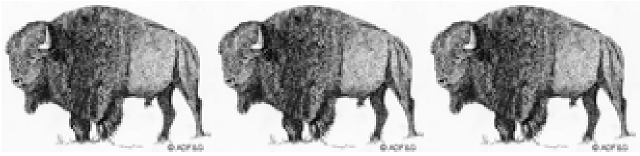

DETERMINING FORAGE AVAILABILITY AND USE PATTERNS FOR BISON IN THE HAYDEN VALLEY OF YELLOWSTONE NATIONAL PARK

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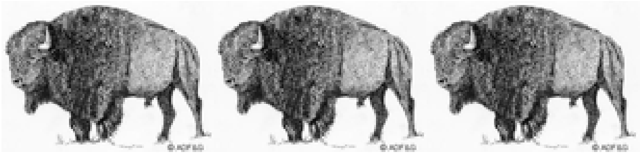

EXECUTIVE SUMMARY

In our original Proposal, we identified 4 objectives:

1. Delineate seasonal forage use patterns by bison in the Hayden Valley;
2. Determine long and short term effects of ungulate foraging on vegetation in the Hayden Valley;
3. Determine efficacy of vegetation monitoring approaches;
4. Estimate annual production and standing crop available during non-growing seasons for herbaceous and shrub layers in major habitat types in the Hayden Valley.

Our efforts to describe forage use by bison focused on assessing finer scale habitat use in a core summer range for bison in YNP. We also collected information on bison food habits and forage quality to begin to explain the “whys” of bison distribution.

Short-term impacts of bison forage utilization were addressed by comparing standing biomass in plots protected from grazing with plots exposed to grazing. Historical data were not available to directly address long-term effects of ungulate foraging in the Hayden Valley, but we were able to indirectly assess some aspects of this question by determining the frequency of repeat grazing over a 3-year period and the rate at which trees along the margins of the Hayden Valley were being killed by bison rubbing

The third objective, determining the relative efficacy of different vegetation monitoring approaches, was accomplished by comparing estimates of standing biomass and biomass utilization obtained via conventional exclosure techniques with estimates based on remote sensing techniques (ground-based and satellite-borne multi-spectral radiometry[MSR]). We addressed efficacy in terms of precision and accuracy of estimates, reliability, and logistical costs at different coverage scales.

The fourth objective, estimation of forage available for ungulates in the Hayden Valley, was achieved using conventional exclosure methodology and remote sensing. We were able to estimate herbaceous biomass production during 3 different years. Exclosures

allowed us to estimated changes in standing crop of herbaceous vegetation at the plant community (conventional cover types, moisture/plant growth form groups, and communities defined by dominant graminoids) and catena (a repeating sequence of communities tied to landscape physiognomy) scales. We developed empirical approaches that allowed us to estimate standing biomass of herbaceous plants from reflectance data obtained from ground-based and satellite-borne multi-spectral radiometry (MSR) units. We demonstrated the potential to estimate biomass of shrubs using the same approaches. We did not have time and resources to complete vegetation maps that would optimize estimates from remote sources, but we have outlined procedures that can be followed in the future to obtain biomass estimates at the landscape scale.

Bison Seasonal Forage Use Patterns in the Hayden Valley -- We examined habitat selection by bison from 2 perspectives: 1) bison selection at the plant community level (using multiple definitions of community, *e.g.* habitat type, dominant species, moisture regime, and plant physiognomy); and 2) dietary selection (by plant species/genus, taxonomic group, and forage quality/quantity). A wide array of data, collected from observation of unmarked bison, fecal counts, microhistological analysis of fecal samples, chemical analysis of vegetation, examination of vegetation for evidence of grazing and rubbing, MSR results, and clipping (in feeding exclusion cages and sites exposed to bison foraging), were used to address this objective.

Delineation of habitat categories **--** Plant communities in the Hayden Valley had to be defined before we could assess bison habitat selection. We defined communities, developed a key to identify plant communities, and developed a 3-tiered classification system that will facilitate mapping based on remote imagery (using a combination of LANDSAT and IKONOS imagery) and can be easily employed by personnel in the field. The comprehensive key we developed (Appendix B) requires field personnel to use <20 plant species to identify vegetation units.

Bison use of vegetation categories **--** We used a point-intercept technique to determine the proportion of different vegetation categorization units in 2 representative areas (the West Alum and Crater Hills blocks) of the study area. Only 3 of the 22 cover types we identified comprised >10% of the 1,668 points measured: *Artr/Feid* (27%); *Arca/Dece* (15%); and *Arca/Feid* (14%). When vegetation was categorized by cover group (based on plant structure and moisture regime), the dry shrub group was the most abundant category (49% of 1,668 points). Other common types included the moist graminoid group (17%), the moist shrub group (16%), and the intermediate graminoid group (13%). When only dominant graminoids were considered, Idaho fescue (*Festuca idahoensis*) was dominant or co-dominant at 57% of the points we sampled. Tufted hairgrass (*Deschampsia cespitosa*) (37% of points), Bearded wheatgrass (*Agropyron caninum*) (9%), Sandberg bluegrass (*Poa sandbergii*) (5 %), and Timber oatgrass (*Danthonia intermedia*)(3%) were also common dominants. Several sedge species (*Carex* spp.) were common in wet sites (dominant or co-dominant at 7% of points).

In summer and early fall, grazed loop surveys indicated that the highest frequencies of grazing occurred in the *Posa* (78% of 51 plots sampled were grazed), *Artr/Posa* (76% of 41 plots), and *Arca/Feid* (68% of 235 plots) cover types. When use was contrasted with availability for cover groups, bison selected the dry shrub and dry graminoid cover groups and avoided moist shrub and moist graminoid types, at least during summer. Data from paired cages and at fixed cage sites also suggested a summer preference for dry plant communities in that bison removed a larger percentage of standing biomass from dry graminoid and shrub types than from wetter types during summer. As with point-intercept data, preferred cover types and cover groups had understories dominated by native xeric bluegrasses (such as *Poa sandbergii*), Idaho fescue, and bearded wheatgrass.

In spring, cages clipped in dry communities, especially those with Idaho fescue or Sandberg bluegrass understories, tended to have the greatest percent offtake and wetter communities the lowest percent offtake. Spring offtake at the fixed cage sites was lower than at paired cage sites, but the mesic grassland site had much lower estimated percent offtake than the drier big sage and silver sage sites.

Our estimates of over-winter offtake from paired and fixed caged sites were possibly influenced by small mammal activity and/or mechanical and biological degradation of residual vegetation, but relative differences between residual vegetation measured inside and outside exclosure cages again indicated much higher proportionate removal of standing vegetation in dry communities than in wetter communities in randomly paired sites.

When we compared offtake only in terms of biomass removed per unit area, bison were able to harvest the same or greater amounts of biomass by taking a relatively low percentage of the standing herbaceous vegetation in many mesic communities as they harvested by taking 50% or more of the standing herbaceous biomass in dry communities. Although we measured high percent offtake and grams offtake in some plant communities, several mesic communities yielded more plant biomass per unit area for bison than the apparently favored dry graminoid communities in spring, summer, and over winter.

Graminoids made up >90% of the overall summer and early fall diets for bison in the Hayden Valley during 1998 – 2000. The graminoid taxa dominant in the summer – early fall diet were not expected based on data we collected from the point-intercept surveys and from clipped plots. Fecal analysis indicated that 49% of the overall summer – early fall diet was comprised of mesic grasses and graminoids (sedges, rushes, etc.) associated with the wet sites bison apparently utilized at low intensities. Of grasses abundant in the favored dry plant communities we identified from point-intercept surveys and clipping, only native bluegrass (probably mostly *Poa sandbergii*) contributed >10% to the overall diet. Idaho fescue, the dominant grass in several dry plant communities apparently favored by bison comprised 8% of the overall summer – early fall diet while tufted hairgrass (*Deschampsia cespitosa*), a dominant graminoid in several communities apparently avoided by bison, made up >9% of the overall summer – early fall diet.

Analyses of nutritional value of 6 common herbaceous taxa indicated that all of the taxa maintained the 7% crude protein level commonly identified as necessary for "maintenance" in cattle during summer and early fall except timber oatgrass (*Danthonia intermedia*). Even this species maintained a minimum crude protein in fall of nearly 6%, a value presumably more than adequate for adult bison. Levels of other macro nutrients, micro nutrients, and digestible energy were reasonable in all of the 6 taxa. Timber oatgrass, the species least frequently ingested of the 6 taxa tested, did have total digestible nutrients to protein (10:1 rather than the 8:1 ratio regarded as a threshold for poor forage quality) and calcium to phosphorus ratios (~4:1 rather than the desired 1 to 2:1) that were undesirable by September, but taxa that were frequently eaten had similar ratios.

Despite superficially contradictory results, our data indicate that bison exhibit a biologically rational grazing strategy in the Hayden Valley. We believe that bison in the Hayden Valley select grasses in dry plant communities until they cannot efficiently harvest them (apparently the threshold for offtake on low growing species such as Sandberg's bluegrass and Idaho fescue is 50-60% during summer). Searches for ungrazed patches or grazed patches with regrowth in favored xeric plant communities drive bison herds to move back and forth across the Hayden Valley during summer and fall. Bison utilize mesic communities adjacent to dry shrub and grass stands throughout the summer and ingest substantial amounts of forage from these moist communities, but they avoid heavy utilization of mesic communities until the easily harvested forage in dry communities is exhausted. The attraction of grasses associated with dry plant communities to bison in the Hayden Valley may be due to some combination of characteristics which we did not discover (perhaps these species are simply better tasting than the mesic graminoids), or use of dry plant communities in preference to mesic communities may be an artifact of the problems heavy animals such as bison have in foraging on wet soils. Bison may make less use of wet sites simply because they become stuck in the mud.

Long and short term effects of ungulate foraging on vegetation in the Hayden Valley -- We did not locate appropriate imagery to identify long term changes in vegetation in our preliminary searches and were forced to abandon attempts to locate this material due to time constraints. We did determine that bison were responsible for >90% of large herbivore activity in the Hayden Valley (based on fecal counts and observation) at the time of our study. Incidental observations indicated that bison were responsible for erosion along trails and in wallows, but we were not able to determine if erosion was increasing. The high level of damage to trees on the margin of the Hayden Valley (91% of trees damaged and 28% dead along the valley margin) demonstrated that ungulates, probably bison, were effective in slowing invasion of the shrub and grasslands by trees or, perhaps, extending grassland into the forest margin.

Short-term impacts were more easily determined. Bison removed significant proportions of spring, summer-fall, and residual winter biomass from the herbaceous component of several grass and shrub communities in the Hayden Valley. In areas we sampled, bison utilized ~25% of new growth in spring (May to early June) over all cover types. Dry and intermediate moisture plant communities were utilized twice as heavily as mesic communities (38% estimated removal versus 14%).

Bison removed 36% of standing biomass (across all common cover types) from June through September. We were unable to detect differences among the 3 growing seasons (1998, 1999, and 2000) we monitored. Over these 3 years, mean percent offtake among cover types varied from >50% (*Posa* and *Artr/Cana*) to <20% (*Carex* and *Dece/Carex*). Plant communities with the lowest productivity (xeric grass and shrub types) tended to experience higher utilization than more productive, mesic plant communities.

