

Ecology of Native Ungulates in the Jackson Valley

Habitat selection, interactions with domestic livestock, and effects of herbivory on grassland and willow communities

Final Report

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Executive Summaries

Part I: Native Ungulates in the Jackson Valley: Elk, Bison, and Moose Habitat Selection, Herbivory, and Interactions with Domestic Cattle

Management of native ungulates in the Jackson Valley, Wyoming, presents a number of unique challenges. The winter range lies on a complex of administrative land areas with a wide diversity of management goals and philosophies, including the National Elk Refuge (NER), Grand Teton National Park (GTNP), and Bridger-Teton National Forest (BTNF). Ungulate management needs on these lands vary from the highest priority to the lowest priority for the land unit. The NER was established in 1912 as a winter range for Jackson Valley elk in response to high winter mortality caused by loss of critical winter range and market hunting. Artificial feeding of the elk was instituted on the NER to mitigate losses of elk winter range habitat to settlement and ranching in the Jackson Hole area, and to alleviate conflicts with ranchers over elk depredation of their livestock feed. Elk are also fed at a number of additional feedgrounds operated by the state of Wyoming in the Gros Ventre River drainage. The Jackson elk herd is currently estimated to number about 15,680 animals, or about 42% over goals set by the state of Wyoming. Additionally, a herd of ~650 accidentally reintroduced bison has been increasing rapidly over the last 35 years, and now winters almost exclusively on the NER feedgrounds. Human developments and habitat alterations, artificial feeding, and high incidence of brucellosis in elk and bison complicate management of free-ranging ungulates in the Jackson Valley. An interagency effort by resource managers in the Jackson Valley is re-evaluating management of elk and bison with the goal of developing a new management plan for both species.

We evaluated herbivory, distributions, and interaction of ungulates in the Jackson Valley, 1996-2001. We studied the effects of native ungulates on grasslands; their partitioning of use of available habitats; and their interactions with domestic livestock that graze this range in the summer. We evaluated habitat selection by three major ungulate species (elk, bison, and moose) in the Jackson Valley, based on observed animal locations. We used best model selection criteria to determine which of eight habitat variables were most important in estimating habitat preference by each species, and applied these best models to the Jackson Valley winter range. We collected information from 1996-2002 on current forage production in habitats used by wintering elk and bison as well as current levels of consumption, or offtake, of that production by wild ungulates. We evaluated effects of grazing by comparing productivity, species diversity, and amount of bare ground inside and outside of several long-term grazing exclosures. Finally, we observed the distribution of wild ungulates in response to grazing domestic livestock and estimated the impacts of grazing domestic cattle on available winter forage base, particularly under drought conditions.

Based on best model selection criteria, we determined that in an average winter, approximately 30% (689 km²) of the 2268 km² ungulate winter range (defined by ungulate distribution as areas \leq 2600 m elevation) was suitable¹ bison habitat, 17% (383 km²) was suitable elk habitat, and 10% (234 km²) was suitable moose habitat. Pronghorn antelope and mule deer habitat selections were not modeled. Overlap in areas of high probability of use by all three common species was not great, even during severe winter conditions. Thirty-one percent of the combined ungulate winter

¹ Suitable is defined as habitats with >50% probability of use by one of the ungulate species.

range was suitable for at least one of the three species of ungulates during severe winters, 5% of the winter range was highly suitable for at least two ungulate species, and <1% was highly suitable for all three species. There was no substantial overlap in preferred winter habitats of elk and bison (when the influence of artificial feeding is removed). A substantial amount of preferred winter habitat for bison in GTNP is not currently being used, due to the availability of feed on the NER and the concentration of bison on the feed.

We found no consistent reduction in total annual production due to grazing, but instead a general tendency toward increased production on grazed sites (10 of 13 comparisons). We concluded there was compensation due to grazing--apparently grazing optimization was occurring in Jackson Valley grasslands. Grazing offtake ranged from moderately high to very high across Valley grasslands (50-60% on native grasslands, 65-90% on managed grasslands). We found few negative influences of grazing on herbaceous species diversity and very minor effects on shrub species diversity. However, we did find significantly greater (nearly 4x more) percentage of bare ground and slightly higher cover of exotic plant species in grazed areas.

Domestic cattle, elk, and bison made substantial co-use of the same managed pastures and native grasslands in summer, resulting in very high use levels (>70%) on these pastures. Elk and bison moved off of the grazed areas during the period of use by cattle, but they used these areas immediately prior to, and immediately after cattle used the sites. There was adequate summer forage for bison, after cattle grazing, even during a very severe drought when forage biomass production was reduced 48-91% below average. However, these high levels of grazing use may not result in optimal foraging for bison from the perspective of forage quality and overall energetic demands for the bison. The high co-use of these summer ranges in fact may result in too much use. We recommend that an evaluation of the nutritional and energetic needs of the bison be conducted in relation to cattle forage use.

Our conclusions concerning the status and vigor of grasslands grazed by ungulates in the Jackson Valley suggest a complex and varied response by the vegetation. We concluded that most of the sites we sampled in the Valley were grazed at high to very high levels due to a combination of moderate summer grazing and high winter grazing on most sample sites. The grasslands demonstrate a number of compensatory responses to grazing—(1) total production, forb production, and graminoid production were not negatively affected by these high levels of grazing, and, in fact, production was higher on grazed sites in most years; (2) these positive responses were likely due to acceleration of nitrogen (N) processes such as N mineralization rates on grazed sites (Stottlemeyer et al. 2003), which provided more highly labile N to plants; (3) plant species diversity was also typically higher on grazed sites. However, we also observed evidence of overgrazing—(1) bare ground was dramatically higher on grazed sites; (2) the most heavily-grazed sites, those with 80% offtake or more, were dominated by exotic plants (*Poa pratensis*, *Bromus inermis*), and the indication was that native plant species could not tolerate these high levels of herbivory. The evidence suggests these hot spots for grazing may be self-perpetuating “grazing lawns” as described by McNaughton (1983) where native plants would be excluded indefinitely, while a high turnover rate for N repeatedly attracts ungulates to the sites.

Part II: A Survey of Willow Communities, Willow Stature and Production, and Correlations to Ungulate Consumption and Density in the Jackson Valley and the National Elk Refuge

Managers in the Jackson Valley are currently re-evaluating their management of elk and bison. A new management plan for both species is the desired product of the interagency effort. The management of woody riparian shrubs, especially willows (*Salix* spp.), cottonwood (*Populus angustifolia*, *P. acuminata*) and aspen (*P. tremuloides*), is a critical issue in this management evaluation process. Managers are concerned over declines in willow, aspen, and cottonwood communities. We conducted three years of research on willow communities on ungulate winter ranges on the National Elk Refuge and in the Jackson Valley to assess the status of willow in the valley, current utilization rates by three large browsing ungulates (elk - *Cervus elaphus*; moose – *Alces alces*; bison – *Bison bison*) and correlations of ungulate abundance and browsing to the status of the willows.

We recognized four general categories of willow use by ungulates in the Jackson Valley based on observations and sampling from winter range willow communities in Yellowstone and Rocky Mountain national parks, avian community characteristics, and stream function. Category I (0-10% consumption) maximizes tall height of willows, large crown sizes, and overall willow abundance across the landscape. These tall willows grow to the edges of streams. The willows benefit the stream aquatic ecosystem by shading of streamsides and due to large amounts of leaf and shoot litterfall. There is higher abundance and diversity of avifauna and, apparently, maximum input to terrestrial soil ecosystem processes. Willow communities in Category II (11-20% consumption) are still healthy and abundant, but willows do not grow over streamsides, they don't shade streams, nor provide as much cover or litter inputs into the stream, which provides habitat and nutrient inputs to aquatic invertebrates and fish. In Category III (21-35% consumption), the size and production of willows is dramatically reduced. Willow patches in Category IV (> 35% consumption) are severely overbrowsed with short, severely hedged plants scattered in small patches. Category IV willow communities have lost much of their ecological function and little avifauna habitat is provided.

There is a high range in ungulate herbivory on willows in the Jackson Valley, ranging from very lightly browsed to very heavily browsed. Our analysis found maximal willow growth (production, canopy size) occurred when consumption rates were ~4-5% and showed sharp declines in willow growth and stature when consumption was above 23%. Winter willow consumption rates averaged $16 \pm 2\%$ across the study area, but consumption was highly variable and ranged from 0 to 47%. Summer consumption rates were lower, ranging from 0 to 8%. Consumption rates were negatively correlated to willow production, willow canopy area, willow canopy volume, and height of both tall and short willow species. Elk density averaged 16.3 ± 4.9 elk/km² and ranged from zero to over 200 elk/km². Moose density averaged 1.9 ± 0.4 moose/km² and ranged from zero to 13 moose/km². Consumption rates were positively correlated to elk densities and negatively correlated to moose densities. Based on best model selection criteria, we concluded that offtake is a better predictor of willow production, canopy area, canopy volume, and willow height than the ungulate density measures. When considering all potential measures of ungulate density (total density, moose alone, elk alone), elk density alone was the best determinant of willow growth variables.

The majority of the willow patches sampled in our study fell into the tallest category (Category I), and over 60% of the sampled patches were in either Category I or II. However, a sizeable portion of the willow landscape is either heavily browsed or overbrowsed (Categories III and IV). Most of these most heavily used willow patches were on the NER. Currently, 33% of the willow patches we measured on the NER and 11% of all the patches we measured in the entire Jackson Valley study area fall into the overbrowsed Category IV. Ninety-four percent of sampled willow patches that were heavily browsed or overbrowsed were within 6 km of feedgrounds.

We concluded the single best index to predict willow status and vigor was consumption rate by ungulates. However, ungulate population size and density is the parameter that managers will modify through harvest regulations. We recommend managers monitor numbers of both elk and moose in order to manage willows, however elk density was the dominant influent on willows and if managers can monitor only one species, that species should be elk. We predict that managers seeking to have the majority of willow communities in Category I height/growth status will need to substantially reduce average elk densities across the entire study area from current average levels of 16.3 elk/km² to 1.9 elk/km². We predict that recovery of all NER willow to Categories I and II would require reducing elk numbers on the NER to between 2,400 and 2,700 elk from the current typical winter numbers of 6,000-6,500 elk. If managers seek to maintain most NER willow communities in Category II after full recovery of all willow stands, elk densities will need to be maintained at a population level of no greater than 3,700 and ideally between 2,750 and 3,150 animals.

Part III: Effects of Long-Term Ungulate Herbivory on Plant and Soil Nitrogen and Carbon, Jackson Valley, Wyoming

In western landscapes, the elimination of predators, loss of migration routes, and the attraction of supplemental forage sources can lead to local over-populations of large herbivores such as elk. Such conditions may contribute to overgrazing on public lands. We studied the effects of elk herbivory on grass and shrub lands in the Jackson Hole region of Wyoming. The study area included lands managed by the U.S. Fish and Wildlife National Elk Refuge, the National Park Service Grand Teton National Park, the U.S. Forest Service Bridger-Teton National Forest, and the State of Wyoming Game and Fish Department.

Study on the grazing effects of large herbivores has generally focused on the more visible ecosystem components such as aboveground plant biomass and diversity. However, also of great ecological significance are the effects of herbivory on the quality of primary production, especially carbon and nitrogen content, and grazing effects on the diverse belowground microbial composition and processes. Belowground biodiversity greatly exceeds that above ground. The soil microbial community accounts for half of ecosystem production, and regulates much of the energy (carbon) and almost all nutrients, such as nitrogen, available to the aboveground biota. Carbon and nitrogen pools take many years, even decades, to accumulate, and thus recovery to normal levels following excess herbivory is a long-term and serious consideration.

Here we summarize results primarily from the second year of a two-year study (2001-02) on the effects of grazing by native ungulates on soil nutrients and processes. We sampled soil inorganic nitrogen (N) pools, total carbon (C) and N pools, net nitrification and N mineralization rates; soil respiration, temperature, and moisture; the C and N content of small roots and aboveground herbaceous production, and ecosystem inorganic N loss in stream water. Most research was conducted during the snow-free season. The study sites were five, >40-yr old exclosures in the Jackson Hole area of Wyoming. The primary research objective was to examine whether elk herbivory accelerated the nitrogen cycle as indicated by increased available inorganic N.

Grazing increased soil bulk density (compaction) and temperature, and reduced soil moisture. The effect of grazing on soil temperature was most apparent at the Miller Butte exclosure, and on soil moisture at the Gros Ventre exclosure.

Elk grazing had little effect on total C and total N pools. Elk grazing had no effect on soil percent C, N, the C:N ratio, the total soil C and N pools, or seasonal change in total soil C and N pools. Soil C content was primarily correlated with moisture. Generally higher moistures increase soil C:N ratios.

Soil CO₂ efflux (C mineralization or soil respiration) provides an index of both microbial and small root respiration rates. Soil respiration rates were correlated with moisture. Grazing reduced growing season soil respiration rates and moisture. With grazing, soil respiration rates were correlated with the total C pool size, but grazing did not alter the percentage of total soil C

content mineralized (respiration) relative to that of the controls (exclosures). Soil C respiration rates and N cycling rates are generally linked.

Grazing dramatically influenced N process and nitrate pools. Grazing increased soil NO_3^- pools, total inorganic N pools, and N mineralization rates. Inorganic N mineralization rates varied by season. Net nitrification rates (generation of NO_3^-) were inverse with soil moisture. Soil NO_3^- pools increased in late summer and NH_4^+ pools declined. The autumn increase in soil NO_3^- pools and net nitrification rates suggests that nitrification of NH_4^+ continued while soil microbial and small root NO_3^- uptake declined. The decline in soil respiration rates concurrent with an increase in soil inorganic N pool size and N mineralization rates suggests that other factors, in addition to grazing, may be affecting soil N mineralization rates. Limited available C (labile carbon) to the soil microbial community likely reduced NO_3^- uptake and increased soil NO_3^- pools. The positive correlation of soil respiration rates and inverse correlation of net nitrification rates with moisture suggests soil moisture was a contributing factor in regulating C availability to the microbial community.

Grazing increased soil exchange resin inorganic N content during winter. This indicates more mobile N, especially NO_3^- , was present in soils during winter. The source of this inorganic N could be from elk, or soil N mineralization rates exceeding biological uptake. Based upon soil inorganic N trends going into winter, the increase in soil inorganic N during winter was likely the result primarily of soil N mineralization rates exceeding microbial uptake. The resin bag NO_3^- content was lower ($P < 0.01$) in summer than winter independent of grazing. This reflects the low net nitrification rates especially in mid-summer.

Above ground, grazing increased summer graminoid production and its C and N content, but had no effect on forb production. Small (<2 mm diameter) and fine (<0.5 mm) roots can account for much of belowground plant production, and are the major components in plant nutrient uptake. Grazing did not alter small root biomass. However, grazing did increase the percentage of small root biomass as fine roots, the fine root C content, and percentage of N in fine roots. The increase in fine root N percentage with grazing could be a response to increased aboveground herbivory and/or the higher soil inorganic N availability. The inverse relationship between fine root C:N ratios and soil inorganic N availability and mineralization rates suggests that the higher fine root N percentage and resin bag inorganic N were the result of increased inorganic N availability with grazing.

We suspect the extra NO_3^- on grazed sites was leached from the system during winter and spring run-off. An indicator of excess ecosystem N availability and loss is the seasonal trend in stream water NO_3^- concentration. Most inorganic N reaching a stream is NO_3^- because, unlike NH_4^+ , soils have little NO_3^- adsorption capacity. The absence of a significant summer decline in Flat Creek NO_3^- concentration indicated unusually high NO_3^- export in stream water. In addition, Flat Creek NO_3^- concentrations were up to an order-of-magnitude greater than might be expected in such a system. We did not monitor stream water chemistry throughout the year. It is likely that the high winter soil inorganic N content (resin bags) coupled with water movement through the soils resulted in still higher stream water NO_3^- and dissolved organic nitrogen (DON) during winter, especially during and following the snowmelt period.

In summary, grazing altered several soil characteristics including compaction, temperature, and moisture. Grazing increased nitrogen mineralization rates, but reduced soil respiration (carbon mineralization) rates. The soil C and N cycles were linked. The decline in seasonal soil respiration rates indicated a decrease in microbial activity. The decline in microbial activity was likely the result of limited available carbon, which was aggravated by low soil moisture. The reduced soil microbial activity lowered its uptake of soil inorganic N, and resulted in an increase in soil available N especially as NO_3^- . Grazing increased belowground fine root biomass and its nitrogen content. This likely improved fine root growth and absorption of nutrients, which could account for the increased aboveground graminoid production with grazing. However, the increased aboveground and belowground growth was not sufficient to fully utilize the extra inorganic N available especially in winter. This nitrogen, primarily NO_3^- , was probably lost from the ecosystem likely in stream water.

Acknowledgements

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Part I: Ecology of Native Ungulates in the Jackson Valley: Elk, Bison, and Moose Habitat Selection, Herbivory, and Interactions with Domestic Cattle

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INTRODUCTION

Management of native ungulates in the Jackson Valley, Wyoming, presents a number of unique challenges. The winter range lies on a complex of administrative land areas with a wide diversity of management goals and philosophies, including the National Elk Refuge (NER), Grand Teton National Park (GTNP), Bridger-Teton National Forest (BTNF), the town of Jackson, private ranches, and private housing developments. Ungulate management needs on these lands vary from the highest priority to the lowest priority for the land unit. To reduce conflicts on private lands, elk and bison are artificially fed alfalfa hay and pellets at several feedgrounds within the Jackson Valley. Feedgrounds are located on the NER, the Gros Ventre Valley (Bridger-Teton National Forest [BTNF]), and south of the town of Jackson.

Human developments and alterations, artificial feeding, and high incidence of brucellosis in elk and bison complicate management of free-ranging ungulates in the Jackson Valley. The NER was established in 1912 as a winter range for Jackson Valley elk in response to high winter mortality caused by loss of critical winter range and market hunting. Artificial feeding of the elk was instituted on the NER to mitigate losses of elk winter range habitat to settlement in the area of Jackson Hole and related livestock ranching operations and to alleviate conflicts with ranchers over elk depredation of their livestock feed. In recent years, the lower end of the Jackson Valley has become increasingly developed, with more housing subdivisions, vacation homes with acreage, and commercial zoning.

The Jackson elk herd is currently estimated to number about 15,680 animals, or about 42% over the agency goals of 11,029 elk (set by the state of Wyoming) for the herd (Lubow and Smith 2003). Agency efforts to reduce the number of elk in the population have been hampered by late migrations of elk both from the interior areas of GTNP, where hunting is not allowed, and late migrations from the less accessible wilderness areas of BTNF. The national park, in cooperation with the state of Wyoming, permits a late elk hunt on portions of GTNP (only those lands east of the Snake River), in order to harvest park segments of the herd. The late hunt, however, has only

been partially successful. Managers are concerned about high densities of elk in the Jackson Valley.

In 1968, a population of 15-16 bison escaped from captivity in Grand Teton National Park and was allowed to roam free in GTNP by local management agencies. In 1975, the bison began wintering on the NER and began using the elk feedgrounds as a food source. Since discovering the feedgrounds, nearly all bison in the herd have wintered on the refuge feedground. As a result of the artificial feed, the population has increased dramatically to its current size of 650 bison (GTNP unpublished data). The presence of a growing bison population in Jackson Hole has caused concern over the potential transmission of brucellosis from bison to domestic livestock. Large concentrations of both bison and elk on the NER feedgrounds provide the opportunity for a higher rate of transmission and infection of the disease in the two species. The *Brucella* organism may be transmitted through ingestion of infected fetuses or fetal membranes, contact with infected tissues, grazing on contaminated native forage, consuming contaminated feed or water, and possibly from contamination by feces left by infected animals (Crawford et al. 1990; T.J. Roffe, USGS, unpublished data). These conditions occur in abundance on the NER feedgrounds during the late winter and early spring where both bison and elk may abort in close proximity, or even right on the feedlines used by elk and bison. Elk are also a significant potential host for *Brucella* (Thorne et al. 1991, Smith et al. 1994). The reduction or cessation of feeding at some, or all, of the feedgrounds has been proposed. However, reduction of feeding will require reductions of elk and bison numbers. Management agencies are concerned that the level of artificial feeding not support more animals than historically inhabited the Valley. Thus, managers are interested in levels of habitat-based carrying capacity for elk and bison. Knowledge of how distributions of native ungulates might change under reduced feeding or cessation of feeding would assist managers in determining locations of potential conflict both between native ungulate species and with private landowners. Analysis of habitat selection of individual ungulate species that are not using artificial feed sources can identify these areas, so that management can be directed in a manner to anticipate and avoid such conflicts.

Grazing by domestic livestock, especially cattle, is a concern, both because of the risk of brucellosis transmission between domestic and native species, and the possibility that livestock may competitively use forage that might otherwise be important to overwintering native ungulates. Domestic cattle grazing allotments are located both in GTNP and BTNF. Livestock grazing is not typically allowed in a national park, however, cattle grazing was grandfathered into the lands that were added to GTNP in 1950. Cattle grazing was permitted to continue in parklands located east of the Snake River where it had occurred prior to the park's designation (Congressional Act 64 Stat. 849, 1950).

Concerns over cattle grazing are as follows:

- 1) Do cattle consume forages that are needed by bison during the summer? The two grazers eat similar forages and share many summer habitats, especially areas around the Kelly hayfields and the Triangle X-Cunningham-Moosehead Flats-Elk Ranch allotments.
- 2) Do cattle consume forages during summer that are needed by elk during winter months and during migratory transition periods? Approximately one-third of the elk herd winters

off of the feedgrounds on GTNP and BTNF lands, where they might encounter ranges already grazed by cattle during the previous summer.

- 3) How much does spring-summer use of areas by bison and cattle overlap? The *Brucella* organism is most typically transmitted from the ingestion of materials from an aborted fetus passed by an infected adult female, either through direct ingestion, or by ingesting the organism off of forages. Habitat overlaps during the bison and elk calving periods would be a serious concern.

The Jackson Valley experienced a severe drought during 2001. GTNP requested the U.S. Geological Survey and Colorado State University to assess the effects of this drought on production, utilization, and availability of forage for bison, elk, and cattle within GTNP. The research team was asked to answer the following questions:

- 1) What were the effects of the 2001 drought on grassland production and relative consumption (i.e. offtake) levels by elk, bison, and cattle?
- 2) How much forage would be required by the Jackson bison herd?
- 3) How much forage was left for native ungulates on grazing allotments after cattle grazing?

Section A. Ungulate Habitat Suitability Models—Projections of Potentially Occupiable Habitat for Elk, Bison, and Moose in the Jackson Valley

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Jackson Valley land and wildlife managers seek predictive maps of all occupiable native ungulate (elk, bison, and moose) habitat in the valley. We conducted multivariate analyses of the available information on bison, elk, and moose distributions and habitat selection. We also conducted a statistical test of multiple habitat variables (snow depths, elevation, slope, aspect, vegetation type) and developed a gradient model to explain the habitat niches that bison and elk could occupy if they were not fed or were fed less. The statistical significance of the relative importance of these parameters is difficult to test, but best model approaches, such as the Akaike's information criteria (AIC), are available to tell us which combination of habitat parameters is the best predictor while being the most economical in terms of number of variables involved in the model (Burnham and Anderson 1992). Using geographic information systems (GIS) techniques, we then applied this best model to the entire valley, including all historic habitat, to present managers with all presently occupiable habitat.

METHODS

The habitats preferred by elk were determined using 786 locations of elk groups gathered during Wyoming Game and Fish Department (WGFD) aerial surveys from 1986-1997. We also used 865 aerial radiotelemetry locations of elk from NER surveys of approximately 168 collared individual elk gathered from 1990-1999. Moose locations (n=622) were obtained from WGFD aerial surveys conducted in January-February 1999-2000. Bison locations (n=519) were obtained from GTNP aerial surveys conducted from 1997-1999. Only winter observations of ungulates (November-April) were used to determine habitat preferences. Only those locations falling within the Jackson Valley study area were used. Our study area corresponds to the boundary depicted in Steele et al. (1999). The southern boundary reaches to the southern edge of the Town of Jackson, the northern edge is at the north end of Jackson Lake, the western edge is about halfway between the crest of the Tetons and the Idaho border, and the eastern edge runs roughly to Togwotee Pass (Fig. 1.1). This boundary roughly encompasses the range of the Jackson elk

herd as defined by WGFD. All common large ungulates potentially use any areas ≤ 2600 m elevation in the Valley.

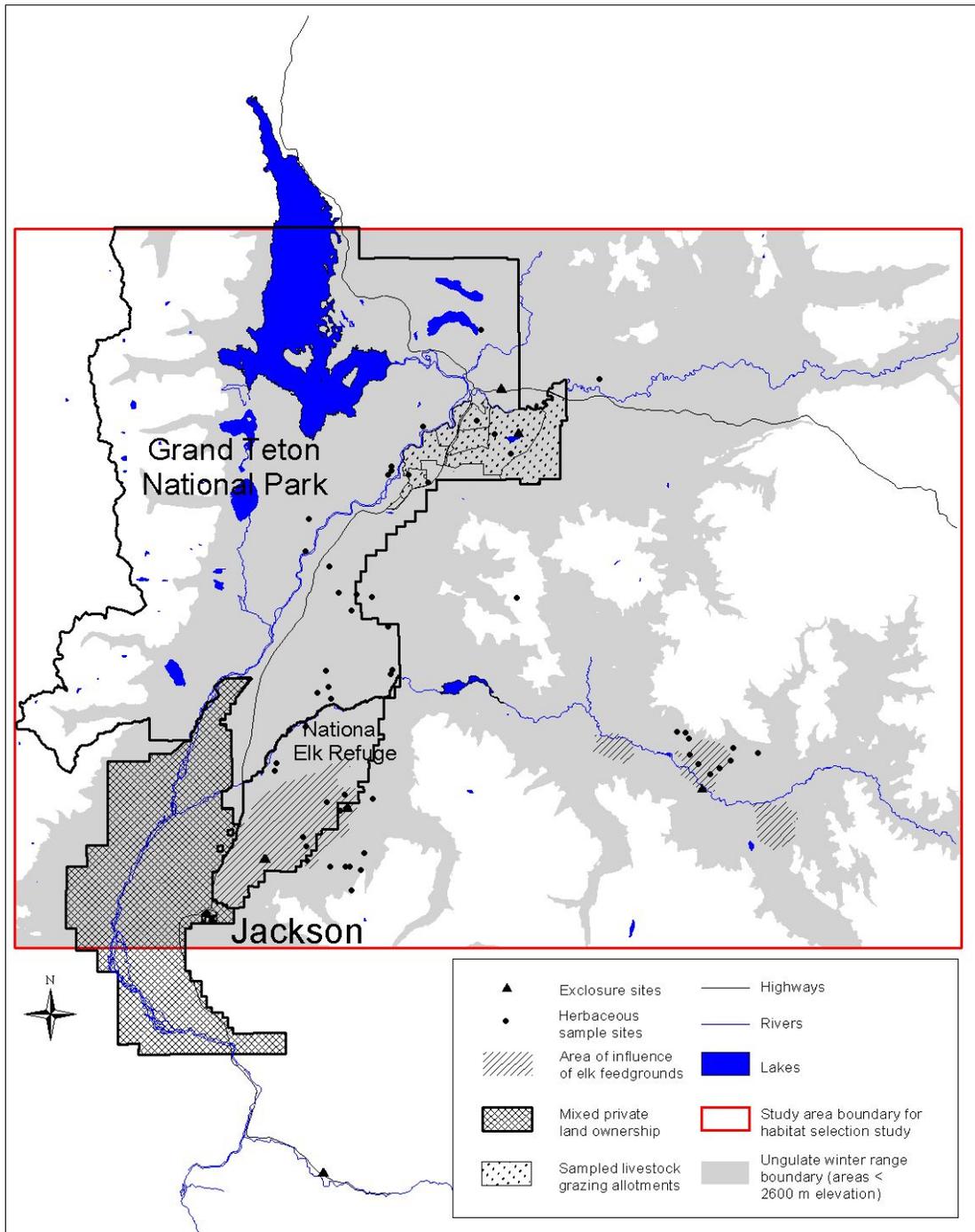


Figure 1.1. Study area and locations of sample sites measured for study of native ungulate habitat selection and herbivory impacts in Jackson Valley, Wyoming.

Information on elevation was obtained from USGS Digital Elevation Models (DEMs) and aspect and slope were derived from these maps using ArcView version 3.2 GIS software. We determined vegetation type using the vegetation map developed for a landscape forage model for this area (Hobbs et al. 2003). We merged maps of lakes and rivers and determined distance to these water sources. About two-thirds of the Jackson elk herd winter at feedgrounds. The feeding affects their movements and alters their habitat preferences. Thus, we only used locations of elk that were not fed. Interpretation of the zone of feeding influence was assisted by a map of elk concentration areas due to feeding provided by Steve Kilpatrick of WGFD (Fig. 1.1). We also compared areas open to elk hunting to un hunted areas to detect any potential avoidance.

The Jackson Valley is a deep snow environment where snow depths, snow density, and snow crusting all influence the distributions of large ungulates. We selected snow water equivalents as the best measure of snow density that can quantify ungulate responses. We used the snow model of Hobbs et al. (2003) to develop maps of snow water equivalents for each day when radiolocation or survey data on ungulates were collected. We then estimated snow water equivalents for each animal location using these snow maps. We also compared habitats that had burned in the last 5 years to habitats that were unburned or burned >5 years ago. Many effects of fire on vegetation, such as effects on forage abundance, forage quality, and species diversity, rapidly diminish over time, and therefore the influence of fire on ungulate habitat selection may decrease over time.

Based on initial analyses, agency feedback, and field observations, we decided to run two separate resource selection models, one for early winter (November and December) and one for late winter (January-April). Snow depths tend to increase during the latter period thus restricting ungulate movement. Snow water equivalent (SWE) data were available through water-year 1999. Since we had a limited amount of moose observation data, half of which were collected in February 2000, we deemed it necessary to use these data in evaluating resource selection models. Therefore, we searched our precipitation data for the last 20 years to find the date with the most similar SWE values to late February 2000. We used the snow map for February 15, 1995 to determine SWE for all 2000 moose observations.

To estimate ungulate habitat selection, we compared the locations of ungulates to a random set of locations. A number of locations equal to the number of observations for each species were randomly generated within the study area using ArcView GIS. We used these random locations to create resource selection functions using logistic regression methods (Boyce and McDonald 1999). Each was randomly assigned an observation date from among the animal observation collection dates so that snow water equivalents could be generated.

We analyzed eight habitat variables for selection by ungulates--vegetation type, distance to water (rivers and lakes), snow water equivalents, elevation, slope, aspect, hunting, and fire occurrence. Locations with missing habitat variables were removed from the data set as well as those within the influence area of the feedgrounds as defined by WGFD personnel (Fig. 1.1) to reduce the influence of artificial feed on habitat selection. Since moose do not frequent feedgrounds, all moose observations were used in this analysis. This reduced the number of locations that were used in the analysis (Table 1.1). We calculated a selection index (w) based on resource selection

functions (the proportion of used resource units of a type of those available) that was calculated by the equation:

$$w_i = p_i / u_i$$

where p_i is the proportion of used resource units in category i , and u_i is the proportion of resource units of category i from all resource units available. This index can be standardized (B_i) to allow more direct comparison between categories of an individual habitat variable. Using a log-likelihood chi-square test (Neu et al. 1974, Manly et al. 1993), we determined whether observed habitat use was significantly different from expected use based on the availability of the habitat. We determined which habitats were preferred using 95% confidence intervals with a Bonferroni correction. This test was performed for all habitat variables except snow water equivalents, since these observations varied based on individual date of animal observations and, therefore, we could not calculate a standard proportion of the area in each category of snow water equivalent.

Table 1.1. Sample size of observed and random animal locations used for habitat selection model testing for elk, bison, and moose in the Jackson Valley, Wyoming.

	Actual animal observations	Random locations
Elk early winter	479	660
Elk late winter	819	884
Bison early winter	222	192
Bison late winter	143	202
Moose	624	624

Logistic regression analyses were performed to determine the best model for predicting habitat selection for each species. The dichotomous response variable was “observed habitat use” versus “randomly generated” locations. Akaike's information criteria (AIC) were used to determine the best model for predicting habitat selection for each species. The resource selection probability function is the probability of selection of any particular habitat in the study area. These probabilities were determined by using the best fitting logistic regression model in the following equation:

$$P_i = \frac{e^{\beta_0 + \beta_1 X_{i1} + \dots + \beta_k X_{ki}}}{1 + e^{\beta_0 + \beta_1 X_{i1} + \dots + \beta_k X_{ki}}}$$

where $\beta_0 \dots \beta_k$ are the parameter estimates in the logistic regression equation and $X_{i1} \dots X_{ki}$ are the values of the habitat variables (van Manen and Pelton 1997; Boyce and McDonald 1999). This provides an index to predict degree of potential selection by each species. Suitable habitat for a species was defined as an area with >50% probability of use by the species in question. We removed areas of spruce-fir, wetlands, and developed/disturbed areas from the final bison late winter habitat selection maps since bison were not observed in those areas in late winter. We

removed human developed and disturbed areas from the final moose habitat selection maps since moose were never observed in those areas.

RESULTS AND DISCUSSION

Both elk and bison significantly preferred sagebrush, aspen, wetlands, and agricultural fields ($P \leq 0.05$, Table 1.2). Unlike bison, elk showed a preference for riparian forest, while bison, unlike elk, preferred wet and dry meadows. Elk tended to avoid flat areas and north-facing slopes, preferring slopes facing southeast, south, southwest, and west. Bison preferred flat areas, as well as southwest, west, and northwest aspects. Elk preferred slopes of less than 15° at elevations of 2000-2600 m. Bison were much more selective in this regard, preferring slopes of $\leq 10^\circ$ at elevations of 2000-2200 m (Table 1.2). Elk and bison were both confined mainly to areas of ≤ 15 cm (6 inches) of snow water equivalent ($\sim 90\%$ of late winter observations), though both species used areas with deeper snow late in the winter (Table 1.2). Elk preferred unhunted areas in the early winter during the hunting season, but then preferred previously hunted areas in late winter following the hunting season. Overall, elk used areas that had been burned within the last 5 years less than expected. Bison showed significant preference for burned areas in early winter, but by late winter, bison use of burned areas decreased (Table 1.2).

Moose preferred willow, riparian forest, wet meadow, and wetlands on flat, north, or south slopes of less than 5° at elevations between 2000-2400 m (Table 1.2). Ninety-five percent of all moose observations were within 1 km of water (streams, rivers, or lakes). Moose were not as restricted by snow, and nearly 50% of moose observations were in locations with 12.5-20 cm (5-8") snow water equivalents. Moose were not observed using any areas that had been burned in the last 5 years. Moose preferred areas where elk were hunted, since the hunt area contained excellent moose habitat (Table 1.2).

The combined winter range (all areas ≤ 2600 m elevation in the Valley study area) for all three ungulates comprised 2268 km² or 56% of the entire 4040 km² study area (Fig. 1.1). This area included the NER, the floor of the Jackson Valley including much of private and developed land near the town of Jackson, a large portion of the Gros Ventre River drainage, and Buffalo Valley.

The best model for predicting both early and late winter elk habitat selection included SWE, distance to water, vegetation type, aspect, slope, elevation, whether the area was open to elk hunting at that time, and occurrence of a fire within the last 5 years. Much of the study area is available to elk during early winter (Fig. 1.2), but later in the winter, the amount of suitable habitat for elk declined (Fig. 1.3). Most late winter suitable habitat was restricted to the Gros Ventre drainage and the southern end of the Jackson Valley (Fig. 1.3).

In a winter of average severity, approximately 383 km² (17.1%) of the ungulate winter range was considered suitable for elk. Of this area, 39 km² of suitable elk habitat was located to the west and south of the NER ungulate fence, and therefore, is presently not accessible to elk (Fig. 1.3a, Table 1.3). In a severe winter, suitable elk habitat drops to 149 km² (6.6%) of which 13 km² is not accessible to elk since it is located outside the ungulate fence (Fig. 1.3b, Table 1.3). Under all conditions, there are parts of the winter range that are non-occupiable because they contain characteristics that make them completely unsuitable (i.e. lakes, extremely deep snow, too steep, poor aspect, etc.).

Table 1.2. Elk, bison, and moose habitat preferences based on percent of total number of animal observed in the Jackson Valley, Wyoming.

