et al. 2003). Even relatively low densities of large herbivores would cause declines in NAPP as they approached the ability of the environment to sustain them. Although some grazing lawns (McNaughton 1979, 1985; Person et al. 2003) and other areas of increased primary productivity (Frank and Groffman 1998) have persisted though time, this ecological condition cannot represent an equilibrium between the density of resident large herbivores and their food supply. Positive feedbacks from more forage of higher quality inevitability would enhance physical condition and increase reproduction of large herbivores (Boyce 1999, Jefferies et al. 2004, Stewart et al. 2005), leading to rapid population growth. Such population growth would result in lower per capita availability and quality of forage to individual animals, and also would initiate reductions in NAPP, thereby producing a strong density-dependent decrease in reproductive output of large herbivores (Kie et al. 2003). Moreover, high densities of herbivores exhibiting density-dependent feedbacks drive successional changes leading to dominance of plant species of lower nutritional value (Pastor and Cohen 1997) or degradation of habitats (Jefferies et al. 2004). Those outcomes mean that factors other than density dependence and migratory life-history strategies must be involved in the maintenance of areas of higher productivity for large herbivores. Density-independent variables, such as rainfall and snow, might play a role in holding some animal populations below K , especially for species that do not exhibit strong density dependence or experience extreme environments. Such factors probably are less important for large herbivores that are better buffered against environmental extremes than smaller-bodied species (Kie et al. 2003). Indeed, precipitation had remarkably little effect on reproduction in elk compared with effects of population density on our study areas (Stewart et al. 2005). Thus, calibrating the density of the herbivore population with respect to K might not only be necessary for managing populations of those mammals (Kie et al. 2003), but also for understanding their effects on ecosystem dynamics, and ultimately biodiversity (Bowyer et al. 2005).

We hypothesize that in addition to migration, predation also could play an important role in herbivore optimization where productive areas are maintained through time by herbivory. Again, some process other than density-dependent feedbacks on reproduction near K must help limit or regulate populations of large herbivores if optimization is to be maintained and a decline in NAPP with increasing densities avoided (Figs. 1, 8, 9). In

ecosystems where large herbivores are naturally regulated, it is unlikely that elevated NAPP is maintained (i.e., herbivores would most likely be on the negative slope of the optimization curve), with possible exceptions of those extremely fertile areas such as Serengeti grasslands. Indeed, this observation might be one of the reasons that herbivore optimization is so difficult to detect in most ecosystems. Such outcomes hold implications for control of predators to enhance prey populations and perhaps the ecosystem processes that support assemblages of large herbivores and the carnivores that prey upon them. Many ecosystems where herbivore optimization and the associated areas of increased primary productivity were described included predator-rich environments (McNaughton 1979, 1983; Molvar et al. 1993; Frank and Groffman 1998). Certainly, predators are capable of influencing sociality in ungulates (Hirth 1977, Berger 1991, Bowyer et al. 2001a), and social gatherings of these large herbivores might have a greater propensity to concentrate feeding activities or urine and feces in particular habitats as a result of predation risk (Molvar and Bowyer 1994, Frank and Groffman 1998, Kie 1999, Bowyer et al. 2001a). Large carnivores recently have been proposed as a contributing factor to maintaining biodiversity through their interactions with large herbivores and the potential for mediating ecological cascades (Bowyer et al. 2005). Indeed, very high population density of herbivores without a concordant increase in predation leads to habitat degradation and trophic cascades (Terborgh et al. 2001, Jefferies et al. 2004, Hebblewhite et al. 2005). If this line of reasoning is correct, then habitat manipulations to enhance or maintain grazing lawns might be ineffective in the absence of high levels of predation, harvest, or other sources of mortality. These unique ecosystem linkages between herbivores and plant species they rely on via the process of herbivore optimization could be more complex than previously suspected, and could require the management of multiple trophic levels for their maintenance.

MANAGEMENT IMPLICATIONS

We demonstrate herbivore optimization in a montane ecosystem at relatively low population densities of elk and correspondingly low levels of herbivory. Most populations of native herbivores that are either naturally regulated by density-dependent processes or regulated by harvest are maintained at much higher population densities than those at which we observed this positive response in NAPP. At higher densities of elk and levels of herbivory, NAPP and forage quality were reduced. Moreover, we only observed a positive response in plant communities that were highly productive, had deeper and more fertile soils, and with ample moisture regimes. Those communities with less fertile soils and lower water-holding capacities did not show pronounced changes in NAPP even at low levels of herbivory. We did not observe positive responses of plants to herbivory during summer when moisture became somewhat limiting in all plant communities.

Grazing optimization has been adopted by some grazing advocates to justify heavy grazing on public and private lands (Painter and Belsky 1993). We advise caution when managing populations of ungulates on montane rangelands in the western United States. Plant communities with lower soil nitrogen and without ample moisture might not exhibit a response consistent

with herbivore optimization at even low levels of herbivory. Our results do not support stocking large densities of ungulates in montane communities, but precisely the opposite. Our results indicate the need to maintain low densities of herbivores if optimizing plant production, forage quality, or maximizing body condition and reproduction of ungulates are the goals.

SUMMARY

We document herbivore optimization in a montane ecosystem. We observed responses of plants consistent with herbivore optimization in response to changing population density of elk in all functional groups of plants including forbs, graminoids, and shrubs. The NAPP and apparent offtake followed an herbivore optimization curve in communities with high NAPP (mesic and logged forests) but that pattern was not pronounced in xeric communities with low NAPP (xeric forest and grasslands). Changes in forage quality in response to herbivory by elk were consistent with predictions from herbivore optimization. We observed no changes in species composition of plants. We did not document changes in soil respiration or N mineralization with changes in population density of elk. Herbivore optimization is likely to occur in ecosystems with ample soil moisture and nutrient availability with low densities of herbivores or in areas where nutrients are transferred into ecosystems via deposition of urine

and feces. We recommend maintaining low to moderate densities of large herbivores in ecosystems if goals are to optimize NAPP and forage quality or to maximize body condition and reproduction of ungulates.

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