Changes in residual vegetation over winter were likely influenced by factors other than bison grazing (*i.e.* small mammal activity, mechanical degradation from snow, and/or activity of bacteria and fungi), but, over all cover types, 45% of residual vegetation disappeared over winter in the 2 winters (1999 and 2000) we sampled. Dry grass types lost 76% of residual vegetation, nearly 3 times the loss recorded for wet graminoid and shrub types (28% disappearance). Disappearance of vegetation over winter was similar (~30%) for all 3 fixed cage sites.

The extent of utilization of the herbaceous standing biomass during the growing season in most plant communities was <50%. This would indicate light to moderate stocking rates were the Hayden Valley being managed for livestock using traditional, conservative pasture management guidelines (*i.e.* "take half, leave half"). (Stoddart and Smith 1955). Frank and McNaughton (1993) have demonstrated that grazing can stimulate production in graminoids in the Yellowstone ecosystem which could mean that offtake of >50% is acceptable in graminoid-dominated plant communities in YNP. However, if bison regraze the same plants during a single grazing season or consistently return to the same plants during consecutive seasons, 50% offtake in the heart of the growing season combined with >30% utilization in early spring, and possibly >70% utilization of residual standing vegetation over winter may be more than some dry plant communities can withstand over long periods of time. In plant communities with understories dominated by Sandberg bluegrass and Idaho fescue, species indicative of xeric plant communities favored by bison, 62% of 110 plots we followed for 2 years were grazed by bison in both years, and 50% of 30 plots we followed for 3 years were grazed by bison in all 3 years. The abundance of timber oatgrass, a species that was consistently low in bison diets, in plant stands that met microclimate, soil, and slope characteristics typical of conditions expected for Idaho fescue stands **may** (we could not definitively identify changes without plant data at our sample sites from the past) indicate that past use of these areas by bison has already led to decreases in graminoids favored by bison.

Efficacy of vegetation monitoring approaches -- We used several approaches to monitoring vegetation status and/or use of vegetation by large herbivores. The “gold standard” for monitoring vegetation biomass and biomass utilization is the grazing exclosure approach. This approach, however, requires extensive and intensive allocation of resources to provide accurate estimates of trends in vegetation production at large scales without labor intensive movement of cages within the growing season; it is potentially subject to biases due to the presence of cages; it cannot accurately detect very light grazing; and results are almost always based on sample sizes that are smaller than desirable and distributed less than ideally. Estimates of standing crop developed from exclosure data were consistent with published estimates for biomass in similar plant communities in other areas indicating that our samples were reasonably adequate and our clipping protocol was appropriate, but we did not determine the contribution of individual plant species to total biomass. Without information on species composition, we could not follow major changes in community makeup that might occur with long term over grazing. Collecting information on biomass by plant species would have added 1 to 3 hours to each plot sampled. Overall time per plot for biomass estimation by plot or by species could be reduced by double sampling (i.e. clipping a few calibration plots and estimating biomass at other plots), but this would also reduce accuracy of estimates and increase the vulnerability of estimates to errors due to poorly trained or motivated personnel.

The point-intercept approach we used in sampling vegetation in the Crater Hills and West Alum blocks with the grazing loop was inexpensive, quick, and allowed us to cover large areas in a short period of time. The estimates of biomass offtake produced using this technique were lower than that those calculated based on clipped plots. This approach did not provide estimates of standing biomass or species composition at individual sample points, and, because this technique called for quick judgments on plant community and intensity of grazing, results could be very subjective, especially with poorly trained or motivated personnel.

A portable MSR unit produced accurate estimates of standing biomass during the growing season with minimal investment of time and labor in clipping plots. When used with calibration clips within a few days of the MSR estimation, our regressions accounted for 84 - 97% of the variability in biomass in vegetation plots (with the inclusion of a classification variable to identify wet sites). When the presence or absence of sagebrush at a sampling point was included as an additional classification variable, we were able to empirically estimate both herbaceous and shrub green at each point with >80% accuracy. The portable radiometer would allow personnel involved in a monitoring program to spend 1 day calibrating the MSR unit to clipped plots, and 1 person could estimate biomass at hundreds or thousands of points per day (with sample numbers limited primarily by distance between sampling points). Although we believe that results are more reliable if calibration plots are clipped within a few days of MSR sample plots, our data suggest that 1 set of calibration plots may provide useful data for biomass estimation over a full growing season or, perhaps, over several years .

We also tested biomass estimation from satellite imagery. This process involved a double-sampling procedure in which regression formulae were developed from the relationship between biomass clipped in 0.75-m^2 plots and reflectance measured at the same plots using a ground-based radiometer and the relationship between biomass estimates obtained with a ground-based radiometer in 45 x 45-m plots and reflectance vales for specific pixels in LANDSAT imagery. Although we were unable to satisfy all the theoretical considerations in developing error terms around estimates, we derived empirical formulae that would explain 83 to 96% of the variability between reflectance and herbaceous biomass estimates – when the moisture (wet vs. dry) and shrub status (presence vs. absence and sage vs. other shrub species) of the pixel was known. This suggests that 1 or 2 days of calibration clipping and measurement of reflectance in 45 x 45-m plots would allow monitoring of standing biomass for the entire Hayden Valley (or for all open vegetation in YNP if imagery were obtained) at a given point in time. Use of fixed reflectance sites (water surfaces, unvegetated soil, roads, empty parking lots, etc.) in calibrations may allow extension of pixel by pixel biomass estimates in herbaceous and shrub communities back in time through the first LANDSAT imagery from the 1970s. This would require geo-referencing of pixels in different images and an accurate map of cover types in the Hayden Valley. We believe that high resolution IKONOS satellite imagery can best provide a reliable means of categorizing grass and shrub communities in the Hayden Valley at a very fine scale.

Annual production and standing crop available during non-growing seasons for herbaceous and shrub layers in major habitat types in the Hayden Valley -- In the Hayden Valley, exclosures set up at the beginning of the growing season and clipped at the end of the growing season should give reasonable production estimates in most plant communities. The exclosure data we collected indicated herbaceous productivity in the Hayden Valley varied from <900 kg/ha in dry graminoid communities (*Feid/Agca*: 874 kg/ha; *Posa*: 894 kg/ha) to >3,300 kg/ha in wet *Carex* communities. Overall, our exclosure cage data indicated that herbaceous plant productivity in the Hayden Valley (~250 km^2) during the 1998-2000 growing seasons varied from 8,900 to 12,000 metric tons. Comparisons of plots protected by cages with adjacent sites open to grazing indicated that large mammals removed 2,800 to 4,200 metric tons per growing season over the same 3 years.

Our preliminary data indicate that regressions derived from the 2-stage sampling scheme we used could accurately predict standing biomass from satellite imagery at the pixel level. This provides a useful device for explicit spatial mapping of standing biomass in graminoid and shrub communities of the Hayden Valley, but it does not yield estimates of productivity in a system where herbivores remove >25% of the annual production over the course of the growing season. With geo-referenced pixels and an accurate map of plant community distribution, satellite imagery does have the potential to answer many questions about bison use of plants. Geo-referencing will allow direct comparison of pixels from one month to another and in the same months over different years to track consistency of plant growth/utilization over time. It would also allow personnel monitoring vegetation to construct a series of pixel-sized exclosures to track changes in biomass in the absence of herbivory by large mammals over time. We strongly urge YNP to complete the vegetation map of the Hayden Valley and to devote resources to LANDSAT imagery interpretation.

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INTRODUCTION

Large ungulates play important roles in ecological processes in many systems in the world (Hobbs 1996). Their movements are determined by vegetation form, availability, and abundance, but they also may influence the vegetation upon which they feed through foraging, trampling, and nutrient cycling (Coughenour 1991). The active and passive aspects of ungulate-vegetation interactions evidently play a major role in shaping winter ranges in Yellowstone National Park (YNP) (Singer *et al.* 1989, Frank 1990, Wallace 1990, Coughenour 1991, Coughenour and Singer 1991, Singer 1992, Frank and McNaughton 1992 and 1993, Merrill *et al.*1994, Tracey and McNaughton 1994 unpubl., Pearson *et al*. 1995, Turner *et al.* 1995, Singer and Harter 1996, National Research Council 2003) and may be important on summer range as well. The impact of ungulates on vegetation in YNP has been hotly debated (Kay and Chadde 1992, Kay 1994, Boyce 1998, Singer *et al*. 1998, Wambolt 1998), but the National Research Council (2003) concluded that large mammals, principally elk (*Cervus elaphus*) and bison (*Bison bison*), had changed vegetation on the Northern Yellowstone Winter Range from conditions existing at the time the Park was proclaimed. The National Research Council (2003) report did not resolve questions about large mammal influence on summer ranges associated with the ungulates in YNP or whether forage availability and utilization on summer range influenced ungulate utilization of forage on winter ranges. We collected data on 1 major summering area, the Hayden Valley, to help fill this information gap.

Prior to our study, investigation of productivity and utilization of forage by ungulates in YNP was limited to studies that relied on small scale clipping, limited numbers of exclosures, indices with limited precision, and/or models that were backed by limited data bases (Singer *et al*. 1989, 1998, Frank 1990, Wallace 1990, Coughenour 1991, Coughenour and Singer 1991, Singer 1992, Frank and McNaughton 1992 and 1993, Kay 1994, Merrill *et al.* 1994, Tracey and McNaughton 1994 unpubl., Pearson *et al*. 1995, Turner et al. 1995, Wambolt 1998). The only early attempt to use landscape-scale remote sensing to investigate plant dynamics (Merrill *et al.* 1993) produced results that were statistically significant but biologically ambiguous. Changes in technology and analysis approaches (Lillesand and Kiefer 1994, Wylie *et al*. 1996, Biondini and Norland, pers. comm.) since Merrill *et al.* (1993) allowed us to collect biologically useful data across large scales.

The Hayden Valley, characterized by open grassland and shrub steppe, serves as a major summer range for bison and elk and is additionally used by bison in other seasons. We used conventional range methodology to determine forage productivity and utilization on smaller scales and a combination of ground and satellite-borne remote sensing (Lillesand and Kiefer 1994) to estimate standing biomass in a spatially and temporally explicit manner over a 3-year period.

Our data collection emphasized summer to early fall production and utilization. In our proposal, we outlined methodology for assessing ungulate utilization of forage in the Hayden Valley during winter, but we reduced our sampling efforts in winter to minimize aircraft disturbance in the area at the request of YNP administrators and to reallocate funds to support other studies which had under-estimated their funding needs.

Data we collected provide a detailed picture of vegetation dynamics in the Hayden Valley and will be crucial to determining ungulate numbers that are sustainable within YNP. Without these data, development of a usable model of vegetation-ungulate dynamics, as proposed by Coughenour (unpubl. 1997) would be impossible.

In our original Proposal, we identified 4 objectives:

1. Delineate seasonal forage use patterns by bison in the Hayden Valley;
2. Determine long and short term effects of ungulate foraging on vegetation in the Hayden Valley;
3. Determine efficacy of vegetation monitoring approaches;
4. Estimate annual production and standing crop available during non-growing seasons for herbaceous and shrub layers in major habitat types in the Hayden Valley.

Some aspects of the first objective, delineation of seasonal forage use patterns of bison, have been covered by the study proposed by Gogan (unpubl. 1997). Data collected for Gogan’s project addresses yearlong habitat use at a coarse scale for the entire range of bison in and outside YNP. Our efforts focused on assessing finer scale habitat use in a core summer range for bison in YNP. We also collected information on bison food habits and forage quality to begin to explain the “whys” of bison distribution.