Habitat variable	p _i	Elk						Bison						Moose		
		Early winter			Late winter			Early winter			Late winter			u _i	B _i	Pref.
		u _i	B _i	Pref.												
Vegetation type																
Sagebrush	15.4	30.7	0.13	+	48.6	0.24	+	44.4	0.08	+	44.3	0.16	+	15.8	0.03	0
Montane Shrub	2.0	2.8	0.09	+	1.5	0.05	-	0	0.00	-	0.3	0.01	-	2.0	0.03	0
Pine	18.6	20.6	0.07	+	12.3	0.05	-	0.4	0.00	-	0.1	0.00	-	2.8	0.00	-
Spruce-Fir	25.8	15.1	0.04	-	11.9	0.03	-	0.2	0.00	-	0	0.00	-	4.2	0.00	-
Douglas Fir	3.3	1.9	0.04	-	2.4	0.05	-	0.8	0.01	-	1.6	0.03	-	1.2	0.01	-
Aspen	3.3	4.8	0.09	+	3.6	0.08	0	7.6	0.07	+	11.6	0.19	+	4.4	0.04	0
Riparian Forest	1.5	7.6	0.32	+	1.4	0.07	0	1.8	0.03	0	0.1	0.00	-	15.9	0.29	+
Willow	3.3	2.5	0.05	-	4.0	0.09	+	2.4	0.02	-	0.3	0.00	-	36.6	0.31	+
Dry Meadow	9.8	5.7	0.04	-	8.9	0.07	-	7.4	0.02	-	18.8	0.10	+	2.2	0.01	-
Wet Meadow	0.6	0	0.00	-	0.5	0.06	0	5.7	0.28	+	0.9	0.08	0	2.6	0.12	+
Wetland	0.8	0	0.00	-	1.7	0.17	+	6.2	0.23	+	0	0.00	-	3.2	0.12	+
Agricultural	2.6	6.2	0.15	+	1.5	0.04	-	23.0	0.26	+	20.8	0.43	+	3.8	0.04	0
Developed	0.4	0	0.00	-	0	0.00	-	0	0.00	-	0	0.00	-	0	0.00	-
Aspect																
Flat	4.0	3.0	0.08	-	1.3	0.04	-	8.8	0.23	+	10.4	0.26	+	9.4	0.25	+
North	13.4	10.2	0.09	-	10.6	0.09	-	11.8	0.09	-	12.6	0.09	0	21.7	0.17	+
Northeast	11.2	3.9	0.04	-	11.4	0.12	0	4.1	0.04	-	1.4	0.01	-	4.6	0.04	-
East	10.6	9.6	0.10	-	9.9	0.11	0	4.9	0.05	-	7.4	0.07	-	5.7	0.06	-
Southeast	11.2	18.0	0.18	+	13.7	0.14	0	4.8	0.04	-	7.4	0.07	-	8.8	0.08	0
South	12.9	15.5	0.14	+	16.8	0.15	+	8.2	0.06	-	6.6	0.05	-	24.5	0.20	+
Southwest	11.5	18.6	0.18	+	15.1	0.15	+	23.9	0.21	+	21.6	0.19	+	7.9	0.07	-
West	12.0	7.5	0.07	-	12.9	0.13	+	15.4	0.13	+	19.4	0.16	+	8.2	0.07	-
Northwest	13.3	13.8	0.12	0	8.3	0.07	-	18.1	0.14	+	13.2	0.10	0	9.1	0.07	-
Slope																
0-5 degrees	24.8	37.6	0.26	+	23.6	0.14	-	83.4	0.79	+	42.3	0.34	+	77.1	0.69	+
5-10 degrees	19.5	17.4	0.15	-	22.3	0.17	+	14.8	0.18	-	34.1	0.35	+	10.6	0.12	-
10-15 degrees	17.9	23.5	0.23	+	22.4	0.19	+	1.6	0.02	-	14.9	0.17	-	6.2	0.08	-
15-20 degrees	13.0	10.5	0.14	-	14.3	0.17	+	0.1	0.00	-	8.5	0.13	-	5.0	0.09	-
20-25 degrees	9.1	8.8	0.17	0	9.7	0.16	0	0.1	0.00	-	0.3	0.01	-	0.7	0.02	-
25-30 degrees	6.4	1.7	0.04	-	5.1	0.12	-	0	0.00	-	0	0	-	0.4	0.02	-
>30 degrees	9.3	0.6	0.01	-	2.6	0.04	-	0	0.00	-	0	0	-	0	0.00	-
Distance to Water																
<0.5 km	53.8	37.6	0.19	+	60.7	0.40	+	61.4	0.39	+	45.3	0.2	-	86.4	0.76	+

Habitat variable	p_i	Elk						Bison						Moose		
		Early winter			Late winter			Early winter			Late winter			u_i	B_i	Pref.
		u_i	B_i	Pref.	u_i	B_i	Pref.	u_i	B_i	Pref.	u_i	B_i	Pref.			
0.5-1 km	31.5	33.1	0.28	+	27.3	0.31	-	22.2	0.24	-	34.0	0.3	0	11.4	0.17	-
1-3 km	14.8	29.3	0.53	-	12.0	0.29	-	16.4	0.38	-	20.7	0.4	+	2.2	0.07	-
Snow Water Equivalents																
0 cm		33.0			3.9			81.2			2.5			0.2		
2.5 cm (1")		43.7			8.4			18.0			22.8			3.1		
5 cm (2")		19.1			15.0			0.4			6.1			30.3		
7.5 cm (3")		3.8			20.1			0.3			17.4			6.6		
10 cm (4")		0.4			23.1			0			14.1			6.7		
12.5 cm (5")		0.02			9.3			0			15.5			12.4		
15 cm (6")		0			10.7			0			13.8			17.7		
17.5 cm (7")		0			3.6			0			5.5			7.2		
20 cm (8")		0			2.8			0			1.0			12.7		
22.5 cm (9")		0			2.1			0			1.0			0.9		
25-37.5 cm (10-15")		0			0.8			0			0.1			2.2		
>37.5 cm (>15")		0			0			0			0			0		
Elevation																
1800-2000 m	6.9	18.4	0.39	+	3.0	0.08	-	0.2	0.00	-	4.5	0.12	-	3.3	0.08	-
2000-2200 m	20.6	30.0	0.21	+	23.5	0.20	+	96.1	0.94	+	94.0	0.86	+	62.5	0.52	+
2200-2400 m	14.4	15.9	0.16	+	33.1	0.40	+	3.7	0.05	-	1.5	0.02	-	29.5	0.35	+
2400-2600	19.2	25.7	0.20	+	30.6	0.28	+	0	0.00	-	0	0.00	-	4.7	0.04	-
> 2600 m	38.9	9.9	0.04	-	9.8	0.04	-	0	0.00	-	0	0.00	-	0	0.00	-
Hunting																
Unhunted area	21.2	27.6	0.59	+	9.1	0.27	-	16.8	0.43	-	15.5	0.41	-	20.5	0.49	0
Hunted area	78.8	72.4	0.41	-	90.9	0.73	+	83.2	0.57	+	84.5	0.59	+	79.5	0.51	0
Fire (within last 5 years)																
Unburned	97.4	96.2	0.41	-	90.2	0.20	+	69.1	0.06	-	94.4	0.31	-	100	1.00	+
Burned	2.6	3.8	0.59	+	9.8	0.80	-	30.9	0.94	+	5.6	0.69	+	0	0.00	-

p_i =percent of habitat i in total study area

u_i =percent of total animals observed using habitat i

B_i =standardized selection index (u_i/p_i)

Pref.=whether the habitat is preferred (+), avoided (-), or used in proportion to its availability (0)

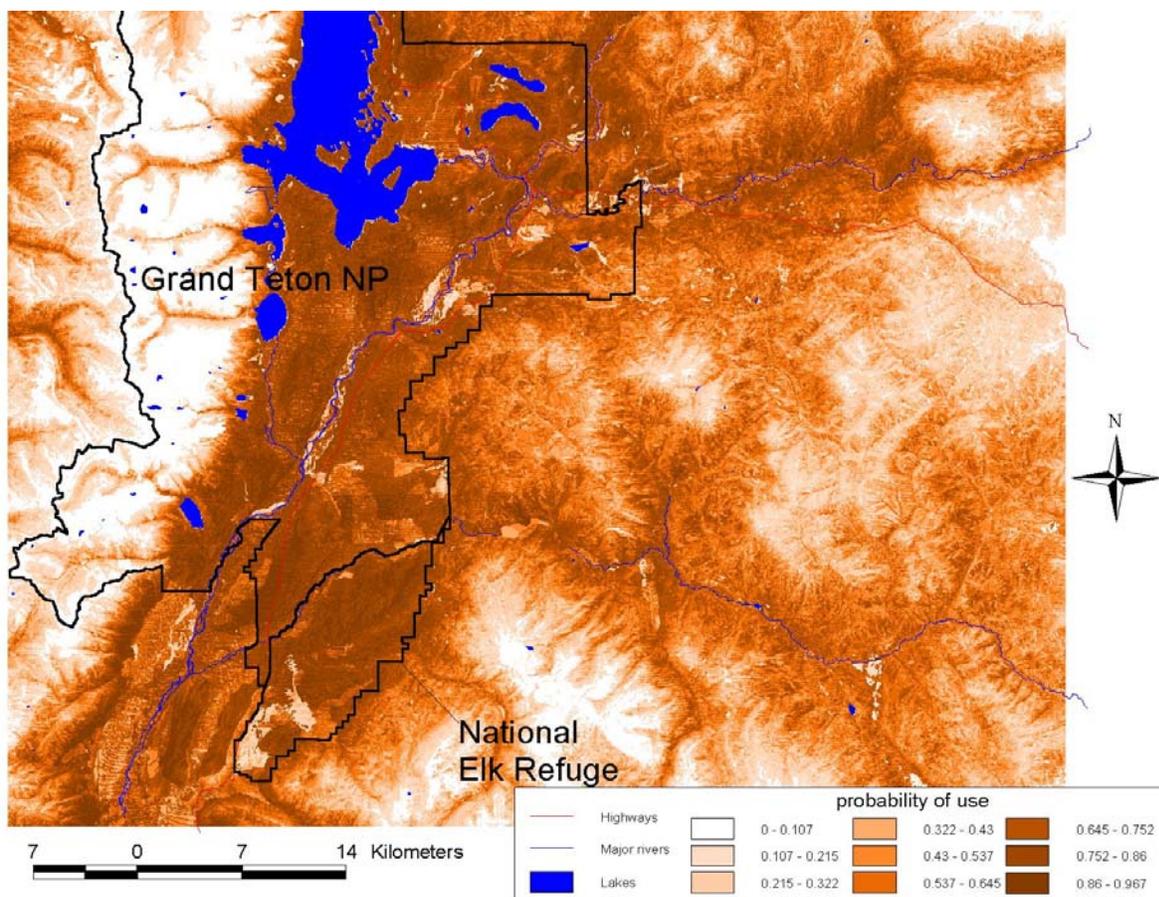


Figure 1.2. Probability of early winter (Nov-Dec) elk use of potential habitats during an average winter in Jackson Valley, Wyoming.

Table 1.3. Percent of ungulate winter range and area (km²) of non-occupiable and suitable (>50% probability of use) ungulate habitats that are available to animals in average and severe winters in the Jackson Valley, Wyoming.

	Average winter				Severe winter			
	Entire winter range		Private land outside ungulate fence		Entire winter range		Private land outside ungulate fence	
	% of area	Area (km ²)	% of area	Area (km ²)	% of area	Area (km ²)	% of area	Area (km ²)
Elk								
Non-occupiable	0.8	17.6	0	0	1.6	35	<0.1	0
Suitable	17.1	383	23.5	39	6.6	149	7.9	13
Bison								
Non-occupiable	26.4	592	11.7	19	28.2	633	11.7	19
Suitable	30.7	689	73.3	121	25.4	569	68.8	114
Moose								
Non-occupiable	1.7	38	8.5	14	3.1	70	8.5	14
Suitable	10.4	234	31.8	52	5.8	130	19.2	32

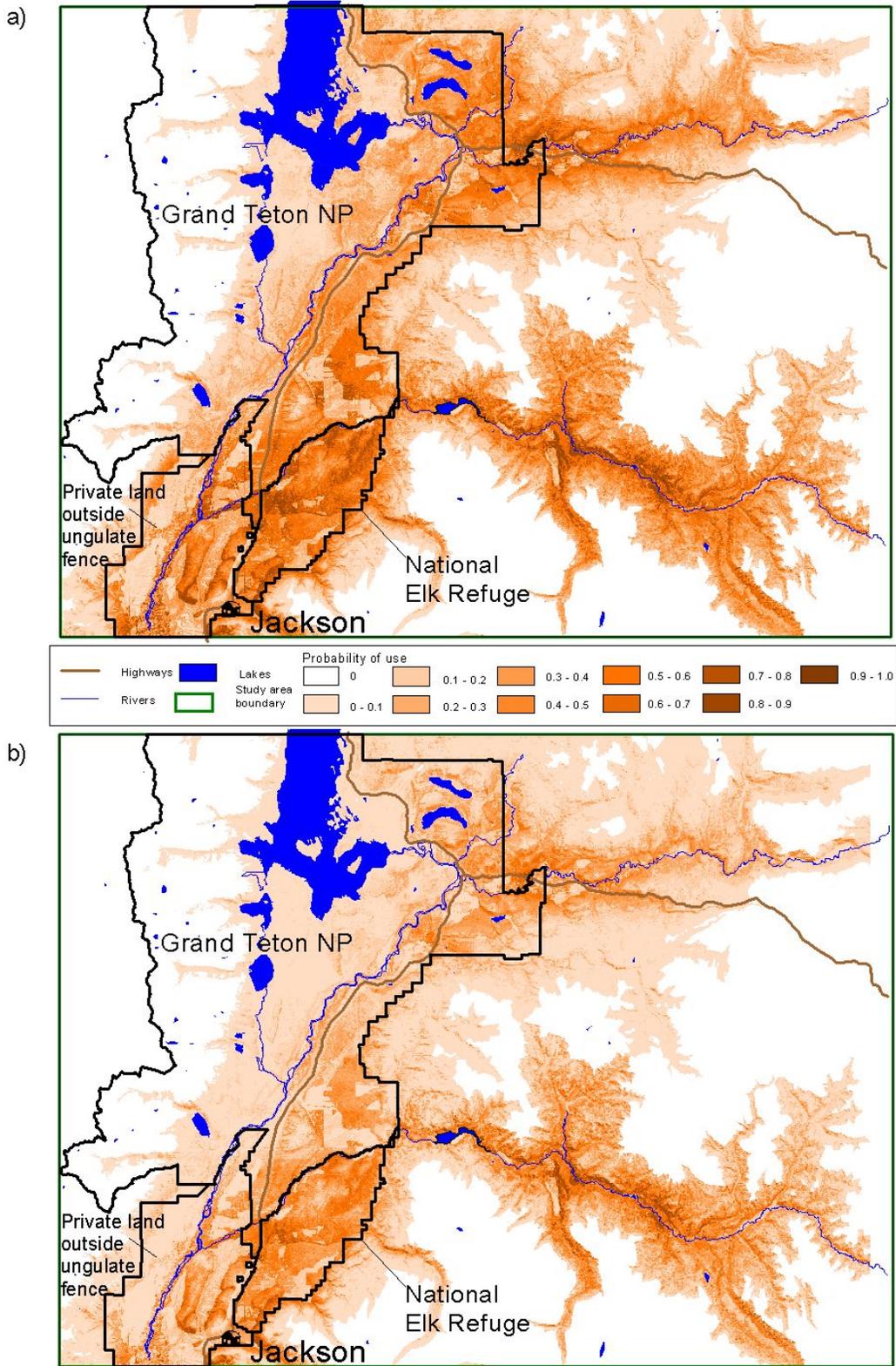


Figure 1.3. Probability of potential use of habitats by elk in late winter (January-April) during an average (a) and a severe (b) winter in the Jackson Valley, Wyoming.

The best habitat suitability models for predicting early and late winter bison habitat selection included SWE, vegetation type, slope, elevation, whether the area was open to elk hunting, occurrence of a fire within the last 5 years, and, for the late winter model, aspect (Figs. 1.4 and 1.5). A larger portion of the winter range (~25%) was suitable habitat for bison, even in a severe winter (Fig. 1.5b), but most of this area was restricted to the NER and areas outside the ungulate fence (Fig. 1.5). The early winter model identified large areas of suitable habitat west of the Snake River and south of the Triangle X ranch which currently don't receive much use (based on observations). The part of this area that lies south of the park boundary likely would not receive much use, even under larger bison population sizes because of development and competing livestock use. However, habitats within the park might receive more use by bison in the future.

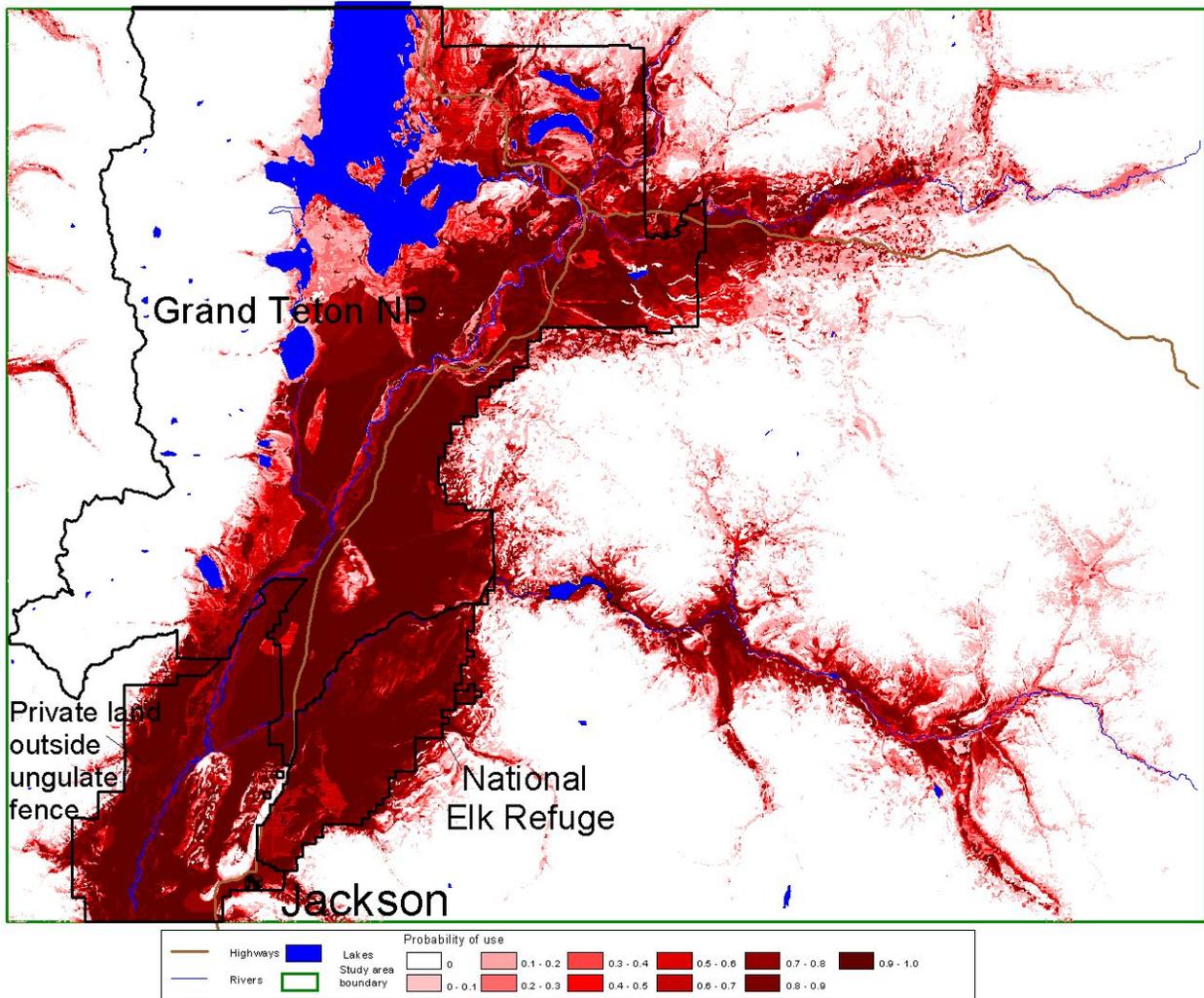


Figure 1.4. Probability of potential use of habitats by bison during early winter (November-December) in the Jackson Valley, Wyoming.

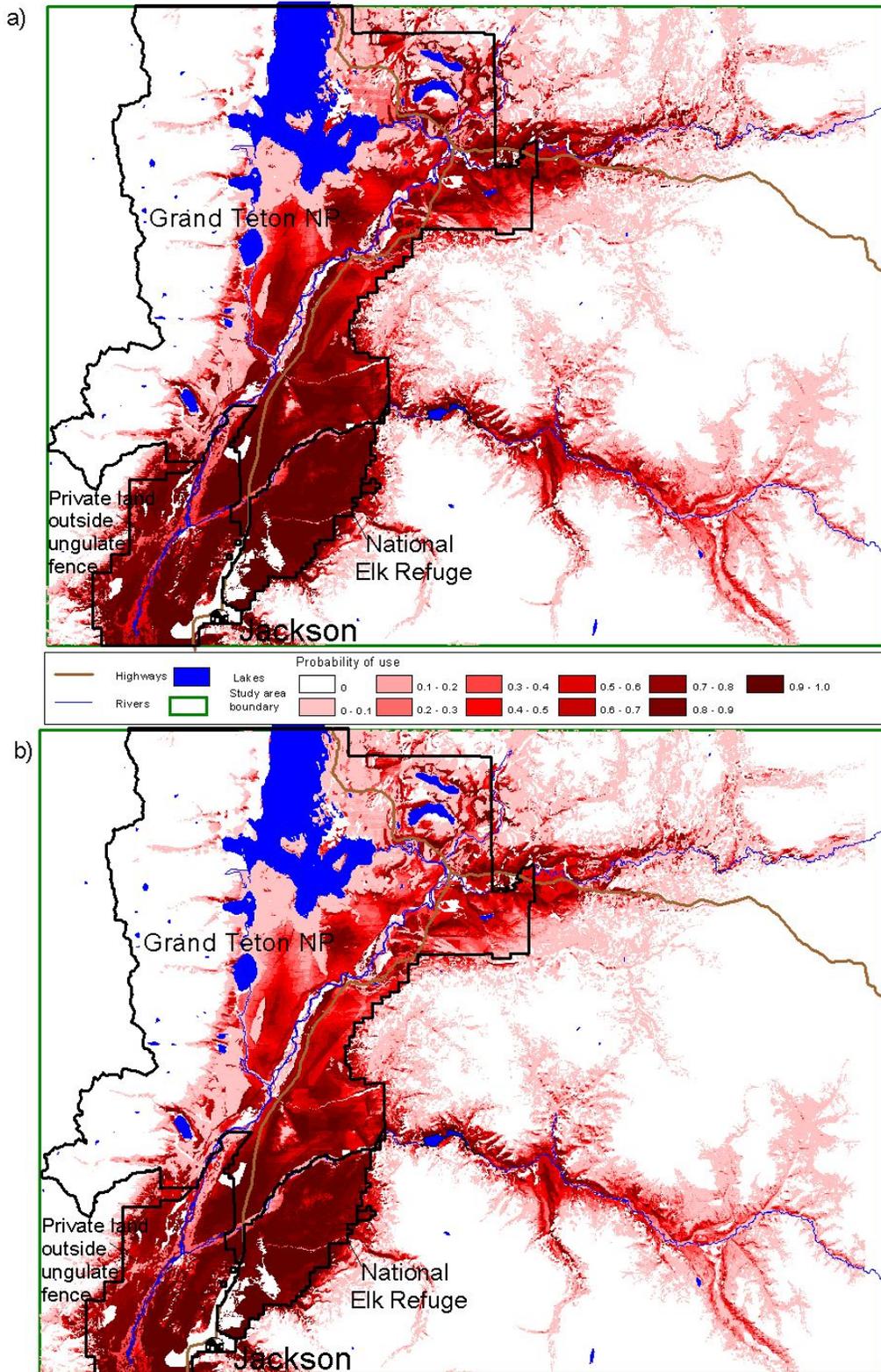


Figure 1.5. Probability of use of potential habitat by bison in late winter (January-April) during an average (a) and a severe (b) winter in the Jackson Valley, Wyoming.

In a winter of average severity, approximately 689 km² of the potential ungulate winter range was considered suitable for bison. Of this area, 121 km² were located to the west and south of the NER ungulate fence, and therefore, is presently not accessible to bison (Fig. 1.5a, Table 1.3). However, in a severe winter, the amount of suitable bison habitat drops to 569 km² of which 114 km² is located outside the ungulate fence (Fig. 1.5b, Table 1.3). There is more habitat that is suitable for bison compared to elk due to the large amount of preferred bison vegetation types (agricultural fields, sagebrush) on the winter range.

Moose habitat selection was best predicted using a model that included SWE, distance to water, vegetation type, elevation, and whether the area was open to elk hunting. We did not have enough data to develop both early and late winter models for moose, but we did model habitat use during an average and a severe winter (Figs. 1.6 and 1.7). Most areas of suitability were located along drainages, particularly of larger rivers and streams, and willow flats near lakeshores (Fig. 1.6). In severe winters, greater snow depths limited suitable habitat to areas along the Snake and Gros Ventre Rivers near the town of Jackson, a willow flat in the Buffalo Valley, and a wetland area of the NER near the feedgrounds (Fig. 1.7). Although moose do not

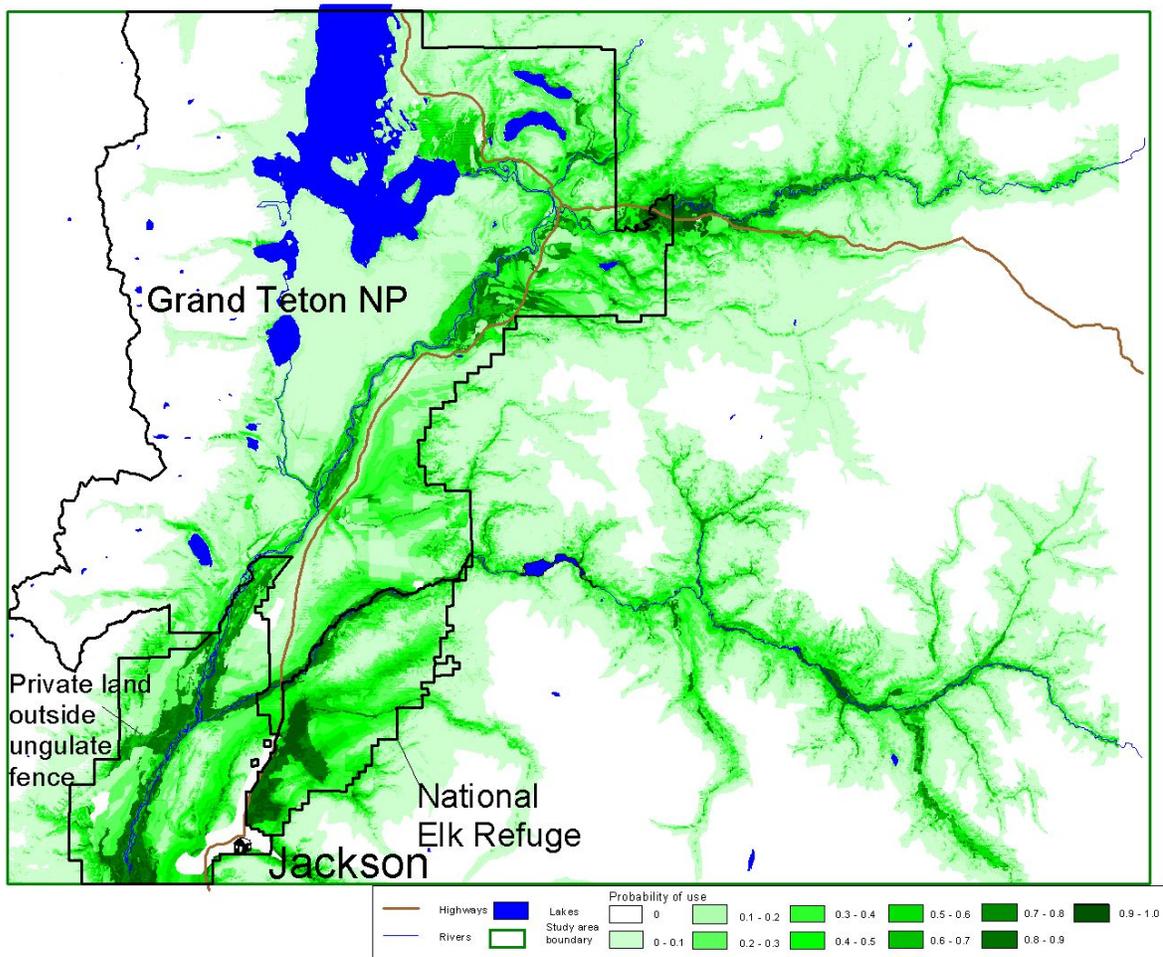


Figure 1.6. Probability of potential use of habitats by moose during a winter of average severity in the Jackson Valley, Wyoming.

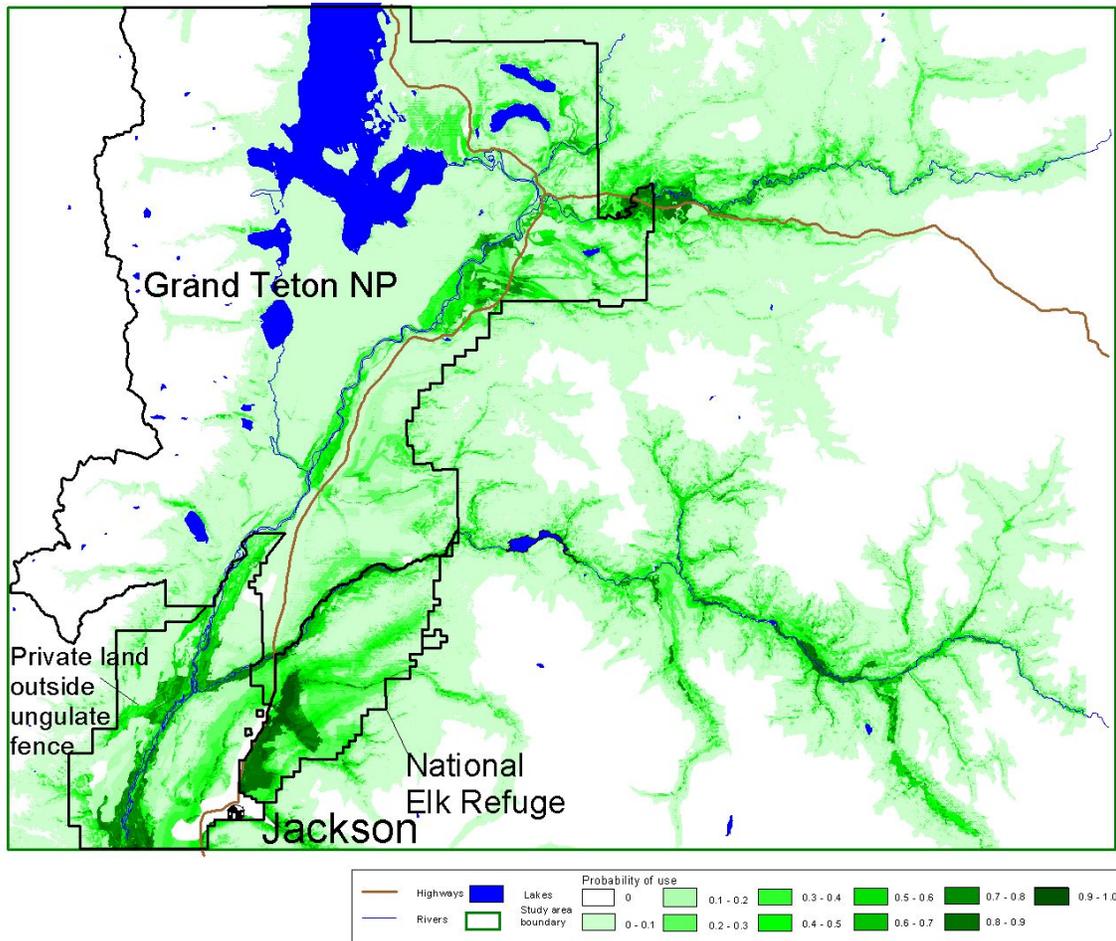


Figure 1.7. Probability of potential use of habitats by moose during a severe winter in the Jackson Valley, Wyoming.

currently use the Flat Creek wetlands of the NER due to reduction of willow available as forage (based on the observations used here and discussions with NER staff), this may be due to the high concentrations of elk on the feedgrounds. This situation might change if feeding were eliminated on the refuge.

There was less suitable habitat for moose compared with elk and bison, since willow, riparian forest, and wetlands were less abundant on the study area than grasslands. In a winter of average severity, approximately 234 km² of the ungulate winter range was considered suitable for moose. Of this area, 52 km² were located to the west and south of the NER ungulate fence (Fig. 1.6, Table 1.3). However, in a severe winter, the amount of suitable moose habitat drops to 130 km² of which 32 km² of this suitable habitat is located outside the ungulate fence (Fig. 1.7, Table 1.3).

Overlap in areas of high probability of use by all three species was not great (Fig. 1.8), even during severe winter conditions. Thirty-one percent of the winter range was suitable for at least

one of the species of ungulates, 5% was suitable for at least 2 ungulate species, and 1% was suitable for all three species (Fig. 1.8).

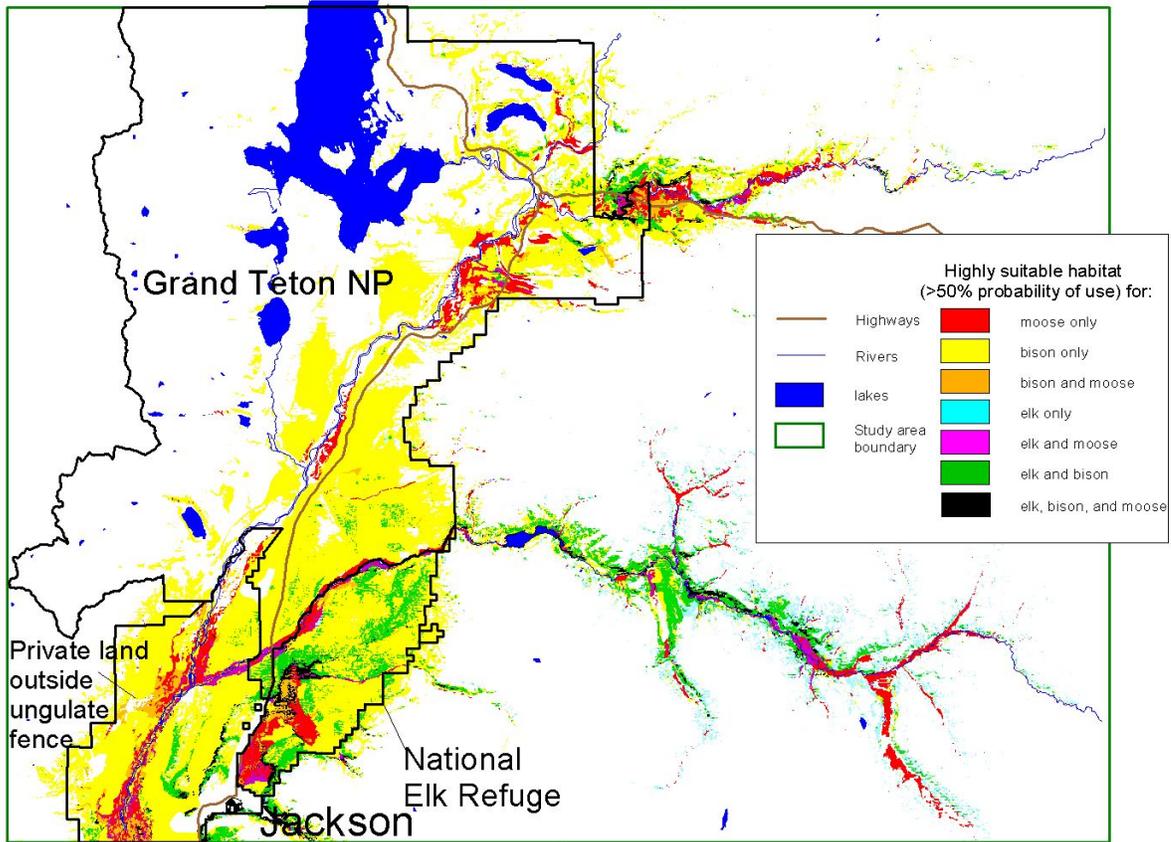


Figure 1.8. Overlap of “highly suitable” potential habitats for elk, bison, and moose during a severe winter in the Jackson Valley, Wyoming.

Section B. Effects of Elk, Bison, and Domestic Cattle Herbivory on Both Native and Managed Grasslands in the Jackson Valley

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Rates of removal and responses of the grasslands to grazing ungulates in terms of production, biodiversity, and vigor. Is there evidence of overgrazing?

Assessment of potential management of wild ungulates in the Jackson Valley requires information about current forage production in habitats used by wintering elk and bison as well as current levels of consumption, or offtake, of that production by wild ungulates. Studies to determine production and offtake on this winter range were conducted from 1996-2001. Sampling over several years can provide managers and modelers information on the range of responses in these variables that can be encountered over several seasons and with varying levels of precipitation.

The potential for overgrazing of western rangelands is typically evaluated using one of the following sets of criteria:

- 1) The Production-Allowable Offtake Approach (Biondini et al. 1998). Production of annual green biomass is measured and the percent offtake (consumption) of this biomass is then estimated by clipping and comparing inside and outside of movable cages. The differences between the grazed and ungrazed (inside the cage) plots are accumulated. Unfortunately, this approach is subjective as levels of percent offtake are judged either “acceptable” or “too much”.
- 2) The Production-Sustainability Approach (McNaughton 1979, 1993; Milchunas and Lauenroth 1993; Frank and Groffman 1998). The production of grazed grasslands is compared with fenced, ungrazed grasslands to determine if the production of grazed sites is sustained. Fertility (nitrogen pools, mineralization rates) and production of the grazed sites is the primary concern, while changes in plant species is not.
- 3) Evidence of Overgrazing (Pengelly 1963; Westoby et al. 1989; Coughenour and Singer 1991; Fuls 1992). Overgrazed ranges are typically thought to possess the following: less production, increased bare ground, plant species alterations to less palatable species, accelerated erosion (more erosion rills, deeper erosional channels), pedestaled bases of plants, more rocks and pebbles on soil surface, and hedged plants.

- 4) Changes in Plant Diversity (Milchunas and Lauenroth 1993). Management of much of the world's grazing land is based primarily on changes in plant species composition. In particular, dominant individual species have been used as indicators of range condition under the increaser-decreaser-invader concept. Ungulates in national parks should not be allowed to exceed levels that impact these diversity values (Wagner et al. 1995). National Park Service (1988) policy states that the natural abundance and diversity of plants and animals should be maintained within the bounds of natural processes. The effect of ungulates on plant diversity may be variable in natural systems depending on environmental conditions, evolutionary history of grazing, and predator limitation (Collins and Barber 1985; Stohlgren et al. 1999). Management for maximum plant species diversity may, in some instances, include management for moderate or even high densities of ungulates. Thus, the grazing system and these major ecological relationships need to be well understood before managers can set goals for plant diversity.

We sampled Jackson Valley grasslands in order to apply these four approaches:

- A) We sampled offtake (percent of annual herbaceous biomass removed) in a very large number of plots located in 10 habitats over five years for both summer and winter grazing offtake. This large and representative sample of grazing offtake across the Jackson Valley landscape (Fig. 1.1) was gathered from a broad range in growing conditions varying from wet (1997) to normal (1998) to very dry (2001). In order to assess the effects of different use levels, we sampled percent offtake outside of five long-term exclosures and compared the plants to those inside the exclosures.
- B) We sampled herbaceous production inside (fenced) and outside of six long-term exclosures. We also conducted a study of nitrogen (N) pools, N mineralization rates, respiration rates, ungulate inputs (feces, urine), and N outputs in a sample of paired fenced-grazed sites. The findings from the N study are detailed in Part III of this report (Stottlemyer et al. 2003).
- C) We inspected the grazed plant communities for any of the traditional criteria for overgrazing.
- D) We sampled plant species diversity at grazed and ungrazed sites at five long-term exclosures.

METHODS

Annual peak production was sampled by clipping all vegetation within 0.25-m² circular plots inside 1-m² movable grazing exclosures that had been randomly placed at the beginning of the growing season in July 1996–1998, 2000, and 2001. All graminoids, forbs, and sub-shrubs within the plot were clipped and sorted into dead and live portions to measure annual peak standing crop. Vegetation was oven dried at 55° C for at least 48 hours and then weighed.

Winter herbaceous offtake (consumption) was determined in 1998, 2000, and 2001 by clipping in spring (prior to green-up), from inside and outside movable grazing exclosures placed at the

end of the previous growing season. Cages were randomly placed again after the spring sampling to capture the early summer consumption that occurs during the time elk are migrating to summer ranges. Percent consumption was calculated using the following formula:

$$\% \text{ consumption} = \frac{100 * (B_i - B_o)}{B_i}$$

where B_i = dry weight of biomass inside grazing cage, and B_o = dry weight of biomass outside of grazing cage. Summer offtake data were collected late June-late July throughout the study area by comparing production inside the grazing cages to standing crop outside the cages. We tested to see whether there was evidence of grazing optimization using second-order regression models of production against previous winter offtake, previous summer offtake, and total annual offtake.

In the Elk Ranch-Moosehead-Cunningham-Triangle X area of domestic livestock allotments, we conducted more detailed studies to differentiate consumption by wild ungulate species (moose, elk, bison, and pronghorn) and domestic livestock. We sampled sites used only by wild ungulates and we compared those to nearby sites (both irrigated and non-irrigated), used by both livestock and wild ungulates. Production and summer consumption data in areas grazed by livestock were collected in late June 2000 and 2001, before the arrival of livestock and again in late September, after livestock were removed. Weekly surveys of ungulate locations were used to apportion the relative consumption during the periods of livestock occupation of the areas.

We evaluated plant diversity and production responses to grazing with the Modified-Whittaker plot technique (Stohlgren et al. 1995). The Modified-Whittaker plot estimates species richness (number of species) and abundance (percent of cover) data at multiple spatial scales by using 1 m², 10 m², and 100 m² subplots nested within a 0.1 ha plot (Fig. 1.9). We located one tenth-hectare plots inside and adjacent to six long-term (30-60 years old) grazing exclosures in GTNP, NER, and BTNF. We chose plots with similar slopes, aspects, and soil and vegetation characteristics within each replicate. Each 20 m X 50 m plot was oriented with its long axis aligned down the fall line of the slope and located at least three meters from exclosure fences. One exclosure was located in wet meadow and willow, as opposed to the more xeric grasses and shrubs at the other sites. As a result, this site was not measured for diversity because of its lack of comparability to any potential paired site, but we did compare herbaceous production and offtake. Analysis of Modified-Whittaker data yields several types of information including: frequency, percent cover and average height for each species present; and frequency and percent cover by: origin (native or exotic), duration (annual, biennial, perennial), growth habit (forbs, graminoids, shrubs, succulents, trees, sub-trees), and by species with less than one percent average cover. We recorded percent cover by rock, soil, litter, standing dead wood, manure, down wood, and standing water for each plot. Modified-Whittaker plots were only measured once during the study. We measured herbaceous plant production annually from 3-5 randomly located 0.25 m² circular plots inside and outside of each exclosure following the methods described above. Plant species that we could not identify in the field were collected and identified at the Park herbarium. Plants that could not be identified at the species level were identified to genus or grouped as unknowns. We conducted all sampling in the first two weeks of June 2000 and in late June-early July 2001 and 2002.

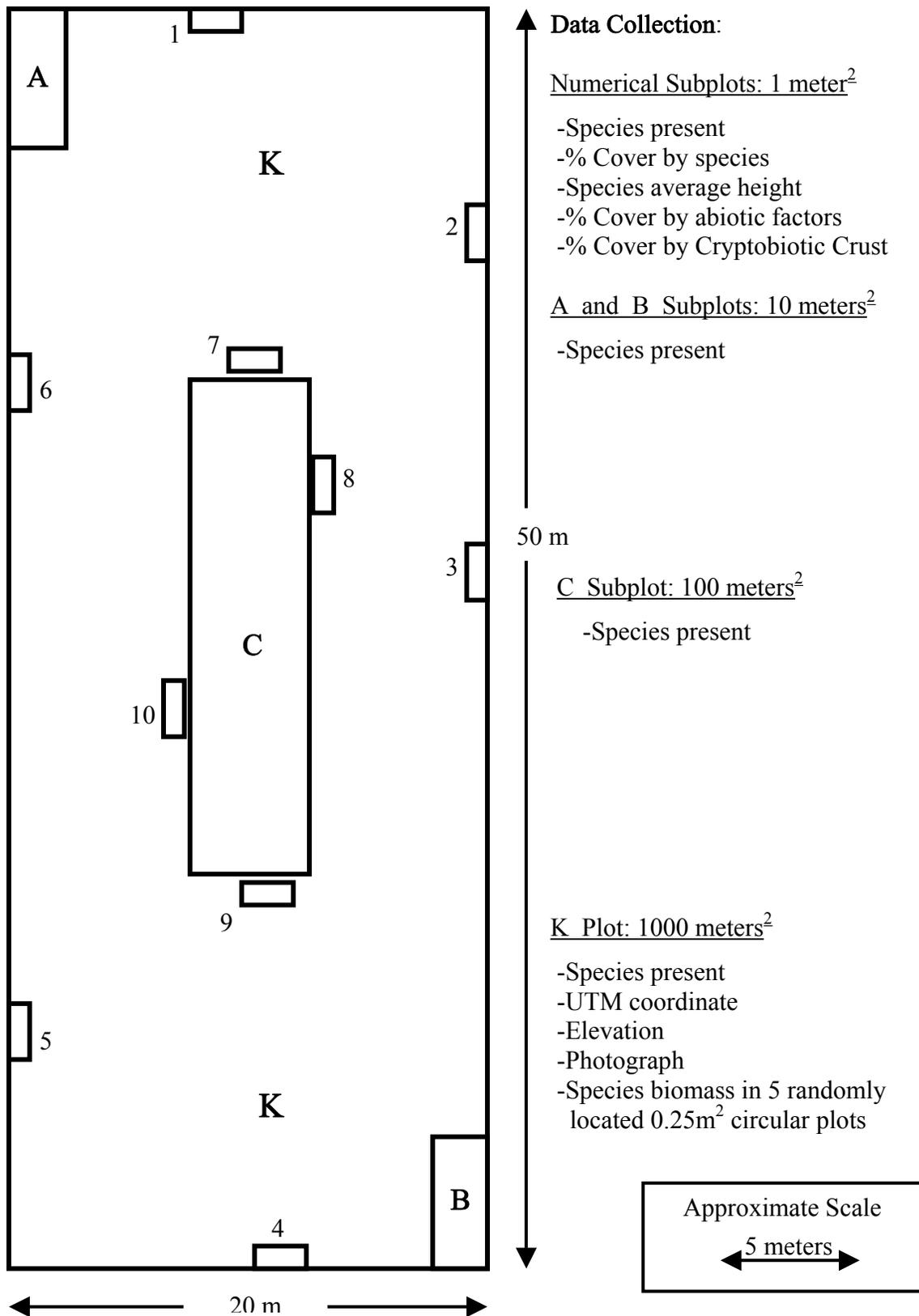


Figure 1.9. Schematic of Modified-Whittaker plot and data collection.

All statistical analyses were conducted using SysStat[®] (version 6.0). Jaccard's Coefficient (Krebs 1989) was used to compare species overlap (1000 m² plot data) between excluded plots and adjacent grazed plots. Jaccard's Coefficient was calculated using the following equation:

$$J=A/(A+B+C)$$

where A = the number of species that were found in both sites 1 and 2, B = species found in site 1 but not in site 2, and C = species found in site 2 but not in site 1. A comparison of two species lists resulting in a similarity coefficient of 1.0 indicates complete overlap, while a coefficient of 0.0 indicates no overlap.

The Shannon-Weaver (1962) diversity index was also used to measure the overall diversity of the plot. Higher index values indicate a more diverse community. Shannon's Index values were calculated with the following equation:

$$H = -\sum_{k=1}^s (P_k) \ln(P_k)$$

where P_k = the proportion of total cover contributed by species k, and s = the number of species found on a site.

Paired *t*-tests were used to compare differences in the frequency and percent cover by species' origin (native or exotic), duration (annual, biennial, perennial), and growth habit (forbs, graminoids, shrubs, succulents, trees, sub-trees) for the five enclosure sites. Analyses were conducted on the 1000 m² plot frequency, 1 m² plot frequency, and the 1 m² plot average frequency data to identify any scale dependent differences. Paired *t*-tests were also used to evaluate differences in production. Differences in Shannon's Diversity Index values (H) between grazed and ungrazed sites were tested using non-parametric methods (Kruskal-Wallis test).

RESULTS AND DISCUSSION

Wild Ungulate Ranges

Winter herbaceous consumption was greatest in burned sagebrush and mixed shrub areas in winter 1997-98 (Fig. 1.10). During the winter of 1999-2000, sagebrush, mixed shrub, mixed grass, and sedge areas were used heavily (>50% consumption of annual biomass). In winter 2000-2001, sage and burned sage areas were used at rates close to 50%, while mixed shrub areas were used at rates close to 60%. Summer consumption of herbaceous forages on our study areas was moderate on areas grazed by wild ungulates only, typically ranging from 15-30% use of the annual production with considerable annual variation (Fig. 1.10). The high degree of heterogeneity in plant productivity that is common in natural plant communities resulted in values of negative average consumption rates in a few sites that were subject to little or no grazing. Unfortunately, a much greater sample size would be necessary to eliminate these negative values and collecting such a large number of samples was too cost-, time-, and labor-intensive to be feasible in this study.

Shallow snow depths in 1999-2000 led to greater availability of herbaceous vegetation and resulted in heavier grazing in herbaceous-dominated sites that winter. There was high variability in consumption rates from year to year, which may be based on ungulate movements in response to weather, snowpack, or increased wolf activity. Apparently, summer elk grazing on select higher elevation meadows on summer ranges within GTNP may locally exceed 60-80% use

(Steve Haynes, GTNP, personal observation). Our study focused on winter and transitional ranges and, we did not sample many of the wet riparian meadows located west of the Snake River and meadows in the high elevation forested zone within the park.

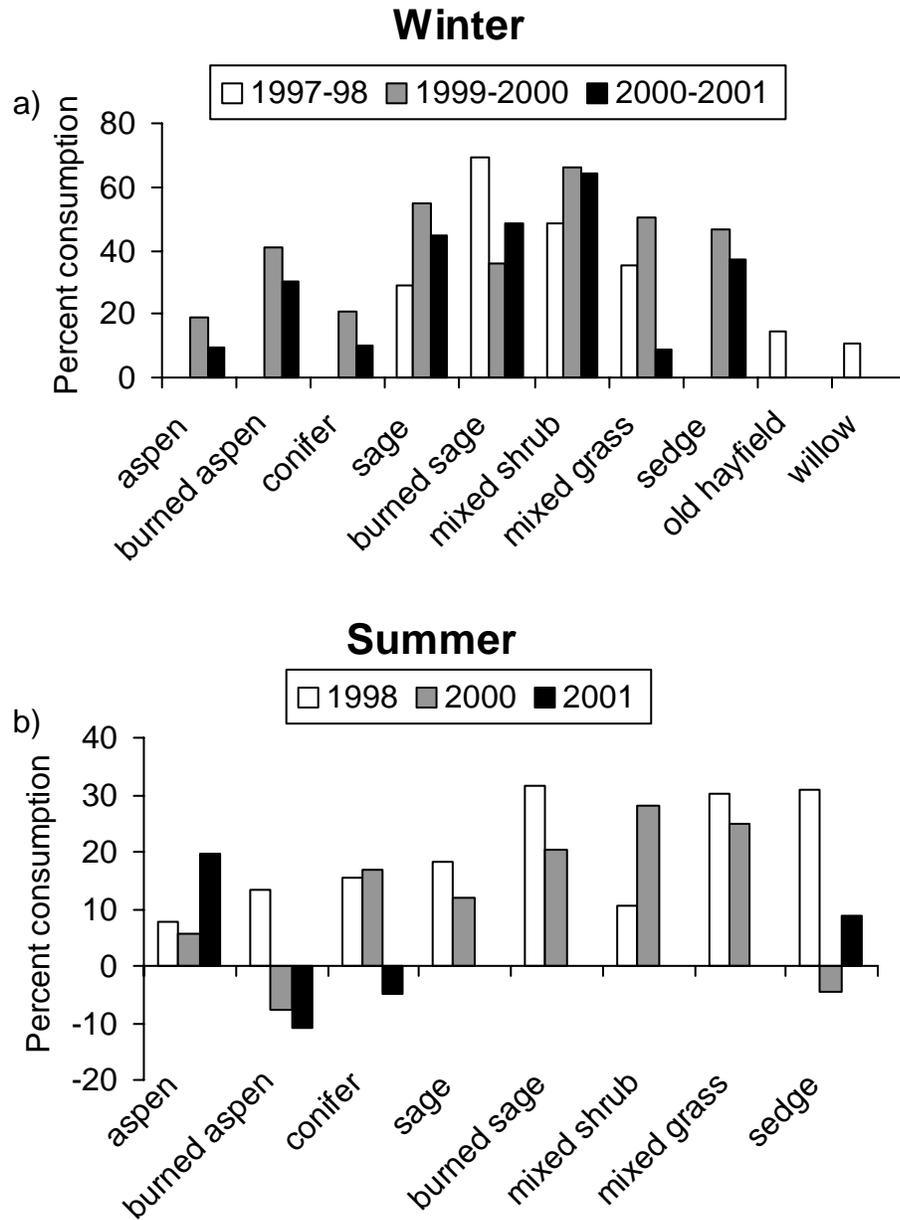


Figure 1.10. Winter (a) and summer (b) consumption rates in different vegetation types on ungulate winter range in Jackson Valley, Wyoming, 1997-2001.

Areas Grazed by Domestic Cattle

Early spring consumption by wildlife (before livestock grazing began) did not differ between irrigated and non-irrigated pastures (Fig. 1.11). Early spring consumption was generally very low and remained low throughout the summer in wildlife-only areas. Consumption rates on wildlife-only areas were significantly lower ($P=0.02$) than areas grazed by livestock (Fig. 1.11) during both summers. Areas of Kentucky bluegrass (*Poa* spp.) near Cunningham Cabin, which were naturally sub-irrigated, but not actively irrigated, were grazed particularly heavily by both livestock and wildlife. We estimated that a large amount of summer offtake on these grazing allotments could be attributed to cattle because over 50% of the total summer herbaceous offtake in irrigated pastures, 34% use in non-irrigated areas, and 85% use in subirrigated *Poa* areas occurred during the period when cattle were present. Concurrent with cattle grazing on these pastures, numbers of bison and elk drop 90-95% in these same areas (see page 47 onward). Thus, we conclude that most of the grazing during this period was by cattle.

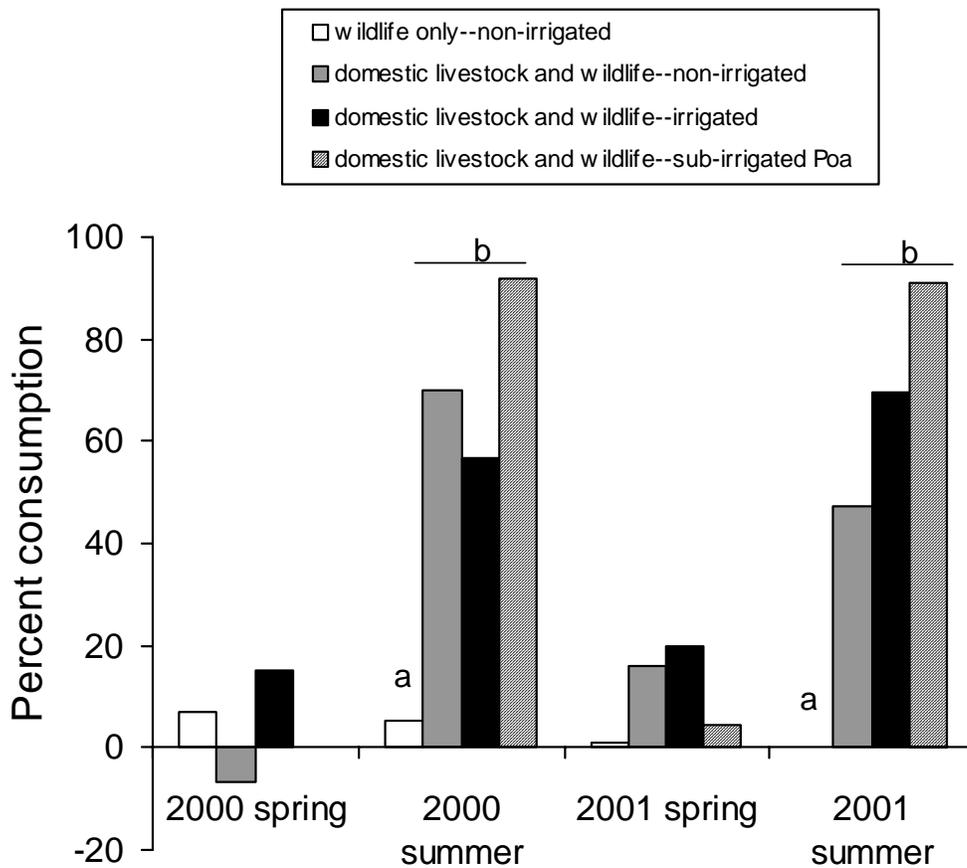


Figure 1.11. Comparisons of spring (prior to domestic cattle grazing) and summer offtake in domestic livestock allotments (wildlife plus livestock) vs. areas grazed by wildlife only in the Jackson Valley, Wyoming, 2000-2001. Different letters indicate significant differences.

Total herbaceous production also showed much annual variability. There was significantly lower production in both 2000 and 2001, which were drought years, compared to 1998, a more normal year (Fig. 1.12). Production values were similar between the years 1996-98. We covered a wide range of the natural variability in production within the four years of our study, since normal, wet, and extreme drought are represented in the years.

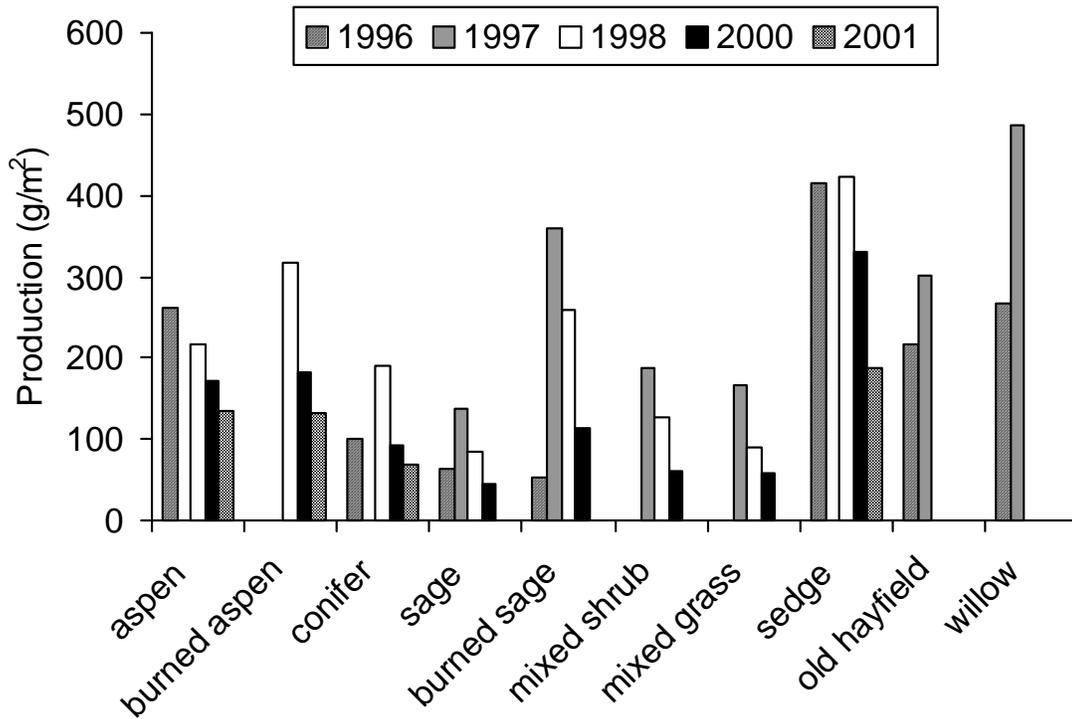


Figure 1.12. Annual herbaceous biomass production on ungulate winter range in the Jackson Valley, Wyoming 1996-2000.

As expected, total herbaceous production was greater ($P < 0.03$) in irrigated pastures than in non-irrigated areas (whether livestock grazed the site or not) and irrigation effectively lengthened the growing season. Herbaceous production on irrigated plots was double that of non-irrigated plots in June 2000, and three times greater by late September 2000 (Fig. 1.13). Standing crop available for wildlife in the fall was greatly reduced by the presence of domestic livestock on both irrigated and non-irrigated pastures. Active irrigation was minimal in 2001, so that irrigated pastures did not have significantly greater production than non-irrigated pastures until the end of September.

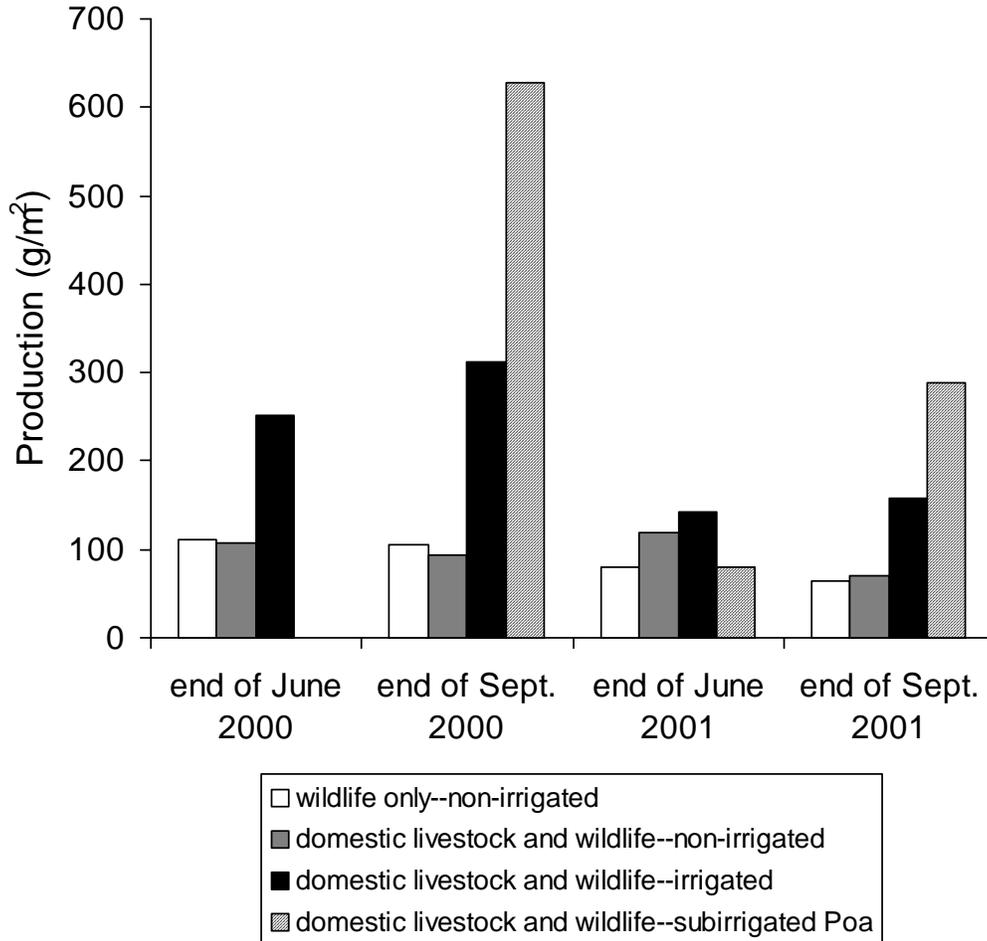


Figure 1.13. Differences in herbaceous standing crop biomass and production between irrigated and non-irrigated pastures that are grazed by wildlife and livestock in Grand Teton National Park, Wyoming 2000-2001.

We found some evidence for grazing optimization, but only due to winter grazing on dry grassland sites. We subdivided the vegetation into three types—(1) wet, highly productive sites (sedge, willow, irrigated pastures); (2) dry, grass-dominated types (sage, mixed grass, mixed xeric shrub, non-irrigated pastures, dry grasslands); and, (3) other productive, moist, forb-dominated sites (aspen, burned aspen, burned sage, and conifer). We found weak, though significant, evidence of grazing optimization in response to winter grazing on dry grassland types ($P=0.02$; $r^2=0.17$; Fig. 1.14). No evidence of grazing optimization was found in the other two more mesic types in response to winter grazing or in any type in response to summer offtake or total annual offtake. Total annual production peaked at winter offtake levels of approximately 40% consumption and begins to drop off rapidly at approximately 60% consumption. At around 80% consumption, production drops below the levels of fenced plots.

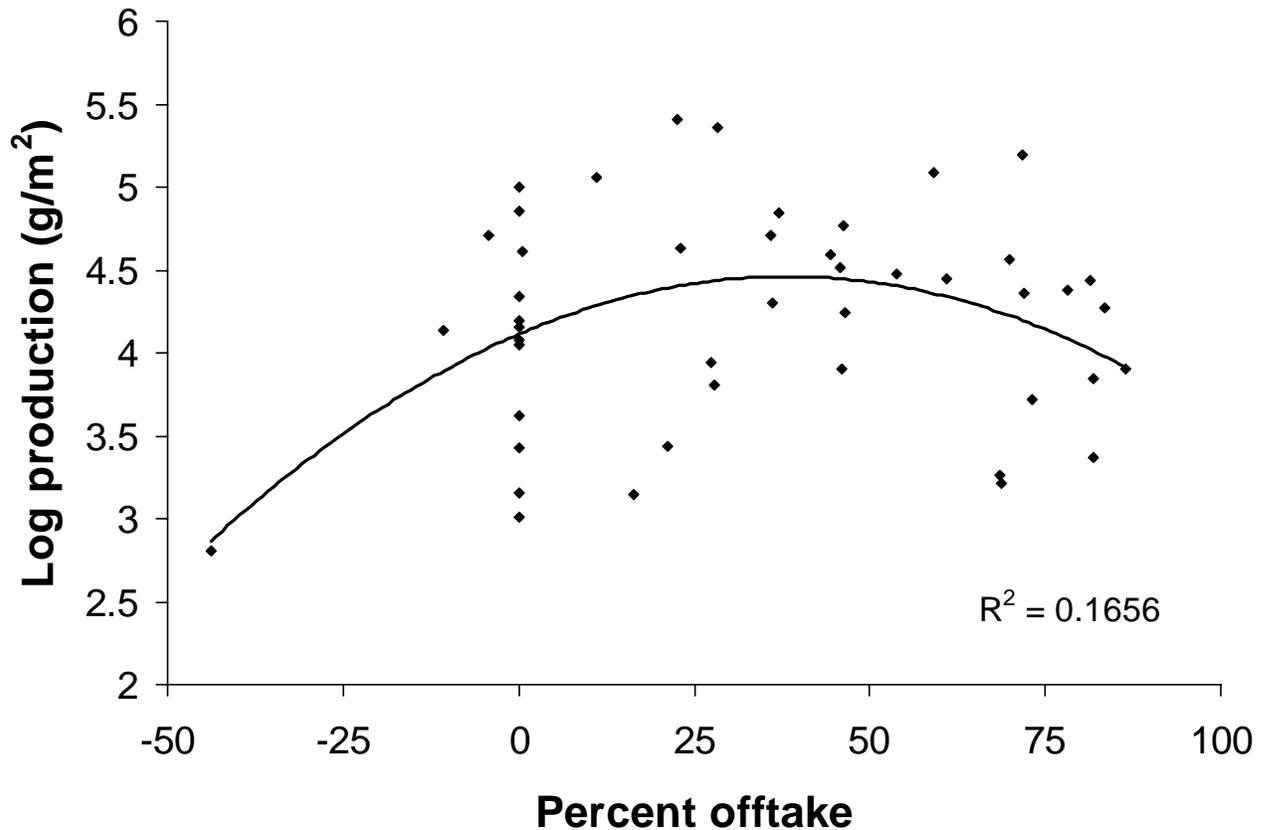


Figure 1.14. Grazing optimization is demonstrated by the relationship between herbaceous plant production and winter percent offtake (consumption) by wild ungulates in dry grassland sites in Jackson Valley, Wyoming 2000-2001.

Native ungulate grazing had little effect on plant species diversity. Species composition, frequency, and percent cover of grazed and fenced sites were very similar. Jaccard's Coefficient indicated a high degree of species overlap for grazed and fenced plots, ranging from 62.3 to 84.3% overlap (Table 1.4). On native grasslands throughout the Rocky Mountains, Stohlgren et al. (1997) found plants at 26 long-term grazing exclosures and their adjacent grazed plots averaged $57.9 \pm 2.8\%$ species overlap. This would seem to indicate that our sites have a high degree of overlap compared to other similar comparisons and thus there appears to be little effect of grazing on plant species diversity in our study sites. Comparison of Shannon's Diversity Index values showed no significant effects due to grazing ($P = 0.251$), also indicating similarity between grazed and fenced areas (Table 1.4). These sites shared five of the ten most abundant species. A few common forage species (*Agropyron spicatum*, *Poa pratensis*) were found in greater abundance on fenced sites (Table 1.5).

Table 1.4. Indices of community similarity (Jaccard's Coefficient) and plant species diversity (Shannon's Diversity Index) for grazed sites and long-term exclosures in the Jackson Valley, Wyoming.

Site	Jaccard's Coefficient (% overlap of species)	Shannon's Diversity Index (H)	
		Grazed	Fenced
Davis Hill	75.4	2.943	2.396
Large NER	84.3	2.226	2.119
Uhl Hill	75.0	2.451	2.393
Miller Butte	71.9	2.675	2.777
Lower Hoback	62.3	2.395	1.406

Table 1.5. Average percent cover of the most abundant species in grazed and fenced plots in the Jackson Valley, Wyoming.

Species	% Cover	
	Fenced	Grazed
<i>Artemisia tridentata</i>	11.1	9.6
<i>Agropyron spicatum</i>	7.6	4.2
<i>Poa fendleriana</i>	5.2	7.0
<i>Poa pratensis</i>	4.6	3.7
<i>Antennaria rosea</i>	3.6	3.9
<i>Phlox muscoides</i>	3.0	3.8
<i>Symphoricarpos oreophilus</i>	2.7	2.2
<i>Artemisia tripartita</i>	3.7	0.4
<i>Purshia tridentata</i>	6.9	0.6
<i>Hesperostipa comata</i>	5.1	1.4
<i>Gutierrezia sarothrae</i>	1.9	2.9
<i>Amelanchier alnifolia</i>	1.7	2.9
<i>Phlox hoodii</i>	1.6	2.6
<i>Agropyron smithii</i>	1.1	4.5

Analysis of the large (1000 m²) Modified-Whittaker plots also indicated few significant differences in plant species diversity between grazed and fenced plots. Grazed plots averaged 43.2 ± 6.6 ($O \pm SE$) species/1000m² while fenced plots averaged 40.0 ± 4.2 species/1000m² ($P=0.44$). At the same large scale, native species richness was greater, 28.9 ± 5.0 in grazed plots compared to 26.7 ± 2.6 in fenced plots ($P=0.58$); and exotic species richness was lower in grazed plots (3.3 ± 1.1) than in fenced plots (4.3 ± 0.9 ; $P=0.89$). Native species cover (1 m² plot data) was lower ($65.0\% \pm 9.6$) in grazed plots compared to fenced plots ($74.5\% \pm 3.2$; $P=0.35$).

There were slightly fewer shrub species (an average of 1.1 fewer species) found in grazed areas ($P=0.030$). The amount of non-vegetative cover (rock, bare soil, litter, duff, manure and wood) was 16.6% higher in grazed areas ($P=0.006$) and this was mainly due to the significantly greater amount of bare ground (bare soil) in grazed ($23.2 \pm 2.1\%$) compared to fenced ($6.4 \pm 1.9\%$; $P=0.008$) areas. There was 1.1% more cover by exotic species in grazed areas ($P=0.090$). No other significant differences between grazed and fenced plots were detected.

Total annual aboveground herbaceous biomass of grazed areas was greater ($43.1 \pm 10.9 \text{ g/m}^2$) than fenced plots ($34.1 \pm 12.4 \text{ g/m}^2$) in 2000 ($P = 0.055$). However, no significant differences were found in production when categories of herbaceous vegetation were inspected separately between grazed and fenced plots (forb, graminoid, subshrub, or individual species). In 2001, the total biomass was $93.9 \pm 22.0 \text{ g/m}^2$ on grazed plots and $76.4 \pm 18.7 \text{ g/m}^2$ in fenced plots, but this difference was not statistically significant ($P = 0.65$). In 2002, the trend was similar with production significantly greater on grazed ($151.0 \pm 37.1 \text{ g/m}^2$) than fenced ($88.9 \pm 16.5 \text{ g/m}^2$; $P = 0.078$) plots. Winter consumption was substantial at all sites (23-72%), except near the Gros Ventre enclosure (Fig. 1.15). Summer consumption rates on these winter and transition summer ranges were generally lower (15-30%), and this use occurred in early spring after green-up and before elk moved to summer ranges (Fig. 1.15).

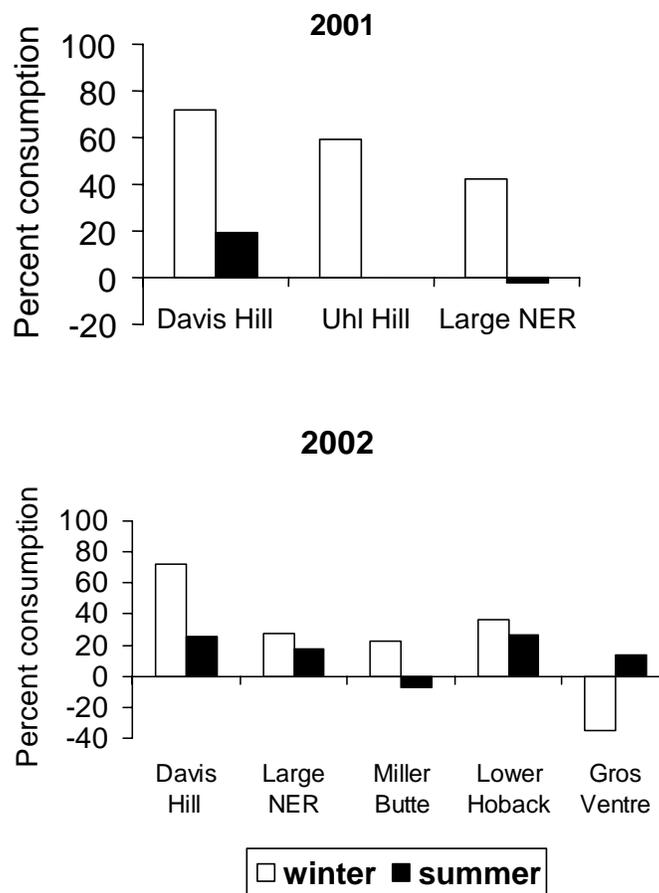


Figure 1.15. Winter and summer percent herbaceous consumption adjacent to long-term enclosure sites in the Jackson Valley, Wyoming, 2001 and 2002.

No sites had significant differences in total biomass between grazed and fenced plots in 2001. In 2000, the only individual sites that showed differences in production were Uhl Hill, which had

higher graminoid production on grazed sites ($P=0.08$), and Davis Hill, which had lower subshrub production in grazed sites ($P=0.06$). Davis Hill and Large NER exclosures had greater graminoid production on grazed plots in 2001 ($P\leq 0.03$). However, the Lower Hoback exclosure showed the opposite trend in 2001 with lower graminoid production on grazed sites ($P=0.08$). In 2002, both the Gros Ventre and Davis Hill exclosures had higher total production ($P\leq 0.04$, Fig. 1.16) in grazed plots. There was higher graminoid production in grazed plots at both sites ($P\leq 0.1$) and higher forb production at Davis Hill. At the Lower Hoback site in 2002, the grazed plots produced more forbs ($P=0.45$), but less graminoids ($P=0.089$).

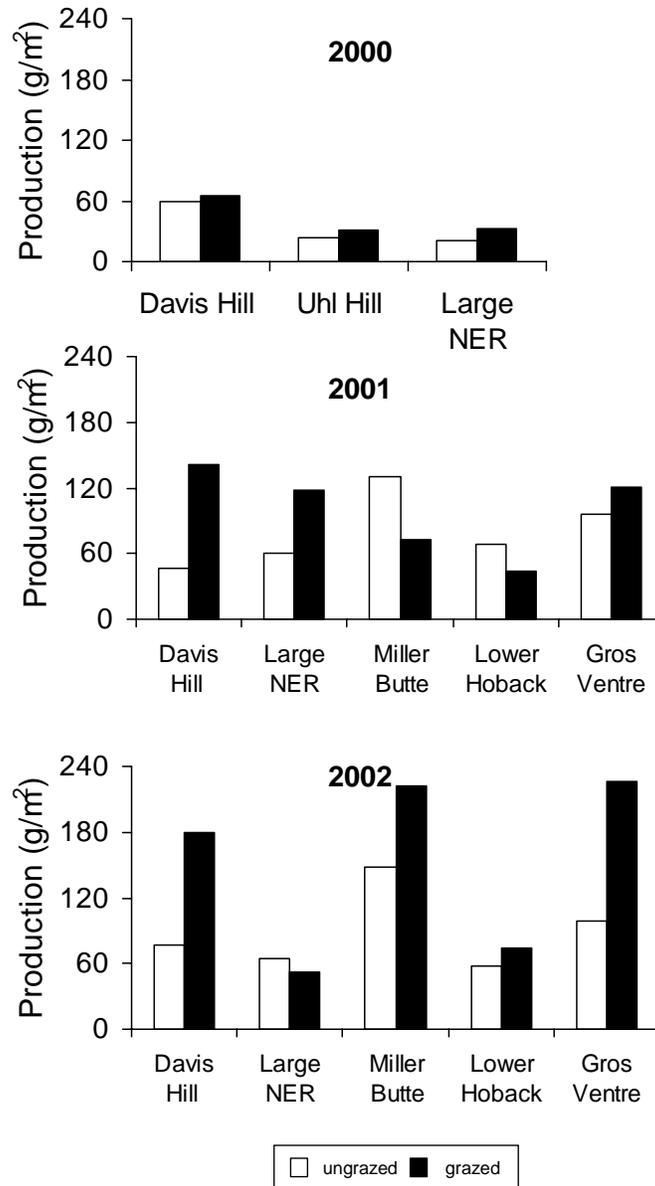


Figure 1.16. Herbaceous production differences between fenced long-term exclosure sites and adjacent grazed areas in Jackson Valley, Wyoming, 2000, 2001, and 2002.

CONCLUSIONS

- 1) We found no consistent reduced production due to grazing. The general tendency was for increased production on grazed sites (10 of 13 comparisons). We concluded there was compensation due to winter grazing. Apparently grazing optimization was occurring in Jackson Valley on dry grasslands in response to winter grazing.
- 2) Grazing offtake ranged from moderately high to very high across the Jackson Valley grasslands. Soil nitrogen mineralization rates (which produce highly usable N for plants) were double on grazed sites (Stottlemyer et al. 2003). These higher amounts of labile N on grazed sites likely account for the ability of the grazed plants (mostly grasses) to more than compensate for the grazing. This facilitation of N cycling due to grazing protects most Jackson Valley grasslands from being overgrazed, with the exception of a few of the most heavily grazed sites.
- 3) We found few negative influences of grazing on herbaceous species diversity and very minor effects on shrub species diversity. Grazed sites had an average of 1.1 fewer shrub species than fenced sites.
- 4) Some of our study results, however, are indicative of overgrazing. There was significantly higher (nearly 4x greater) percentage of bare ground, and slightly higher cover of exotic plant species in grazed areas. We did not study species changes in the managed grasslands and subirrigated *Poa* grazing lawns due to a lack of exclosures. It appears that native grasses cannot sustain the very high grazing levels at these sites (60-90%) and only Eurasian grasses (bromes, *Poa* spp., exotic wheatgrass) that are better adapted to sustain multiple grazing events each growing season were found on these sites.

Nitrogen processes may, in fact, be optimized at some intermediate level of ungulate herbivory as well. The work of Biondini et al. (1998) suggests this--nitrogen acceleration did not occur at the highest rates of offtake, such as 80 or 100%. To verify this for the Jackson Valley would require more work. Preliminary work on Jackson Valley sites (see Part III, Stottlemyer et al.) indicated increased mineralization on grazed sites. Future work should be focused on identifying the relationship between nitrogen acceleration, grazing offtake, and soil moisture levels. It would also be necessary to sample within more defined strata of grassland types and to sample some of the types of special concern such as summer range meadows within GTNP.

Grazing optimization has rarely been verified as we have done here for the Jackson Valley. A great deal of information can be obtained from optimization curves (Fig. 1.14), depending upon one's perspective. For example, if maximum production is a manager's goal—underutilized range (in this case, <40% consumption), optimal use (40-60% consumption), and overutilized forage use rates (>80% consumption) can be identified (Fig. 1.14). If maximum forage production is not a goal (e.g. in a national park) other information, such as the effect of ungulates on increasing their own ecological carrying capacity (i.e. at peak levels of forage optimization), and the magnitude of that increase, can be identified.

Effects of cattle on forages and habitats used by native ungulates

We studied the amounts of summer range habitat overlap between cattle and native ungulates and their combined use of forages. Our objectives of this work were:

- 1) To document any locations of co-use of areas by cattle, horses, bison, elk, and pronghorn.
- 2) To document any active avoidance of the cattle by the native ungulates.
- 3) To determine the amount of combined summer use of forages by bison and cattle to estimate the extent to which cattle grazing limits forage for bison.
- 4) To determine if cattle consume forages in summer that are needed by elk during the winter. (Bison have few forage needs in winter, since, at present, they primarily use the feedgrounds.)

METHODS

We quantified effects of domestic ungulates on wild ungulate density and distribution during the summers of 2000 and 2001. We surveyed wild ungulates (elk, bison, pronghorn) and domestic ungulates (cattle, horses) in an area where a herd of 1000 cattle were grazed in late summer. This area is centered on the Triangle X, Cunningham, Moosehead Flats, and Elk Ranch grazing allotments (Fig. 1.17). We looked at the distribution and densities of wild ungulates before, during, and after cattle were put on the grazing allotments. A few horses were present throughout the summer on most of the allotments.