Short-term impacts of bison forage utilization were addressed by comparing standing biomass in plots protected from grazing with plots exposed to grazing. Historical data were not available to directly address long-term effects of ungulate foraging in the Hayden Valley, but we were able to indirectly assess some aspects of this question by determining the frequency of repeat grazing over a 3-year period and the rate at which trees along the margins of the Hayden Valley were being killed by bison rubbing. We also began exploratory surveys to monitor invasion by exotic plants in the valley.

The third objective, determining the relative efficacy of different vegetation monitoring approaches, was accomplished by comparing estimates of standing biomass and biomass utilization obtained via conventional exclosure techniques with estimates based on remote sensing techniques (ground-based and satellite-borne). We addressed efficacy in terms of precision and accuracy of estimates, reliability, and costs at different coverage scales.

The fourth objective, estimation of forage available for ungulates in the Hayden Valley, was achieved using conventional exclosure methodology and remote sensing. We were able to estimate herbaceous biomass production during 3 different years. Exclosures allowed us to estimated changes in standing crop of herbaceous vegetation at the plant community (conventional cover types, moisture/plant growth form groups, and communities defined by dominant graminoids) and catena (a repeating sequence of communities tied to landscape physiognomy) scales. We developed empirical approaches that allowed us to estimate standing biomass of shrubs and herbaceous plants from reflectance data obtained from ground-based and satellite-borne multi-spectral radiometry (MSR) units. We did not have time and resources to complete vegetation maps that would optimize estimates from remote sources, but we have outlined procedures that can be followed in the future to obtain biomass estimates at the landscape scale.

Funding was provided by the U.S.G.S. Biological Resources Division under a contract administered by Dr. Peter J. Gogan (BRD) through a cooperative agreement with Montana State University.

STUDY AREA

The Hayden Valley covers ~ 250 km^2 in the center of YNP (Fig. 1). The Yellowstone River flows through the eastern edge of the valley, and this valley was once an arm of Yellowstone Lake. Glacial action over lake sediments produced a gently rolling topography in the valley. When the most recent glaciers retreated (approximately 13,000 B.P.), clay from lake sediments and fine grained till created a tight soil which impedes water penetration. Wind and water erosion have modified exposed locations, but many areas are still impervious to water. Hayden Valley soils, possibly aided by fire and ungulates, have limited colonization by trees, leaving the valley open with a complex of shrub, grass, and sedge communities interspersed with a few islands of trees.

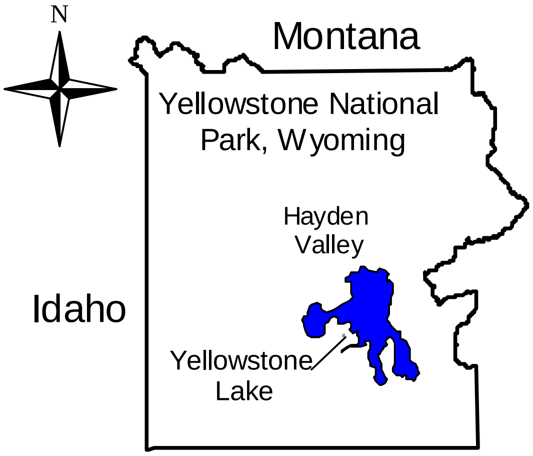
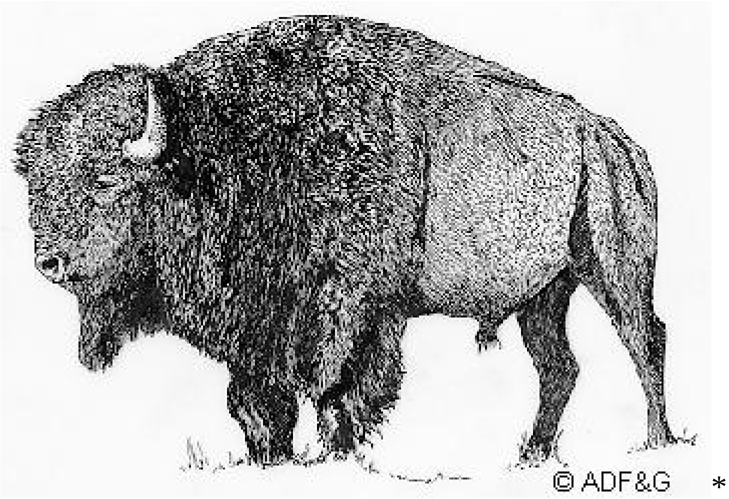


Fig. 1. Boundary of Yellowstone National Park showing the approximate location of the Hayden Valley.

The Hayden Valley lies at an elevation of 2,300 - 2,500 m. Average precipitation at the Lake Weather Station, the nearest station with long-term data, averages 52 cm, and the station reports an average 196 days of snow cover per winter (Farnes et al. 1999). Winters are severe with deep, crusted snow in low areas that persists from early November to mid May. Deeper snow drifts on leeward slopes often persist into late June after harsh winters. Although archeological evidence indicates indigenous people occupied the area around Yellowstone Lake as early as 9,600 years B. P., human activity was limited to summer use or short incursions in other seasons. Currently, elk utilize the valley during summer and fall and bison throughout the year. Bison use is highest in summer, but some bison remain in the valley until late winter and, if they leave, they usually return by mid spring.



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METHODS

Delineation of Vegetation Types

The Hayden Valley contains a patchy, heterogeneous mix of grassland, shrubland, and wetland cover types interspersed with islands of trees. Lake sediments, elevation, and microclimate have resulted in a combination of plant communities which may not collectively exist elsewhere. Existing layers from a Geographic Information System (GIS), conventional paper maps, or even an encompassing classification system capable of delineating vegetation at the scale and juxtaposition found in the Hayden Valley were not available prior to initiation of our study.

We augmented the predominately upland habitat types of Mueggler and Stewart (1980) with riparian and wetland habitat and cover types of Hansen *et al.* (1995) in a classification system able to delineate variability and existing plant associations of the Hayden and nearby Pelican Valleys of Yellowstone Park. Although some of the types we delineate are true habitat types, we refer to all as cover types for consistency. A key to cover types based on general reconnaissance and 119 plots and descriptions of each cover type can be found in Appendix B. Our types can be considered an extension of previous classification systems of the area by Despain (1990) and Graham (1978) and can be readily combined into their types and those of Mueggler and Stewart (1980) or Hansen *et al.* (1995), as noted in cover type descriptions. Graham (1978) provides a plant list specific to the Hayden and Pelican Valleys. We used a minimum map unit of 1 are (0.01 ha) for defining distinct patches of vegetation.

We used 3 vegetation classification schemes in our analyses. When sample sizes permitted, we looked at utilization of individual cover types by bison (underlying hypothesis: bison discriminate among plant communities in making foraging decisions) The second classification scheme involved combining cover types into groups based on life forms of the overstory and understory (underlying hypothesis: bison discriminate among vegetation units primarily based on growth forms of dominant plants and/or moisture regime of the community). Our third classification scheme ignored shrubs and concentrated solely on understory dominants (underlying hypothesis: bison are grazers [Reynolds *et al.* 1982] and, therefore, should discriminate among plant communities primarily on the basis of herbaceous plants in the understory rather than presence or absence of shrubs). The grouping based only on understory species assumes bison would utilize a *Festuca idahoensis* type and an *Artemisia tridentata / Festuca idahoensis* type in a similar manner because both have the same dominant herbaceous understory species.

Use of Exclosures

The "gold standard" for estimating vegetative production involves the use of exclosure cages to deny animal access to vegetation in a plot, with the use of dry weight of plants clipped in protected plots as the estimate of productivity for the period of the exclosure (Cox and Waithaka 1989, Higgins *et al.* 1994, Litvaitis *et al*. 1996). Utilization by grazing animals for that period is conventionally determined by comparing standing biomass within exclosures to biomass in unprotected plots. Although the exclosure approach is regarded as the most precise field-based methodology available for estimating vegetative productivity, it is far from perfect. Exclosures are time and labor intensive, may not take stimulation of forage production by grazing into account (Frank and McNaughton 1993), do not account for differing rates of phenology and senescence among plant species, limit observers to samples from small portions of a study area which may or may not be representative (Porwal et al. 1996), may be subject to cage effects, provide a refuge for insects or small mammals that consume biomass “saved” from excluded animals, and are subject to considerable errors in sample collection if field personnel are not carefully trained, well motivated, and tightly monitored (Brown 1954, Stoddart and Smith 1955, Higgins *et al*. 1994, Litvaitis *et al*. 1994). We attempted to minimize these problems and assess their impacts on our estimates of productivity and offtake where possible.

During the growing season, all exclosures used in this study were left standing for an entire growing season rather than moving them at intervals to account for compensatory growth. A discussion of movable and season-long exclosures and methods for determining productivity in grazing ecosystems can be found in McNaughton *et al.* (1996). We acknowledge compensatory growth may occur to increase estimates of protected vegetation but chose season-long exclosures for the following reasons: 1) statistical errors and discrepancies in calculating productivity using movable cages (McNaughton *et al*. 1996); 2) difficulty of matching movement frequency of cages to reflect the intensity of herbivory, plant regrowth rate, and any changes in plant selection by ungulates over time; 3) logistics of clipping and moving all cages and unprotected plots in a timely fashion to prevent differences due to timing of data collection; 4) the growing season in the Hayden Valley is generally very short (90% of biomass growth occurs between early June and mid August) where herbaceous production occurs as a single strong pulse with a shorter time period for regrowth to occur than other grasslands, thus potentially reducing the amount of regrowth and the need to use movable exclosures.

Therefore, estimates of productivity and utilization from our study may be better viewed relative to “exclusion of large mammal grazing” rather than absolute estimates.

Factors increasing vegetation production inside exclosures will increase estimates of ungulate offtake, while factors reducing biomass of protected plots will decrease estimates. Protection from drying effects of wind inside exclosures and increased moisture availability from dew condensing on caging material and dripping onto the ground are microclimatic factors which may increase vegetation growth inside exclosures. Deposition of metals in the soil from caging material and greater accumulation of snow inside exclosures during winter may have a net positive or negative effect. Although deposition of metals has occasionally been mentioned as influencing growth, we did not consider it a truly viable possibility from galvanized material in relatively short term exclosures, and we did not attempt to account for this potential bias. To determine overall potential effects of cages on herbaceous growth, we conducted a paired comparison between plots clipped inside and outside exclosures within a fenced area excluded from grazing by large mammals.

Cage effect estimation -- We selected 12 pairs of plots in an Idaho fescue (*Festuca idahoensis*) grassland of the Bridger Mountains, northwest of Bozeman, Montana. The Bridger site was selected because an adequately sized protected area for determination of cage effects was not available within Yellowstone Park. However, the elevation and vegetation type were similar to the most common vegetation type of the Hayden Valley. Paired plots had similar biomass and species composition of vegetation, and we tried to select pairs to cover the range of productivity within the area. One plot of each pair was randomly selected to receive a 1m x 1m x 1m tall exclosure constructed of

~10 cm square mesh utility fencing with 1m x 1.3 cm diameter rebar posts at 2 diagonal corners. The remaining plot of each pair was marked for subsequent location with wooden carpenter's shims driven to ~5cm of ground level at each corner (1x1m) and circled with household cotton twine to delineate areas equal in size to exclosures and to provide accurate relocation of plots for clipping. Plots were selected in spring of 2000 and total standing crop (current year's growth and any other standing vegetation) was clipped in fall 2000. Exclosures and marked locations of paired plots outside exclosures were left standing over the winter and the exact locations, as determined from obvious circles left from previous clipping, were again clipped fall 2001. Plots clipped in fall 2000 provided a comparison of cage effect on standing crop (current year's growth and old standing dead) during the growing season, while plots clipped in fall 2001 provided a comparison of cage effect for an entire year strictly on new growth. The comparison for an entire year included the possibility of increased moisture availability from drifted snow accumulation in winter and rainfall or dew during the growing season. We also visited cage sites in the Hayden Valley during mid and late winter to visually determine if snow accumulated to a greater depth inside exclosures.

Small mammal effects at cage sites -- We attempted to determine if exclosures that excluded large mammals provided a refuge for small mammals in the Hayden Valley, either due to potentially greater vegetation amounts or "additional cover" provided by the presence of exclosures. Small mammal activity was recorded inside and outside exclosures of all plots we clipped, determined by existence of runways or haystacks, as 1 of 3 disturbance levels within each plot; none = no activity present, slight

= 1-7%, moderate = >7%. Chi-square analysis was used to determine differences in distributions of small mammal activity and Kruskal-Wallis rank-sum tests were used to determine significant differences in vegetative weight from small mammal activity.

Vegetative regrowth in the Hayden Valley following grazing may be less than other areas due to the short growing season, but nonetheless the potential exists. Sixteen plots clipped in conjunction with other field work at approximate peak standing crop were clipped again at the end of the growing season during 2000 to determine amounts of regrowth. Plot frames were placed within the visually obvious boundary of the first clipping and vegetation was clipped to a height of ~1cm above ground level both times. Sites were not protected from grazing but were revisited at ~16 day intervals and examined for grazing within a 5m diameter area around plots.

Fixed cages -- The most common method for placing an array of exclosures at a single site is a random pattern. This approach requires a large enough sample size to account for heterogeneity of vegetative biomass within the site. Dawes (1998) found that 10 seasonal exclosures per site was probably not enough to determine vegetation removal by large mammals in the Madison Junction area of Yellowstone Park. Based on visual observations of less heterogeneity in biomass within most vegetative types of the Hayden Valley versus Madison Junction, small sizes of patches containing similar vegetation for exclosure placement, logistics of moving exclosures strong enough to withstand damage by bison, and aesthetics of exclosures to Yellowstone Park visitors, we chose to use 20 exclosures at each of 3 sites.

Three sites near the public road in the Crater Hills area of the Hayden Valley were selected for multi-year vegetation biomass measurements. These sites encompassed common vegetation complexes (catenas) in the Hayden Valley and included: 1) a hillside dominated by big sagebrush (*Artemisia tridentata*) with an Idaho fescue understory; 2) a mountain silver sagebrush (*Artemisia cana* ssp. *viscidula*) community with an understory generally dominated by tufted hairgrass (*Deschampsia cespitosa*) on level ground; and 3) a wet meadow site with no shrubs and a mix of communities dominated by mesic graminoids. In order to include an area large enough for placement of exclosures over a 3-year period and to provide reasonable consistency in the vegetation we sampled, we were forced to create irregularly shaped boundaries for the big sage and mesic graminoid sites. The silver sage site was rectangular.

The silver sage site was predominately of the *Arca/Dece* cover type with a small part of the northwest portion containing *Arca/Feid-Dain*. The big sage site was similar in shape to an inverted "U" on a hillside with a small gully containing *Arca/Dece* running from the inside of the "U" in a downhill direction. All cells and exclosures at the big sage site were maintained on the upland portions, predominately *Artr/Feid* with several cells containing *Artr/Feid-Dain*. In order to maintain cages within mesic vegetation (*Dece/Carex* and wet *Carex* types) at the mesic graminoid site, delineated cells for cage placement resembled the shape of a "U" with a tail. The inside of the "U" contained *Arca/Dece*. GPS files defining overall perimeters, boundaries of vegetative types containing exclosures, boundaries of vegetative inclusions, and surface areas for sites, and vegetation types within sites were created. The same sites were used in all years of the study to provide information on forage offtake patterns at the same sites over time (hence our designation of the 3 sites as "fixed sites").

We deviated from a completely random design to accommodate pairing of plots and to avoid shrubs. A paired placement with cages in close proximity to each other is preferred over purely random placement to minimize variations in vegetation, soils, topography, and microclimate (Ratti and Garton 1994). We avoided placing cages or unprotected plots at sites with sagebrush because bison rarely utilize browse (Meagher 1973, Peden 1976, Reynolds *et al.* 1982). Sagebrush was not present at the mesic graminoid site, but juxtaposition of wetland vegetation required a similar approach to insure that all cages and unprotected plots were placed in comparable vegetation. Because we avoided shrubs, our estimates of production and offtake at fixed sites apply only to herbaceous vegetation.

At each fixed site, we first delineated all 25m x 25m cells that would fit within predefined site boundaries. This was accomplished using a pace pole and compass prior to receiving our Global Positioning System (GPS) receiver in 1998 and afterward by using a real-time correction GPS receiver with an advertised accuracy of <1m (Satloc Corp.).

Twenty random cells were selected (with replacement) at each site during spring of 1998, 1999, and 2000. All locations large enough for an exclosure without including sagebrush were marked in each cell with numbered pin flags. Numbers on the pin flags were used to randomly select 4 locations within each cell, 1 to receive an exclosure during the growing season, 1 to be paired with the exclosure when plots were clipped at the end of the growing season, 1 to receive an exclosure during the winter, and the last one to be paired with the winter exclosure when they were clipped in spring. Locations not receiving exclosures were marked with orange-painted 10cm long nails pushed to <1cm of ground level. We collected and averaged a minimum of 30 GPS locations at each orange-painted nail to provide precise locations for relocating plots or potential plots if nails were lost. GPS data were collected when the location on the GPS receiver was stable and the Horizontal Dilution of Precision (HDOP) was $\leq$2.0. Exclosures (1.2x1.2m base and 1.5m tall) were made of 10-cm mesh cattle panels with steel t-posts wired to cattle panels at diagonal corners.

Paired cages -- The development of highly accurate GPS equipment allowed us to use a second configuration of exclosures to assess productivity and utilization over many more vegetation types and over larger areas than we used at fixed sites. After a general reconnaissance, the “Crater Hills Area” in the eastern part of the valley was selected because it contained patches of all cover types present in the Hayden Valley. The 4.1km^2 area we defined was selected solely on the presence of all different cover types and was not explicitly intended to represent cover types in proportion to availability.

Lack of adequate vegetation data defining vegetation in a spatially explicit manner or even the capability to develop it prior to the start of our study prevented us from using stratified random sampling for selection of exclosure sites and unprotected plots. Therefore, we walked through the Crater Hills area in mid-July of 1998 and selected 50 widespread representative patches of vegetation from our defined cover types.

Patches were selected across the full extent of the area to avoid clumping exclosures. Two similar ~1m diameter paired plots, based on biomass and species composition of vegetation, were selected in each patch within ~25 m of each other. One of the paired plots within each patch was randomly selected to receive an exclosure, and the location of the unprotected plot was recorded using an average of at least 30 GPS readings. The process of selecting paired plots was repeated after clipping vegetation in each time period (fall of 1998, spring and fall of 1999, and spring of 2000). We used adjacent or nearby patches of vegetation for subsequent time periods when the patch was too small to accommodate more than one independent pair of plots or site current conditions were not suitable (due to wallow creation, excessive trampling at a site prior to our arrival at the site, slow snow melt, or flooding) for using the same patch in consecutive years. Weight and bulk of transporting material any distance from the road prevented us from using the relatively sturdy type of exclosures we used at the 3 fixed sites. Therefore, exclosures were similar in construction to those we used in our test of cage effects in the Bridger Mountains, with the addition of 2 inverted “J” stakes to hold down corners without posts.

Due to encouraging results the first year, we added the 4.8 km^2 “West Alum Area” in the western end of the Hayden Valley during the summer of 1999. Selection of paired plots in the West Alum area during summer and fall of 1999 and spring of 2000 was identical to the Crater Hills area. We used only 30 exclosures in this area due to the difficulty of transporting exclosure material 8 to 15 km to the site.

Prominent topographic features, such as ridge tops, tree lines, and the road through the Hayden Valley, were used to define boundaries of each area. Exclosures and unprotected plots from the West Alum and Crater Hills areas will be referred to as "paired plots" for convenience. Paired plots provide the ability to estimate forage removal on a larger "regional" scale than fixed sites.

Non-native clover (*Trifolium repens* and *T. hybridum*) was identified in 2 patches totaling <1ha, 1 patch each in the Crater Hills and West Alum areas. We selected 5 paired plots in each patch and placed exclosures in them during summer of 2000. Due to the small area occupied by non-native clover, limited number of patches, and potential biases of clustering cages in small areas, clipped plots of non-native clover were used only for descriptive purposes in estimating productivity, offtake, and in assessing potential spread of these non-native species. Data from non-native clover plots were not included in statistical analysis of clipped data in relation to grazing.

Sampling conventions common to all cage sites -- Circular 0.33-m^2 plots were clipped to a height of ~1 cm above ground level at the center of cages and unprotected locations from fixed sites and paired plots when cages were moved at the end of the growing season (September to early October) and early in the growing season (mid May to early June) when snow conditions allowed us to begin field work. Samples clipped at the start of the growing season were sorted into "new growth" (green plant biomass produced in the spring prior to clipping) and "residual vegetation" (vegetation from the previous growing season). All vegetation clipped at the end of the season was considered "standing crop" and undoubtedly included indefinite amounts of dead vegetation from previous years in addition to the current year. We believe that attempting to separate previous year's dead biomass from current year's growth at the end of the growing season is unnecessary for communities in the Hayden Valley. Sorting previous from current year growth in early autumn is difficult and subjective (Coughenour 1991) and biomass from previous years is unlikely to contribute significantly to total biomass because of relatively rapid decomposition rates in most herbaceous communities. Differential decomposition rates among vegetation types would pose the greatest concern if biomass from previous years is not separated, and, for that reason, we separated standing crop between current year and previous years' growth to test its impact on productivity estimates at the 3 fixed sites in fall of 2000. We found that growth from previous years made a negligible contribution to total biomass clipped in early autumn in all of the communities represented at fixed sites.

We clipped and sorted early spring growth from 20 plots at each fixed site into forbs and graminoids when cages were first set up in spring 1998 to estimate the relative contribution of graminoids and forbs to productivity. In all subsequent clipping, herbaceous biomass was not divided into forb and graminoid components. All clipped vegetation from fixed sites and paired plots was bagged, dried at 70^{o} C for at least 48 hours in a drying oven, and weighed ($\underline{+}$ 0.1 g accuracy).

Vegetation clipped from fixed sites and paired plots in spring and fall allowed us to look at vegetation removal, productivity, and biomass availability for 3 seasonal periods covering the entire calendar year: 1) early spring growth; 2) entire growing season; and 3) non-growing season. Amounts of new growth from exclosures in spring provided estimates of early spring productivity and differences between exclosures and unprotected plots provided estimates of offtake of early spring growth. Likewise, amounts of standing crop in fall provided estimates of total productivity and offtake for an entire growing season. Cages used to estimate standing crop in fall were placed in their locations after clipping in spring and we assumed any offtake of early spring growth we measured this early in the growing season would be accounted for in fall estimates by compensatory plant growth. The amount of vegetation from unprotected plots outside exclosures in fall represented the amount of forage available at the start of winter. Exclosures were repositioned in fall after clipping vegetation and subsequently clipped in spring to complete an annual cycle. Differences in residual vegetation between protected and unprotected plots in spring provided the amounts of offtake for the non-growing season (late fall to early spring).