We conducted 14 systematic surveys between May 31, 2000 and August 3, 2000, and 19 additional weekly surveys between May 24, 2001 and September 27, 2001. We recorded and mapped all elk, bison, pronghorn, mule deer, horse, and cattle groups observed during each survey. The survey area was covered by vehicle on established roads, usually with two observers. Most of the survey area was visible from the vehicle, although in some locations observers left the vehicle to survey areas obscured by shrubs or topography. Some areas were not visible at all. The same routes, and the same short (20-200 m) walks to observation points were covered during each survey.

In 2000, observations were plotted on 1:24,000 USGS topographic maps. We conducted surveys in the evening and sometimes at first light. Eight surveys were completed before cattle were put on the grazing allotments, and 6 were conducted while cattle were present in the survey area. Based on the larger numbers of animals observed during morning surveys in 2000, we always conducted morning surveys in 2001, beginning at first light. We conducted 9 surveys before cattle were present, 4 while cattle were present, and 6 after cattle were removed from the survey area. Observations were plotted using a Global Positioning System to determine the observer's location, then using a laser range finder and compass to calculate the animals' position. In cases where animals were out of laser range, observations were plotted on 1:24,000 USGS topographic maps.

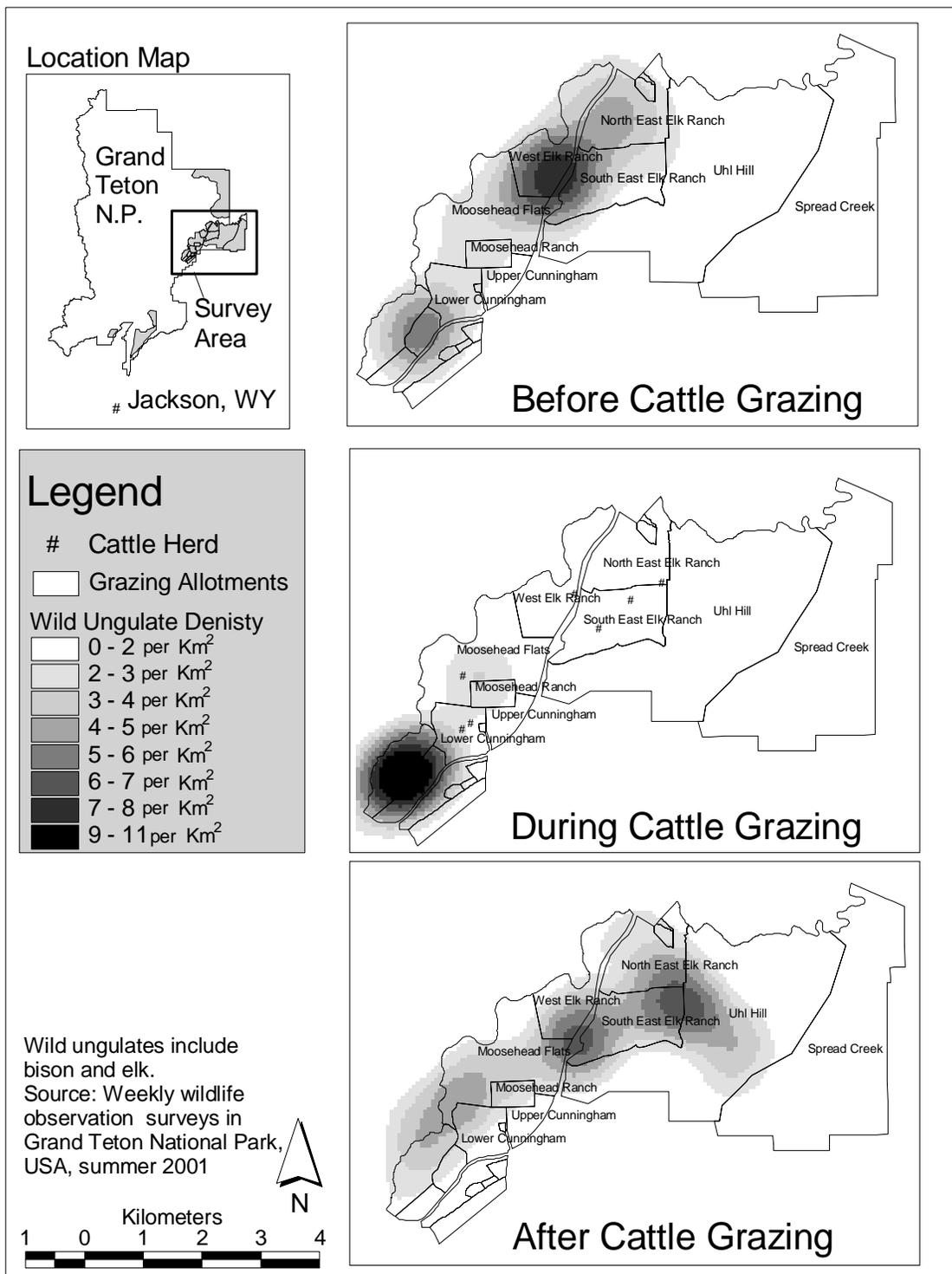


Figure 1.17. Wild ungulate distribution and density before, during and after cattle put-on dates in Grand Teton National Park, Wyoming, summer 2001.

We calculated the density of wild ungulates before cattle, while cattle were present, and during the first six weeks after cattle were taken out (2001 only) of the survey area using ArcView's density function with a kernel estimator, and a 2 km search radius (Fig. 1.17). We tested to see if the number of elk, bison, and pronghorn differed before, during and after cattle were put on grazing allotments in Grand Teton National Park. In 2001, we examined cases of elk and bison presence at the same time as cattle on individual allotments and at the same time as cattle were present anywhere in the entire survey area. We used the one-way rank sum Wilcoxon test, a nonparametric statistic comparable to a *t*-test, because a *t*-test was inappropriate in this case due to the small sample size and lack of normal distribution of the data.

We measured herbaceous standing crop on the four Kelly Hayfield pastures (NW, SW, NE, SE) and the three North Gros Ventre pastures (South, Middle, and North) in mid-July 2001 by clipping all herbaceous vegetation in five 0.25m² circular plots at each site. At the time of sampling, the NW Kelly and the North Gros Ventre South Pasture had been grazed by cattle for 5-7 days. All other pastures had only been grazed by wildlife in 2001. The Middle and South portions of the North Gros Ventre pastures were paired for comparisons, and highly productive areas near Blacktail Butte were sampled and compared separately from less productive areas away from the butte. The NW Kelly pasture was paired for comparison with the SW Kelly pasture. Offtake levels on cattle-grazed pastures were estimated following the formula:

$$\frac{SC_u - SC_g}{SC_u}$$

where SC_u = the average standing crop biomass of the ungrazed pasture and SC_g = the average standing crop biomass of the cattle-grazed pasture. We sampled locations in the NW, SW, and SE Kelly Hayfields during a normal precipitation year (1996), a wet summer (1997), and a drought (2001). Due to uneven sample sizes, we used non-parametric tests (Kruskal-Wallis One Way Analysis of Variance) to determine differences between years. We also compared production and offtake rates on the Mormon Row Burn area of Antelope Flats. This area is widely used by bison during the summer.

We measured offtake levels on the irrigated East Elk Ranch in mid-August 2001, after 6-8 days of cattle grazing. On the non-irrigated West Elk Ranch pasture, cattle had been grazing for at least six days when we measured offtake. Because of the patchiness of grazing, two plots outside the grazing cages were measured. Selection of one of the uncaged plots followed the methods we previously described, while the other uncaged plot was selected from the nearest area to the cage that was "obviously" grazed by cattle. We estimated an "average" offtake (or consumption) rate that was assumed to be the mean offtake level over all forages on these pastures. We also estimated a "preferred" offtake rate that was assumed to be the level on preferred forages and was determined using the "obviously" grazed plot.

Average summer bison densities are high in the vicinity of the Kelly Hayfields, North Gros Ventre Pasture, and Antelope Flats (Fig. 1.18). Lower productivity and increased livestock grazing pressure in this area could reduce the forage base available to bison and increase their use of other foraging areas. To determine this, we used aerial surveys of bison locations that were conducted every other week during the summers of 1997-1999. We calculated bison density for each summer month (May-Sept) for each year using ArcView's density function. We

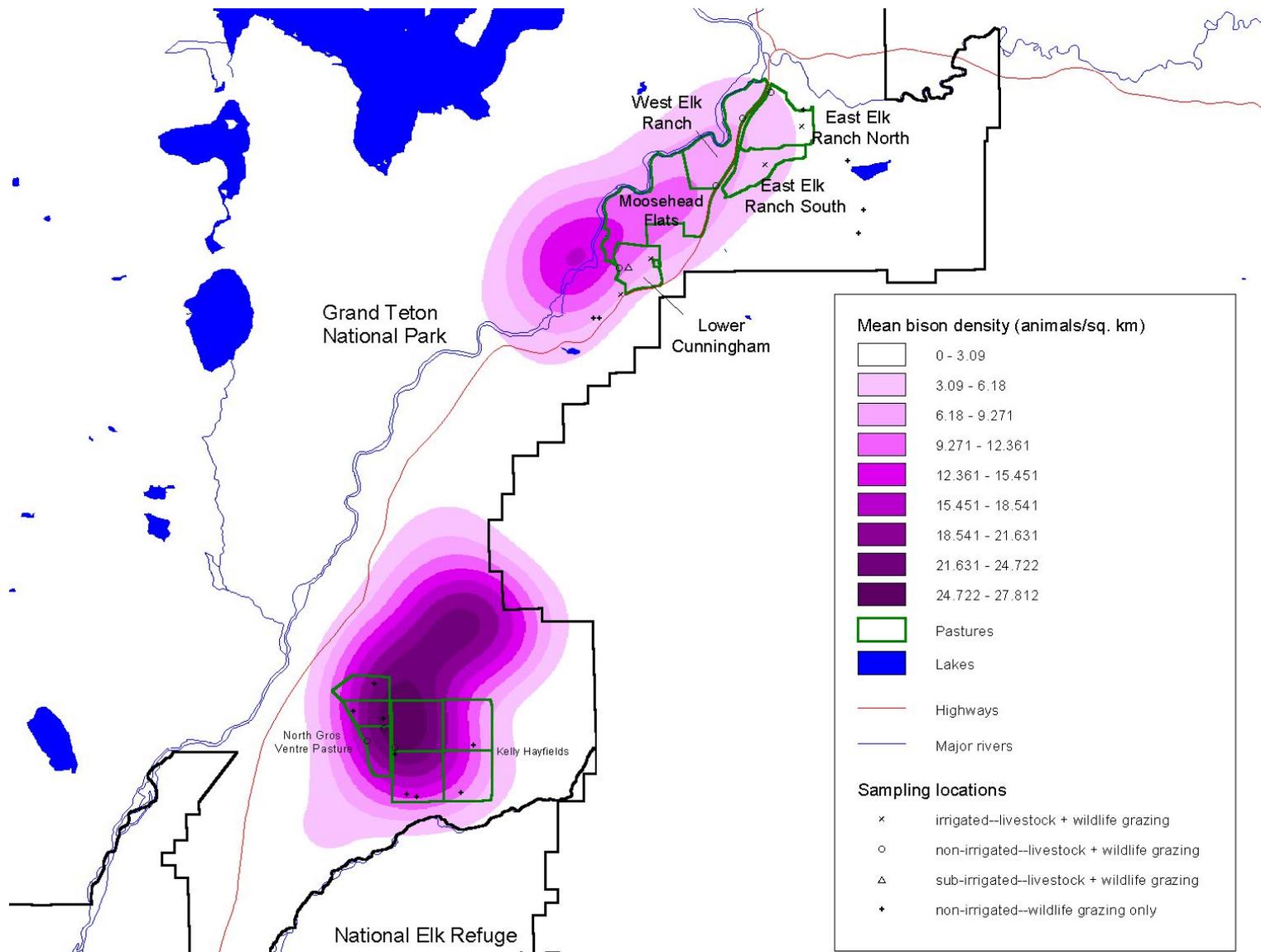


Figure 1.18. Relative summer bison density (averaged over 3 summers, 1997-1999), livestock grazing areas, and sampling locations in Grand Teton National Park, Wyoming.

then averaged all months for each year to get an average summer density each year, then averaged all available years (Fig. 1.18). Based on our standing crop biomass measures, we determined the forage available on this core of the bison summer range in August 2001. We then calculated the forage requirements for the bison herd between August and the end of October 2001. By late October-early November, the majority of the bison herd typically moves south several kilometers onto the NER. Estimation of forage requirements follows the methods of Hobbs et al. (2003). We calculated average daily forage consumption for each bison assuming each animal consumes dry matter equivalent to 2% of its body weight each day. Average body size for 4 sex and age classes were estimated from literature (Meagher 1973, Houston 1982), and year 2000 population counts for each sex/age class were obtained from GTNP biologists (Table 1.6). Sub-adult animals were grouped with adults. We used this information to estimate herd size in 2001, calculating a calf crop that was 19% of total population size (as per 2000), 10% mortality of previous years calves, and 5% mortality of all other age classes (Table 1.6). This estimate seems to fit with current population size estimates in 2001 of approximately 650 bison (Steve Haynes, GTNP, personal communication).

Table 1.6. Average estimated body weight and numbers of bison in each age/sex class for the Jackson bison herd in Grand Teton National Park, Wyoming.

Age/sex class	Average body weight (kg)	2000 population size	Estimated 2001 population size
Calves	160	90	105
Yearlings	270	90	81
Cows	585	198	231
Bulls	900	195	228
Total		573	645

RESULTS AND DISCUSSION

Native Ungulate-Cattle Distributions

Native ungulates avoided pastures during the period when domestic cattle grazed there. In 2000, our surveys showed that before cattle were present, the average numbers of elk, bison, and pronghorn seen per survey were 112.9, 44.5, and 5.8, respectively. During cattle grazing, the averages dropped to 65.3, 15.8, and 5.3, respectively. No surveys were conducted after cattle were removed from the study area. Both elk and bison numbers dropped during cattle grazing ($P = 0.05$ and $P = 0.08$, respectively), but there was no change in pronghorn numbers ($P = 0.40$; Fig. 1.19). Elk and bison use dropped in every individual allotment while the cattle herd grazed the pasture (Table 1.7). The average number of cattle grazed on the area was 1,011.3. The average number of horses before cattle grazing was 22, during cattle grazing it was 33.8.

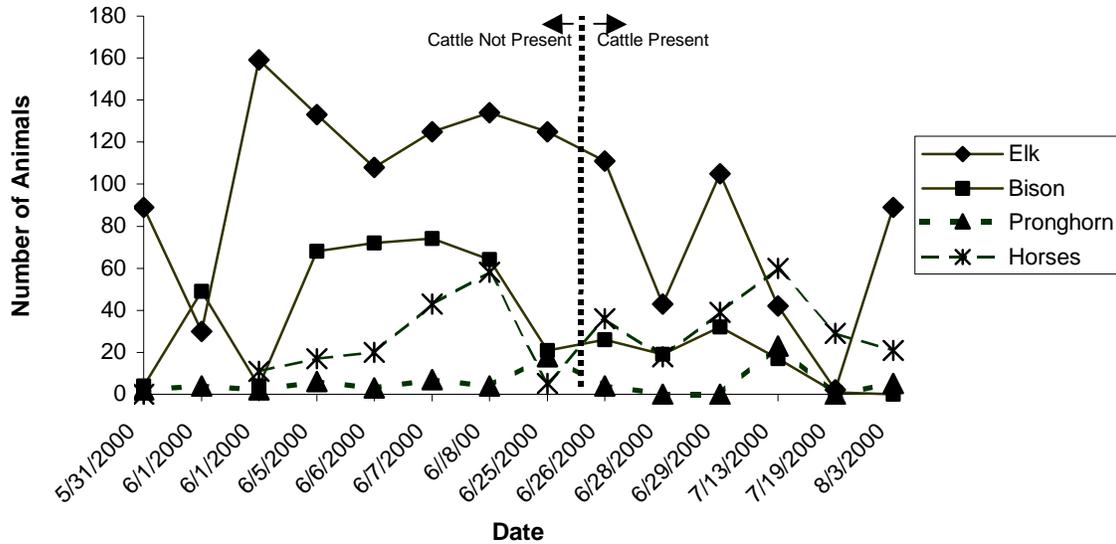


Figure 1.19. Total numbers of wild ungulates seen during wildlife observation surveys in the Jackson Valley, Wyoming, summer 2000.

Table 1.7. Average elk and bison counts per survey on Grand Teton National Park, Wyoming grazing allotments before and during cattle grazing, 2000.

Grazing Allotment	Bison		Elk	
	Before Cattle Grazing	After/during Cattle Grazing	Before Cattle Grazing	After/during Cattle Grazing
North East Elk Ranch	0.67	0.00	8.42	0.00
South East Elk Ranch	3.64	0.67	15.27	0.67
Lower Cunningham	2.38	0.00	16.00	1.33
Uhl Hill	11.85	0.00	9.85	0.00
West Elk Ranch	15.13	2.17	26.63	14.50

In 2001, we observed an average of 68.9 elk, 56.7 bison, and 7.4 pronghorn per survey before cattle were present. While cattle were in the survey area, the numbers dropped to 21.2, 24.3, and 0 respectively. After the cattle were taken out of the survey area the counts increased to 63 elk, 81.2 bison, and 3.7 pronghorn per survey (Fig. 1.20). The average number of cattle grazed on the area was 1,002.5. The average number of horses per survey before cattle was 74.2, 17.3 while cattle were present, and 33 after cattle. When the survey area was examined as a whole, we did not observe any significant differences in elk or bison numbers before, during, or after cattle (Table 1.8).

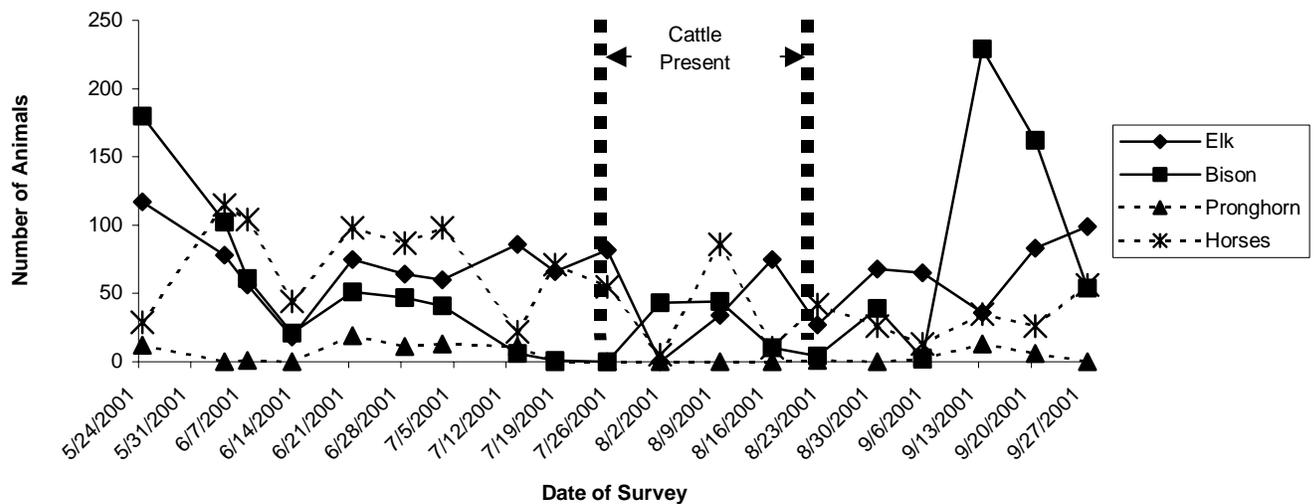


Figure 1.20. Total numbers of wild ungulates seen during wildlife observation surveys in the Jackson Valley, Wyoming, summer 2001.

Bison numbers in cattle-grazed allotments were greater before cattle were present when compared to when cattle were present ($P < 0.001$). Bison numbers on the cattle-grazed allotments increased again after cattle were removed ($P = 0.094$). Bison numbers were higher after cattle were removed than before cattle grazing ($P = 0.004$). Average elk numbers were greater before cattle than when cattle were present ($P \leq 0.0041$). On the same allotments where cattle were grazed, elk numbers increased again after cattle were removed ($P = 0.055$). However, this number was lower than the number of elk seen prior to cattle grazing ($P = 0.025$).

Numbers of some wild ungulate species dropped to zero, or near zero, during observation sessions immediately prior to the arrival of cattle on the northern pastures. However, activity on these cattle grazed pastures begins in advance of cattle arrival when range hands arrive to fix fences and set out salt blocks in preparation for the cattle. In addition, since cattle trail in slowly from the south, their impending arrival can be heard before their actual appearance on these grazing allotments. The combination of these factors may lead to movement of wild ungulates out of the area prior to the actual presence of grazing cattle. The fact that the numbers of wild ungulates increased following the removal of cattle in 2001 gives a strong indication of their avoidance of these areas during the cattle grazing period.

In 2000, before cattle, we observed wild ungulates mostly in the Elk Ranch area with a second concentration to the south by the Cunningham pastures and some use of the Uhl Hill allotment. While cattle were present, the pattern of use shifted away from cattle to Uhl Hill, the area south of Cunningham, and the northwest corner of the Elk Ranch. After cattle, the wild ungulate activity on the West Elk Ranch shifted from the southern portion of the allotment to the northern part. Most of the domestic ungulate use of the West Elk Ranch is in the southern portion. In the Lower Cunningham-Triangle X area, the wild ungulate use moved west and away from domestic use. Similarly, in 2001 before cattle were present in the survey area, bison and elk used the Elk Ranch allotments heavily, with a second center of use south of the Cunningham pastures (Fig.

Table 1.8. Comparison of elk and bison abundance in response to cattle grazing in Grand Teton National Park, Wyoming, 2001. Entire survey area encompasses all grazing allotments as opposed to only those that were being grazed by cattle at the time of survey.

Condition		Calculation	Entire survey area	Cattle-grazed allotments only
Bison	Before Cattle	Average number of animals	56.70	7.12
		Number of observations	9	45
	Cattle Present	Average number of animals	24.25	0.50
		Number of observations	4.00	20.00
		<i>P</i> value with before cattle	0.26	0.0007
	Cattle on same allotment	Average number of animals		0
		Number of observations		6
		<i>P</i> value with before cattle		0.0001
		<i>P</i> value with during cattle		0.3421
	After cattle	Average number of animals	81.83	7.67
		Number of observations	6	30
		<i>P</i> value with before cattle	0.95	0.004
		<i>P</i> value with during cattle	0.47	0.094
		<i>P</i> value with same allotments		0.022
	Elk	Before Cattle	Average number of animals	68.89
Number of observations			9	45
Cattle Present		Average number of animals	21.22	0.6
		Number of observations	4	20
		<i>P</i> value with before cattle	0.54	0.004
Cattle on same allotment		Average number of animals		0
		Number of observations		6
		<i>P</i> value with before cattle		0.0003
		<i>P</i> value with during cattle		0.1626
After cattle		Average number of animals	63.00	4.37
		Number of observations	6	30
		<i>P</i> value with before cattle	0.95	0.026
		<i>P</i> value with during cattle	0.61	0.413
		<i>P</i> value with same allotments		0.055

1.17). Fewer wild ungulates were observed after cattle were put onto grazing allotments, and those that remained moved south, far away from cattle use. After the cattle were removed, wild ungulates returned to allotments grazed by cattle, but in lower densities, particularly the Elk Ranch pastures.

A drought in 2001 may have caused some changes in density and distribution. In 2000, wild ungulates made frequent use of the non-irrigated Uhl Hill and Spread Creek allotments, while there was almost no use of these allotments in 2001 (Fig. 1.17). In 2001, an average of 48 elk were seen per survey while cattle were present, while an average of 65 elk per survey were observed in 2000. However, bison may have actually increased – an average of 16 in 2000 while cattle were present but 24 in 2001. This may be because the cattle grazed allotments south of our survey area heavily before being brought north. This was done in an attempt to lessen the impact

of cattle grazing during the drought on the Elk Ranch-Cunningham-Moosehead-Triangle X allotments. Wild ungulates used our survey area both in the summer and winter months, and the goal of park management was to leave some forages in the northern grazing lands for wild ungulates in winter. Bison have historically used the areas around Kelly/Mormon Row throughout the entire summer, but due to the extraordinarily heavy cattle grazing in 2001, they may have left in favor of pastures in the survey area.

Standing crop biomass was significantly lower in 2001 than either 1996 or 1997 ($P \leq 0.10$; Table 1.9) in the Kelly Hayfields. Since 1997 was a very wet year with significantly greater biomass than 1996, we made closer examination of differences between 2001 and 1996. Offtake levels were extremely high in both the productive (90% offtake) and non-productive (76% offtake) areas of the South sub-unit of the North Gros Ventre pasture. Offtake on the NW Kelly pasture was 35% after 7 days of grazing. However, the NW Kelly pasture is 3 times larger than the South portion of the North Gros Ventre pasture (Table 1.10). Production was significantly lower (48-91% lower) on the Antelope Flats/Mormon Row Burn area than any other year recorded ($P = 0.004$), but offtake levels, primarily by bison, were similar to other years and averaged around 17%.

Table 1.9. Comparison of standing crop biomass on the Kelly Hayfields between wet (1997), average (1996), and drought (2001) years. 1997 crop was significantly greater ($P < 0.05$) than both 2001 and 1996.

Pasture	Standing crop biomass (g/m ²)					P-value
	2001 (mean ± se)	2000 (mean ± se)	1998 (mean ± se)	1997 (mean ± se)	1996 (mean ± se)	
Kelly North	43.6 ± 13.5			481.8 ± 10.7	257.2 ± 36.1	0.014*
Kelly Central	86.7 ± 5.5			435.7 ± 59.9	136.0 ± 9.7	0.025*
Kelly South	66.9 ± 7.6			461.5 ± 102.1	105.0 ± 14.2	0.101*
Antelope Flats (Mormon Row burn)	65.6 ± 11.6	127.0 ± 20.5	213.0 ± 10.2	717.5 ± 128.3	174.1 ± 55.6	0.004**

*P-value between 1996 and 2001

** P-value between 2001 and all other years

Percent offtake by wildlife by late June was not significantly different between 2000 and 2001 ($P > 0.10$) in the Elk Ranch-Lower Cunningham-Triangle X pastures. However, production was significantly lower (44-66% lower) in 2001 for irrigated pastures than all other years ($P = 0.02$, Kruskal-Wallis test statistic = 9.85; Fig. 1.11). Production on non-irrigated livestock pastures and non-irrigated areas grazed by wildlife only, was not different between 2000 and 2001 ($P > 0.10$). Offtake on the East Elk Ranch irrigated pastures was high (>60%) after only a few days of grazing by cattle (Table 1.11). Consumption was much higher on the East Elk Ranch where elk are concentrated in a smaller area compared to the larger West Elk Ranch-Moosehead Flats allotments (Table 1.11). Offtake was greater on the north pasture of the East Elk Ranch than the south pasture, but offtake on the non-irrigated part of this north pasture was about half as great as

on the irrigated sections. Already the offtake rates on these pastures exceed generally accepted sustainable levels, and further grazing may impact future productivity of these areas.

Table 1.10. Production and pasture size for the Kelly and North Gros Ventre pastures, Grand Teton National Park, Wyoming, July 2001.

Pasture	2001 standing crop biomass (g/m ²) mean ± se	Area (km ²)
North Gros Ventre		
South--productive	14.2 ± 4.0	0.88
South--non-productive	17.1 ± 7.1	
Middle--productive	140.4 ± 10.9	1.40
Middle--non-productive	71.5 ± 8.8	
North	142.1 ± 19.4	1.24
Kelly Pastures		
NW	43.6 ± 13.5	2.60
SW	67.9 ± 10.3	2.59
NE	47.4 ± 11.4	2.52
SE	38.8 ± 6.4	2.51

Table 1.11. Offtake rates on average and for "preferred" areas of the East and West Elk Ranch pastures after 6-8 days of cattle grazing in late July-early August 2001, Grand Teton National Park, Wyoming.

Pasture Locations	Offtake rate (%)	
	All forages	Preferred forages
Irrigated pastures ^a	60.8 ± 20.4	67.8 ± 5.7
East Elk Ranch North Pasture	81.2 ± 8.1	73.5 ± 7.2
East Elk Ranch South Pasture	40.4 ± 18.8	62.0 ± 13.6
Non-irrigated pastures ^a	38.3 ± 4.0	45.8 ± 7.6
East Elk Ranch North Pasture	36.8 ± 21.2	60.9 ± 17.7
West Elk Ranch--North End ^b	32.1	40.2
West Elk Ranch--South End	45.9 ± 25.1	36.3 ± 20.0

^aMean of sites sampled for this category.

^bOnly one cage available for sampling--all other cages destroyed by ungulates

We estimated that the bison herd would need 634,580 kg of forage still available on their current core summer range to meet their requirements from August 2001 until they moved onto the NER around the beginning of November 2001 (82 days). Cattle forage use included losses due to trampling and therefore used approximately 13.5 kg per animal per day (Steve Haynes, GTNP, personal communication). The 841 cattle grazed on park lands in 2001 required 11,442 kg of forage per day. Estimated total available standing crop in the area where bison densities were >3 bison/km² was 9,081,218 kg in 2001. However, 14.26 km² of the area falling within the >3 bison/km² density contour was used less than 3% of the time by bison and apparently were not preferred areas of use. Therefore, we felt it was more accurate to also summarize the available forage in terms of area used by bison greater than 3% of the time. Using this area, standing crop on the core preferred bison summer range was estimated at 7,833,385 kg in 2001. The East Elk

Ranch standing crop estimates were adjusted for 38 days of bison grazing (the time period from sampling at June 20 to July 28, 2001 when cattle were put on the East Elk Ranch) at an approximate density of 4 bison per km² in this area (Fig. 1.18) and using an average bison body size of 485 kg. The West Elk Ranch-Moosehead Flats-Lower Cunningham complex standing crop estimates were adjusted for 52 days of bison grazing (June 20-August 10, 2001) at an average density of 8 bison per km². There was greater bison use in this area because cattle were only trailed through and previous observations show that bison continue to use this area during the summer, whereas they tend to move off the East Elk Ranch when cattle arrive (Fig. 1.17). We calculated standing crop on all allotments plus the Kelly Hayfield and North Gros Ventre pastures in August 2001 at 2,145,465 kg (Table 1.12).

Only 756,723 kg of standing crop herbaceous forage remained on the Kelly Hayfield-North Gros Ventre pastures by mid-August 2001 and little forage remained beyond the estimated needs of the bison in this area alone (Table 1.12). Forage still remained on the East Elk Ranch, but less than would have been required for cattle until the end of September 2001 and this would require grazing at ~88% offtake of 2001 production. If cattle continued grazing on the Elk Ranch, almost no forage would be available in these pastures in 2001 for bison and elk moving to winter range. This did not leave much room for error in the timing for moving animals between pastures, or for less than complete use of some forages on some areas. An average of 34% of production on the northern pasture complexes are willow or wetland/sedge, which may be unpalatable and/or highly sensitive to grazing. These estimates may be conservative since calves of domestic cattle were not included as individuals in the number of cattle grazing in the park, and these calves may remove a greater amount of forage late in the season when they are older.

Estimated total herbaceous production on core bison summer range in 2001 was 11,731,185 kg when all forage areas were used, and 10,335,758 kg when preferred forage areas were used. Using the generally accepted target of 50% offtake as a sustainable level of grazing, 5,903,965 kg of forage would have been available for grazing ungulates using the "all forage areas of bison summer range" scenario, and 5,206,283 kg would have been available under the "preferred forage areas for bison" scenario. The forage requirements for bison for the entire summer season was 1,423,935. Technically, the available forage on the bison summer range met the requirements of both species, but there was no predicting the use patterns of bison under drought conditions. For example bison might remain on GTNP summer range for an additional month or more if forage production was poor on the NER, or if mild winter conditions allowed the bison to continue to utilize park ranges, requiring an additional 232,163 kg of forage. Our calculations did not take into account the impact of elk grazing and their forage requirements, particularly as they transition to their winter range. While elk use a wider range of habitats than bison, drought would also affect forage availability on these habitats. Groups of over 100 elk were observed on the park grazing allotments in August and groups of 20-30 elk were commonly seen in the area throughout the summer.

Table 1.12. Production, measured and available standing crop, and estimated ungulate use since sampling dates, on grazing allotments in Grand Teton National Park, Wyoming, summer 2001.

Grazing Unit	Size (km ²)	Standing crop measured ^a	Days cattle use ^b	Estimated forage use by cattle	Days bison use ^c	Average bison density (bison/km ²)	Estimated forage use by bison (kg)	Available standing crop (kg)	Estimated total production (kg)
East Elk Ranch South	2.00	254,148	6	68,652	38	4	2,964	182,532	300,099
East Elk Ranch North	3.11	469,481	8	91,536	38	4	4,609	373,336	491,483
Total East Elk Ranch Complex								555,868	791,582
West Elk Ranch	3.38	376,779							502,118
Moosehead Flats	6.09	446,919							559,541
Lower Cunningham	1.84	169,472							173,098
Total of West Elk-Moosehead-Lower Cunningham Complex								832,874	1,234,757
NW Kelly Hayfields	2.60	113,360			25	17	10,774	102,586	
SW Kelly Hayfields	2.59	175,861			25	17	10,733	165,128	
NE Kelly Hayfields	2.52	119,448			25	17	10,443	109,005	
SE Kelly Hayfields	2.51	97,388			25	17	10,401	86,987	
North Gros Ventre South	1.22	19,093			25	17	5,056	14,037	
North Gros Ventre Middle	1.06	112,307			25	17	4,393	107,914	
North Gros Ventre North	1.24	176,204			25	17	5,138	171,066	
Total Kelly-North Gros Ventre Complex								756,723	
Totals								2,145,465	

^aStanding crop measured approximately June 20, 2001 on East Elk Ranch-West Elk Ranch-Lower Cunningham-Moosehead Flats. Measured approximately July 16, 2001 on Kelly Hayfield-North Gros Ventre pastures, after 12 days of cattle grazing in 2 of the pastures.

^bUse July 16-August 10, 2001.

^cUse by bison after sampling date of June 20 through August 10, 2001.

CONCLUSIONS

- 1) Domestic cattle, elk, and bison made substantial co-use of the same managed pastures and native grasslands in the Triangle X-Cunningham-Elk Ranch complex. Forage use of non-irrigated grassland plots averaged 63.2% consumption, while use of irrigated pastures averaged 80.8%. One subirrigated site dominated by *Poa* spp. averaged >90% combined use. These are very high combined forage utilization rates by combined native and domestic ungulates on managed pastures. Most western range managers seek to limit grazing use to $\leq 50\%$ of the forage produced.
- 2) Elk and bison moved off of areas while they were grazed by cattle. But elk and bison used these areas immediately prior to, and immediately after cattle grazing. Most of the bison present were bulls (the cow-calf segment of the population summers to the south in the Kelly-Antelope Flats area), and bulls are unlikely to transmit the *Brucella* organism. Since there is almost no bison calving in the northern GTNP managed pastures, and since the cattle do not arrive on the ranches until two months after the peak of bison calving, transmission of brucellosis is unlikely between the two ungulates in the GTNP pasture setting. Still, there remains a small prospect of transmission.
- 3) There was adequate summer forage for bison, after cattle grazing, even during a very severe drought year when forage biomass production was reduced 48-91% below average. However, we could not conclude there were no effects of the cattle grazing on bison. The amount of combined use of some areas was extraordinarily high—80-90% combined use. Bison grazed more than their “preferred” areas, at least in 2001, in order to meet their forage needs. Grazing at these high levels may result in sub-optimal foraging for bison for forage quality and overall energetic demands. High co-use of summer ranges may result in too much use. We would need to evaluate the nutritional and energetic needs of the bison to determine if any deficiency occurs. We recommend further investigations of foraging energetic demands for bison.

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Part II: A Survey of Willow Communities, Willow Stature and Production, and Correlations to Ungulate Consumption and Density in the Jackson Valley and the National Elk Refuge

Report to the National Elk Refuge and Grand Teton National Park

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INTRODUCTION

Managers in the Jackson Valley are currently re-evaluating their management of elk and bison. A new management plan for both species is the desired product of the interagency effort. The management of woody riparian shrubs, especially willows (*Salix* spp.), cottonwood (*Populus angustifolia*, *P. acuminata*) and aspen (*P. tremuloides*), is a critical issue in this management evaluation process. Managers are concerned over declines in willow, aspen, and cottonwood communities. This report summarizes research conducted over a 3-year period on one of those communities—willow communities on ungulate winter ranges on the National Elk Refuge (hereafter NER) and in the Jackson Valley. We report here on the status of willow in the valley, their current utilization rates by three large browsing ungulates (elk - *Cervus elaphus*, moose – *Alces alces*; bison – *Bison bison*) and correlations of ungulate abundance and browsing to the status of the willows.

We recognized four general categories of willow use by ungulates in the Jackson Valley ranging from lightly to heavily browsed. These categories were developed by an independent science panel convened to address issues surrounding the ecological condition and avian response in willow, aspen, and cottonwood communities on the National Elk Refuge (Dobkin et al. 2002). The categories were based on observations and sampling from winter range willow communities in Yellowstone and Rocky Mountain national parks (Singer et al. 1994, 2002). These categories are further characterized by avian community composition (Dobkin and Wilcox 1986, Dobkin 1994, Ohmart 1994, Tewksbury et al. 2002) and stream function (Platts 1979, Hickin 1984, Skolvin 1984, Platts and Nelson 1985, Platts et al. 1985, Beschta and Platts 1986, Chaney et al. 1990) based on extensive studies of similar systems elsewhere in the Rocky Mountains and Intermountain West (Table 2.1, Fig. 2.1).

The optimum stage of willow stature and growth varies depending upon the goals or views of a particular management program. For example, an aquatic ecologist or manager, and an avian specialist are likely to favor all management that features Category I, or very lightly browsed

Table 2.1. Criteria for classifying degree of ungulate browsing pressure on willow stands in the National Elk Refuge and Jackson Valley, Wyoming.

	Ungulate consumption (%)	Mean height (cm)	Mean canopy area (m ² /ha)	Current annual growth (kg/ha)	Willow effects on stream	Avian community characteristics	Typical bird species ¹
Category I Unbrowsed to lightly browsed (Fig. 2.1a)	0-10	212	8400	4700	Thickets shade stream Stem, leaf, and shoot fall yield nutrient input and invertebrate habitat Peak bank stability and flood resistance	Peak species richness	
Category II Moderately browsed (Fig. 2.1b)	11-20	150	5100	2700	Thickets absent; shade reduced Reduced stem, leaf, and shoot fall Less bank stability and flood resistance	Reduced species richness; Nesting habitat diminished	Calliope Hummingbird Willow Flycatcher Gray Catbird Northern Waterthrush MacGillivray's Warbler Wilson's Warbler Yellow-breasted Chat
Category III Heavily browsed (Fig. 2.1c)	21-35	151	5500	3000	Willows discontinuous along bank Much-reduced shading and nutrient inputs Impaired bank stability and flood resistance	Substantially altered	Lazuli Bunting Fox Sparrow Lincoln's Sparrow Western Meadowlark Vesper Sparrow Brewer's Blackbird
Category IV Overbrowsed (Fig. 2.1d)	>35	97	2000	800	Willow height suppressed; some reduced to shoots in herb layer Greatly reduced nutrient input Minimal bank stability and flood resistance	Greatly altered; wet meadow or grassland species predominate	Brown-headed Cowbird

¹A gradient of change in bird species will occur with a decline in diversity of species as the structure of willow community declines (Berger et al. 2001).