Calculation of forage availability and herbivore offtake over winter was complicated by the logistics of field sampling. In the severe environment of the Hayden Valley, residual vegetation would decline during the non-growing season due to actions of bacteria and fungi and from mechanical losses due to wind and snow compaction in the absence of herbivores. For estimating offtake, this situation could be accommodated by adjusting estimates for cage effects (*i.e.* differences in rates of vegetation disappearance in plots protected by cages versus those not protected by cages – if differences existed) and then comparing residual biomass at protected and unprotected sites with the difference assumed to represent herbivore offtake.

Another problem involved our inability to sample plots prior to the initiation of early spring growth. This problem occurred because we could not sample caged and uncaged plots until most snow had disappeared from the Hayden Valley. This delayed access provided time for subnivean plant growth and growth at sites that shed snow early. Graminoids were especially difficult to deal with because green vegetation in spring could be due to new leaves appearing from plant bases or regrowth in leaves produced in the previous growing season (Stoddard and Smith 1955); therefore, new and past year's growth could not be easily differentiated as it could with forbs. To resolve this problem, we assumed that leaves originating from grass and sedge clumps that were all green were current year's growth and those with brown tips were the previous year's growth and that errors in distinguishing early spring growth from residual vegetation in graminoids should not affect comparisons between protected and unprotected plots since sorting errors between plots should be equal. This allowed us to estimate "new spring growth" in caged and uncaged plots and to use the difference as an estimate of herbivore offtake of new growth in spring.

Two additional problems remained: 1) estimating biomass present at the end of the growing season that was not available to herbivores overwinter (*i.e.* the vegetation lost to biological and mechanical degradation); and 2) determining if non-growing season decomposition and early spring regrowth patterns differed substantially among vegetation types. For the 2 periods when we had data for standing crop in fall and residual vegetation in spring (1998-1999 and 1999-2000), we calculated the "maximum" and "minimum" amount of intrinsic biomass loss that occurred over winter at each of our 3 fixed sites. Maximum overwinter loss (to factors other than grazing by large mammals) was estimated by subtracting the weight of standing dead biomass measured inside exclosures set up at the end of the growing season and measured the following spring from standing biomass measured outside exclosures in fall.

For estimates of minimum loss of residual vegetation to factors other than grazing by large herbivores, we used the same approach but added a correction for greenup of graminoid leaves produced in the preceding growing season to the overwinter weight of dead vegetation measured in spring. Because forbs did not initiate regrowth in leaves produced in the previous growing season, we needed to determine what percentage of spring growth was attributable to graminoids. We used the average proportion of graminoids from the 20 plots we clipped at each fixed site during initial cage layout in spring 1998 (Appendix A, Table 42) to estimate the amount of graminoids in spring new growth for 1999 and 2000 and assumed that #25% of the green leaves in graminoids in spring were regrowth of old leaves. Using these assumptions, we added 25% of the weight of green graminoids in plots protected from grazing over winter to the dead standing biomass in caged plots and 25% of the green graminoid biomass in unprotected plots to the weight of dead standing vegetation in unprotected plots to obtain “corrected” estimates of residual biomass. Overwinter loss was expressed both in grams and in percentages. Similar estimates for paired plots were not calculated because we did not have percentages of forbs and graminoids for all cover types.

For each clipping period, we tested for significance of differences between protected and unprotected plots among years and vegetation types using Analysis of Variance (Zar 1999), and calculated 95% simultaneous confidence intervals using Tukey’s method (Kramer 1956) to test for significant differences between pairs. We used t-tests for site differences between standing crop outside exclosures in fall and inside exclosure in spring (intrinsic winter loss) because exclosures were moved between the 2 periods. All statistical tests were conducted using S-plus statistical software (Insightful 2001) unless otherwise noted.

We have chosen to use the term “offtake” instead of “utilization” when referring to differences in vegetative biomass between protected and unprotected plots. The word “utilization” denotes use and generally implies use by ungulates in a grazing study. Differences between protected and unprotected plots may result from influences of the cage itself or by small mammals and insects in addition to ungulates.

Remote Sensing for Estimating Standing Crop

Using GPS equipment for paired plots in the Crater Hills and Alum Creek areas allowed us to estimate productivity and offtake across a much larger area and for a greater number of vegetation types than the traditional approach of multiple cages at fixed sites. However, extrapolation of results across the entire Hayden Valley from either method, our desired goal, depends on sites being unbiased representations of the entire area. Techniques which are less sensitive to site bias and incorporate larger areas could increase accuracy and precision of productivity and offtake estimates, and for this task we used satellite imagery. Satellite imagery provides a census of large areas, albeit at the spatial scale of the imagery, and, therefore, can provide an estimate of standing crop on a spatially explicit scale for the entire Hayden Valley. Estimates of standing crop in fall from our fixed cage sites and from paired plots offered a unique opportunity for testing the efficacy of methods utilizing remote sensing techniques.

Use of remote sensing is based on differences in reflectivity and absorption of electromagnetic energy in different wavelengths (Lillesand and Kiefer 1994). Blue, green, red, near-infrared, and mid-infrared are commonly used wavelengths for differentiating vegetation. Red and blue light are absorbed by chlorophyll in the photosynthetic process, near-infrared light is reflected by mesophyll tissue due to damaging effects on actively growing vegetation, while mid-infrared reflectance is generally dependent on water content in vegetation.

Satellite imagery, often using the normalized difference vegetation index (NDVI), has long been used to estimate vegetative biomass (Anderson et al. 1993; Wylie at al. 1996, 2002; Lillesand and Kiefer 1999). However, a number of sampling issues have reduced accuracy, precision, and general use of estimates. Multispectral radiometers aboard satellites measure the amount of reflected light for each pixel of an image, but the corresponding pixel area on the ground is too large to obtain direct biophysical measurements of vegetative biomass (e.g. ~30x30m for Landsat TM series) and must be sub-sampled. Sampling issues not unlike those encountered using exclosures may arise when estimating biomass for an entire pixel-sized area. Plant phenology and species composition must also be considered. Our desire was to estimate only the herbaceous portion of vegetation but the influence of shrub species on reflectance and biomass estimates must be considered, as must changes in reflectance of plants that occur during phenological progression.

We modified the methods of Wylie et al. (1996, 2002) in a double-sampling process to relate biomass of small clipped plots across the entire Hayden Valley using a portable radiometer and satellite imagery. In a multi-step process, vegetative biomass was related to reflectance from the portable radiometer (Pearson et al. 1976), the radiometer used as a sampling tool to estimate biomass over larger areas, and then biomass estimates of the larger areas were related to pixels of satellite imagery. The entire process was repeated for each estimate we made. We tried to complete all data collection within 3-4 days before or after a satellite overpass and attempted to make estimates at 16-day intervals in conjunction with Landsat satellite overpass dates between early July and mid September each year. Successful completion of estimates was dependent on acquisition of cloud-free satellite images and adequate weather in the days prior to and after a satellite overpass to accomplish all ground related sampling.

The intent of the first step was to relate the entire range of vegetation characteristics to reflectance readings from the portable radiometer, not to characterize the area from our samples themselves. Therefore, plots were visually selected rather than relying on random sampling methods to encompass the range of vegetation cover types and all amounts of herbaceous and shrub biomass. We used a Cropscan (Cropscan Rochester, Minnesota) portable radiometer to obtain reflectance data in the same wavelengths as the first 5 bands of Landsat TM imagery (Blue: 450-520 nm; Green 520-600 nm; Red: 630-690; Near-Infrared: 760-900; and Mid-Infrared:1550-1750 nm). The instrument calculates percent reflectance to account for differing atmospheric conditions by simultaneously measuring irradiance and radiance and includes a cosine correction for angle of irradiance.

Height of the radiometer was adjusted to sample 0.75-m^2 circular plots at ground level. We took 3 successive readings of each plot with the radiometer and averaged them. All readings were taken at a maximum sun angle of 60 degrees from solar zenith and minimum irradiance of 400 watts/m^2. Current year's growth of herbaceous vegetation (obvious green plant biomass plus current season's growth which has senesced) was clipped from the entire 0.75 m^2 circular plot to within ~1 cm of ground level and collected. Green biomass was stripped from sagebrush plants and collected separately from herbaceous vegetation after measuring height and canopy diameter in both the longest axis of the canopy and perpendicular to the longest axis of sagebrush plants. Percent greenness of herbaceous vegetation in each plot was estimated visually. Between 12 and 35 plots were sampled in each time period for which an estimate was made. All vegetation was dried for a minimum of 48 hours at 70^{o} C in a drying oven before weighing. Linear regression was used to relate vegetative biomass to reflectance.

Prior to conducting fieldwork, we calculated NDVI from a July 1996 scene of Landsat 5 imagery as a pixel by pixel pseudo estimate of vegetative biomass for the Hayden Valley and selected areas from the image for field sampling with the portable radiometer. We used an iterative process to define categories of NDVI in the image and selected areas from each category such that: 1) each area contained a grid of at least 3 x 3 pixels that were as homogenous in NDVI values as possible; and 2) selected areas must cover the range of NDVI categories, therefore representing the range of vegetative biomass in the Hayden Valley. The process yielded 8 locations (Table 1) that met our criteria. We located the corresponding locations on the ground with our GPS receiver and laid out a 45x45m plot within each area using a 75m tape and GPS receiver. Plot boundaries were in the ordinal directions and corners were permanently marked to allow exact relocation. Systematic sampling was chosen over random sampling (Ratti and Garton 1994), and samples were taken at a distance of 5 m along transects spaced 5 m apart to collect 81 reflectance readings in each grid with the portable radiometer (0.75-m^2 circular plots at a maximum sun angle of 60 degrees from solar zenith and minimum irradiance of 400 watts/m^2). Permanently marking corners and using a tape to lay out grid locations along plot boundaries with pin flags allowed us to sample almost the exact same locations in each time period.

Table 1. Minimum and maximum values of NDVI from July 12, 1996 Landat 5 imagery for pixels within areas used to sample biomass with a portable radiometer.

Grid number	Minimum NDVI	Maximum NDVI
1	0.23	0.26
2	0.32	0.34
3	0.41	0.44
4	0.46	0.49
5	0.50	0.52
6	0.54	0.57
7	0.58	0.61
8	0.70	0.73

We also selected 12 30x30m plots covering the range of vegetative biomass and cover types present in the Hayden Valley. Plots were centered in areas of visually homogeneous vegetation at least 100m in diameter, plot boundaries were in the ordinal directions, and locations of corners were determined by averaging 30 GPS positions using methods previously described to facilitate plot relocation. As with the 45x45m plots, readings were taken with the portable radiometer using a systematic sampling pattern at 5m intervals, providing 36 reflectance readings for this plot size. We will refer to both the 45x45m and 30x30m plots as “grids” for convenience in differentiating them from clipped plots.