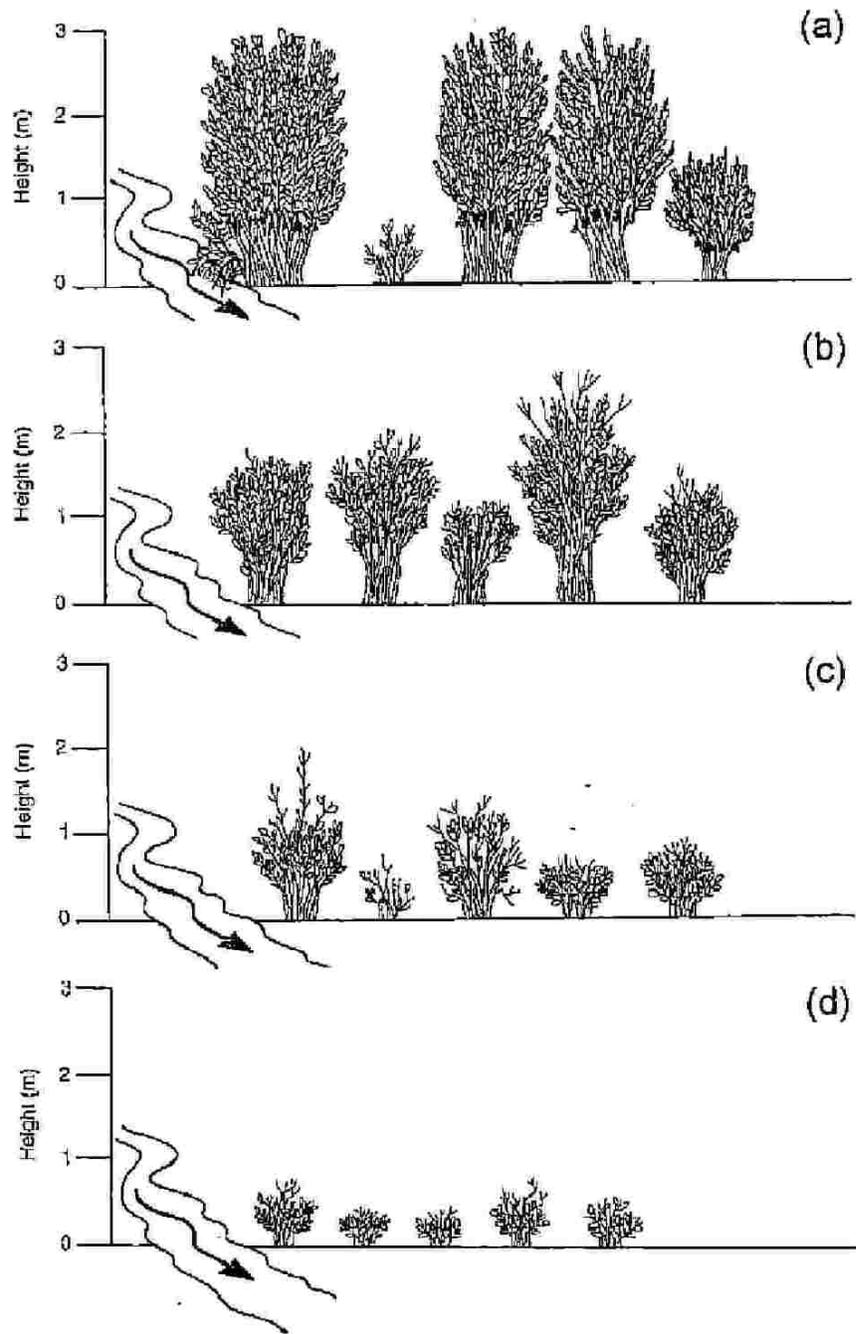


Figure 2.1. Four categories of willow response to browsing pressure identified for Jackson Valley, Wyoming. Category I is unbrowsed or lightly browsed (a); Category II is moderately browsed (b); Category III is heavily browsed (c); and Category IV is overbrowsed (d). Taken from Dobkin et al. 2002.

willows. Category I maximizes tall height of willows, large crown sizes. Willows grow to the edges of streams. There are ecosystem benefits to the stream aquatic ecosystem from shading of streambanks and large amounts of leaf and shoot litterfall into the stream. This organic material initiates cycles of nutrient spiraling. This corresponds to low densities of ungulates across the landscape. A wildlife manager interested in management of big game may be far more likely to favor management of Category II willows (moderately browsed – 11-20% use) and moderate densities of harvestable ungulates, and even some patches being in Categories III and IV. The artificial feeding of ungulates is likely to result in some willow patches near feedgrounds always being in Category III or IV—heavily browsed or overbrowsed. To some managers, the feeding program is worth the price of overbrowsing a few patches of willows, providing willows are generally in a healthy state across the remainder of the landscape. Fencing a few patches of willows near feedgrounds is also a management option. Those managers seeking to protect avian and aquatic habitats would find large areas of overbrowsed willows to be objectionable.

The purpose of this report and analysis is not to determine for managers which stage of willow stature and growth is most appropriate for the various land management of the valley, but rather to predict which willow stature and growth variables will result from different levels of ungulate abundance. Managers, and the public, can then decide the most appropriate levels of ungulate abundance.

In our analysis, we searched for any evidence of browsing optimization of willows in the Jackson Valley. Optimization is the maximization of plant growth at some moderate level of grazing (see Fig. 2.2). Optimization might be a goal of many managers, since browse production and forage to harvestable ungulates are maximized at this point. Grazing optimization has been reported from some ecosystems (McNaughton 1979, 1983, 1993; Oldemeyer 1981; Danell et al. 1985; Frank and McNaughton 1993), but some authors report optimization is rarely found in western rangelands (see review by Painter and Belsky 1993).

The final objective of our analysis was to predict, for the National Elk Refuge: (a) at what level of reduced densities of elk would all willows recover to willow categories I and II across the NER, and (b) once recovered, what densities of elk would be sustainable with healthy, persisting stands of willows on the NER.

METHODS

We sampled 2000-2002 production, and winter and summer consumption of willows. Initially, 15 willow sites were randomly selected in four strata of winter elk and moose densities: high elk and low moose densities (South end of NER), medium elk and medium moose densities (Gros Ventre drainage near Upper Slide Lake and Cottonwood Creek), medium elk and high moose densities (North end of NER and Grand Teton National Park areas near Triangle X and Wolff Ridge), and low elk and moose densities (Buffalo Valley and along the Rockefeller Parkway). These strata were determined using elk and moose survey data provided by Wyoming Game and Fish Department. Only three sites were available in the high elk-low moose density strata and these were confined to the southern end of the NER. Additionally, two of these sites were burned during prescribed burning in May of 2000. After analyzing 2000 data, we determined that the strata were not reflecting a wide enough range of elk and moose densities, and based on additional moose location data provided by Wyoming Game and Fish Department, we added 3

additional sites that were measured in 2001 (near the Gros Ventre River in Bridger-Teton National Forest along Dry Cottonwood Creek, and near Beaver Creek and near Bar BC Ranch in Grand Teton National Park).

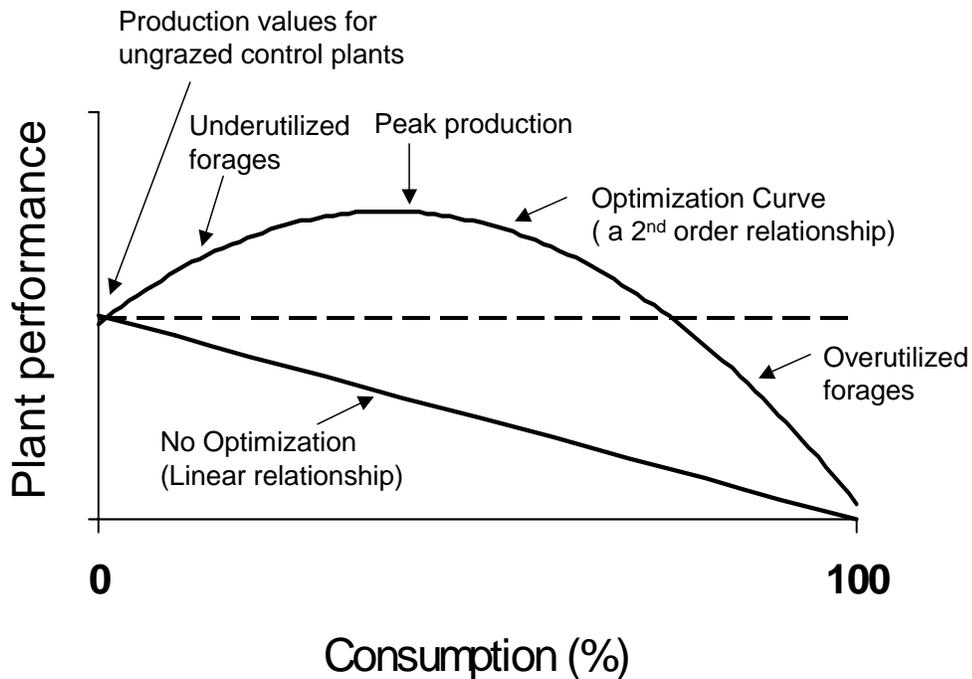


Figure 2.2. Conceptual examples of relationship between plant performance variables and consumption rate when grazing optimization is present (2nd order model, i.e. a hump-shaped curve) and when no optimization (linear relationship) is evident.

Three 9.3 m² randomly selected circular plots were established at each willow study site. We averaged across all plots in a site for each year to provide data for each sample point used in analysis. Data collected on each shrub in all plots included species; shrub canopy diameters (widest and perpendicular to widest diameter); shrub height; number of stems; and an estimate of percent of canopy dead. On every fourth individual of each shrub of each species a subsample of the number of browsed and unbrowsed leaders; diameters at twig base, tip, and point of browse; and leader lengths were also collected. Winter consumption was measured before leaf bud break in May, and summer consumption was measured in August. Percent leader use was determined using the equation:

$$\% \text{ leaderuse} = \frac{a}{a + b}$$

where a = number of browsed leaders and b = number of unbrowsed leaders. Average percent twig removed was determined using the method of Jensen and Urness (1981) and Pitt and Schwab (1990) following the formula:

$$\% \text{ twiguse} = \frac{100(D_p - D_t)}{D_b - D_t}$$

where D_p = twig diameter at point of browsing, D_t = diameter of a representative sample of unbrowsed twig tips, and D_b = basal diameter of current year's twig growth. Total consumption was determined by multiplying % leader use by % twig use. For short, single stem, densely growing species, such as wolf willow (*Salix wolfii*), we measured all plants within 1 m² plots, then determined the amount of the circular plot which was contiguously covered by these species and estimated production for the entire 9.3 m² plot based on the measured 1 m² plot.

Annual production was determined following methods of Singer et al. (1994). Average twig weight was calculated from linear regression of dry weight (dependent variable) on twig length or green twig basal diameter. Ten to twenty twig samples were taken from all willow species as well as from shrubby cinquefoil, *Potentilla fruticosa*, (which was also quite common in most sites) at each site. Separate regression equations were developed for each species and each density category for each year. R^2 values ranged from 0.63-0.93 for 2000. We found that the best regressions were based on both twig lengths and green basal diameters in 2000, and thus we gathered sufficient data in 2001 to create these regressions. R^2 values ranged from 0.70-0.98 in 2001. The biomass of each willow plant where twig measurements were taken was estimated by multiplying average twig weight x average number of twigs per stem x number of stems per plant. Regression equations were then developed relating canopy area or volume to production for these plants. These regressions were used to estimate biomass for the remaining plants that had no twig measurements. These r^2 values ranged from 0.64-0.94. Willow species were divided into two height categories--those species that are naturally of short stature (< 1.5 m greatest height, *S. wolfii*, *S. candida*, *S. farriae*), and those which have the potential to grow greater than 1.5 m (*S. boothii*, *S. bebbiana*, *S. geeyeriana*, *S. planifolia*).

Managers need to know at what density of ungulates, and at what consumption level, there is a negative effect on plant sizes and plant growth. We correlated ungulate abundance to willow structure and production variables. Willow structure and growth parameters included: annual willow biomass production, willow height, stem and plant densities, plant canopy area and plant volume. These variables were correlated to consumption levels at each site, to ungulate use indices based on fecal plots, and to ungulate densities. Moose density and elk density outside the NER were calculated from annual Wyoming Game and Fish Department aerial surveys conducted in February 2000-2002. Elk densities on the NER were calculated by averaging several pre-feeding ground surveys conducted by Bruce Smith (U.S. Fish and Wildlife Service) on the NER from early December through the beginning of feeding (usually late January or early February) 2000-2002. We calculated average elk and moose densities across the entire study area using ArcView 3.2 software density function with a kernel estimator and a 2,000 meter search radius.

Elk and moose densities are difficult to directly compare since moose are larger than elk, they consume more forage per day, and more of their diet is composed of willow and other woody browse. We estimated the average intake of willows by each species in order to compare their relative impacts on the shrubs (Table 2.2). We calculated daily intake rates of willow by elk for each willow site by multiplying the average elk density by the average daily intake rate for an adult elk (5 kg dry wt, Hobbs [1979]) multiplied by the estimated percent of diet which is comprised of willow where willow patches are present (10%, Hobbs et al. [1981]). We calculated daily intake rates of willow by moose by multiplying the average moose density by

the average daily intake rate for an adult moose (16 kg dry wt, Peterson [1955]) by the estimated percent of the winter moose diet that is comprised of willow (75%, Harry [1957]). We correlated all willow structure and growth variables to univariate and multivariate models using the independent variables of elk and moose density, elk and moose intake rates, total intake rates, and the ratio of moose to elk intake rates. In cases where elk density, and thus intake rate was zero, we substituted an intake rate of .000001 kg/day in order to calculate the ratio.

Table 2.2. Herd size and daily forage intake rates of moose and elk in the Jackson Valley, Wyoming.

	Moose	Elk	Total
Total number of animals in study area	890	15,600	16,490
Percent of diet which consists of willow	75	10	
Average daily forage intake (kg dry weight/animal/day)	16	5	
Total species intake rate of willows (kg dry weight/species/day)	10,680	7,800	18,480

In order to detect any grazing optimization we used Akaike’s Information Criteria (AIC) to determine best model selection of univariate, multivariate, and second order regression models for both density and offtake. Grazing optimization, or any positive response by plant growth at moderate ungulate density or consumption rates, is important for managers to identify, should it occur.

We could not differentiate browsing by moose, elk, or bison on willows. In order to assess the relative activity by each species of ungulate, we counted fecal piles for each species at the willow study patches. An index of ungulate species use was calculated by counting the number and species (elk, moose, bison) of fecal piles found within each 9.3 m² fixed radius circular plot used for measuring willows. These fecal counts were conducted before willow measures were taken in spring 2002 to assure a minimum disturbance of fecal piles by research teams prior to collection of the data on shrubs. This data was only available for 2002 and the pellet data were applied to all years of data for the analysis. Correlations were conducted using first- and second-order regression equations. Where appropriate, dependent variables were log transformed to stabilize variance. Statistical analyses were performed using SAS statistical analysis software ver. 8.0.

Study Area

We identified eight species of willow occurring in our study sites—Booth’s willow (*S. boothii*), Geyer willow (*S. geyeriana*), Wolf’s willow (*S. wolfii*), sageleaf willow (*S. candida*), Farr’s willow (*S. farriae*), Bebb willow (*S. bebbiana*), plain-leaf willow (*S. planifolia*) and false mountain willow (*S. pseudomonticola*). The highest diversity of willow species occurred in the area of highest elk density on the south end of the NER (Table 2.3). This area was also where spring prescribed burning was conducted in 2000 and it is unknown whether this may have contributed to the high diversity. Other shrub species found in the study area included *Potentilla fruticosa*, *Betula glandulosa*, *Rosa* spp., *Ribes* spp., and occasional *Artemisia tridentata* and *A. cana*.

Table 2.3. Shrub species occurrence in Jackson Valley, Wyoming willow study sites, 2000-2002.

Site name	Location	<i>Salix</i> species							Other species							
		<i>S. boothii</i>	<i>S. geyeriana</i>	<i>S. wolffi</i>	<i>S. candida</i>	<i>S. farrariae</i>	<i>S. bebbiana</i>	<i>S. planifolia</i>	<i>S. pseudo-monticola</i>	<i>Artemisia tridentata</i>	<i>Betula glandulosa</i>	<i>Lonicera involcrata</i>	<i>Potentilla fruticosa</i>	<i>Ribes spp.</i>	<i>Rosa spp.</i>	<i>Tetradymia canescens</i>
GTNP and Parkway sites																
EL-MH1	Buffalo Valley		x									x				
EL-MH2	Buffalo Valley	x	x	x								x				
EL-ML3	Rockefeller Parkway		x													
EL-ML4	Rockefeller Parkway		x	x												
EL-ML1	Beaver Creek	x	x										x		x	
EL-ML2	Bar BC ranch	x	x										x		x	
EL-MH3	Cunningham Cabin	x	x									x				
EL-MH4	Wolff Ridge	x	x						x			x				
BTNF--Gros Ventre Sites																
ELM-ML3	Upper Slide Lake	x	x													
EMH-MH2	Dry Cottonwood Creek	x	x	x									x			
EMH-MH3	Cottonwood Creek	x		x	x	x				x			x		x	
EMH-MH4	Cottonwood Creek	x	x						x				x			x
EMH-MH1	Dry Cottonwood Creek	x	x								x	x	x			
NER sites																
ELM-ML1	NER Gros Ventre Gate	x	x											x		
ELM-ML2	NER-across river from campground	x	x										x		x	
EH-ML1	NER visitor center	x	x					x	x	x			x			
EH-ML2	Flat Creek Inn	x	x		x								x	x		x
EH-ML3	NER valley center		x			x								x		

RESULTS AND DISCUSSION

Winter willow consumption rates were moderate in general across the study area and averaged $16.1 \pm 2.0\%$. But consumption was highly variable and ranged from 0 to 47.4%. Any consumption values greater than 30% are likely detrimental to the plants, while 45-47% use is exceptionally high (Singer et al. 1994, 2002). Summer consumption of willows was lower; rates ranged from 0 to 7.6%. Consumption rates were negatively correlated to willow production ($P=0.0002$, $r^2=0.29$; Fig. 2.3a), willow canopy area ($P<0.0001$, $r^2=0.40$, Fig. 2.3b), willow canopy volume ($P<0.0001$, $r^2=0.48$, Fig. 2.3c), and height of both tall and short willow species ($P=0.001$, $r^2=0.22$ for tall stature species; $P=0.03$, $r^2=0.33$ for short stature species, Fig. 2.4). Elk density averaged 16.3 ± 4.9 elk/km² and ranged from zero to over 200 elk/km². Moose density averaged 1.9 ± 0.4 moose/km² and ranged from zero to 13 moose/km² (Fig. 2.5).

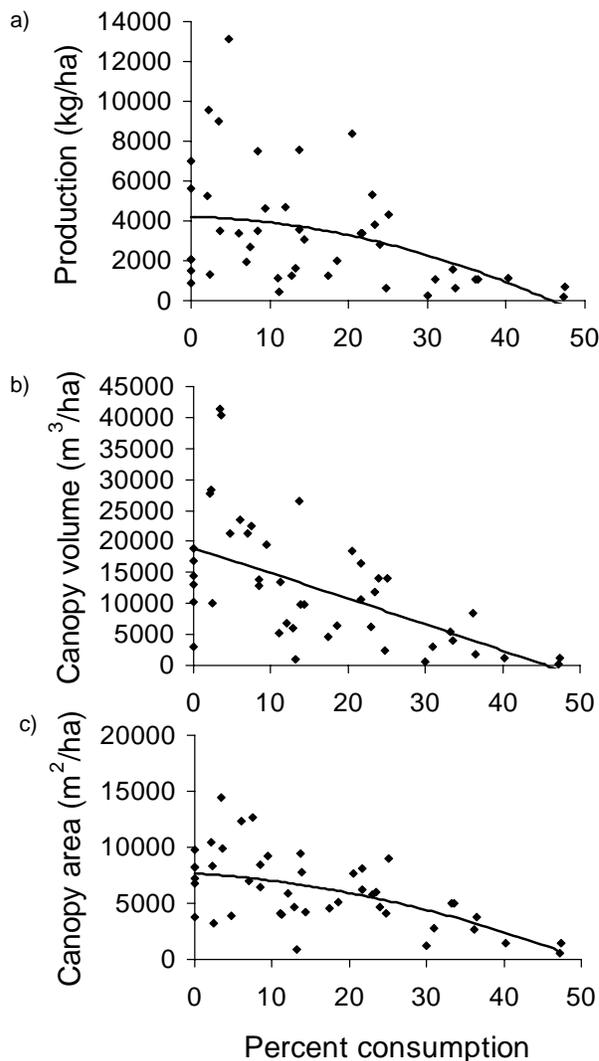


Figure 2.3. Relationship between percent winter consumption rate of willows by ungulates and willow production (a), canopy volume (b), and canopy area (c) in the Jackson Valley, Wyoming, 2000-2002. Optimization is present, but very weak.

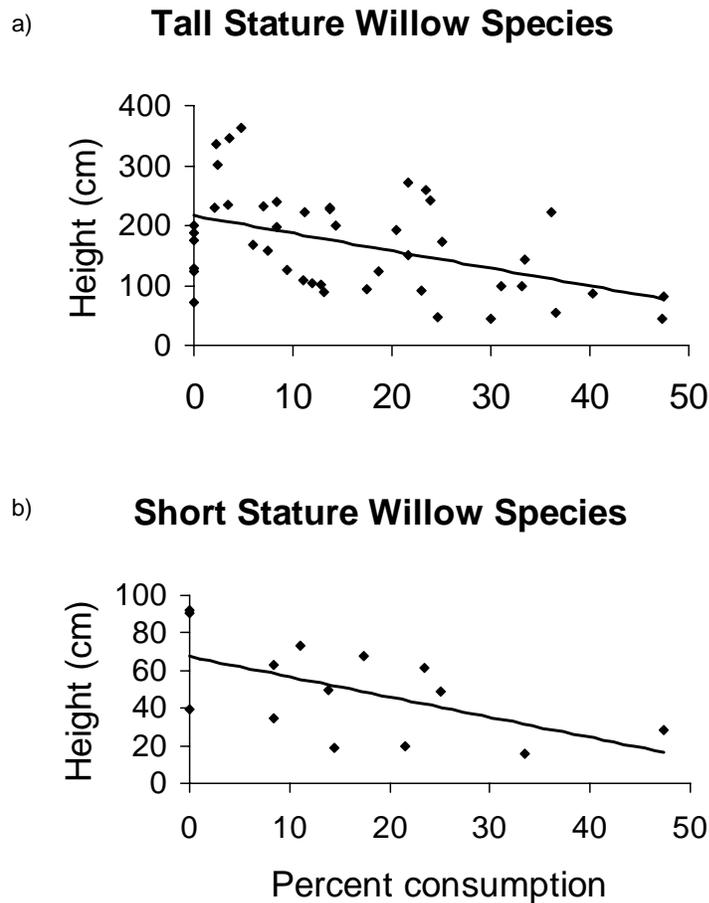


Figure 2.4. Relationship between percent winter consumption rate of willows by ungulates and willow heights for both tall stature species (a), and short stature species of willow (b) in the Jackson Valley, Wyoming, 2000-2002.

Consumption rates were positively correlated to elk densities ($P < 0.0001$, $r^2 = 0.45$) and negatively correlated to moose densities ($P = 0.07$, $r^2 = 0.07$, Fig. 2.6). We predicted there would be a positive correlation between ungulate densities and consumption rates on willows. A good relationship (i.e. high r^2 value) is useful to managers, since then consumption rates could be predicted from ungulate densities alone, thus saving time and money. Information on ungulate densities can be rapidly sampled from a few aerial surveys, while information on consumption rates is very time consuming to gather. We found willow consumption rates were strongly correlated to elk density ($P < 0.0001$), but the amount of the variance explained was only moderate ($r^2 = 0.45$). Thus, predicting consumption rates from elk density information alone provides only a rough approximation. Percent leader use (average number of twigs that are browsed) is strongly correlated to consumption rates ($P < 0.0001$, $r^2 = 0.91$) and might be considered as a quicker, easier alternative to measuring consumption rates. The amount of variance explained by moose density alone was very low ($r^2 = 0.07$), and using moose densities alone is not recommended when evaluating willow browse rates.

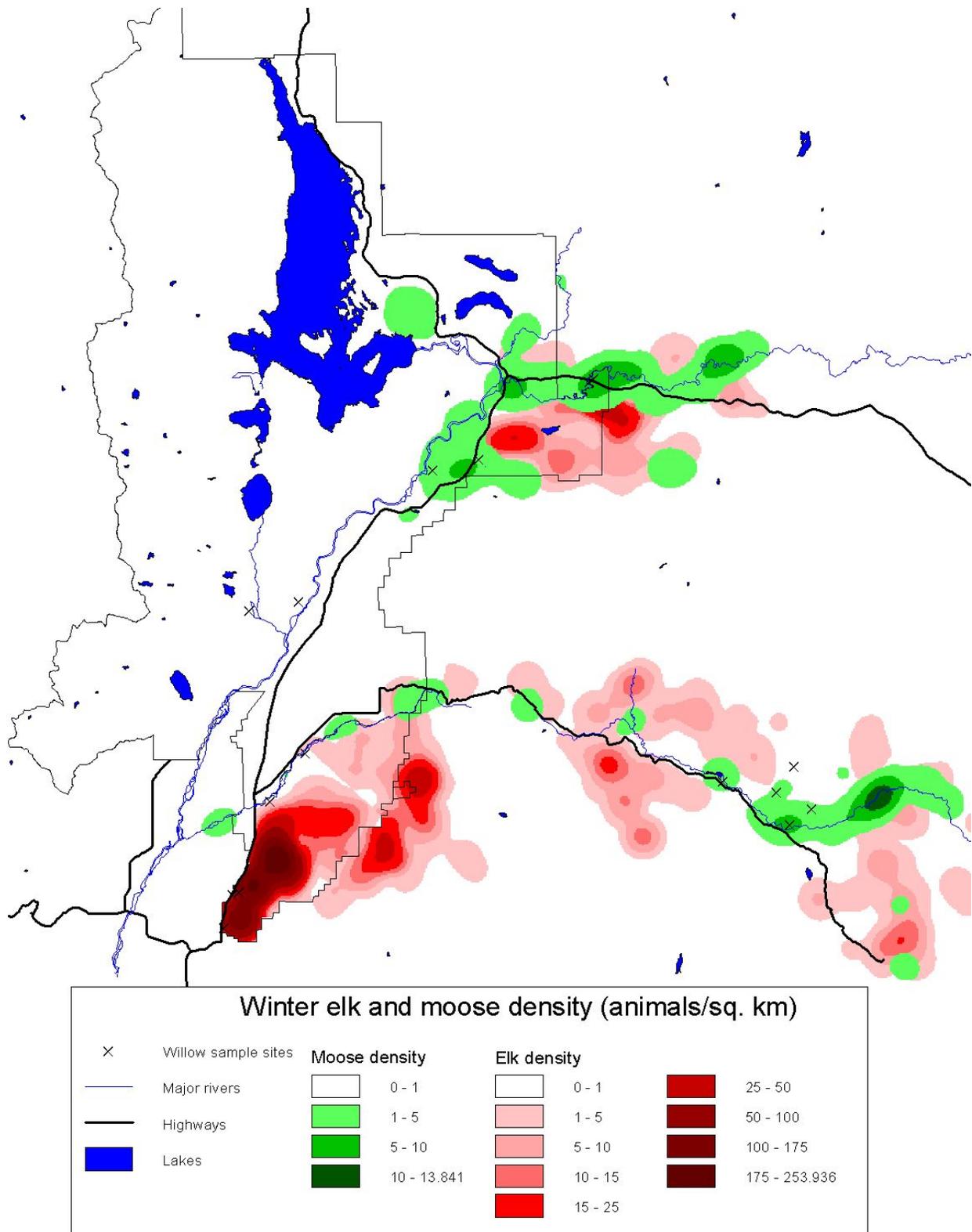


Figure 2.5. Moose and elk densities (animals/km²) averaged over several winters (2000-2002 for elk; 1999-2000 for moose) in the Jackson Valley, Wyoming.

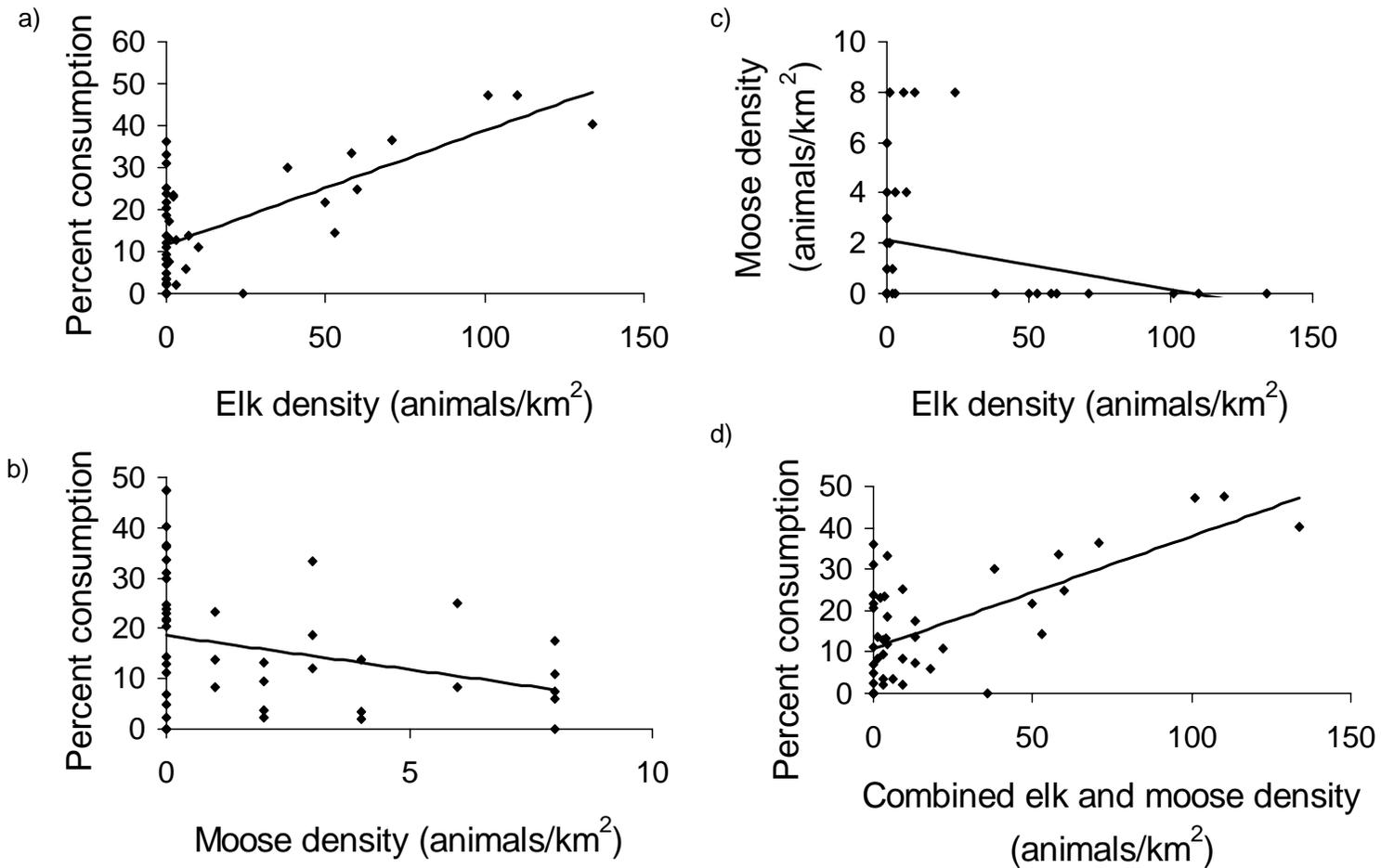


Figure 2.6. Relationship between percent winter consumption rate of willows by ungulates (a,b) and elk and moose (a,b,c) density in the Jackson Valley, Wyoming, 2000-2002. The negative relation to moose density is apparently explained by the fact that moose density is negatively correlated to elk density ($P= 0.09$, $r^2 = 0.06$) and elk are having the dominant influence on vegetation. When elk and moose densities are combined (d), the relation to percent consumption of willows is once again positive ($P < 0.0001$, $r^2 = 0.42$).

We found only very weak evidence for browsing (grazing) optimization of willows in the Jackson Valley. While AIC values indicated that second-order regression models (i.e. graphical evidence of optimization) were the better choice for predicting production, canopy volume and canopy area, but not height, from consumption rates, overall improvement in r^2 values was minimal. The general correlation is strongly negative and provides very weak evidence for browse optimization in willows in this area (Fig. 2.3a-c). This is in contrast to patterns seen in Rocky Mountain National Park, where second-order regression models best explained the relationship between willow growth characteristics and consumption rates. The data indicated browsing optimization in Rocky Mountain National Park with a peak in growth around 21% consumption and negative effects at rates greater than 37% (Fig. 2.7).

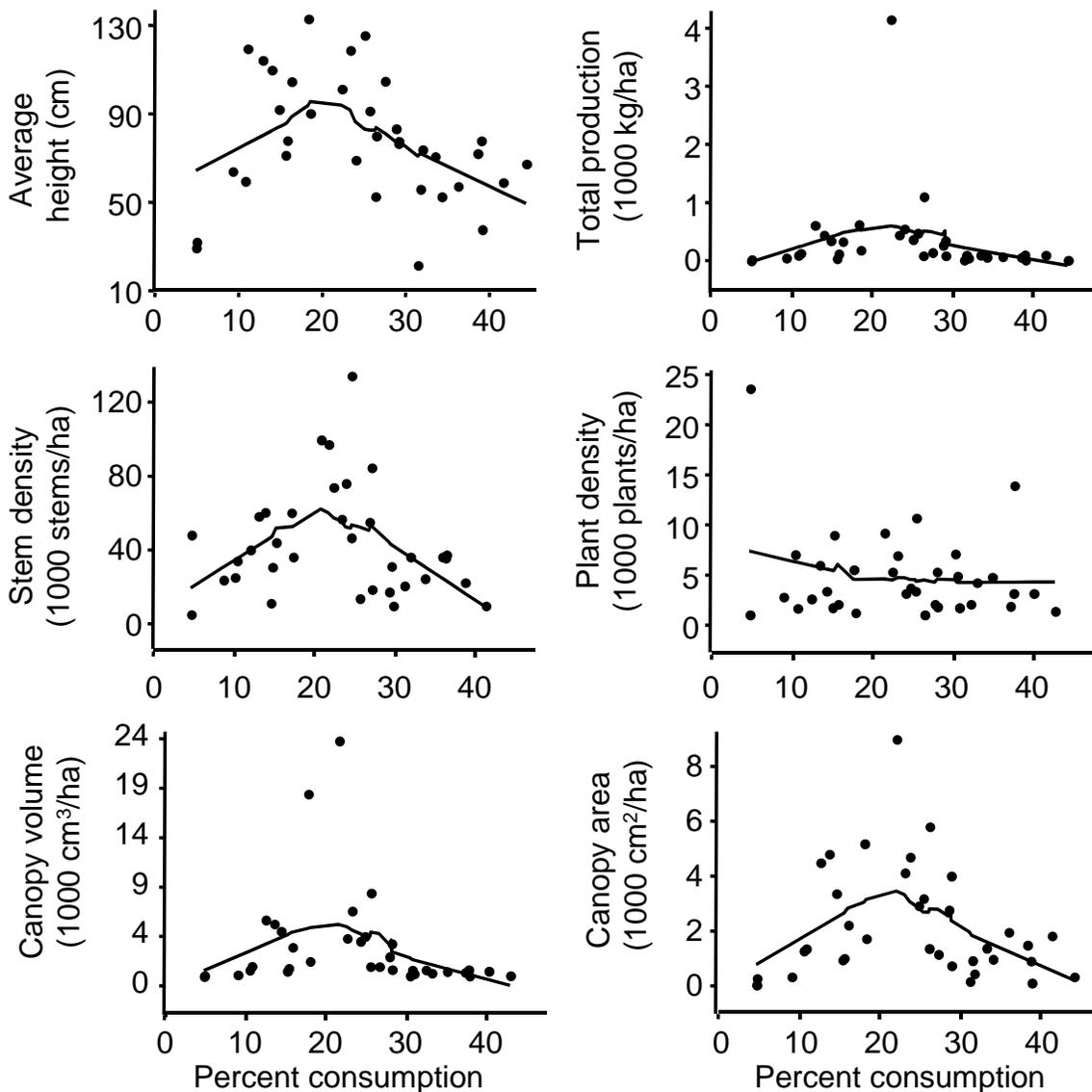


Figure 2.7. Relationship between willow growth characteristics and percent consumption in Rocky Mountain National Park, Colorado, 1994-1998. Optimization is strongly suggested by the peaks in growth at moderate (~21%) consumption levels.

However, there are several differences between the two study areas. The Jackson Valley study covers a much larger area (~1500 km²) than the Rocky Mountain National Park study (~100 km²); both elk and moose browse on Jackson Valley willows, while only elk browse Rocky Mountain National Park willows; and unbrowsed and lightly browsed willows are much more prevalent in the Jackson Valley study than the Rocky Mountain National Park study (Tables 2.4 and 2.5). In fact, in the Rocky Mountain National Park study, no unbrowsed willow patches were available in the winter range, except those protected by elk-proof exclosures.

Table 2.4. Characteristics of willow stands subjected to varying winter consumption levels on willows in the Jackson Valley and Gros Ventre drainage, Wyoming.

	Category I 0-10% offtake mean ± SE	Category II 11-20% offtake mean ± SE	Category III 21-35% offtake mean ± SE	Category IV >35% offtake mean ± SE
Number of samples	18	10	12	5
Average height (cm)*	212.0 ± 19.4	150.0 ± 19.3	151.2 ± 22.7	97.2 ± 31.9
% plants showing height decline	21.5 ± 4.9	18.8 ± 4.1	14.4 ± 4.5	30.0 ± 20.0
Willow CAG production (kg/ha)	4692 ± 796	2657 ± 682	2968 ± 682	825 ± 177
Willow canopy area (m ² /ha)	8361 ± 716	5064 ± 726	5461 ± 635	1983 ± 569
Willow plant density (# willows per ha)	2758 ± 555	4140 ± 953	3689 ± 608	1971 ± 439
Willow stem density (# stems/ha)	159409 ± 22873	150950 ± 32822	175612 ± 24565	136165 ± 83379
Average % live canopy	77.4 ± 3.0	76.1 ± 3.0	80.9 ± 3.9	77.8 ± 10.7
Average % dead canopy	22.6 ± 3.0	23.9 ± 3.1	19.1 ± 3.9	22.2 ± 10.7
Average number shrub species (per 9.3 m ² plot)	1.7 ± 0.2	2.2 ± 0.1	2.9 ± 0.3	1.7 ± 0.2
Average number willow species (per 9.3 m ² plot)	0.6 ± 0.1	1.2 ± 0.1	1.2 ± 0.2	0.8 ± 0.2
Avg. number non-willow shrub species (per 9.3 m ² plot)	1.3 ± 0.1	1.4 ± 0.1	1.9 ± 0.3	1.2 ± 0.2

*Only includes willows that naturally grow to heights > 1.5 m

Table 2.5. Characteristics of willow stands subjected to varying consumption levels in Rocky Mountain National Park, Colorado.

	Category I 0-10% offtake mean ± SE	Category II 11-20% offtake mean ± SE	Category III 21-35% offtake mean ± SE	Category IV >35% offtake mean ± SE
Number of samples	3	10	16	6
Average height (cm)	42.0 ± 11.1	97.4 ± 7.3	78.6 ± 6.6	62.0 ± 5.8
Willow CAG production (kg/ha)	27.8 ± 14.4	297.7 ± 67.6	526.4 ± 25.16	64.2 ± 16.6
Willow canopy area (m ² /ha)	230 ± 92	2652 ± 529	2742 ± 594	1117 ± 317
Willow plant density (# willows/ ha)	9200 ± 7247	4082 ± 845	4602 ± 698	4773 ± 1904
Willow stem density (# willow stems/ha)	25926 ± 12453	40297 ± 5116	54702 ± 9210	27909 ± 4441

The four categories of willow use are based upon multiple factors of stream function and avian community composition, in addition to willow community characteristics. Therefore, the lack of difference between Categories II and III for several willow growth parameters (height, canopy area, production) in the Jackson Valley is not surprising (Table 2.4). Willow growth parameters broke down more neatly into four categories when a two-year sample (years=2000-2001, n=33) was used (Dobkin et al. 2002), than the larger three-year sample (years=2000-2002, n=45; Table 2.4). Upon analysis of the current data, we redefined offtake levels used to categorize willow sites using winter consumption rates of willows only, whereas in earlier reports (Dobkin et al. 2002), total annual consumption rates on all shrubs in a site was used. We chose to categorize by winter willow consumption rates because willow was the focus of this analysis, and because winter consumption rates were substantially higher than summer rates and had greater influence on willow growth parameters (Figs. 2.3 and 2.4).

In order to assess the relative impacts of elk vs. moose on willows, we ran a multivariate model which included both elk and moose densities. We used AIC (Akaike's Information Criteria) to determine whether elk density alone, moose density alone, or both densities combined was the best model. Elk density was overwhelmingly ($P \leq 0.007$; $r^2 \geq 0.18$) more important than was moose density in predicting most willow growth and willow size parameters, however moose density alone best predicted stem and plant density (Table 2.6). Willow production ($P = 0.0003$, $r^2 = 0.27$), canopy area ($P < 0.0001$, $r^2 = 0.37$), canopy volume ($P < 0.0001$, $r^2 = 0.46$), and heights were all negatively correlated to elk density ($P = 0.004$, $r^2 = 0.18$ for tall stature species; $P = 0.007$, $r^2 = 0.47$ for short stature species, Fig. 2.8), but willow plant density ($P = 0.03$, $r^2 = 0.10$), stem density ($P = 0.02$, $r^2 = 0.11$), and canopy area ($P = 0.0$, $r^2 = 0.09$) were weakly positively correlated to moose density (Fig. 2.9). This may indicate that moose browsing has a less detrimental effect on willows than heavy elk browsing. It should be remembered, however, that high elk densities are on the order of 10 times higher in number of animals per km² than high moose densities, such that "high" elk densities are much higher than "high" moose densities for the Jackson Valley.

Table 2.6. Comparison of models of elk and moose density versus willow size and growth variables. Lower AIC values indicate a more parsimonious model. * indicates best model.

	Model AIC value		
	Elk density alone	Moose density alone	Elk and moose density combined
Willow CAG production (kg/ha)	0.7581*	1.0327	0.8064
Willow stem density (stems/ha)	0.7261	0.6314*	0.6840
Willow canopy area (m ² /ha)	-0.0483*	0.3257	-0.0301
Willow canopy volume (m ³ /ha)	0.7355*	1.3292	0.7894
Willow plant density (plants/ha)	0.1519	0.0457*	0.0981
Willow height—tall species (cm)	9.7641*	9.9546	9.7647
Willow height—short species (cm)	7.3678*	7.9779	7.6245

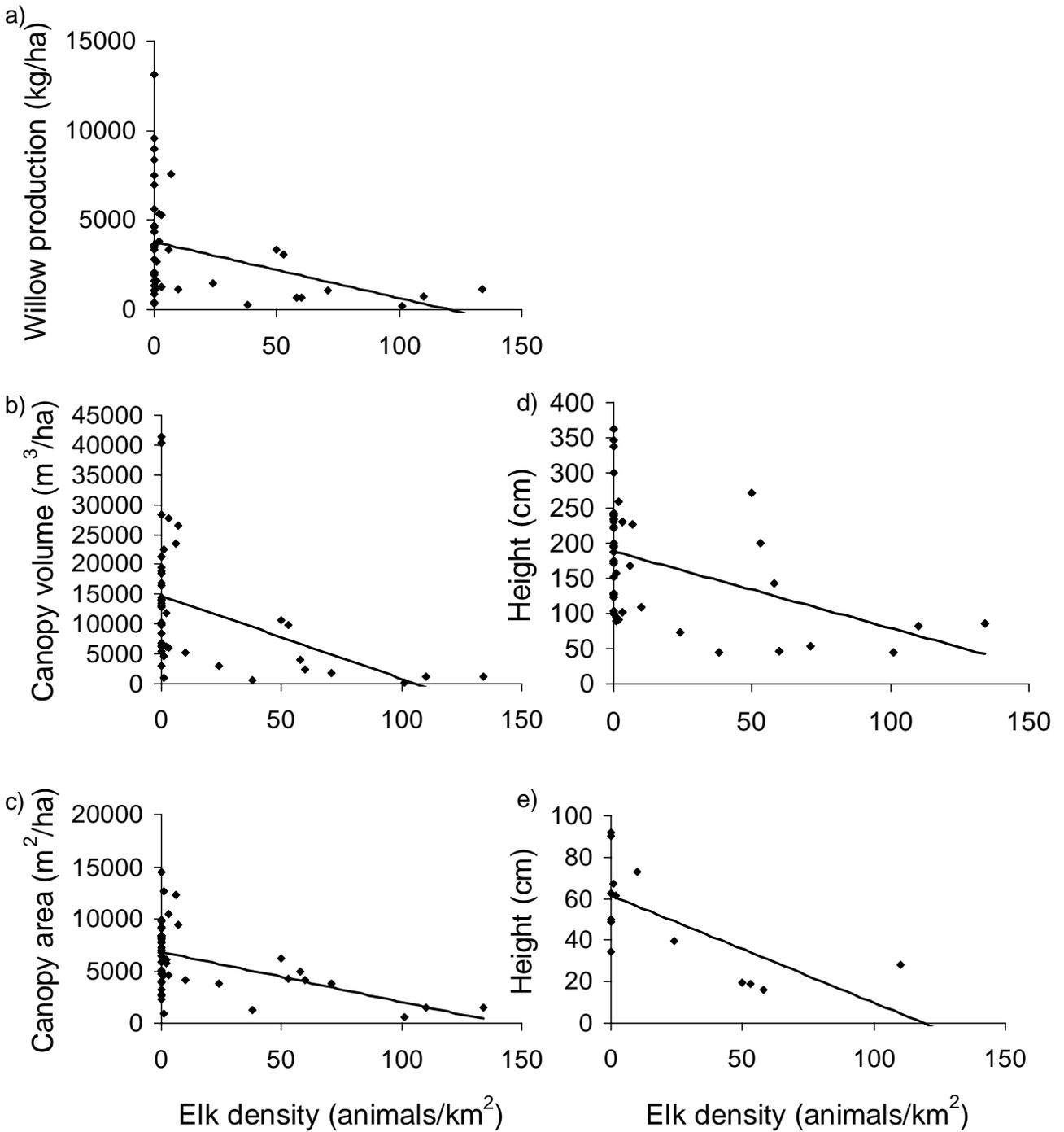


Figure 2.8. Relationship between winter elk density and willow production (a), canopy volume (b), canopy area (c), and height of tall (d) and short (e) stature species in the Jackson Valley, Wyoming, 2000-2002. Elk densities are from Wyoming Game and Fish Department and National Elk Refuge surveys 2000-2002.

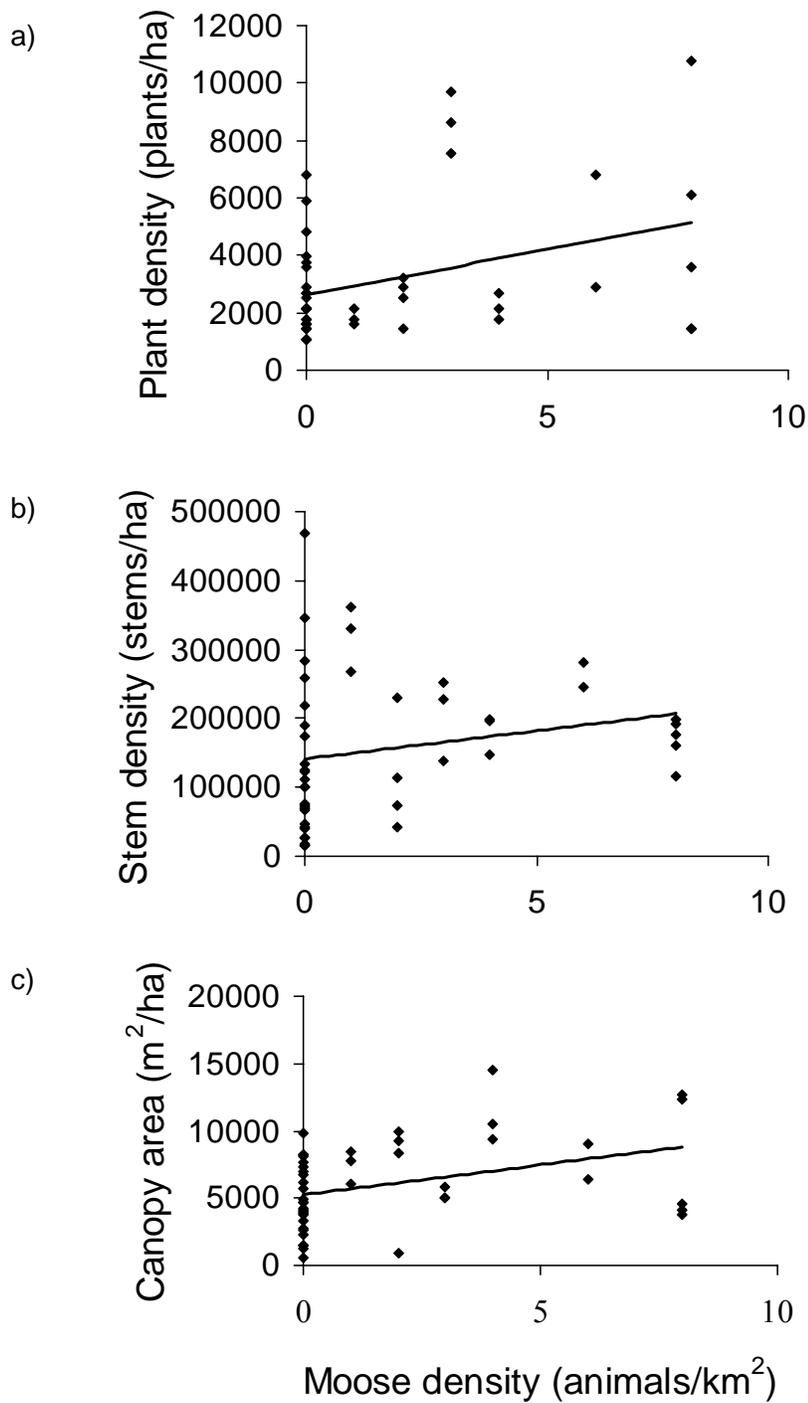


Figure 2.9. Relationship between winter moose density and willow plant density (a), stem density (b), and canopy area (c) in the Jackson Valley, Wyoming, 2000-2002. Moose densities are from Wyoming Game and Fish Department surveys in 1999 and 2000.

Willow canopy area and volume were also negatively correlated to elk use index based on fecal pellet plots ($P=0.02$, $r^2=0.12$ for canopy area; $P=0.06$, $r^2=0.08$ for canopy volume), and willow production was weakly positively correlated to total ungulate use index ($P=0.08$, $r^2=0.07$), but no other willow production variables were correlated to elk, moose, or bison use indices. In fact, based on fecal pellet groups, no bison activity was found within any of our study willow patches, although there was evidence of bison activity close by. Bison are occasionally observed browsing on willows in the study area.

Intake rates by elk and moose ranged from 0 to 165 kg/day (Fig. 2.10). Production, canopy area, canopy volumes, and height were all negatively correlated to elk intake rates, while stem density, canopy area, and plant density were all positively correlated to moose intake rates. However, only stem and plant densities and height of tall stature species were correlated to combined intake rates. Willow stem and plant densities were positively correlated to total intake rate, while heights were negatively correlated. Although moose consume more willow in their diet than elk (Table 2.2), elk removal tends to be concentrated, particularly on the NER and specifically on stands in Categories III and IV (Fig. 2.11, Table 2.7). Removal of an equivalent percentage of willow biomass from these less productive stands has greater impact than similar removals from more productive stands (Fig. 2.12). While it may seem surprising that total intake rates are not better correlated to the willow growth variables when looking at total intake rates listed in Table 2.2, it should be remembered that total intake at any individual site is confounded by the fact that only one of the ungulate species was found to be using most willow sites (Fig. 2.11). Moose, for example, tend to browse in more productive stands (Table 2.7). Heights were not correlated to the ratio of moose to elk daily intake, but all other variables were positively correlated ($P \leq 0.10$) to this ratio, though weakly so ($r^2 \leq 0.14$).

Table 2.7. Relative production and offtake of willow stands browsed primarily by elk, moose, or both ungulates in the Jackson Valley, Wyoming.

Predominant browsing ungulate species	Production (kg/ha)	% offtake	Production removed (kg/ha)
Elk	1602 ± 489	31 ± 4	392 ± 103
Moose	4264 ± 616	12 ± 2	407 ± 69
Moose and elk approximately equal	3525 ± 859	12 ± 3	378 ± 124

Based on AIC criteria, we concluded that offtake is a better predictor of willow production, canopy area, canopy volume, and willow height than ungulate density measures. When considering only ungulate density, elk density was the best determinant of willow growth variables. However, willow stem and plant density were best predicted based upon moose density.

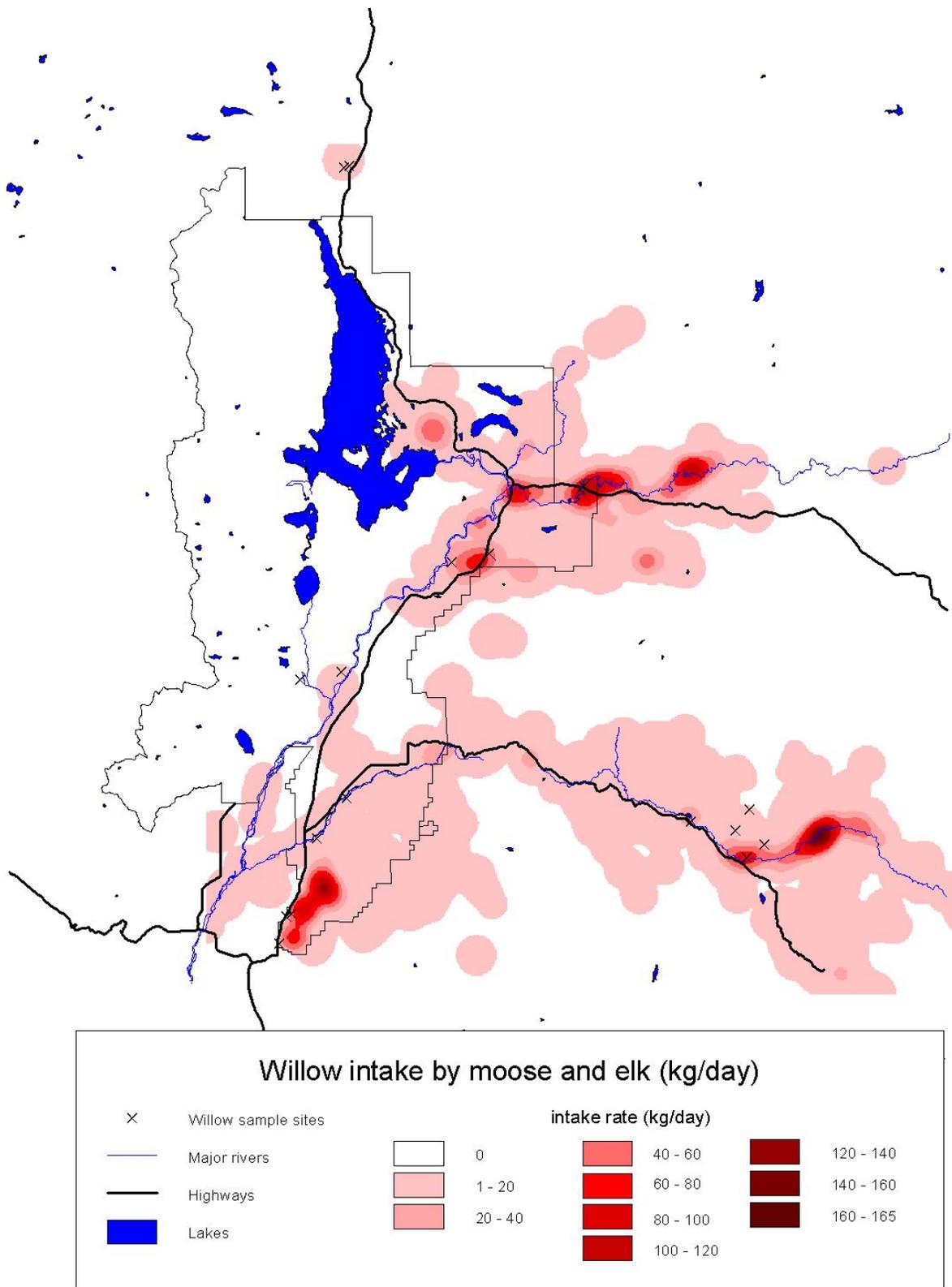


Figure 2.10. Average estimated daily moose and elk intake rates of willow (averaged over winters 2000-2002 for elk and 1999-2000 for moose) in the Jackson Valley, Wyoming.

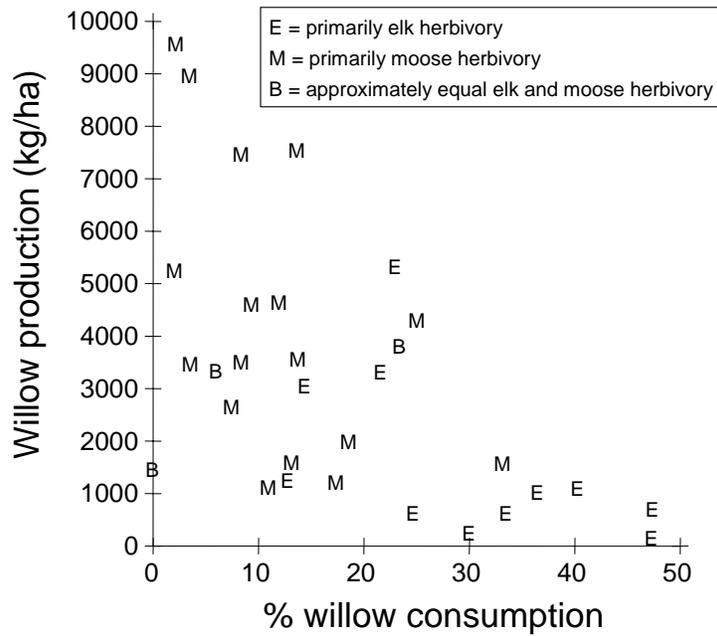


Figure 2.11. Distribution of moose and elk in willow patches with varying annual production and consumption levels in the Jackson Valley, Wyoming, 2000-2002.

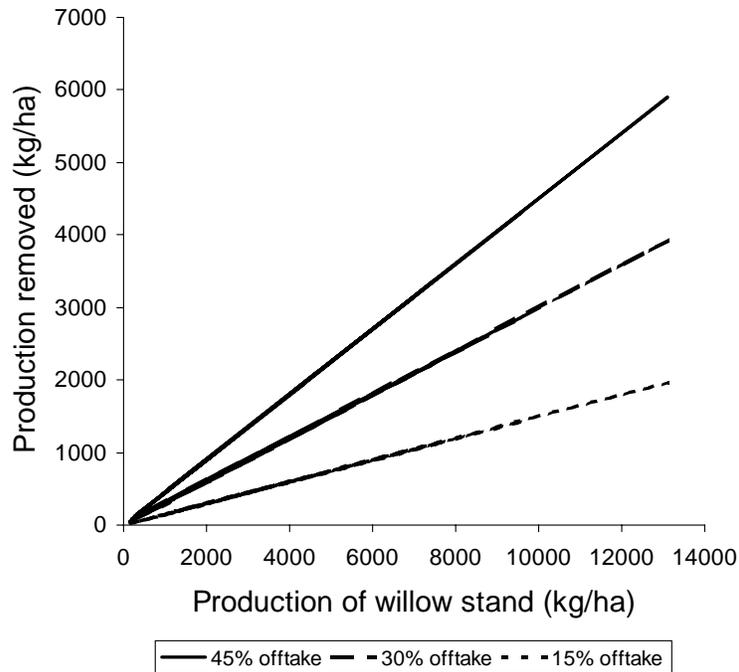


Figure 2.12. Effect of various levels of offtake (consumption rate) of willows on removal of annual production from willow stands. As the production of willow stands increased, the same percent of offtake resulted in a higher biomass removal (kg/ha).

CONCLUSIONS

We concluded the single best index to predict willow status and vigor was consumption rate. However, ungulate population size and density is the parameter that managers will modify through harvest regulations. We recommend managers monitor numbers of both elk and moose in order to manage willows. If managers can monitor only one species, that species should be elk. We do not recommend monitoring moose alone, because moose density was negatively correlated to elk density (Fig. 2.6c), and elk density was the dominant influent on willows. Thus monitoring and managing for moose densities alone would be misleading.

Our analysis found maximal willow growth (production, canopy size) occurred when consumption rates were ~4-5% and showed sharp declines above 23%. There is a high diversity in the status of willows in the Jackson Valley, ranging from very lightly browsed to very heavily browsed. The majority of the willow patches sampled in our study fell into Category I, the tallest willow type. Over 60% of the sampled patches were in either Category I or II. However, a sizeable portion of the willow landscape is either heavily browsed or overbrowsed, but it is important to consider the location of these patches. Ninety-four percent of sampled willow patches that were heavily browsed or overbrowsed were within 6 km of feedgrounds.

Managers need to decide which type of willows they want to manage for. Tall willows result in high abundance and diversity of avifauna, and maximum input to terrestrial soil ecosystem processes (Berger et al. 2001; Dobkin et al. 2002; Singer and Schoenecker 2003). Willow abundance across the landscape will be maximized if all willows are in Category I. Managers seeking to have the majority of willow communities in Category I height/growth status will need to substantially reduce average elk densities across the entire study area from current average levels of 16.3 elk/km² to 1.9 elk/km².

If managers seek to maintain most willow communities in moderately tall Category II for height and growth parameters, average consumption needs to be 11-20% and elk densities will need to be reduced to ~7.5 elk/km². Willow communities in Category II will still be healthy and abundant, but willows will not grow over streamsides, they will not shade streams, nor provide as much cover or litter inputs into the stream, which provides habitat and nutrient inputs to aquatic invertebrates and fish. Category II willow communities will not provide as much habitat for avifauna, although avifauna habitat will be greater than in Category III or IV willow patches (Dobkin et al. 2002). Willows in Category II are productive in terms of annual dry weight biomass of shoots that are produced, however, we found no clear-cut, unambiguous evidence of any maximal biomass production for Category II over Category I willows as we found in the Rocky Mountain National Park ecosystems (Fig. 2.7; Singer et al. 2002).

In willow Category III (21-35% consumption), the size and production of willows is dramatically reduced. Heights of willows are only 70% that of Category I, and canopy cover and production are 65% of Category I. We predict that if elk densities of 35 to 60 elk/km² are present across the NER, most of the willow patches on the NER will be in Category III.

Willow patches in Category IV (> 35% consumption) are severely overbrowsed. Willow plants are short, severely hedged and scattered in small patches. Willow communities have lost much of their ecological function, and little avifauna habitat is provided. As the amount of

overbrowsing increases in riparian woody communities, bird communities change from a diverse community dominated by several species of warblers and vireos, gray catbirds, and several woodpeckers; to a simple community dominated by starlings, cowbirds, black-billed magpies, northern flickers, and meadowlarks (Dobkin et al. 2002). Currently, 33% of the willow patches we measured on the NER and 11% of all the patches we measured in the entire Jackson valley study area fall into the overbrowsed Category IV (Table 2.8). When considering both Categories III and IV, 80% of the willow patches combined on the NER are either heavily browsed (Category III) or clearly overbrowsed (Category IV). Biologists concerned primarily with promoting aquatic and avifaunal habitat, would rate both Category III and IV willows as poor habitat.

Table 2.8. Percent of willow patches in 4 browse categories on the National Elk Refuge and in the Jackson Valley, Wyoming, 2000-2002.

Willow status		Ungulate consumption (%)	% of measured NER willow patches	% of measured patches in entire Jackson Valley study area
Category I	Unbrowsed to lightly browsed	0-10	6.7	40.0
Category II	Moderately browsed	11-20	13.3	22.0
Category III	Heavily browsed	21-35	46.7	26.8
Category IV	Overbrowsed	>35	33.3	11.1

Recommendations to Restore Willows on the NER

If managers desire to recover willows back to healthy stands that are tall enough to escape herbivory by elk, the number of elk currently wintering in concentrated areas on the south end of the NER would have to be reduced. This reduction could be achieved by reducing or eliminating the amount of feeding that occurs in this area. Currently, offtake on the stands we measured throughout the NER averages 28.6%, and on the south end of the NER near the feedgrounds this offtake increases to 32.8%. In recent years, only about 6,000 elk have been fed annually on the NER feedgrounds. Our observations on the northern elk winter range of Yellowstone National Park have found substantial height release of willows when offtake levels dropped to approximately 13%. This height release has translated to recovery of heavily browsed willow patches to willow thickets, the interior of which can often escape browsing by elk entirely because of the increased height and protection of close growing branches. In a timeframe of 6-8

years of reduced browsing levels, thickets have developed from formerly hedged willow patches (F. J. Singer, unpublished data).

Assuming a linear relationship between reduction of elk numbers and reduction in offtake levels, elk numbers would have to be reduced 55-60% to achieve target consumption rates to release the heights of willows. We predict mean elk numbers would need to be reduced to between 2,400 and 2,700 animals on the NER, for at least 6-8 years to initiate recovery of willows on the south end of the NER to healthy stands. Willow recovery leads to additional recovery by changing site conditions and the potential for recovery. Full recovery of these areas might take 2-3 decades or more. Currently, the south end of the NER has about 1,480 acres of existing willow in categories III or IV, all within close proximity to feedgrounds and therefore, subject to the highest elk densities on the NER (Fig. 2.13). Some of this acreage includes areas where willow is still the dominant cover type, while in others *Potentilla fruticosa*/*Carex* spp. is now the predominant vegetation classification. Most willows in these areas are less than 0.5 m tall and heavily browsed (Eric Cole, National Elk Refuge, personal communication). There is an additional 238 acres of willow along the Gros Ventre River in the north end of the NER and these willows are mostly Category II and III stands (Fig. 2.13). Willow is the dominant shrub species in these areas and plants tend to be taller and more productive.

The recovery of willow stands under this treatment protocol (elk reduced to 2,400-2,700 animals on the NER for 6-8 years) would apply only to those patches where willows are still the dominant vegetation. Willow patches height-released in Yellowstone National Park were still ~1 m tall and occurred at a density of about 4 plants per 10m² plot. We predict willows that now occur as a component of an herbaceous community (scattered individual plants, 45-85 cm tall, at densities of only 1-3 plant per 10m² plot) along Flat Creek in the NER will take much longer to fully recover.

Low stature-low density patches of willows may take much more active disturbance or management to fully recover, such as fencing, flooding, or the return of beaver. Currently, there is almost no recruitment of willows along Flat Creek. Willows cannot establish in heavy grass or sedge cover, such as exists along Flat Creek. Willow seedlings or recruits require open, bare, moist sites. Willows may recruit new individuals in the following manners: (a) in the moist deposits left immediately, the first year or two, following the breach of a beaver dam; (b) on frequently flooded point bars of streams; and (c) in old stream channels. Recruits may develop by sexual (seed) or asexual (rooted stems, shoots) means. Beaver activity increases the amounts of stems and shoots in the stream and deposits that may later root and develop on moist sites. The return of beaver to portions of Flat Creek will promote willow habitat through the watering of larger areas and through the creation of suitable sites for re-establishment of willow. The Gros Ventre drainage in the NER supports more beaver activity and more adequate recruitment of willow.

The recovery of willows will require lower elk densities (estimated $\leq \sim 2,500$ on the NER) than will the number of elk to stabilize willow communities once willows are fully recovered. We predict to maintain recovered willows on the NER in mostly Category II, would require holding the elk population at a maximum level of no more than $\sim 3,700$ animals. This estimate assumes

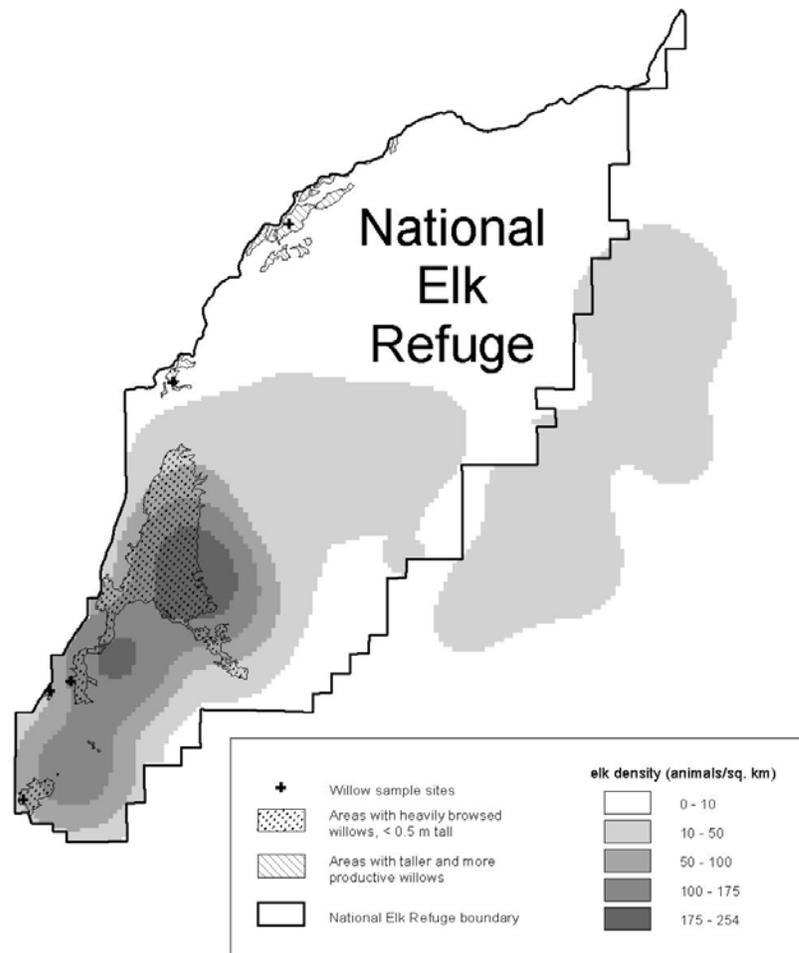


Figure 2.13. Area and characteristics of existing willow cover as it relates to elk density on the National Elk Refuge, Wyoming, 2002.

that a linear reduction in the number of animals from ~6,000 to ~3,700 would equate to a linear and proportionate reduction in offtake levels from 32.8% to 20%. However, since the average offtake of category II willows in our study was 15%, it would be prudent to maintain a population of 2,750-3,150 elk (~10-25% more elk than to recover willows) once willows are recovered on the NER. We emphasize that we cannot predict all of the effects of reduced artificial feeding and/or reductions in elk numbers on the distribution and foraging behavior of the remaining population. These numbers are conditional estimates and lower (or possibly higher) populations may be supported while maintaining healthy willow stands on the NER. Thus, any management program should include monitoring of vegetation and should be adaptive.

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Addendum to USGS-CSU Willow Report to NER, 23 June 2003

We attempted to determine the amount of willow in each of the four general categories of willow use on the National Elk Refuge (NER) based upon elk densities. Currently ~1677 acres of willow have been identified on the entire NER. Our study team has identified 4 categories of willow based on percent utilization by large ungulates and associated height and vigor:

Category I—Tall, vigorous willows browsed only 0-10%.

Category II—Productive willows, not quite as tall or dense, browsed moderately 11-20%.

Category III—Short willows browsed 21-35%.

Category IV—Very suppressed, scattered willows browsed >35%.

We developed a regression relationship to predict offtake of willows based on winter elk density throughout the Jackson Valley. We used an equation in which the intercept was forced through zero assuming that at very low elk densities on the NER offtake would be negligible. However, if tall willows recovered in the Flat Creek area of the NER, a small number of moose would likely begin to spend winters in the area. Based on the regression relationship, we predicted the amount of current willow in each category with 3 scenarios in elk numbers: (1) current elk numbers (~6,500); (2) a 30% reduction in elk numbers (elk reduced to ~4,500); and (3) a 70% reduction of current elk numbers (elk reduced to ~2,500).

We estimate approximately 80% of willows on the entire NER are currently in the suppressed categories III and IV (Table 2.9). While reducing elk densities 30% would substantially increase the amount of taller willow in class II, 72% of all NER willow patches would remain in categories III and IV. A much more drastic reduction in elk density would be required to restore the majority of willow patches (about 70%) to tall vigorous category I and II willows (Table 2.9).

Table 2.9. Predicted category of willow and percent utilization of willow on the National Elk Refuge, Wyoming, based upon current and hypothetically reduced elk densities.

Category of willow and average percent utilization	Acres of willow in each category (% of all willow area)		
	Current elk density*	Elk density reduced 30%**	Elk density reduced 70%***
Category I—Lightly browsed (0-10% offtake)	237 (14%)	250 (15%)	531 (32%)
Category II—Moderately browsed (11-20% offtake)	86 (5%)	215 (13%)	610 (36%)
Category III—Heavily browsed (21-35% offtake)	232 (14%)	390 (23%)	536 (32%)
Category IV--Overbrowsed (>35% offtake)	1122 (67%)	823 (49%)	0

*Current elk density equates to average numbers of elk (~6,500) wintering on the NER, 2000-02.

**30% reduction in elk density estimated to simulate reduction to ~4,500 elk

***70% reduction in elk density estimated to simulate reduction to ~2,500 elk

Part III: Effects of Long-Term Ungulate Herbivory on Plant and Soil Nitrogen and Carbon, Jackson Valley, Wyoming

Report to the National Elk Refuge and Grand Teton National Park

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INTRODUCTION

Large herbivores can have long-term effects on the biomass, biodiversity, and nutrient cycling of forests and grasslands (Burke et al. 1989, Pastor et al. 1993, Frank et al. 2000, Singer and Zeigenfuss 2002). Herbivores can alter nutrient cycling, especially nitrogen (N), which may limit ecosystem production and biodiversity. Large herbivores alter nutrient cycles by direct impact through trampling, grazing and browsing, and by spatially redistributing nutrients through feces and urine. The latter may increase the presence of more labile forms of carbon (C) and N, which in turn can accelerate soil N processes. Such effects can interact with soil conditions such as temperature, moisture, and total C and N pools, which further regulate nutrient cycles.

With heavy grazing or browsing of plant biomass, soil N mineralization rates may decline along with net primary production and its quality (Pastor et al. 1993). On nutrient-poor sites, grazing and browsing may require plants to invest significant energy to produce and maintain elevated concentrations of defensive compounds to protect aboveground tissues (Coley et al. 1985). Since plants vary in this ability and such investments are especially taxing on nutrient-poor sites, the additional stress may alter both above- and below- ground biodiversity and function.

The potential for overgrazing by native large herbivores in western national parks, national forests, and wildlife refuges has been a long-term natural resource issue (Wright et al. 1933, Wright 1999, Singer and Zeigenfuss 2002). Numerous conditions can elevate and redistribute populations of large herbivores. The loss of predators, incompatible conterminous land use, and blocking of historical migration paths by human development are common factors. In some instances, the redistribution of large numbers of herbivores has led to use of supplemental feeding programs, especially in winter, by federal and state agencies. Supplemental feeding can add significant amounts of limiting nutrients to the terrestrial and aquatic ecosystem.

Here we summarize results from a 2-yr study on the effect of elk herbivory on shrub and grasslands by comparison research using five long-term (>40 yrs old) exclosures located in the National Elk Refuge, Bridger-Teton National Forest, and Grand Teton National Park, Jackson Valley, Wyoming (Fig. 3.1). We investigated seasonal change in soil inorganic N pools, total C

and N pools, net nitrification and N mineralization rates; soil respiration, temperature, and moisture; and the C and N content of aboveground herbaceous production and small roots. The primary objective was to examine whether elk herbivory accelerated N cycling.

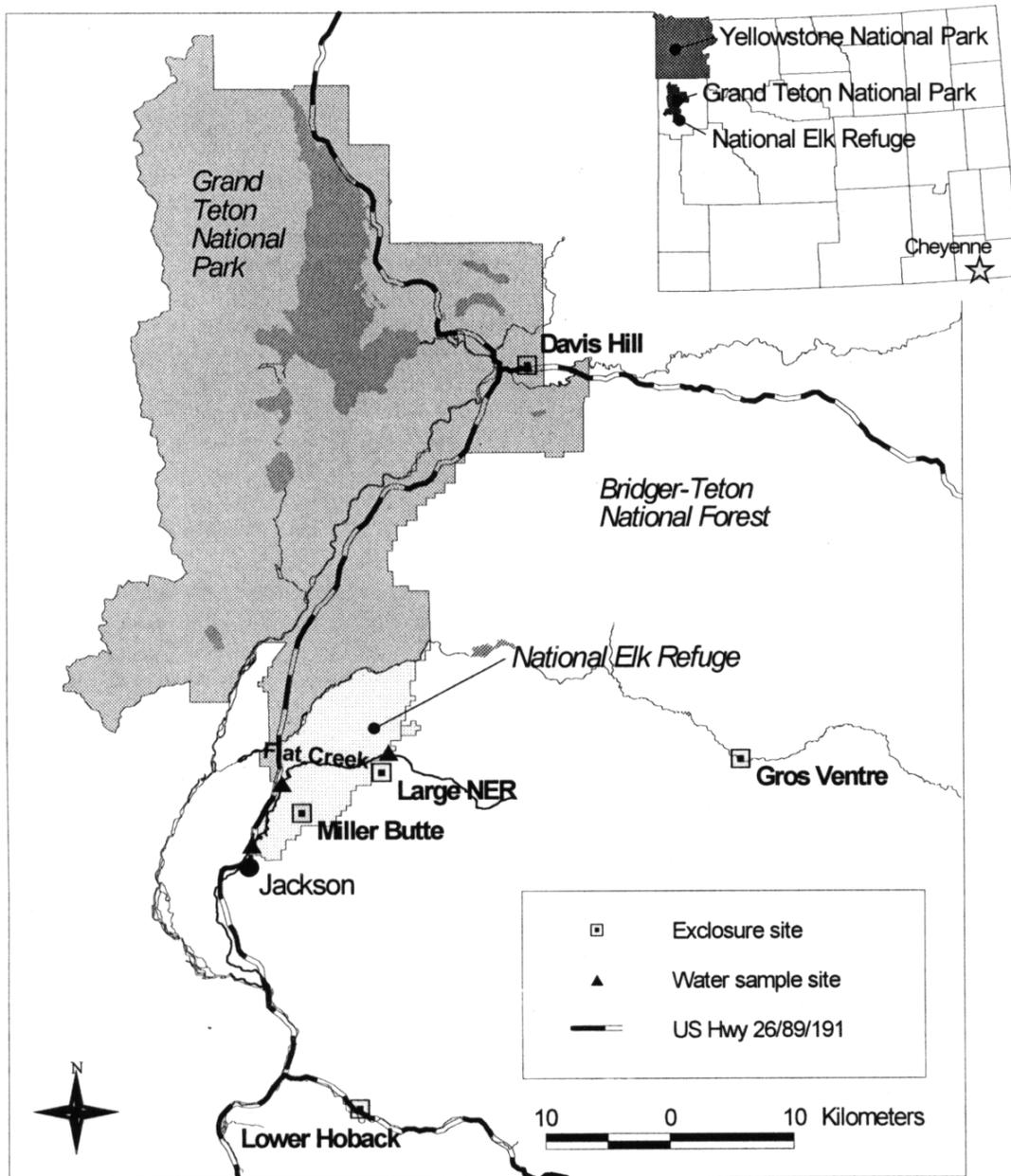


Figure 3.1. Location of exclosure study sites and water sampling points for study of effects of ungulate herbivory on plant and soil carbon and nitrogen, Jackson Valley, Wyoming.