Rain and cloudy conditions that preclude use of remote sensing techniques are a common occurrence in the high elevation local of the Hayden Valley. Emphasis during each estimate of standing crop was the collection of enough clipped plots to develop a relationship between vegetative biomass and reflectance for that time period and sampling the 8 *a-priori* delineated 45x45m grids, all within a short time period of the satellite overpass. During each time period, we also attempted to sample the 30x30m grids, but unsuitable weather prevented us from sampling all 12 in all time periods.

The regression developed between clipped plots and reflectance from the portable radiometer during each time period was applied to portable radiometer readings taken within grids to estimate biomass within each grid. We calculated variograms for each grid to model autocorrelation and used block kriging (Gamma Design Software 2002) as a more precise method than point kriging (Webster et al. 1989) to interpolate biomass across the extent of each grid. Total estimated biomass in each 45x45m and 30x30m grid was proportionally reduced to the size of a pixel of satellite imagery and assigned to the corresponding pixel of satellite imagery with the greatest overlap of sample area. Linear regression was used to relate estimated grid biomass to pixel reflectance. Regression results were then applied to remaining pixels within the scene to estimate biomass on a pixel by pixel basis for the entire Hayden Valley.

Use of the portable radiometer was also incorporated into other aspects of our work. Reflectance readings were taken of all paired plots in the Crater Hills during the first selection period in July 1998. We calculated NDVI of plots as an estimate of biomass and conducted a paired t-test between protected and unprotected plots as a pseudo-comparison of the same initial biomass between pairs.

We also used the portable radiometer to provide non-destructive estimates of vegetative biomass and offtake at fixed sites during the middle of the growing season. Reflectance readings were taken of protected and unprotected plots with the radiometer and converted to biomass estimates using regressions from the closest time periods we calculated the relationship between clipped biomass and reflectance. Although mid-summer biomass estimates of fixed sites have a regression error term associated with them, a bias should not exist between estimates from protected and unprotected plots when applying the regression. Under this assumption, we treated each estimate as a sample to allow testing for differences using ANOVA tests similar to clipped data.

Indices of Animal Use

Grazed loop surveys -- We used the grazed-loop technique (U. S. Forest Service 1977) in the Crater Hills and West Alum areas at the end of the growing season in 1999 and 2000. Metal loops, 12.7 cm in diameter attached to a 0.75-m pole, were lowered to the ground at randomly paced intervals along transects providing comprehensive coverage of each area. We recorded grazing level, cover type, and location with a GPS receiver at each location. As defined by the grazed loop technique, grazing of less than 5% by weight of forage within loops was recorded as ungrazed and >5% is recorded as grazed. In samples with >5% grazing, we classified sites as level 1 (vegetation height > 7 mm) or level 2 (vegetation height < 7 mm) grazed. This allowed us to analyze results using a 2-class system (grazed versus ungrazed) and a 3-class system (no grazing, level 1 grazing, level 2 grazing). We also used the grazed loop method at the 3 fixed exclosure sites in 1999 and 2000 to compare percent removal from this method with removal estimates from exclosures.

Cover type was recorded at each grazed-loop sample site to provide an estimate of cover type availability in the Crater Hills and West Alum areas. Use versus availability was tested using simultaneous confidence intervals (Marcum and Loftsgaarden 1980) based on a 2-class division (grazed versus non-grazed) and a 3-class division (no grazing, level 1 grazing, level 2 grazing). We did not use goodness-of-fit test prior to constructing intervals because it is not necessary for intervals to be valid (Byers et al. 1984) and may of questionable use (Cherry 1996).

Counts of large mammals and their feces -- Fecal counts were conducted on 3 different scales throughout the Hayden Valley as another way to assess relative use by bison and elk. In the Crater Hills and West Alum areas, bison and elk feces from the current season within ~5m of exclosures were counted in spring 2000 as an indication of relative use by each species during winter and again in fall as an indication of use during the growing season. At fixed sites, all bison and elk feces within site boundaries were broken apart or flattened by stepping on them when exclosures were first set up in spring 1998. We then counted and broke apart or flattened all ungulate feces when plots at fixed sites were clipped to obtain numbers of bison and elk feces over the same period as clipped vegetation data.

Fecal counts were also made at ~16 day intervals during the growing seasons of 1998, 1999, and 2000 in the 8 45x45m plots we used for estimating standing crop with remote sensing techniques. Fecal deposits within the 8 plots were marked or removed at the start of each growing season, subsequently counted and marked each 16-day period similar to methods for fixed plots, and summed for each growing season.

Observations of bison and elk were recorded at the 3 fixed cage sites from the time exclosures were set up in spring until they were moved at the end of summer each year. Field work throughout the Hayden Valley prevented us from setting random survey times; therefore, surveys were conducted whenever we could survey all 3 sites within ~10 minutes of each other. Animals were often seen adjacent or within several kilometers of sites but only animals within boundaries used for cage placement were recorded. We also recorded numbers of bison and elk observed when we systematically surveyed blocks in the Crater Hills and West Alum areas to determine the distribution of feeding bison, and we had access to total counts from aerial surveys conducted by Hess (2000). Although other large mammals (mule deer, grizzly bears, moose, etc.) were occasionally seen in the Hayden Valley, we made no attempt to calculate their numbers, distribution, or contribution to forage utilization.

Fecal counts and counts of animals (except those from fixed sites) were intended solely for relative comparisons between numbers of bison and elk. Our methods at fixed sites allowed analysis of site and seasonal differences in addition to relative use. Fecal densities and animal densities at fixed cage sites were calculated based on surface area estimates in GPS files defining overall perimeters of fixed sites and boundaries of vegetative inclusions within fixed sites and converted to numbers per hectare for specific sampling periods. We used Analysis of Variance (Zar 1999) to test for differences among sites, seasons, and site by season interactions in bison and elk fecal densities. Differences among years were not tested due to small sample sizes and because year influences should be accounted for within the season variable. Since observational surveys of fixed sights were only conducted during the growing season, we only tested for differences among sites for density of observed animals.

Fecal counts and numbers of animals have long been used as indicators of animal use. Since fall clipping and fall fecal counts both represent the same time period (growing season), we used fecal density and observed animal density as separate predictor variables in linear regression for forage removal during the growing season. During the spring period, fecal counts correspond to clipping and analysis of both spring new growth and residual vegetation from the previous year. To account for the overlap of spring fecal counts across 2 offtake estimates, we used fecal densities as a predictor variable for offtake of spring new growth and residual vegetation individually and to predict their combined offtake. Individual season regressions contained small sample sizes, consisting of samples from the 3 fixed sites over 3 growing seasons and 2 non-growing seasons, but served as a means of identifying potential trends. Additionally, we conducted "yearlong" regressions by combining fecal densities from both seasons as the predictor variable and total offtake of standing crop in fall, residual vegetation, and new growth in spring as the response variable.

Estimates of Herbaceous Productivity and Offtake

We used our 2 configurations of exclosure placement, multiple cages at fixed sites and paired plots across large areas, in conjunction with cover type availability from grazed loop surveys to extrapolate herbaceous production and forage offtake of the combined Crater Hills and West Alum areas and for the entire Hayden Valley. Separate estimates were conducted as a comparison of traditional methods using multiple exclosures at sites in comparison to our paired plot method.

For this process, the onscreen utility of ArcView GIS (ESRI 2000) was used to calculate approximate area of the Crater Hills area, the West Alum area, and total contiguous grassland of the Hayden Valley excluding islands of trees. Summed area of the Crater Hills and West Alum areas was multiplied by percent availability of cover types from grazed loop surveys to estimate total area of each cover type within the combined Crater Hills and West Alum areas.

Estimates based on data from paired plots required extrapolation of production estimates for several cover types for which we did not have clipped data, while estimates using data from fixed sites required us to group communities at the fixed sites into broad vegetation types. Descriptions of cover types are given in Appendix B. Acronyms for types appear in Table 2.

For estimates based on paired plot data collected in the Crater Hills and West Alum areas we grouped cover types (see Appendix B for cover type descriptions and acronym definitions). The *Arca/Feid-Dain* cover type was represented by *Artr/Feid-Dain.* The *Artr/P*osa cover type was represented by *Posa*, and the Sage/dry *Carex* cover type was represented by averaging the 3 cover types (*Artr/Feid*, *Arca/Feid*, *Arca/Dece*) occurring adjacent to it. Productivity estimates of the miscellaneous forb and thermally influenced cover types were assumed to be the same as that calculated for clover, the only other forb-dominated cover type. Estimates of offtake by weight were calculated based on similar groupings of cover types except that offtake of miscellaneous forb and thermally influenced types was considered to be 0 due to lack of offtake data for these types and small total area (3.2ha) they were estimated to collectively occupy in the Crater Hills and West Alum areas.

After we derived estimates of production (standing biomass at the end of the growing season in plots protected from grazing) and offtake (difference between standing biomass in cage and biomass in an adjacent equivalent plot at the end of the growing season) on a per unit area basis for each vegetation category, we multiplied these values by the area of each vegetation category in the Crater Hills and West Alum areas. Estimates for the Hayden Valley were calculated by extrapolating production in the Crater Hills and West Alum areas to the entire valley under the assumption that the proportions of cover types within sample areas were similar to proportions for the entire valley.

For estimates using fixed sites, we first combined areas of cover types into the 3 broad vegetation categories represented by fixed sites. The mesic graminoid fixed site was assumed to be representative of *Dece/Carex*, wet *Carex*, *Salix*/*Carex*, and *Caca* cover types (see Appendix B for descriptions and acronym definitions). The silver sage fixed site was assumed to have productivity equivalent to the *Arca/Dece, PoFr/Dece*, and *Dece* cover types and to 3 forb-dominated cover types found in intermediate moisture environments. The big sage fixed site was assumed to be representative of herbaceous productivity in all dry graminoid and dry shrub cover types.

We then multiplied estimates of production and offtake by the surface areas of classes comparable to vegetation in the fixed sites found in the Crater Hills and West Alum study sites. Estimates for the Hayden Valley were based on extrapolation of values from the Crater Hills and West Alum sites to the entire valley. Total percent offtake for estimates based on paired cages and fixed sites was calculated by dividing offtake estimates by production estimates and multiplying the resulting decimal fraction by 100.

We also used data from grazed loop surveys in conjunction with U.S. Forest Service (1977) procedures to calculate a third estimate of productivity. The grazed loop estimate was calculated using the “Mixed Grass Prairie” graph (U. S. Forest Service

1977) for all cover types from the *Feid* and *Posa* understory groups (Table 3) and the "Mountain Meadows" graph (U. S. Forest Service 1977) for the *Dece* and wet *Carex* understory groups (Table 3). Because data from 1998, 1999, and 2000 from exclosures were combined for offtake estimates, we combined 1999 and 2000 data from grazed loop surveys to provide a comparison between methods. We estimated that any effect of including 1998 data in exclosure estimates and using 1999 and 2000 data for grazed loop estimates would only minimally influence the difference between grazed loop estimates and estimates from exclosure data. Excluding 1998 data would slightly increase estimates of offtake by weight, but the corresponding slight increase in production would result in similar estimates of percent offtake from exclosure data.

Influences on Vegetation

Estimates of frequency of repeated grazing by ungulates and small mammals -- Detrimental effects of excessive grazing occur from repeated offtake over consecutive years rather than a single year, in addition to timing and amount of vegetation removal. Presence of indicator plant species is often used to identify excessive grazing if the species composition of healthy climax vegetation in an area is known (Stoddart and Smith 1955), but the paucity of historical data on vegetation in the Hayden Valley would make it difficult to determine if changes in species composition have occurred or if they occurred prior to or after increases in bison populations. As an alternative, we used data collected from exclosures to provide information on amounts and timing of vegetation removal. Secondly, we looked at the occurrence of repeated grazing as a way to assess the probability a ~1m^2 patch of ground will be grazed once or multiple times within a 3-

year period. The combination of amount and timing of offtake in conjunction with occurrence of repeat grazing may aid in identifying the potential for excessive grazing and the vegetative types most at risk.

Prior to clipping vegetation during our first sample period in 1998, we recorded the presence of ungulate grazing by 1 of 3 categories (none = <5% by weight grazed, slight = 5-20%, obvious = >20%) in a ~1-m diameter area containing unprotected 0.33-m^2 plots at paired and fixed cage sites. We also categorized small mammal activity in plots (none, slight, heavy) which could occur in addition to ungulate grazing when runways were obvious. We used GPS to relocate each unprotected plot clipped in 1998 during fall 1999 and 2000. Ungulate grazing and small mammal activity levels were again recorded. This provided information on the same plots spanning 3 consecutive years. Likewise, we recorded ungulate and small mammal use of plots first used in 1999 and relocated them in 2000 to record use over 2 years. Plots selected each year were used independently for each occurrence category to avoid skewing data for tests and cover all categories for the period of this study. Plots first used in 1998 are the only ones that provide information for the 2-year period of 1998 and 1999 in addition to all 3 years. They were combined with plots selected in 1999 to encompass a data set covering both 2-consecutive year periods of the study, 1998-99 and 199-00. Excluding the plots grazed 3 consecutive years from data sets of 2-year periods while maintaining actual sample sizes would have biased results of the 2-consecutive year test against a vegetation type with a high occurrence of grazing in all 3 years.

Fixed sites occupy small areas of relatively homogeneous vegetation in relation to areas containing paired plots. Grazing at 1 location within a fixed site may influence grazing at other locations within the site to a greater extent than within the much larger and vegetatively heterogeneous Crater Hills and West Alum areas. Therefore, analysis of fixed sites and paired plots was conducted separately due to differences in spatial scale each cage configuration represents. We used chi-square tests of proportions to test the null hypothesis of the same probability of grazing among all vegetative types for each category of repeated grazing when sample sizes were large enough. Fisher's exact tests were used when expected counts <5 were encountered. If the null hypothesis for all types was not accepted (*P*<0.05), separate tests were conducted between each vegetative pair. Similar analysis was conducted for repeated occurrence of ungulate grazing and offtake from small mammals.

Impacts of ungulates on forest-grassland boundary -- We hypothesized bison may be disrupting the forest boundary due to the number of girdled and dead trees along forest margins, remains of mature trees far from the forest edge, and observations of bison scraping bark from trees with their horns. Elk may also damage trees, but the relatively small number of observed elk and presence of antlers or horns capable of causing damage only on male elk (as opposed to both sexes for bison) suggests bison may be the greatest contributor to girdled trees. Potential disruption of forest margins by bison would be a relatively recent event since <300 bison probably occupied the Hayden Valley between ~1880 and 1968 (Meagher 1973). Questions of interest were: 1) what was the extent of damage; 2) was damage related to tree size; and 3) could cumulative damage over ~30 years disrupt forest boundaries?

We selected 25 random locations along forest boundaries from topographic maps and navigated to them with a GPS receiver. From the random locations, a minimum of 25 trees in each direction along the forest boundary and within ~2 m of the edge were inventoried. We recorded size of trees (sapling = 5-10 cm dbh, pole timber = 10-20 cm dbh, mature = >20 cm dbh) and the extent ungulate rubbing had damaged individual trees (1 = no damage when existence of scrapping was not present, 2 = scraped, when bark was scraped off but less than 20% of the tree by circumference was girdled, 3 = 20-50% of the tree circumference was girdled by ungulate scraping, 4 = >50% of the tree circumference girdled, 5 = dead trees with visual evidence of scraping). We used chi-square tests of proportions to test the null hypothesis of the same probability of damage among tree size and separate tests between pairs when the null hypothesis was not accepted ($P<0.05$).

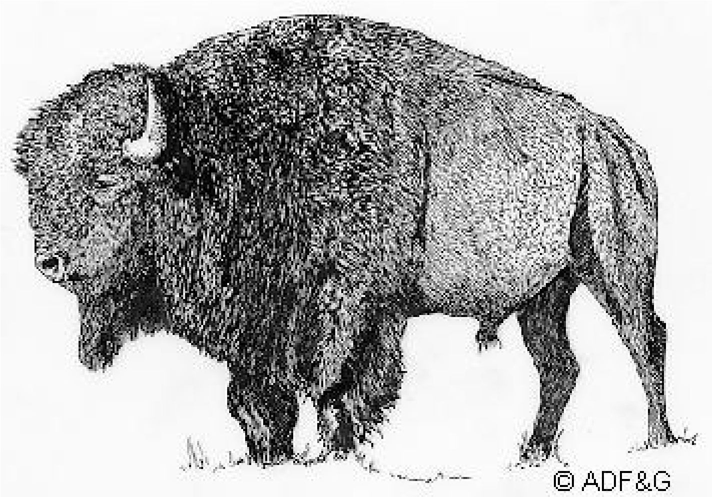
Nutritional Quality of Forage and Plant Composition in Fecal Samples

Forage nutritional quality -- In early, mid, and late summer of 2000, we randomly collected current year's growth of graminoid species forming the basis of cover types and groupings of cover types (*Festuca idahoensis*, *Poa sandbergii*, *Deschampsia cespitosa*, and a composited mix of the 2 most common sedges forming wet carex meadows, *Carex aquatilis* and *C. rostrata*). Cursory observations of grazing patterns during field work indicated an avoidance of *Danthonia intermedia* and selection for *Carex nebraskensis*. Therefore, we also collected samples of these 2 species for examination of obvious differences in nutrient levels. Multiple plants (>25) from several locations were composited into each sample. Standard chemical constituent analyses (nitrogen, minerals, water content, acid detergent fiber, etc.) were conducted on all samples (Midwest Laboratories, Inc., Omaha, NE).

Plant nutrient results were compared relative to each other and to assumed nutritional requirements of bison rather than for absolute differences among plants. Due to the limited amount of specific literature pertaining to nutritional requirements of bison, we took a conservative approach and used published requirements for cattle (base levels of no weight gain and not pregnant or lactating) as a basis for assessing nutrition of collected plants. Bison digest forage more efficiently than cattle (Peden et al. 1974, Hawley et al. 1981); suggesting nutritional requirements of cattle are more restrictive than those of bison.

Forage crude protein (CP) content below 7% may not supply the needs of rumen bacteria in cattle, causing consumption to decrease to the point it may be difficult to meet energy requirements (McDonald et al. 1973), while 54% total digestible nutrients (TDN) in forage is considered a minimal requirement for maintenance (National Research Council 1984). However, the TDN: CP ratio is also important. A ratio >8 may indicate there is a deficiency of protein relative to energy (National Research Council 1984, 1989). We used these levels of CP, TDN, and the CP: TDN ratio as base levels to assess the adequacy of protein and energy for plants we collected. We also compared plant mineral content in relation to cattle requirements and calculated calcium to phosphorus ratios. In cattle, a 1:1 to 2:1 ratio of calcium to phosphorous is considered optimal, and ratios greater than 8:1 have been suggested to interfere with ruminant phosphorus metabolism.

Plant composition in feces -- We assessed seasonal diet composition by examining plant fragments in feces (Sparks and Malechek 1968). We collected bison feces throughout the Hayden Valley in early summer (~July 1), mid-summer (~Aug 5), late summer (Sept 10) and, during 1 year, in the fall (Oct 12). Equal sub-samples from 10 fecal piles formed a composite sample for each time period. Botanical composition was expressed as percent relative cover of identifiable plant fragments in 200 random microscopic fields (Washington State University, Wildlife Habitat Laboratory, Pullman). Correction factors for differential digestibility of plant species were not applied.



RESULTS

Cover Types

The *Artr/Feid*, *Arca/Dece*, and *Arca/Feid* cover types (see Appendix B for key to cover types and descriptions) were the most common types in the Crater Hills and West Alum areas, based on 1,688 random points from grazed loop surveys (Table 2). *Salix/Carex*, sage/dry *Carex*, and cover types in the forb or thermally influenced plant group occurred least, with $\leq$0.3% of the total area in each of these cover types. General reconnaissance indicated percentages of cover types in the Crater Hills and West Alum areas (Table 2) were probably similar to amounts in the entire Hayden Valley, and percentages were also similar to reported amounts with one notable exception when we compressed our types into corresponding types of Graham (1978). The proportion of wet *Carex* meadow we calculated from grazed loop surveys of the Crater Hills and West Alum areas was lower than the 14% reported by Graham (1978), because the Crater Hills and West Alum areas do not contain large wet sedge meadows such as occur along the Yellowstone River. Omission of riverine wet sedge meadows led to a higher estimate (by 7.5%) of the proportion of the *Artr/Feid* type than reported by Graham (1978). Proportions of all other types derived from grazed loop surveys were within 3% of estimates reported by Graham for the whole Hayden Valley (1978).

The vegetation classification scheme in Table 2 is a conventional grouping of cover types based on inclusion of a shrub canopy, if present. We also defined cover groups based on relative abundance of 3 common grass species and a set of sedges common in moist site. Grouping of cover types by these 4 graminoid understory groups

Table 2. Cover types identified in the Hayden Valley, cover group membership, corresponding acronyms, and percent area estimated in the Crater Hills and West Alum areas from grazed loop surveys during 1999 and 2000.

Cover group Cover type	Acronym	Percent area
Dry shrub group		
Artemisia tridentata / Festuca idahoensis	Artr/Feid	27.0
Artemisia cana / Festuca Idahoensis	Arca/Feid	13.9
Artemisia tridentata / Festuca Idahoensis-Danthonia intermedia phase	Artr/Feid-Dain	2.4
Artemisia cana / Festuca Idahoensis-Danthonia intermedia phase	Arca/Feid-Dain	0.6
Artemisia tridentata / Agropyron caninum.	Artr/Agca	2.8
Artemisia tridentata / Poa sandbergii	Artr/Posa	2.4
Artemisia / Dry *carex* phase	Sage/dry carex	0.3
Moist shrub group		
Potentilla Fruticosa / Deschampsia cespitosa	Pofr/Dece	0.4
Artemisia cana / Deschampsia cespitosa	Arca/Dece	15.3
Wet shrub group		
Salix / carex	Salix/Carex	0.0
Dry grass group		
Ridge top *Poa sandbergii*	Posa	3.0
Intermediate grass group		
Festuca Idahoensis / Agropyron caninum	Feid/Agca	6.2
Festuca Idahoensis / Deschampsia cespitosa	Feid/Dece	6.8
Moist / wet graminoid group		
Calamagrostis canadensis	Caca	0.8
Deschampsia cespitosa	Dece	9.1
Deschampsia cespitosa / Carex	Dece/Carex	5.0
Wet *carex* spp.	Wet Carex	2.4
Forb or thermally influenced plant group		
Non-native clover (*Trifolium* spp.)	Clover	0.1
Miscellaneous forb	Misc. Forb	0.3
Thermal vegetation	Thermal Veg.	0.1
Non-vegetated		
Erosive / disturbed (not thermal)	Eros/Dist	1.1
Thermally influenced	Thermal Gnd.	0.1

(Table 3) allowed us to examine habitat availability from the standpoint of bison forage. In effect, 2 general differences existed between combining cover types into cover groups or into understory groups. The dry shrub group and the intermediate grass group both contain *Festuca idahoensis* dominated cover types and these were combined into the *Feid* type rather than being placed in separate groups due to the presence of sagebrush. Second, cover types containing *Deschampsia cespitosa* (tufted hairgrass) from wet grass and moist shrub groups were combined as a *Dece* grass type rather than separated using conventional methods. Total percent of understory groups for the Crater Hills and West Alum areas were 59.7% for *Feid*, 25.6% for *Dece*, 5.4% for *Posa*, and 7.4% for Wet *Carex*.