METHODS

Site Description

Five exclosures from 40 to 65 yrs old and their conterminous area were studied. The Lower Hoback, National Elk Refuge (NER), and Gros Ventre exclosures were located in the Bridger Teton National Forest, the Miller Butte exclosure was located in the National Elk Refuge managed by the U.S. Fish and Wildlife Service, and the Davis Hill exclosure was east of Moran Junction, Grand Teton National Park (Fig. 3.1).

The 1985-2002 mean summer (June - August) temperature in the region was 19.3° C (National Climate Data Center). During the study, the mean summer temperature was 20.1° C.

Temperatures throughout this region are warming slightly (0.17° C/decade). The 1985-2002 average precipitation in the region was 44 cm. The mean annual precipitation amount during 2001-2002 was 38 cm. There was no significant trend in annual precipitation amount during the last 20 yrs.

Annual inorganic N deposition at National Atmospheric Deposition Program (NADP) station WY98 at Gypsum, Wyoming, averaged 0.84±0.24 kg/ha during the past two decades. There has been a slight increase ($P < 0.05$, $r^2 = 0.24$, mean = 0.02 kg/ha) in annual inorganic N deposition during this time. Deposition during the study period was slightly below average (<0.8 kg/ha/yr) because of the reduced precipitation amounts. Seasonal inorganic N in wet deposition was greatest ($P < 0.01$) during summer (0.35 kg/ha, June - August, NADP). Winter mean cumulative inorganic N inputs from September through May averaged 0.5 kg/ha (50 mg N/m²).

The Lower Hoback exclosure (31 x 31 m) was established in 1938, and is located just north of US Hwy 189/191 in Hoback Canyon. The exclosure is located near the Wyoming Game and Fish Dept's Fish Creek winter feeding ground. The exclosure has a south aspect. Soils are well-drained gravelly loams. Inside the exclosure dominant plant species include big sagebrush (*Artemisia tridentata*), needle-and-thread grass (*Hesperostipa comata*), antelope bitterbrush (*Purshia tridentata*), carpet phlox (*Phlox hoodii*), arrowleaf balsamroot (*Balsamorhiza sagittata*), and mutton bluegrass (*Poa fendleriana*). On grazed areas, big sagebrush, western wheatgrass (*Pascopyrum smithii*), needle-and-thread grass, mutton bluegrass, arrowleaf balsamroot, and littleleaf pussytoes (*Antennaria parvifolia*) predominate.

The Miller Butte exclosure (84 x 130 m) is located on the north end of Miller Butte in the National Elk Refuge. The exclosure has a NNE aspect at 1940 m elevation. Soils were formed in loess and are dominated by loam and silt loam. The grazed areas are subjected to large groups of elk that come to winter at the Refuge feeding grounds. The site shows some signs of recent elk activity within the exclosure. Inside the exclosure, dominant plant species include three-tipped sagebrush (*Artemisia tripartita*), Kentucky bluegrass (*Poa pratensis*), mountain snowberry (*Symphoricarpos oreophilus*), Columbia needlegrass (*Achnatherum nelsonii*), and broom snakeweed (*Gutierrezia sarothrae*). Outside the exclosure broom snakeweed, mutton bluegrass, carpet phlox, Columbia needlegrass, mountain snowberry, and wood rose (*Rosa woodsii*) are dominant.

The National Elk Refuge (NER) exclosure (113 x 125 m) is located on US Forest Service land along the eastern boundary of the National Elk Refuge. The exclosure was established in 1952

on a WNW slope at 2100 m elevation. Soils are gravelly loam, silt loam, and loam formed from volcanic and sedimentary rock and loess. The area is subjected to large herds of wintering elk that come into the adjacent National Elk Refuge to feed. The enclosure has been breached by elk in the recent past, but repairs have been in place since 2000. Dominant plant species inside the enclosure include mutton bluegrass, rose pussytoes (*Antennaria rosea*), *Phlox muscoides*, junegrass (*Koeleria macrantha*), western and bluebunch (*Agropyron spicatum*) wheatgrasses. Outside the enclosure *Phlox muscoides*, mutton bluegrass, bluebunch wheatgrass, rose pussytoes, junegrass, and stemless goldenweed (*Haplopappus acaulis*) predominate.

The Davis Hill enclosure (47 x 62 m) is located inside the eastern boundary of Grand Teton National Park, on a hillside with a SSW aspect at 2136 m elevation just east of Moran Junction and north of US Hwy 26/287. The enclosure was established in 1963. Soils are very well drained gravelly loams and silt loams derived from alluvium. Dominant species inside the enclosure are bluebunch wheatgrass, antelope bitterbrush, mountain snowberry, arrowleaf balsamroot, horsebrush (*Tetradymia canescens*), and Oregon grape (*Mahonia repens*). Outside the enclosure serviceberry (*Amelanchier alnifolia*), arrowleaf balsamroot, locoweed (*Oxytropis* spp.), sedges (*Carex* spp.), and bulbous bluegrass (*Poa bulbosa*) dominate.

The Gros Ventre (GV) enclosure (61 x 61 m) is located in the Bridger-Teton National Forest within the Gros Ventre River drainage 5 km SE of Upper Slide Lake and just SW of the confluence of the Gros Ventre River and Fish Creek. The enclosure was established in 1958. The enclosure is situated along a flat alluvial area S of the river at an elevation of 2400 m. Soils are a brownish gray fine sandy loam. The riparian zone is vegetated by the *Salix boothii*/*Carex utriculata* (*rostrata*) community and *S. geyeriana* while *S. drummondiana* and *S. wolfii* may be present (Youngblood et al. 1985). The understory is dominated (38% mean area) by graminoid species (*Carex utriculata*, *C. aquatilis*, *Calamagrostis canadensis*, and *Juncus balticus*) and some forbs (13% of area). Graminoids and forbs cover 39% of the area within the enclosure and 63% outside.

Field Procedures

Soil inorganic N pools, net N mineralization rates

From 5 to 20 sample points were randomly located within each enclosure (control) and in the conterminous area (grazed). The number of sample points at each enclosure was determined by vegetation diversity, and were equal for grazed and control. Sample points within the enclosures were >5 m from the fenced perimeter, and >15 m to 25 m external the enclosures. No sample point was <1 m distance from another.

We estimated NO_3^- - N and NH_4^+ - N pool size and inorganic N mineralization rates monthly from May through September using the closed top core method (Adams and Attiwill 1986). Following removal of any Oi layer, the top 10 cm of soil was sampled using a 5.3 cm diameter plastic tube. Paired cores were pulled from each sample point. One core from each pair, which represented a nonincubated sample, was placed in a Whirl Pac and returned to the field laboratory and stored at 2°C. The other core was left in its sample tube, capped, and returned to the same hole for incubation. Any displaced Oi layer was then replaced adjacent the tube. After approximately 30 d, the field-incubated sample was removed and returned to the field laboratory for extraction.

Following field collection, soil samples were refrigerated at the field lab for <5 d at 2°C. This time was needed for sample collection from all 5 exclosures. Soil moisture was determined on non-incubated samples by oven drying (105°C for 24+ h) a subsample with percent moisture expressed as g H₂O/soil dry weight. Bulk density was calculated from the total oven dry weight / total sample volume. A large subsample was then sieved (2-mm sieve), and the >2-mm fraction weighed and discarded. The <2-mm fraction was weighed and split into two subsamples; one subsample was extracted for NO₃⁻ - N and NH₄⁺ - N using 2M KCl, and the other frozen for total C and N analyses.

Soil respiration rates

From May to October 2002, we measured monthly soil respiration rates (CO₂ efflux) from the soil surface within and adjacent each exclosure. The objective was to use CO₂ efflux as an index of soil microbial and small root respiration rates, the rate change with soil temperature and moisture, and to define relationships between soil respiration rates, N mineralization rates, and soil total C and N pools. We used the dynamic method (PP System Model 2 Infrared Gas Analyzer). Fifteen points were randomly located within each control and 15 in the conterminous grazed area. Minimal distances from the exclosure perimeters were similar to the N mineralization study. Soil respiration sample points were permanent for the study period, and measurements were taken from bare soil. Any Oi (litter) present was removed, the measurement taken, then the Oi layer replaced. Only the Gros Ventre site had a continuous Oi layer. Respiration rates were taken as close to the middle of the day as possible. This limited the number of exclosures visited each day so respiration measurements were taken over a period of several or more days each month. No measurements were taken after rain when soil moisture and temperatures rapidly change.

Soil Resin Bags

Potential change in seasonal inorganic N availability was estimated using ion exchange resin bags (Binkley and Hart 1989). In September 2001, early May 2002, and September 2002 approximately 15 ion exchange resin bags were placed within and external each control. The resin bag locations overlapped with the N mineralization sample points. Resin bags were pulled in May 2002 and September 2002. Resin bags were constructed in two compartments--one containing anion resin and the other cation resin. Each bag compartment was approximately 5 cm x 5 cm with a glue bead separating the two. Bags were placed in mineral soil at a depth of 7 cm below the Oi. After collection, the resins from each bag were combined for extraction using 2M KCl.

Small Roots

We conducted a one-time sampling of small root biomass and its chemistry in early September 2002. Samples were collected using a 5.3 cm diameter sharpened tube driven into the soil to a depth of 10 cm. Five cores were collected from each control and grazed area near the N mineralization sample points. Cores were returned to the field laboratory where roots were separated from soil by washing in a flat pan. The separated roots were then divided into <0.5 mm (fine) and 0.5 - 1.5 mm (small) diameter samples, oven-dried, weighed, and stored until analyses for total C and N.

Herbaceous Vegetation Production and Offtake

In April and early July of 2002, herbaceous production from 3-5 randomly located 0.25 m² circular plots was clipped to the ground. The number of plots was the same in the control and with grazing. The clippings were separated into growth form (forbs, graminoids), oven-dried, weighed, and stored until laboratory analyses for C and N. The April samples represented dead herbaceous material not consumed since the previous fall, and the July samples represented new production in 2002. To complete the measurement of production and offtake by large herbivores on grazed sites, similar clippings were taken from replicated 1 m² cages located >10 m from the fenced perimeter of each control plot.

Stream Chemistry

From early May to late October 2002, stream water chemistry was monitored at three locations in the National Elk Refuge (Fig. 3.1): where Flat Creek enters the Refuge along its eastern boundary, at the Fish Hatchery, and at the bridge where Flat Creek leaves the Refuge and enters the city of Jackson. Samples were collected weekly unless the discharge was unchanged when stream chemistry was sampled every two weeks. Water samples were collected in amber 250 ml Nalgene polyethylene bottles. Sample bottles were pre-rinsed in deionized water, dried, and then twice rinsed with stream water before sample collection. Samples were refrigerated at 2°C, and shipped to the laboratory in Ft. Collins, Colorado.

Laboratory Analyses

Ten-gram sieved soil subsamples were extracted with 50 ml of 2 M KCl, and NO₃⁻ - N (cadmium reduction) and NH₄⁺ - N (indo-phenol) determined on a Lachat autoanalyzer (Lachat Instruments, Milwaukee, WI). Net NO₃⁻ - N mineralization for each 30-d period was estimated by the difference between initial and final NO₃⁻ - N content. Total net N mineralization rates were determined by the difference between initial and final NO₃⁻ - N and NH₄⁺ - N content.

Soil, root, and plant tissue C and N content was analyzed on a Leco 1000 CHN analyzer. Samples were oven-dried then finely ground prior to analysis.

Stream water samples were analyzed in the laboratory at Ft. Collins. The stream water pH, conductance, and alkalinity were determined on a Mann Tech PC Titrant auto-titrator (Cosa Instr. Co., Gelp, Canada). Separate filtered (0.45 µm) subsamples of stream water were analyzed for macro ions (Ca²⁺, Mg²⁺, Na⁺, K⁺, NH₄⁺, PO₄⁻, Cl⁻, NO₃⁻, SO₄²⁻) using Waters ion chromatographs.

Data Analyses

The data presented here were primarily from the period September 2001 to October 2002. The most intensive data gathering occurred during the snow-free period from April to October 2002. We examined the effect of grazing on all five exclosures combined using t-tests (Systat). The t-tests were used to compare the effect of grazing on basic soil properties, soil inorganic N and total N pools, N mineralization rates, soil total C pools and C respiration rates, and plant production biomass and small root C and N content. Analyses were confined to soils dominated by herbaceous vegetation. Some shrubs were present at Miller Butte, Davis Hill, and Gros Ventre, however, except for inside the Gros Ventre exclosure, shrub cover was not pervasive. All C, N, and biomass results were presented on a unit area or unit weight basis using

appropriate conversion factors. Except to provide some descriptive data, the sites were not analyzed individually.

RESULTS

Soils

Bulk density, temperature, moisture

Grazing increased soil bulk densities 9% ($P < 0.01$; Table 3.1). The increases were most evident at Lower Hoback, Davis Hill, and Gros Ventre. Soil moisture and temperature were inversely correlated (Tables 3.2 & 3.3). Grazing increased ($P = 0.07$) soil temperatures at a 5 cm depth beneath the Oi layer (Fig. 3.2). The temperature increase was most apparent at Miller Butte. Grazing decreased soil moisture ($P < 0.05$) with the largest difference at Gros Ventre.

Soil C and N Pools

Grazing had no effect on soil C and N percentages, the C:N ratio, or total soil C and N content (Table 3.1). The soil total C and N pools were correlated (Tables 3.2 & 3.3). There were no differences in early (June) and late summer (September) soil C or N percentages. In the controls (exclosures), the soil total C pool was correlated with temperature and moisture. With grazing the soil total C pool was correlated with moisture.

Soil C mineralization rates

Soil respiration rates peaked in late June. Soil respiration rates were highest ($P < 0.01$) at Gros Ventre and lowest at NER. The range in mean respiration rates among the five exclosures (0.78 mg C/m²/d) was an order-of-magnitude greater than the effect of grazing (0.07 mg C/m²/d). July was the only month respiration rates were greater ($P < 0.05$) in the controls.

Grazing reduced ($P < 0.05$) soil respiration rates (Fig. 3.2). The grazing effect was most evident at Lower Hoback ($P < 0.001$) and Gros Ventre ($P < 0.01$). On grazed sites, soil respiration rates and the total soil C pool size were correlated, but the percentage of soil total C respired did not differ from the controls. Soil respiration rates were also correlated with moisture and net N mineralization rates (Table 3.3).

In the controls, soil respiration rates were correlated with total N pools and inversely correlated with temperature (Table 3.2). Soil respiration rates and moisture were positively correlated, and inversely correlated with soil NH₄⁺ - N pools and net nitrification rates.

Soil inorganic N Pools

Grazing increased soil (0 - 10 cm depth) NO₃⁻ - N ($P < 0.05$) and total inorganic N pool size ($P < 0.01$; Fig. 3.3), but did not alter the soil NH₄⁺ - N to NO₃⁻ - N ratio (Fig. 3.4). In late summer, soil NO₃⁻ - N pools increased and NH₄⁺ - N pools declined resulting in a NH₄⁺ - N to NO₃⁻ - N ratio approaching unity by September. The NH₄⁺ - N pool was correlated with the NO₃⁻ - N, and total C and N pools (Table 3.3).

Table 3.1. Summer (June-September) soil characteristics and graminoid biomass, carbon, nitrogen, and C:N, Jackson Valley, Wyoming.

Site	Soil					Graminoids			
	Bulk density (g/m ³)	% moisture	%N mean \pm s.d.	%C mean \pm s.d.	C:N	Shoot: root	C (kg/m ²) mean \pm s.d.	N (kg/m ²) mean \pm s.d.	C:N
Hoback									
ungrazed	1.00	14.6	0.23 \pm 0.04	2.7 \pm 0.6	11.7 \pm 0.6	0.44	14.5 \pm 8.4	0.41 \pm 0.24	35.0
grazed	1.17	14.3	0.21 \pm 0.03	2.6 \pm 0.4	12.0 \pm 0.4	0.68	9.5 \pm 3.6	0.26 \pm 0.10	35.7
Miller Butte									
ungrazed	0.90	22.4	0.48 \pm 0.18	5.9 \pm 2.2	12.6 \pm 2.6	0.08	7.2 \pm 4.5	0.21 \pm 0.13	33.4
grazed	0.98	19.9	0.43 \pm 0.09	5.0 \pm 1.2	11.4 \pm 1.0	0.32	52.0 \pm 69.0	1.70 \pm 2.30	30.7
NER									
ungrazed	12.7	9.3	0.17 \pm 0.05	4.2 \pm 1.6	25.0 \pm 10.0	0.04	4.8 \pm 2.7	0.16 \pm 0.09	29.7
grazed	1.18	9.3	0.16 \pm 0.04	4.0 \pm 1.9	25.0 \pm 9.2	0.04	5.4 \pm 2.2	0.19 \pm 0.07	28.3
Davis Hill									
ungrazed	1.05	9.4	0.28 \pm 0.13	3.9 \pm 1.6	14.4 \pm 2.4	0.28	11.2 \pm 8.1	0.28 \pm 0.18	37.9
grazed	1.22	9.0	0.20 \pm 0.06	3.1 \pm 0.6	16.1 \pm 3.6	0.88	29.0 \pm 6.1	0.82 \pm 0.17	35.2
Gros Ventre									
ungrazed	0.91	31.8	0.25 \pm 0.13	5.1 \pm 2.4	21.5 \pm 4.9	0.08			
grazed	1.03	25.7	0.29 \pm 0.13	5.9 \pm 1.7	22.1 \pm 5.2	0.24	49.7 \pm 9.3	1.63 \pm 3.10	30.6

Table 3.2. Correlation coefficients among monthly soil net mineralization rates, CO₂ efflux, soil moisture, soil temperature (5 - cm depth), and inorganic and total N pools inside exclosures (ungrazed), Jackson Valley, Wyoming.

	Soil Temp (°C)	Moisture (%)	C Mineralization	NO ₃ ⁻ pool	NH ₄ ⁺ pool	Net nitrification	Net N mineralization	Total C pool	Total N pool
Soil Temp (°C)	1.00								
Moisture (%)	-0.65***	1.00							
C Mineralization	-0.43**	0.57***	1.00						
NO ₃ ⁻ pool	0.56***	-0.22*	-0.20	1.00					
NH ₄ ⁺ pool	0.15	-0.05	-0.25*	0.57***	1.00				
Net nitrification	0.47***	-0.41**	-0.37**	0.23	0.09	1.00			
Net N mineralization	0.17	-0.02	0.05	0.31*	-0.02	0.46***	1.00		
Total C pool	0.30*	0.27*	-0.11	0.41***	0.28*	0.15	-0.02	1.00	
Total N pool	0.12	0.16	-0.27*	0.09	0.33*	-0.08	-0.22	0.78***	1.00

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3.3. Correlation coefficients among monthly soil net mineralization rates, CO₂ efflux, soil moisture, soil temperature (5 - cm depth), and inorganic and total N pools outside exclosures (grazed), Jackson Valley, Wyoming.

	Soil Temp (°C)	Moisture (%)	C Mineralization	NO ₃ ⁻ pool	NH ₄ ⁺ pool	Net nitrification	Net N mineralization	Total C pool	Total N pool
Soil Temp (°C)	1.00								
Moisture (%)	-0.62***	1.00							
C Mineralization	0.06	0.24*	1.00						
NO ₃ ⁻ pool	0.07	-0.22*	0.05	1.00					
NH ₄ ⁺ pool	-0.04	-0.06	-0.10	0.58***	1.00				
Net nitrification	-0.02	-0.35**	-0.11	0.41**	0.28*	1.00			
Net N mineralization	0.41**	0.07	0.32*	-0.12	-0.04	-0.26*	1.00		
Total C pool	-0.12	0.44***	0.32*	0.15	0.42**	-0.12	0.27*	1.00	
Total N pool	-0.20	0.27*	-0.17	0.09	0.56***	0.01	-0.07	0.41**	1.00

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

In the controls, soil NO_3^- - N pools were correlated with soil temperature and inversely with moisture (Table 3.2). The inorganic N pool size was inversely related to soil respiration rates. The soil NO_3^- - N pool was correlated with NH_4^+ - N and the total C pool, and the NH_4^+ - N pool with total N (Table 3.2). The range in inorganic N pool size (237 mg N/m^2) in the controls was greater than on grazed sites (54 mg N/m^2).

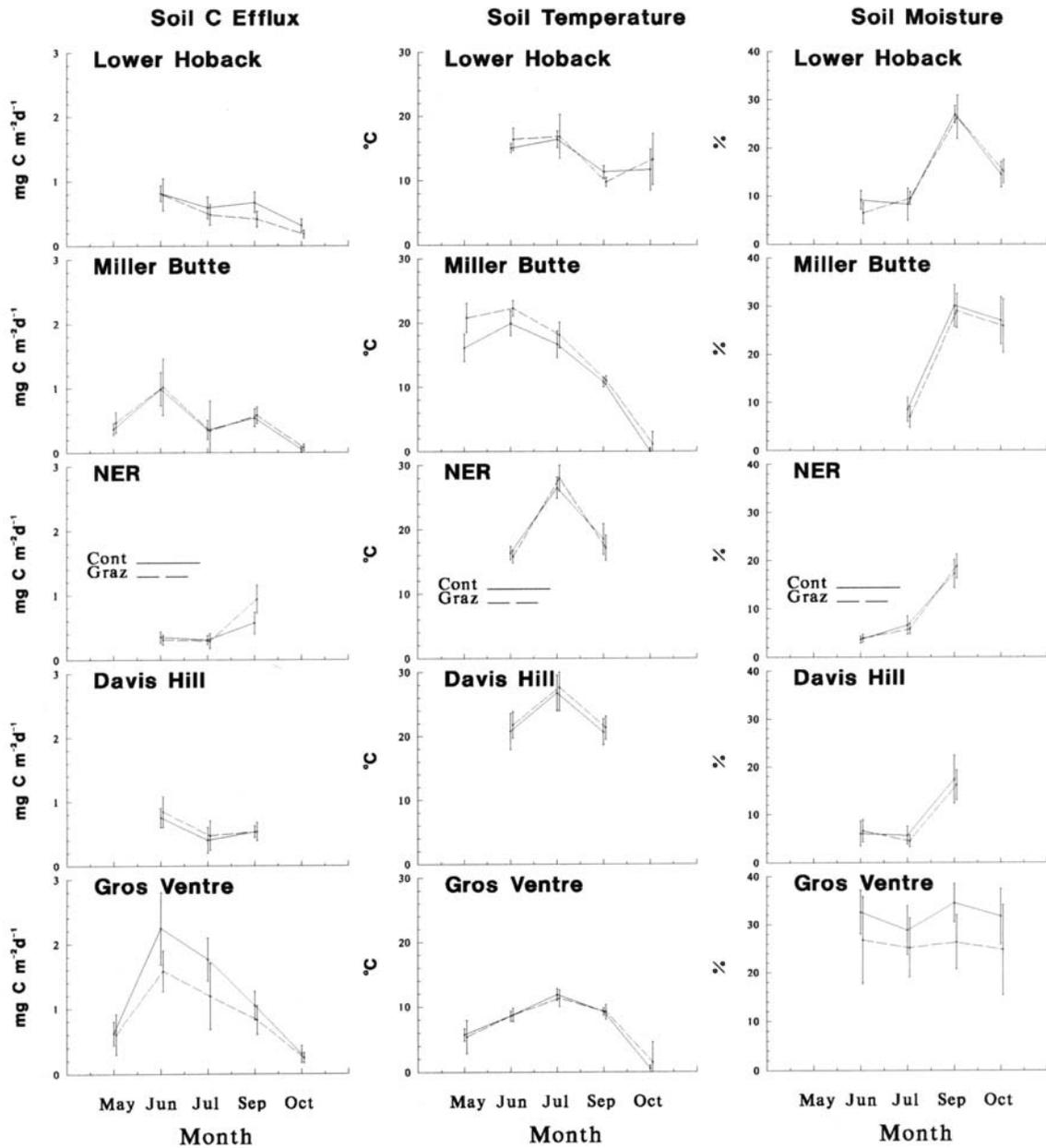


Figure 3.2. Seasonal mean mid-day soil temperatures, moisture, and soil surface C emission rates in exclosures (controls) and with grazing, Jackson Valley, Wyoming. Bars represent standard deviation.

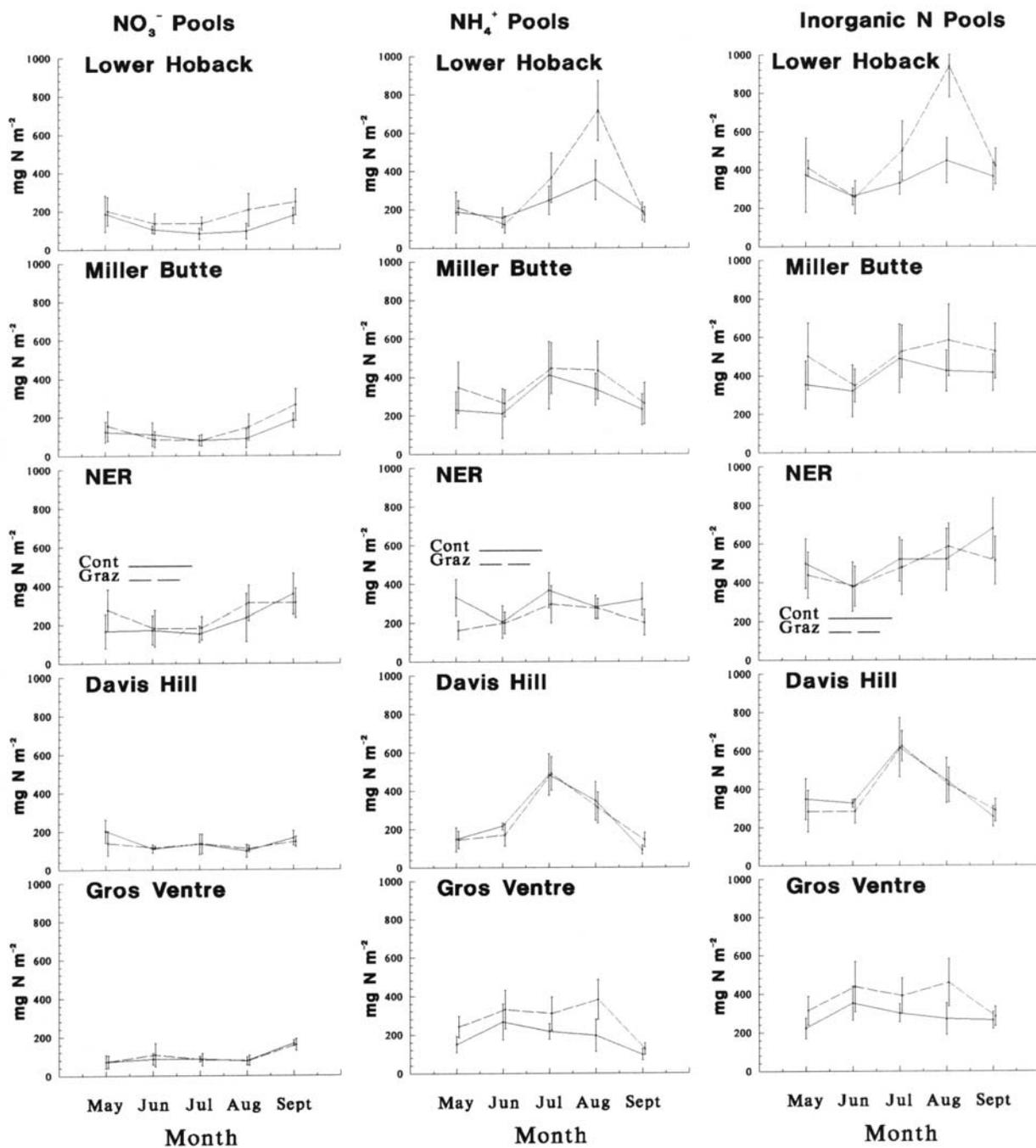


Figure 3.3. Seasonal change in inorganic N pools (NO_3^- , NH_4^+ , inorganic N) in exclosures (controls) and with grazing, Jackson Valley, Wyoming. Bars represent standard deviation.

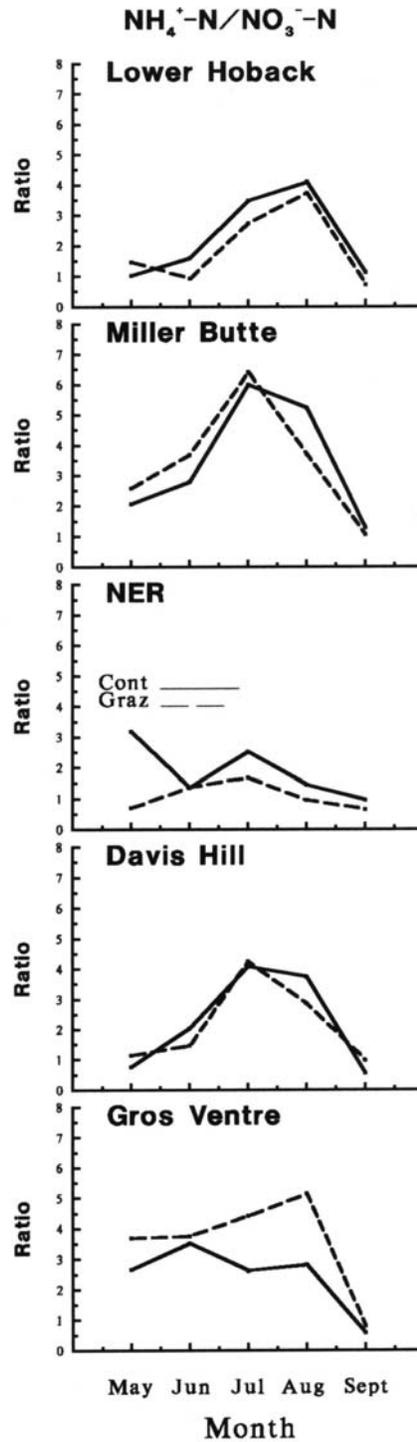


Figure 3.4. Seasonal change in the $\text{NH}_4^+ - \text{N} / \text{NO}_3^- - \text{N}$ ratio in soil inorganic pools, in exclosures (controls) and with grazing, Jackson Valley, Wyoming.

Soil net N mineralization rates

Grazing increased net nitrification ($P < 0.01$) rates, and total net N mineralization rates by an average 45% ($P < 0.05$; Fig. 3.5). The increase was about one-third the mean net N mineralization rates of the controls. Seasonally, net nitrification rates were lowest ($P < 0.001$) in August and highest ($P < 0.001$) in September. Net N mineralization rates were highest ($P < 0.001$) in June and lowest ($P < 0.001$) in September. With grazing, net nitrification rates were correlated with soil NO_3^- and NH_4^+ pools, and inversely correlated with soil moisture (Table 3.3). Net N mineralization rates were correlated with soil temperature and respiration, and inversely with net nitrification rates (Table 3.3).

In the controls net nitrification rates were correlated with soil temperature and inversely with moisture and soil respiration rates (Table 3.2). The range in growing season net N mineralization rates was greater in the controls (9.8 mg N/m²/d) than with grazing (1.8 mg N/m²/d; Fig. 3.5).

Resin bag N content

The resin bag NO_3^- content was lower ($P < 0.01$) in summer than winter (Fig. 3.6). Grazing increased ($P < 0.001$) winter resin NO_3^- and total inorganic N content. In the controls, summer resin bag NO_3^- content was positively correlated to net nitrification rates ($P < 0.10$) and with grazing to net N mineralization rates ($P < 0.10$).

Biomass

Fine/small roots

Fine root (<0.5 mm diameter) biomass exceeded ($P < 0.001$) that of small (>0.5 - 2 mm) roots by >2 fold (Fig. 3.7). In the controls, fine roots made up 56% of the total root biomass ($P < 0.01$) and with grazing, 72% ($P < 0.001$). Grazing had no effect on root C content (Fig. 3.7). The fine root C content, 72% of total root C, was greater ($P < 0.01$) than that in small roots and proportional to fine root biomass. In the controls, there was no difference in C content by root size. Grazing had little effect on root N content or C:N ratio (Fig. 3.8). Fine root N content (71%) exceeded ($P < 0.001$) that of small roots, and the fine root C:N ratio (27) was lower ($P < 0.001$). In the controls the fine root N content was 64% of the total ($P < 0.05$), and with grazing 80% ($P < 0.001$).

In the controls, soil respiration rates were related to fine root biomass ($P < 0.10$), its C content ($P < 0.01$) and C:N ratio ($P < 0.001$). The fine root C:N ratio was inversely correlated ($P < 0.001$) with soil NO_3^- pools, net nitrification rates, total net N mineralization rates ($P < 0.05$), and positively correlated ($P < 0.05$) with soil NH_4^+ pools. With grazing only net nitrification rates were correlated ($P < 0.05$) with fine root biomass and its C and N content.

Herbaceous production

Grazing increased summer ($P = 0.05$) graminoid production, its N and C content, and the C:N ratio within cages external the exclosures. Grazing had no effect on forb production, its C and N content, or dead graminoid or forb biomass. The dead graminoid C:N ratio was greater ($P < 0.01$) in the controls. Grazing increased the average ratio of graminoid production to fine root biomass, but the increase was not significant.

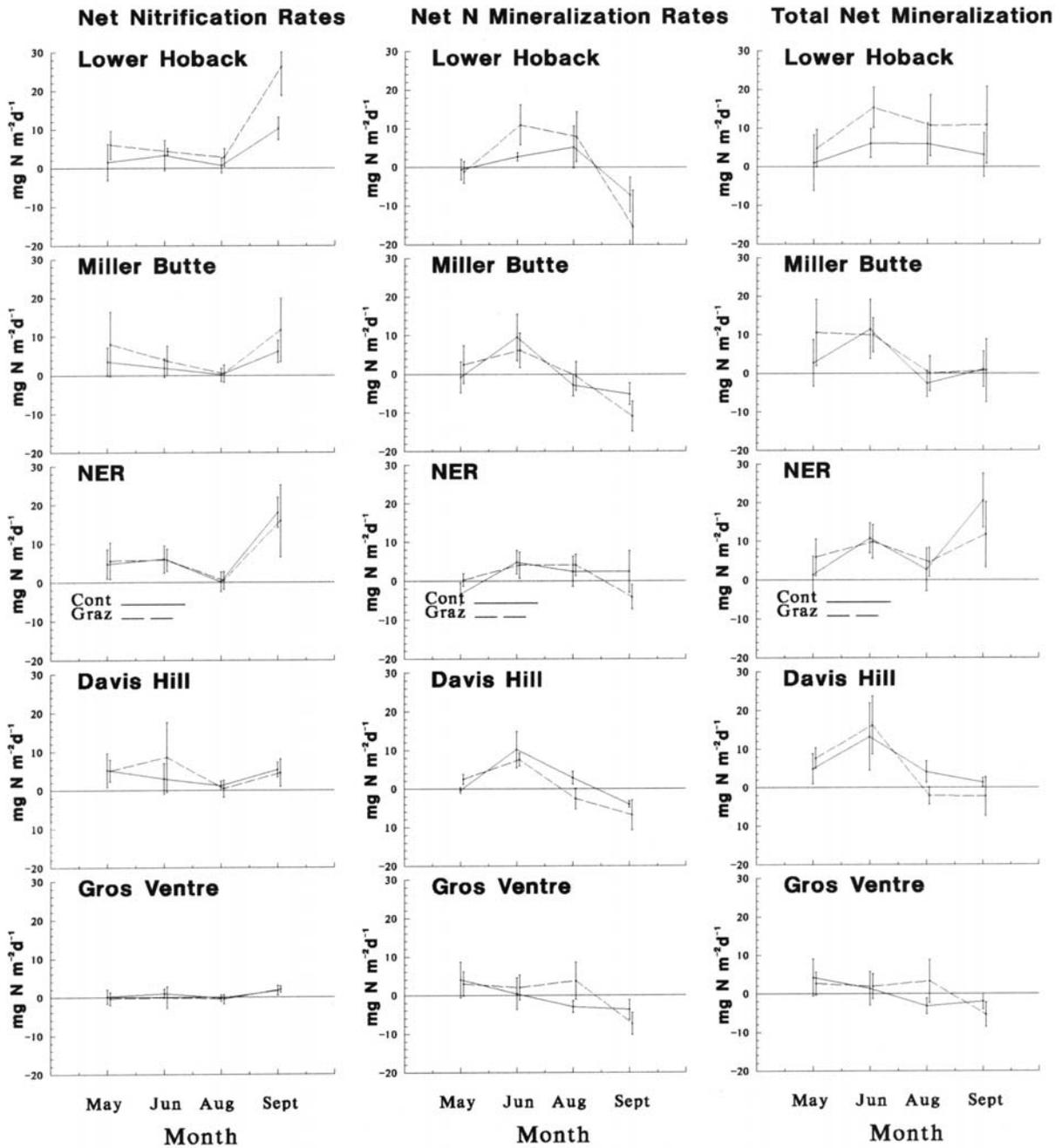


Figure 3.5. Means and standard deviation (bars) for net nitrification, net N mineralization, and total net N mineralization, in exclosures (controls) and with grazing, Jackson Valley, Wyoming.

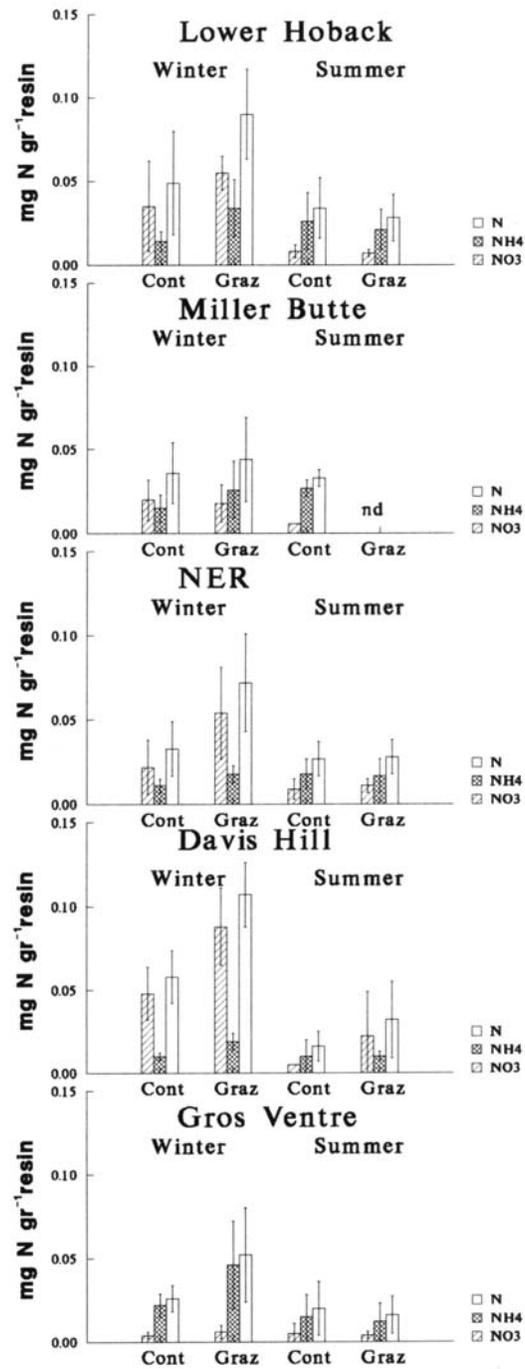


Figure 3.6. Mean and standard deviation (bars) of inorganic N in resin bags left over winter (September - May) and summer (May - September), in exclosures (controls) and with grazing, Jackson Valley, Wyoming. nd equals "no data".

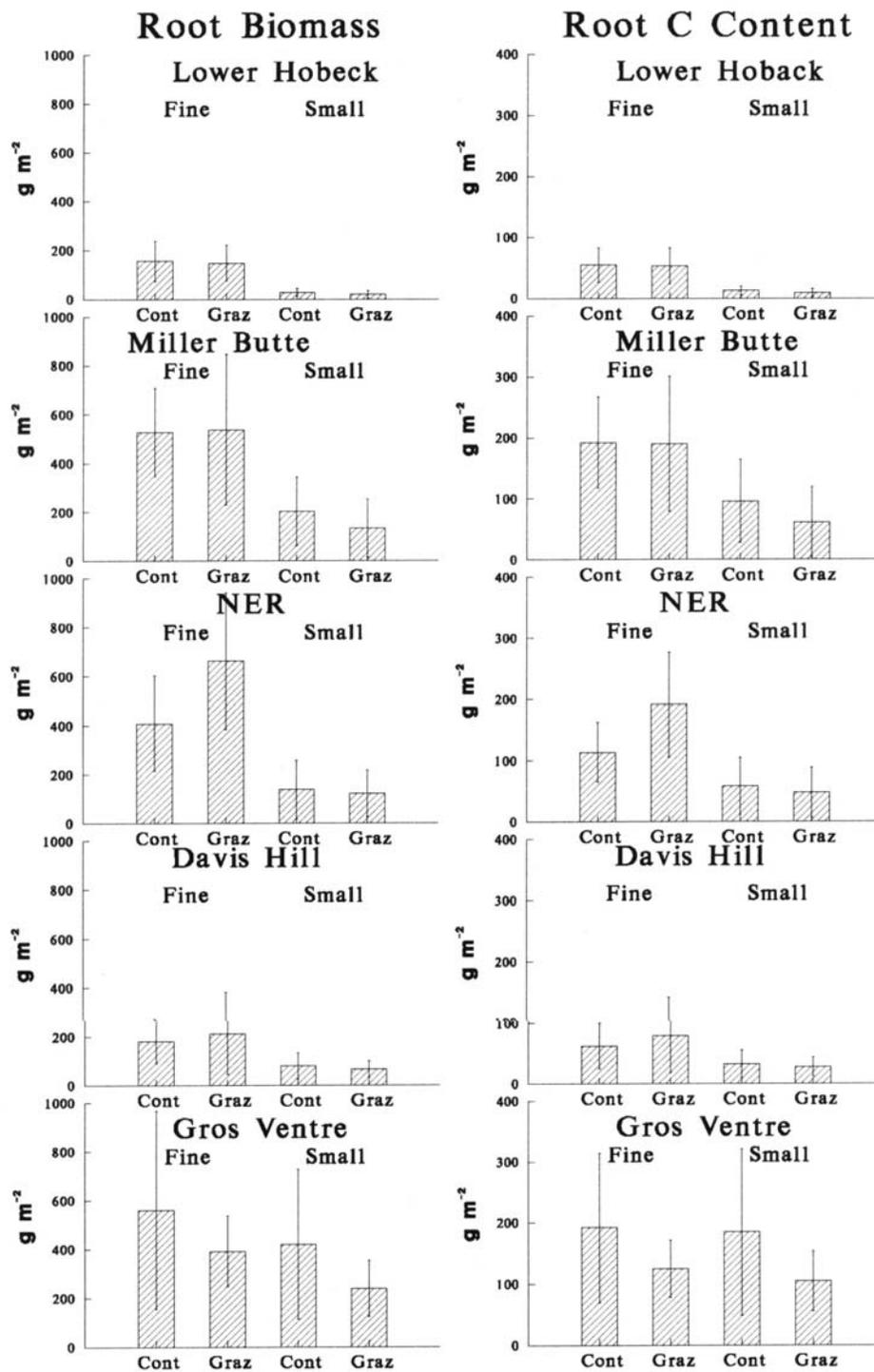


Figure 3.7. Mean and standard deviations (bars) of small (<0.5 mm diameter) and larger (0.5 - 2 mm) root biomass and carbon (C) content in exclosures (controls) and with grazing, Jackson Valley, Wyoming.

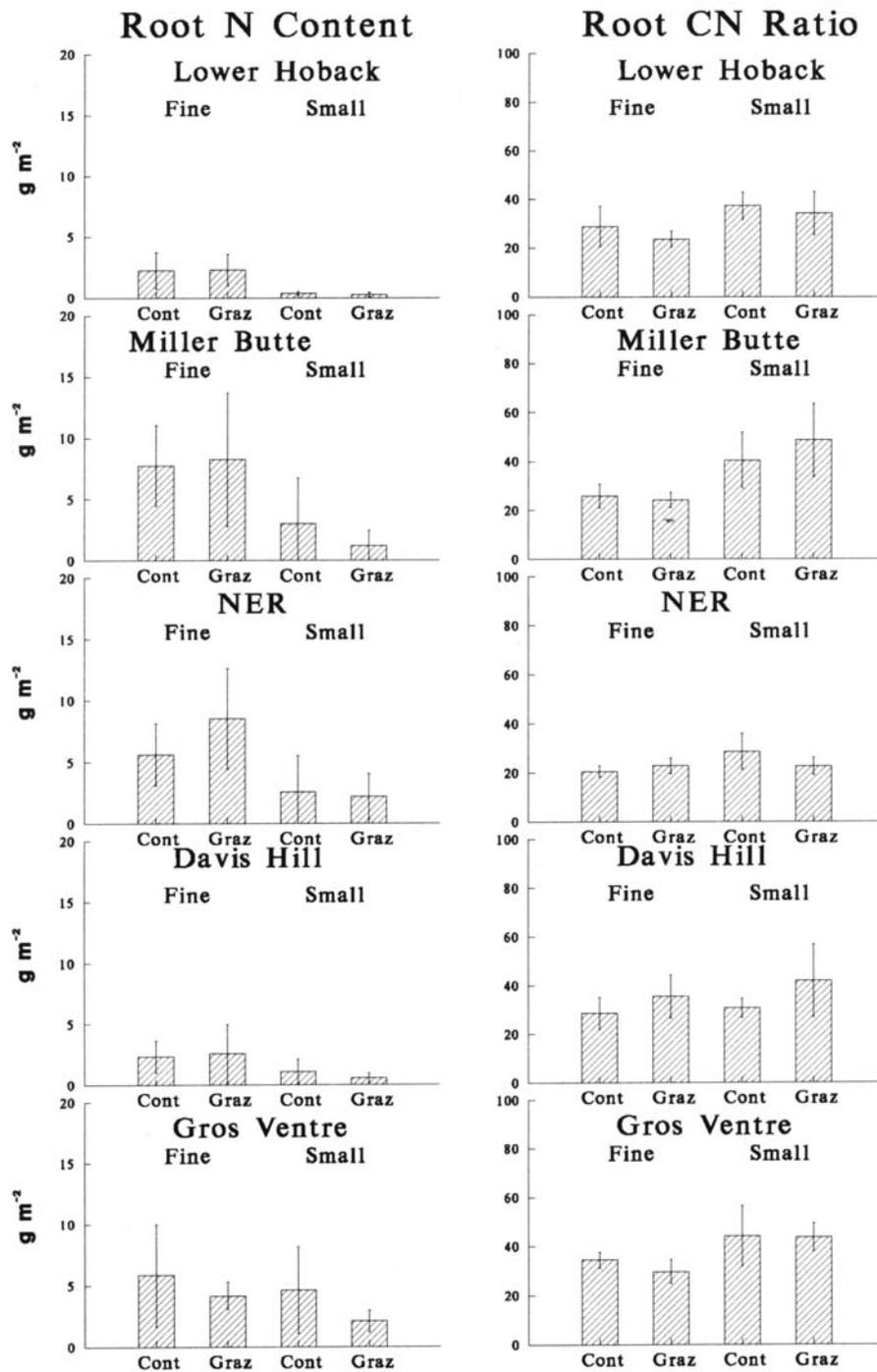


Figure 3.8. Mean and standard deviations (bars) of small and large root nitrogen (N) content and C:N ratio in exclosures (controls) and with grazing, Jackson Valley, Wyoming.

DISCUSSION

Climate and N inputs

Compared with the longer-term record, there were no major deviations in regional temperature or local N deposition during the 2001-2002 study period. Annual precipitation was about 15% below average.

From September to May, inorganic N deposition in wet precipitation averaged 12% of the mean soil inorganic N pool in the top 10 cm (Fig. 3.3). Annual inorganic N deposition averaged 20% of mean soil inorganic N pools. Unless dry deposition of N or wet precipitation dissolved organic N (DON) were significant contributors, atmospheric N inputs were small relative to soil inorganic N pools. Further evidence for the modest precipitation contributions comes from examining the precipitation NH_4^+ - N to NO_3^- - N ratio which was low (mean 0.68) relative to soil ratios (Fig. 3.4).

Soils

The five sites in the present study varied in dominant vegetation, slope, aspect, and elevation. Yet growing season soil C and N mineralization rates, soil moisture, and total C and N pool size varied only by 2 - 3 fold. Topography and climate can be important factors in setting grassland soil conditions, and their effect can result in much variation in soil characteristics (Frank et al. 2000). But in the present study, it appears the similarity in basic soil characteristics limited variation in soil C and N pools and processes among sites. The similarity suggests that differences between grazed and control plots largely reflected the long-term effects of elk herbivory.

In the present study, soil coarse material fractions (>2mm diameter) were low (5% to <25%) at all sites. In recent study on the effects of elk grazing on soils in Rocky Mountain National Park, Colorado, Binkley et al. (2002) found similar increases in soil bulk density near recently established exclosures especially on soils with few rocks. Their results suggest that soil compaction by ungulates occurs relatively quickly following exclosure placement, and the present study suggests further change with time may be minimal.

The higher soil temperatures with grazing were likely the product of lower soil moisture, a less extensive surface litter layer (not quantified), and increased bare ground (Zeigenfuss et al. 2003). The higher and more uniform soil moisture levels at Gros Ventre were the product of increased precipitation amounts at greater elevations, a uniform alluvial soil texture, and a well-developed uniform $2 \pm$ cm deep Oi (litter) layer.

Soil C and N Pools

The absence of a grazing effect on soil C:N ratios suggests that even after four decades large herbivores do not alter net N inputs. The effects of grazing on soil conditions, especially moisture, likely had a greater effect on total C pools as indicated in this and other studies (Stark and Grellmann 2002). At the landscape level, soil C pools and C:N ratios commonly increase with soil moisture.

In this study, there were no seasonal (June and September) differences evident in soil total C or N content, and early May soil inorganic N pools were at or below average (Fig. 3.3). This

finding suggests that winter elk N inputs had little direct effect on growing season soil N pool size in the enclosure vicinity. In a study in Yellowstone National Park, Frank and Groffman (1998) found elk grazing had no effect on soil N or C percentages. Binkley et al. (2002), using recently established enclosures, found little effect of elk grazing on C and N pool size in Rocky Mountain Park. Stark and Grellman (2002) had similar results in a study of large mammal grazing in arctic tundra. The studies suggest that, even after decades of grazing with some soil compaction, there were few effects on basic soil characteristics as texture, N%, or C%. However, Pastor et al. (1993) in a study of moose browsing in boreal forests on Isle Royale National Park, Michigan, found generally higher soil N and C pool sizes inside older enclosures.

Soil C mineralization rates

Soil C and N mineralization rates are often correlated with total soil C and N pools (Pastor et al. 1993, Frank and Groffman 1998, Stottlemeyer 2001). In the present study, the absence of a grazing effect on total C and N pool size indicates that differences in soil C and N mineralization rates were regulated by other factors.

The higher soil respiration rates in the controls likely reflected the more favorable soil moisture levels and moderate temperatures (Fig. 3.2). Soil respiration rates had a greater range in the controls (0.41 to 1.19 mg C/m²/d) than with grazing (0.46 to 0.89 mg C/m²/d) which suggests factors not related to grazing accounted for much of the variation in soil respiration rates. The differences in range also indicate the importance of landscape factors in accounting for variation in soil respiration rates.

At all enclosures except Davis Hill, early season variation in soil respiration rates was greater. This suggests the labile C supply was higher then, and that more recalcitrant C sources were the dominant respiration substrate later in the growing season. At most sites, soil respiration rates declined after June despite near optimal soil temperatures (Nadelhoffer et al. 1991) through September and increased or steady soil moisture levels (Fig. 3.2). Soil respiration rates reached their lowest level (<0.3 mg C/m²/d) in October limited likely by low available C and temperatures (Fig. 3.2).

Grazing also reduced soil C mineralization rates in arctic tundra independent of soil nutrient availability (Stark and Grellmann 2002). An increase in soil nutrient availability, as NO₃⁻ - N, is often rapidly immobilized by the microbial community (Nadelhoffer et al. 1991, Zogg et al. 2000, Stark and Grellmann 2002), which may be reflected in soil respiration rates. However, in the present study, net nitrification rates were inversely correlated (controls) or unrelated (grazed) to soil respiration rates. This result suggests that grazing limited soil microbial respiration rates by reducing microbial biomass which in turn limited NO₃⁻ uptake relative to N mineralization rates (Hart et al. 1994). Soil microbial biomass and respiration rates can decline rapidly in some ecosystems when soils are thawed and labile C becomes limiting (Lipson et al. 2000). A reduction in soil labile C could reflect herbivore offtake of more nutrient-rich plant production. In the present study, grazing did increase summer graminoid production and its C and N content. However, there was no evidence that biomass quality available for autumn and winter offtake by herbivores was higher.

More likely variation in soil labile C reflected variation in fine root turnover rates (Burton et al. 2000). Rapid fine root turnover can provide substantial labile C to soil microbial groups (Boone et al. 1998). Grazing did increase the percentage of N content in fine roots, but the relationship between fine root turnover and soil nutrient status is not clear (Burton et al. 2000). Still for the present study, the seasonal trends in net C and N mineralization rates appear best explained by a loss in microbial biomass in response to limited labile C.

In the controls, soil respiration rates were correlated with fine root biomass and its C and N content (Figs. 3.2 & 3.7). This finding indicates the contribution fine root respiration may make in overall soil respiration rates at these sites.

Soil inorganic N Pools and net N mineralization rates

The autumn increase in soil NO_3^- pools and net nitrification rates (Figs. 3.3 & 3.5) suggests that nitrification of NH_4^+ continued while soil microbial and small root NO_3^- uptake declined. The inverse relationship between soil NO_3^- - N pool size with moisture and the positive correlation between soil respiration and moisture suggests that moisture limited microbial and fine root NO_3^- uptake on both control and grazed sites. The effect of moisture likely was indirect. At all but one enclosure, soil respiration rates declined during the season as soil moisture held steady (Gros Ventre) or increased. This suggests labile C was increasingly limited to the microbial community during the summer and fall. Even under adequate moisture conditions, soil available C can quickly become limited resulting in a rapid loss of soil microbial biomass and respiration rates (Lipson et al. 2000). Burke et al. (1989) showed strong correlations between net and gross N mineralization rates in sagebrush steppe. As their incubations progressed in time, net N mineralization rates became a greater proportion of gross rates. Hart et al. (1994) found a similar pattern in a longer-term laboratory study. They attributed the inorganic N build up to limited labile C, which reduced microbial N demand.

The late season trends in soil inorganic N may help account for why over-winter resin bag NO_3^- contents were elevated (Fig. 3.6). Soils have little capacity to adsorb NO_3^- , and it is likely with increased seasonal moisture coupled with decreased biotic uptake that much of the excess NO_3^- was mobilized to below the rooting zone and eventually lost in stream water (Fig. 3.9). Elevated soil NO_3^- levels are common in winter in the absence of herbivores even where soils may freeze, and soil NO_3^- losses are reflected in winter and early spring stream water (Mitchell et al. 1996, Stottlemeyer and Toczydlowski 1999).

The inverse correlation between net N mineralization and nitrification rates with grazing suggests increased nitrifier competition for inorganic N at the expense of uptake by plants and heterotrophs. The positive correlation between net N mineralization and nitrification rates in the controls supports this hypothesis. The range in mean net N mineralization rates in the controls was 5.7 mg N/m²/d and with grazing 9.8 mg N/m²/d. Grazing increased the variation in net N mineralization rates, primarily net nitrification (Fig. 3.5).

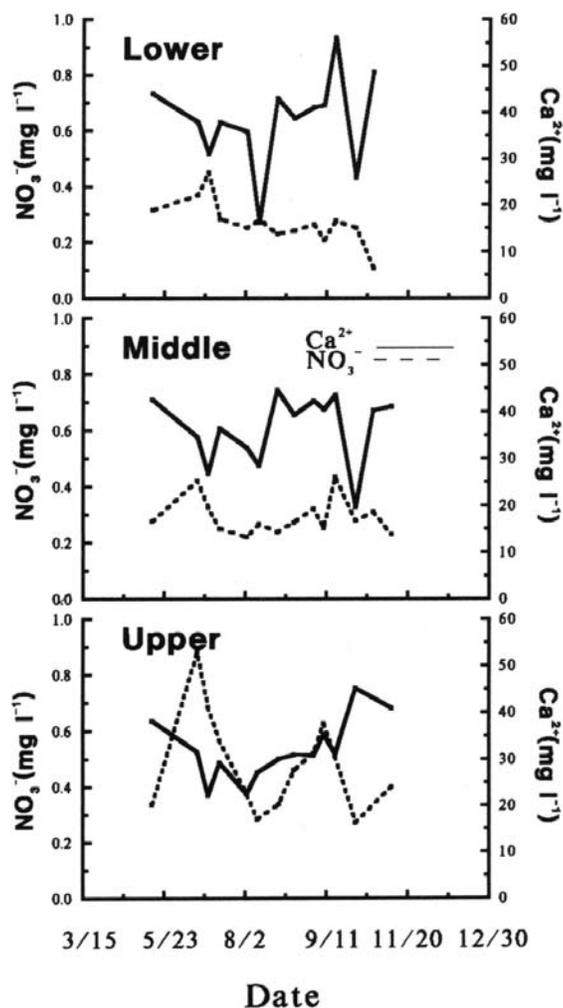


Figure 3.9. Seasonal change in stream water Ca^{2+} and NO_3^- concentrations at stations above (Upper), within (Middle), and downstream (Lower) of the National Elk Refuge, Jackson, Wyoming.

Extrapolating spring - autumn N mineralization rates to year-round, N mineralization rates in the controls ($1.6 \text{ g N/m}^2/\text{yr}$) were about 25% lower than found by Frank and Groffman (1998) in Yellowstone grasslands. Growing season net N mineralization rates are generally the lowest of the year because of increased immobilization. The resin bag data indicate that soil available N in

winter was greater than in summer which would likely increase estimates of annual N mineralization rates.

The larger inorganic N pools and net N mineralization rates with grazing likely contributed to the greater graminoid production. The greater variation in N mineralization rates with grazing may also contribute to increased variation in plant production among sites.

Resin Bags

Seasonal resin bag N content indicated that grazing promoted winter inorganic N leaching or loss from surface soils (Fig. 3.6). The largest potential surface soil NO_3^- losses came on grazed sites during winter. Part of the NO_3^- adsorbed by over-winter resins likely came from the late autumn increase in soil NO_3^- pool size and increased net nitrification rates (Figs. 3.3 & 3.5). However, adsorbed NH_4^+ was also higher on resins during winter when the autumn inorganic N pool size and total net N mineralization rates were low.

The year-round resin results coupled with low early spring soil inorganic N pool size and net N mineralization rates suggest that most of the N adsorbed to over-winter resins was the result of winter soil mineralization with possible contributions by elk. Winter soil net N mineralization rates can exceed summer rates where soils do not freeze (Stottlemeyer and Toczydlowski 1999), and over-winter resin bags placed where there is little or no herbivory can show high adsorbed N content (Stottlemeyer 2001). The processes regulating soil N mineralization from N uptake differ in quality and magnitude and response to environmental conditions. Such factors likely accounted for the high winter resin N contents.

Biomass

Under nutrient-rich conditions, one hypothesized effect of herbivory is a shift in vegetation composition toward fast-growing plants that increase nutrient uptake and may enrich plant production quality (Chapin 1991). As litterfall, the enriched production decomposes more rapidly, further accelerating the nutrient cycle.

Another potential response to herbivory is an increased allocation of resources to fine root biomass to accommodate for increased offtake. In the present study, there were some differences in shoot and root chemistry with grazing but few were significant compared with the controls. For example, with grazing there was a shift in the relative amounts of biomass to fine roots, fine root N content, and a decline in the fine root C:N ratio. By implication, this suggests grazing may have affected the aboveground biomass resource allocation. Graminoids are one group that respond to a nutrient-rich environment (Post and Klein 1996). In the present study, graminoid biomass clippings of summer production within cages external the exclosures suggest grazing did promote production. But graminoid clippings from cages had a higher C and N content and C:N ratio ($P=0.05$), which does not indicate nutrient enrichment of herbaceous production.

In forest ecosystems, increases in soil nutrient status may slow fine root turnover and its contributions to labile C (Burton et al. 2000). Fine root metabolic activity can be greater when N availability is greater. However, in the present study, soil respiration - the sum of microbial and fine root respiration - was lower with increased N availability from grazing. This again suggests that soil metabolic activity was limited by available C.

Stream water inorganic N

It is impractical, likely impossible, to compute an accurate N budget for the Flat Creek watershed owing to the spatial and temporal variation in land use and seasonal hydrologic manipulations. The Flat Creek watershed is large (10,750 ha) with a relatively small portion of it impacted by high-density elk grazing and supplemental feeding. The stream drains the Gros Ventre Range, and travels about 20 km before entering the National Elk Refuge. The watershed has been gauged below the Refuge for 14 years by the USGS (Wyoming station 13018000), and peak discharge (mean 2457 l/s) occurs on average June 23 during snowmelt at the higher elevations.

In high solute concentration stream water, as Flat Creek (Fig. 3.9), base cation solutes as Ca^{2+} decrease in concentration as stream water discharge increases. During the May-June 2002 period, the time span where most snowmelt enters streams in this region, stream water Ca^{2+} declined as NO_3^- concentrations peaked with increased discharge. The USGS hydrologic data for 2002 were not yet available, but the change in stream water Ca^{2+} concentration suggests discharge peaked June 25-27, 2002 at the upper station and a week later near the mouth. The peak in stream water NO_3^- concentration, which made up about 75% of the streamwater inorganic N concentration, occurred May 26 at the upper station and 7-9 d later at the mouth. At peak discharge, the inorganic N output from the watershed was about 0.16 mg N m/s/d, a small fraction of that available from soil pools (Fig. 3.3). Inorganic nitrogen outputs likely peaked earlier concurrent with peak stream water NO_3^- concentrations. This occurred when stream discharge was >50% of peak.

Short of an intensive year-round hydrologic study with stream water chemistry, it appears the watershed was retaining inorganic N relative to atmospheric N inputs. However, stream water inorganic N concentrations were still an order of magnitude higher than usually found in forested watersheds of this region.

SUMMARY

It appears elk herbivory increased soil N mineralization rates and inorganic N pools primarily by reducing labile C availability to soil microbes. This hypothesis was supported by the lower soil respiration rates with grazing. Limited soil moisture was likely a contributing factor in C supply. Soil processes had less variation among grazed sites than within the controls. The reduced variation may have been a response to greater recalcitrant C forms and lower soil moisture with grazing. Elk urine and fecal N additions likely added to the N cycle, but this study did not show any direct evidence of an effect. This result was likely due to the seasonal disconnect between elk presence and growing season N cycling. It is probable any seasonal elk addition to the N cycle could be lost during spring snowmelt. Stream water NO_3^- concentrations through the growing season suggest the ecosystem was losing relatively high amounts of inorganic N.

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ADDENDUM

Potential Influence on Nitrogen Inputs due to Elk Using Feedgrounds on the National Elk Refuge (NER).--There may be enrichment of grasslands near feedgrounds due to the ingestion and excretion of nitrogen (N) from the alfalfa pellets fed to elk on the NER. In 2001-2002, 2,314.6 tons of alfalfa pellets were fed to elk and bison on the NER, of which 16.5% was protein (16.5 % protein \div 6.25 = 2.64% N). Approximately 61.1 tons of N is potentially added to the ecosystem from the alfalfa fed. Pellets are fed in order to reduce waste, to reduce the bulk of the material handled, and to increase the mechanical efficiency of the feeding. Managers are concerned there may be enrichment of N on the southern one-half of the NER due to the feeding. The ecological implications of any enrichment are not known. Any additional N inputs may simply increase production on some sites, or there may be ecological alterations of the ecosystem.

Our goal was to quantify the extent of any N enrichment on the NER due to artificial feeding. We selected the winter of 2001-2002 as a prototype winter for sampling—approximately 6,021 elk were fed 1,870 tons of alfalfa pellets. This was roughly an average winter for feeding activities on the NER. The feeding of alfalfa pellets is calculated by the NER to approximately substitute for the natural daily requirements for elk of 5kg per day, but elk may additionally feed beyond these requirements by foraging on native grasses and sedges, both near to, and up to 2 km away from, the feed lines. USGS crews observed elk for all daylight hours and for limited periods at night with night vision scopes. In fact, most elk were observed to drift away from the feed lines, particularly by evening (the pellets are fed in the morning, typically 0900 to 1130 hr) and to forage on grasses and sedges often located 1 or 2 km from feed lines. Distances moved from the feedgrounds (maximum distance moved = 6.5 km; average daily distance = 2.1 km) were recorded, as were hours/day of foraging on native forages (O = 8 hours/elk/day). These observations, combined with input from WGFD biologists, resulted in a map of the approximate total area (6,190 ha) used by fed elk (Fig. 3.10).

We estimated the influence on nitrogen inputs to the soil surface due to elk, based on fed (NER) and non-fed elk in the Jackson Valley. We conducted fecal surveys on the NER and at 5 exclosure sites in spring 2002. We counted the number of elk fecal piles and pile size on 262 plots of 9.3 m² in size located on 11 transects on the NER and from 25 plots of 9.3m² in size at 5 study sites (5 per site) of elk off feed. These surveys were used to estimate average elk fecal piles/m² and average fecal pile mass.

We estimated the proportion of elk piles attributed to elk on native forage during early winter, on alfalfa feed through mid-winter, and on greening native forages in spring on the NER. The number of elk days on native forage in early winter were calculated by tallying weekly surveys of elk numbers on the south end of the NER from late October 2001 until feeding commenced in mid-January 2002. These surveys were conducted by Bruce Smith (NER). Numbers of elk on feed were taken from reports of the National Elk Refuge for 2002. Numbers of elk days on native forage in spring were calculated by reducing the total number of elk fed gradually over a six-week period following the cessation of feeding. Observation by NER personnel indicated that elk began to leave approximately 3 weeks after feeding ended on March 29, 2002, and that nearly all were gone by May 10, 2002 (Bruce Smith, NER, personal correspondence). We

totaled the number of elk days for all three periods and then calculated the proportion each period contributed to this total.

We estimated N deposition due to elk feces from the grams of fecal N that were deposited by: (a) elk feeding on native forage in early winter; (b) elk on feed; and (c) elk feeding on greening native forage in spring. Fecal N was determined using the following equation:

$$\text{grams fecal N} = \% \text{ N of feces} * \text{dry weight biomass (g)/fecal pile} * \text{average \# piles/m}^2 \text{ deposited at the end of winter season} * \text{proportion of piles deposited by elk in each time period}$$

where % N of feces = $0.77 + (0.49 * \% \text{ N in forage})$ [Mould and Robbins 1981]. Each time period had a different forage N value and therefore contributed different amounts of total fecal N. Grams of urinary N was estimated based on the ratio of urinary to fecal deposition rates from Schoenecker et al. (2002), using the formula:

$$\text{grams urinary N} = U_{\text{ratio}} * \text{fecal N}$$

where $U_{\text{ratio}} = 0.976798596$.

We estimated percent N of NER native forages from Bailey (1999) and production from data collected by NER staff during summer 2001. We estimated percent N of supplemental feed based on values found in Smith et al. (1997). Percent N of native forages eaten by elk off feed was determined from our plant samples from spring and summer 2002 adjacent to 5 enclosure sites and production was sampled on these same plots in summer 2001. We also sampled production and N concentration of plants inside the long-term enclosures to determine N yield with no grazing.

We estimated the average amount of grazing offtake by fed elk on the NER from 1997 samples from 10 plots of 0.25m^2 at grazing cages located within the primary zone of foraging by fed elk (within 1-2 km of feedgrounds). Offtake on the NER was estimated at 65% based on these samples, and this approximate number was also verified by sampling in 2001 and 2002 by Eric Cole of the NER staff (E. Cole, National Elk Refuge, personal communication). Offtake for off feed sites was sampled at 15 plots of 0.25m^2 size from grazing cages adjacent to the 5 long-term enclosures. Offtake at off feed sites was estimated to be 53%. We estimated grams N removed from plots by multiplying the percent offtake by the N yield of the biomass (plant N concentration multiplied by plant production). Percent plant N was averaged between winter and summer samples to account for grazing that occurred in summer and fall when nitrogen levels in plants are higher than in winter.

Atmospheric nitrogen deposition was estimated from records of the National Atmospheric Deposition Program for site WY98, located at Gypsum Creek, approximately 50 mi. SE of Jackson. We totaled reported atmospheric deposition of NH_4 , NO_3 , and inorganic N for summer 2001 through spring 2002.

Conclusions.--Elk grazing on native forages on our off-feed sites was substantial and averaged 53%. Due to this heavy grazing, N inputs were less on grazed (off-feed) compared to paired

enclosed (fenced) sites (Table 3.4). However, we concluded there was enrichment of N onto sites used by elk that visited feedgrounds. N inputs due to elk at these sites were about double compared to sites located away from feedgrounds, i.e. off feed sites (Table 3.4). Overall, N deposition from elk feces and urine was greatest in areas where feeding occurred and decreased as distance from feed lines increased—particularly to the north where the bison are fed (Fig. 3.11). We are uncertain as to the ecological implications of the enrichment. Much of the excess N could be leached into the water table, or to nearby streams during spring runoff. Accelerated N concentration in streams on the NER from spot sampling suggests this could be the case, but this needs to be determined—some uptake by greening plants is also likely. The ultimate destination of the N and any ecological effects of the additional N would require additional studies.

Table 3.4. Inputs and outputs of nitrogen to the soil surface due to the influence of elk in the Jackson Valley, Wyoming, winter 2001-2002.

	All grazed sites influenced by nearby feedgrounds on the NER (on feed)	The 1% of all on feed sites with maximal inputs of N due to elk*	Grazed sites near feedgrounds (off feed)	Ungrazed areas (fenced)
N Inputs Due to Elk				
Fecal/Urinary N (kg N/ha)	13.45	65.8	3.82	0
Ungrazed plant N yield (kg N/ha)	3.5	0	7.44	7.7
Atmospheric deposition (kg N/ha)	2.87	2.87	2.87	2.87
N outputs Due to Elk**				
Plant N yield removed by grazing (kg N/ha)	6.32	9.82	8.38	0
Difference--the total inputs minus outputs due to elk grazing and depositions (kg N/ha)				
	+13.5	+58.85	+5.75	+10.57

*On 63 ha of the NER (~1% of study area), fecal and urinary N deposition exceeds 50 kg N/ha, with an average of 65.8 kg N/ha. Approximately 5 ha of this area has fecal and urinary N deposition exceeding 100 kg N/ha with a high of ~112 kg N/ha.

**Volatilization of urine not sampled. Likely only 10% of urinary N based on the work of Schimel et al. (1986) and Detling et al. (1988).

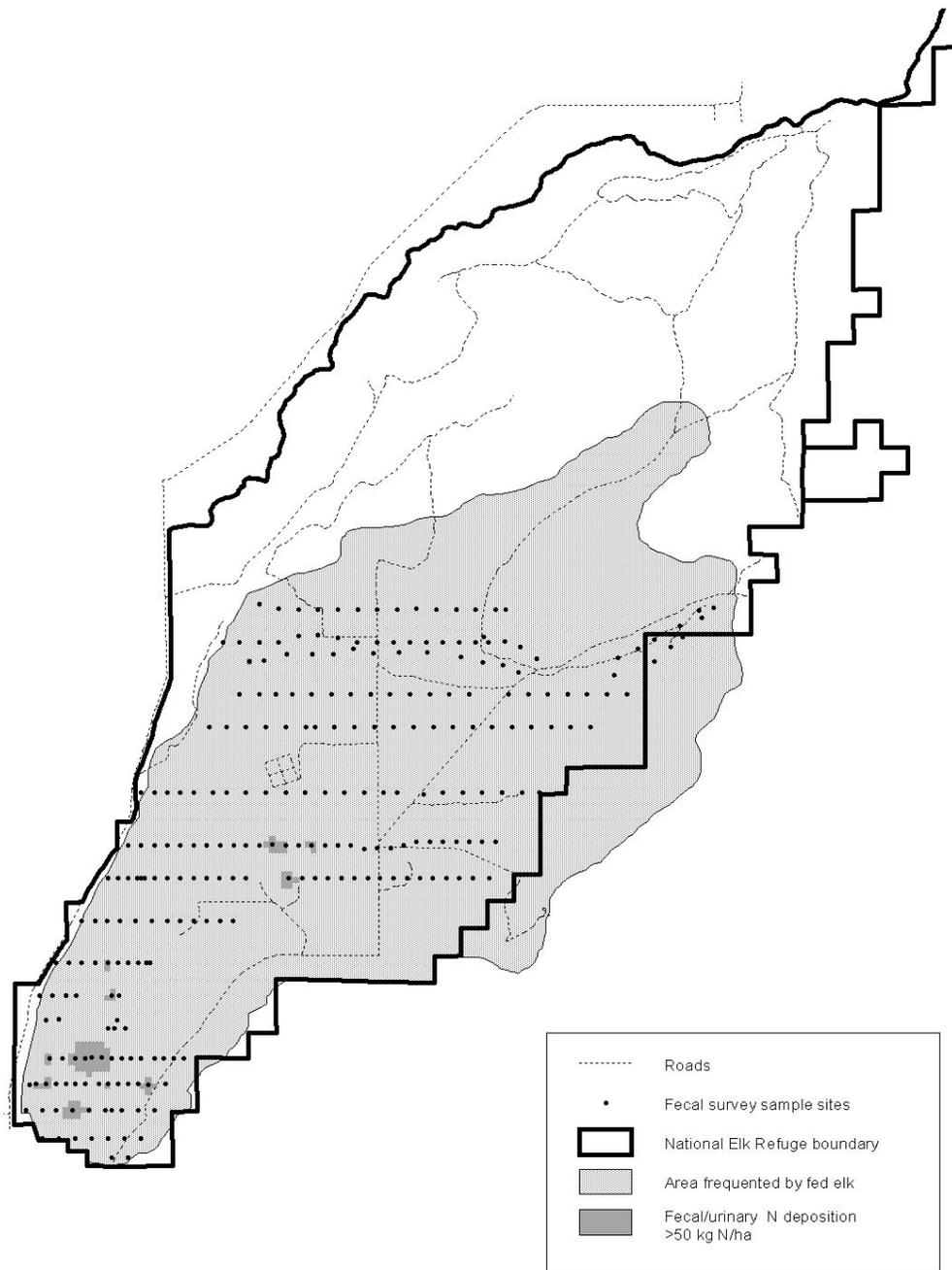


Figure 3.10. Map of our survey transects for elk fecal piles on the National Elk Refuge (NER), late winter 2001-2002. The portion of the NER frequented by elk that use the feedgrounds (i.e. fed elk) and areas of very high fecal/urinary nitrogen deposition are identified.

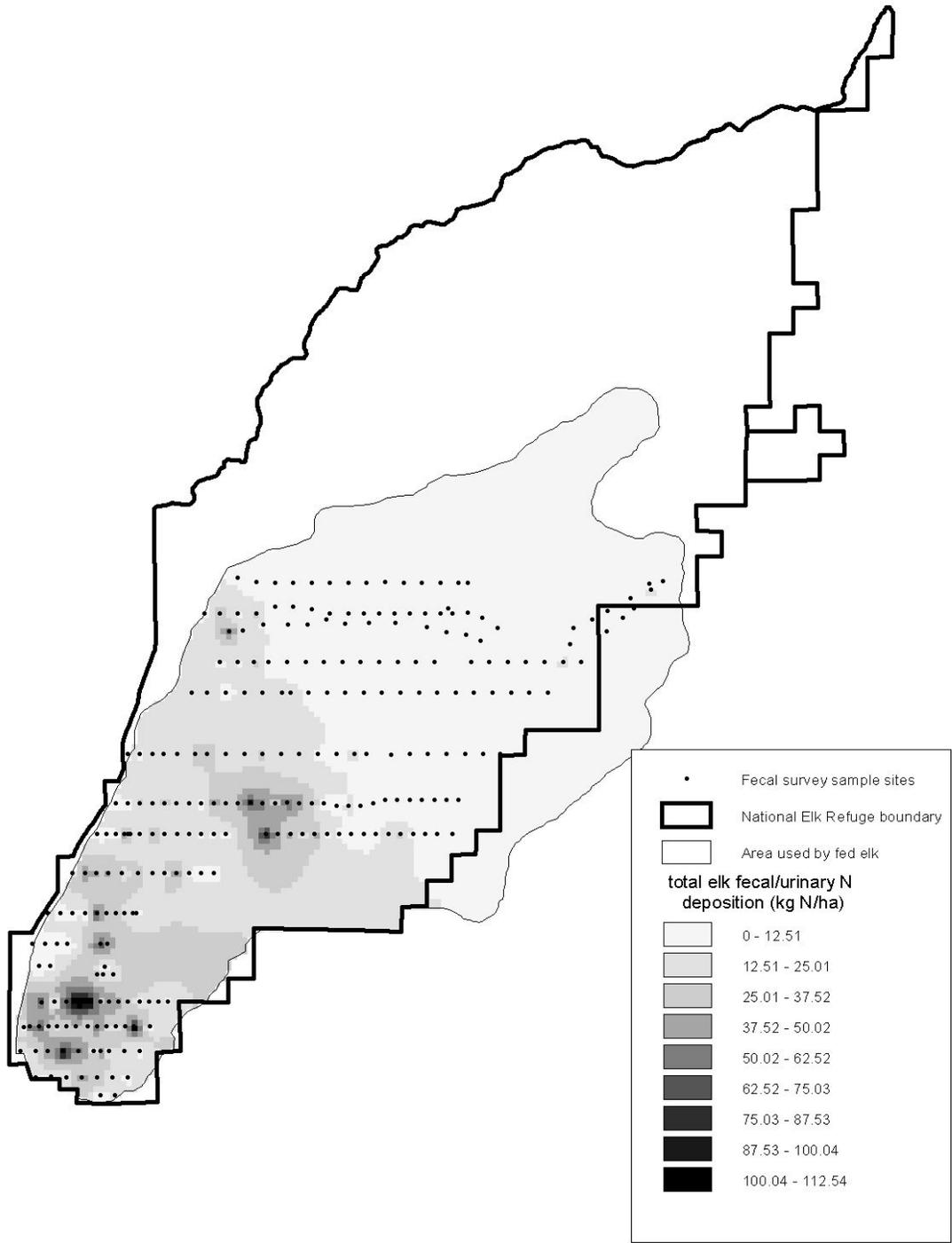


Figure 3.11. Estimated depositions of nitrogen (N) due to elk fecal and urinary depositions on that portion of the National Elk Refuge used by elk that visit feedgrounds.

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