We used cover types, cover groups, and graminoid understory groups in analyses of production and offtake for paired cage sites in the Crater Hills and West Alum areas. The sage/*Carex* cover type, cover types representing non-vegetated areas, plant communities dominated by forbs or thermally influenced vegetation, and wet shrub communities were not included in analyses. These communities were identified due to their uniqueness, but they represent small portions of the landscape (< 1%) and were not sampled adequately for statistical analysis. In our opinion, considering them inclusions of adjacent types was also inappropriate because the species composition in these types is quite different from adjoining areas. Deleting them from consideration of bison forage dynamics in the Hayden Valley is justifiable because they cover a minute proportion of the area and, with a few exceptions, provide little forage for grazing ungulates.

Salix/Carex, non-native clover, and thermal vegetation may provide forage for bison but are very site specific types and collectively comprised 0.2% of the Crater Hills and West Alum area. We observed *Salix/Carex* and non-native clover in 2 locations of the Hayden Valley, but we did not encounter them during grazed loop surveys. The sage/*Carex* cover type is probably a phase of a *Festuca idahoensis* or *Deschampsia* *cespitosa* cover type, but we excluded it due to its very limited presence and aberrant species composition compared to either *Artr/Feid* or *Artr/Dece*.

Table 3. Cover types categorized by graminoid understory groups from grazed loop surveys in the Hayden Valley during 1999 and 2000.

Graminoid group Cover type	Acronym
Festuca idahoensis (FeId) grass type	
Artemisia tridentata / Festuca Idahoensis	ArTr/FeId
Artemisia cana / Festuca Idahoensis	ArCa/FeId
Artemisia tridentata / Festuca Idahoensis-Danthonia intermedia phase	ArTr/FeId-DaIn
Artemisia cana / Festuca Idahoensis-Danthonia intermedia phase	ArCa/FeId-DaIn
Artemisia tridentata / Agropyron caninum.	ArTr/AgCa
Festuca Idahoensis / Agropyron caninum	FeId/AgCa
Festuca Idahoensis / Deschampsia cespitosa	FeId/DeCe
Poa sandbergii (PoSa) grass type	
Ridge top *Poa sandbergii*	PoSa
Artemisia tridentata / Poa sandbergii	ArTr/PoSa
Deschampsia cespitosa (DeCe) grass type	
Potentilla Fruticosa / Deschampsia cespitosa	PoFr/DeCe
Artemisia cana / Deschampsia cespitosa	ArCa/DeCe
Calamagrostis canadensis	CaCa
Deschampsia cespitosa	DeCe
Wet Carex grass type	
Wet *carex* spp.	Wet Carex
Deschampsia cespitosa / Carex	DeCe/Carex
Salix / carex	Salix/Carex

Relationship between Vegetative Biomass and Reflectance from a Portable Radiometer

We took reflectance readings with the portable radiometer and clipped corresponding vegetation during 12 time periods during 1998 – 2000. The strongest regressions, as determined by multiple R-squared values, were obtained for the herbaceous component of vegetation rather than the combined biomass of herbaceous plants and sagebrush. Multiple R^2 values for herbaceous biomass ranged from 0.84 to

0.97 for each time period individually, and 0.81 for all dates combined (Table 4). Best regressions were obtained using reflectance of red and near infrared light (NIR) as continuous variables and an indicator variable for plots of the wet *Carex* cover type ($\geq$90% wet *Carex* spp.).

Differences in coefficients among dates and the weaker relationship for all dates combined resulted from differences in phenology among plots. We were able to define a "phenology" variable to account for differences. However, results are preliminary at this time. We were able to predict biomass of sagebrush (R^2 ~ 0.72) independent of herbaceous biomass after using classification trees to predict plots containing sagebrush (~85% accuracy).

Table 4. Variable coefficients and multiple R^2 for regressions between reflectance from a portable radiometer and herbaceous vegetation for each time period and all dates combined during 1998, 1999, and 2000 for the Hayden Valley.

Year		Regression coefficients				
Dates	N	Intercept	Red	NIR	Carex	R^2
1998						
17-20 July	35	-118.01	-3.94	7.43	125.55	0.86
1-6 August	32	151.25	-19.37	1.50	90.58	0.87
16-23 August	22	8.59	-10.28	5.21	71.08	0.90
1999						
8-11 July	32	-26.86	-3.82	4.02	95.49	0.94
23 July	15	-1.77	-5.77	4.48	140.36	0.98
24-26 August	30	29.14	-10.54	5.34	134.14	0.94
10-11 September	12	68.65	-12.78	5.30	74.27	0.92
2000						
27 June - 3 July	21	-85.34	-2.58	5.90	NA[1]	0.84
13-16 July	24	38.39	-6.58	3.23	95.24	0.89
29 July - 2 August	18	126.06	-16.59	3.26	187.56	0.89
14-17 August	20	-37.36	-6.08	6.39	118.38	0.89
7-10 September	17	-196.05	-4.59	13.03	147.58	0.97
All dates combined	278	-14.26	-4.14	4.26	137.17	0.81

[1] Plots containing only carex were not clipped during this time period.

Exclosures

Exclosure distribution, numbers, and durability -- Of the 300 total exclosure cages (5 time periods x 3 sites x 20 per site) used at the 3 fixed sites during this study, 5 cages (~3%) were pushed over by animals and plot pairs were not clipped, resulting in sample sizes of less than 20 per site on several occasions. We found 65% of the nails marking plot locations outside exclosures at the fixed sites, did not find 33%, and 2% had been pulled up by animals and were found within ~2 m of origin. When nails marking plots were not found, we located plots to the nearest 0.1 m with our GPS receiver. HDOP was always <2.0 during relocation of plots and we held the antenna of the GPS receiver over a location until we achieved a consistent reading for the desired position.

In the Crater Hills and West Alum areas, 77 of the 346 total cages we placed during the study (22%) were pushed over by animals and did not provide data. Damage to cages and our selection process of sites resulted in unequal sample sizes among cover types and vegetation groupings. Nails were not used to mark unprotected plots. Consequently, plot locations were located with the GPS in the same manner as fixed sites when nails were not found. A paired t-test between NDVI of protected and unprotected plots when the first set of plots were selected in the Crater Hills area in1998 indicated no difference in biomass as measured by NDVI (t = -0.10, df = 49, p = 0.92), indicating our selection process between protected and unprotected plots in the Crater Hills and West Alum areas was not biased.

Reliability of exclosure methodology as an index of forage offtake -- Using differences between vegetation protected from grazing by exclosures and vegetation accessible to grazing ungulates as an indicator of forage offtake is contingent on: 1) comparability of protected plots and plots accessible to foraging ungulates; 2) sufficient use by ungulates to create a measurable difference in biomass between protected and unprotected plots; and 3) absence of factors that could influence differences in protected and unprotected plots other than grazing.

Were caged and uncaged plots comparable? The first required condition, comparability of protected and unprotected plots is primarily a function of sample design. Sample design at fixed sites assured caged and protected plots would contain similar plant species and the close proximity of pairs decreased potential differences in productivity while maintaining a random placement. We minimized bias and maximized comparability in our selection of paired plots in the Crater Hills and West Alum areas by selecting pairs containing similar species composition and biomass and randomly assigning which plot from the pair was caged. Both sampling designs provided a high degree of comparability between pairs of protected and unprotected plots and allowed a pair-wise approach to analysis for both exclosure configurations.

Was utilization by ungulates detectable? The ability to detect a measurable amount of offtake attributable to ungulate grazing was investigated in a 2-step approach: 1) we tested all pairs to determine if unprotected plots had lower biomass values than plots protected from grazing; and 2) we compared pairs of plots with evidence of grazing in the unprotected plot to pairs without evidence of grazing to determine if estimated offtake was higher where grazing was visually obvious.

Paired t-tests comparing protected and unprotected plots (one-sided tests of the hypothesis that cage biomass was greater than unprotected plot biomass) at fixed sites indicted standing crop at the end of the growing season and residual vegetation in spring were higher in cages than paired unprotected 0.33-m^2 plots, but there was not a difference for new growth in spring (Table 5) which had slightly higher mean biomass outside exclosures. For paired plots in the Crater Hills and West Alum areas, one-sided paired t-tests indicated biomass was higher in caged plots for growing season clips (standing crop in fall) and spring clips (including both residual vegetation and new growth) (Table 5). The aggregate pattern suggested caged plots had more biomass than uncaged plots.

Table 5. Mean weights (SD) and differences (g) between protected and unprotected plots for the fixed sites and paired plot locations (Crater Hills and West Alum combined) for 1998 - 2000 combined in the Hayden Valley. Test results are for paired t-tests (one-sided, greater biomass inside cage).

Configuration		Protected	Unprotected			
Vegetation type	n	Mean (SD)	Mean (SD)	Diff. (g)[a]	Paired-t	P
Fixed sites						
Standing crop	175	52.3 (27.5)	46.2 (29.8)	6.1	3.94	<0.001
New growth	120	9.8 (6.3)	10.6 (8.8)	-0.8	-1.90	0.87
Residual	120	23.3 (18.2)	16.9 (15.0)	6.3	3.74	<0.001
Paired plots						
Standing crop	166	52.2 (30.3)	35.6 (28.0)	16.6	11.97	<0.001
New growth	103	32.8 (15.4)	25.8 (13.5)	7.0	5.26	<0.001
Residual	103	20.7 (16.6)	13.7 (14.4)	7.0	6.31	<0.001

[a] Mean difference between protected and unprotected plots (protected - unprotected)

Our failure to find a difference in new spring growth between caged and uncaged plots at fixed sites when we did find that caged plots had more spring growth than uncaged plots in the paired cage comparisons was most likely an artifact of differences in clipping dates between cage configurations during a period of rapid plant growth. Work was always completed at fixed sites as soon as the area was accessible in the spring (~mid-May). Sampling the fixed sites required 2 to 3 weeks so paired plots in the Crater Hills and West Alum could not be sampled until at least 2 to 3 weeks after the fixed sites. This delay provided a longer period of growth (and allowed a longer period for grazing) in paired cages compared to fixed sites.

To determine if offtake was higher where grazing was visually obvious, we compared **unadjusted percent offtake** (**UPO** = [biomass inside exclosure – biomass outside exclosure] / biomass inside exclosure) of pairs with visual evidence of grazing in the unprotected plot of the pair to pairs without evident grazing in the unprotected plot. The “obvious grazing” category was only recorded 3 times at the silver sage site and not at all for the mesic graminoid site, so the 2 grazing categories were combined into a “grazed” category so we could look at fixed sites individually.

UPO was greater for “grazed” pairs than for “ungrazed” pairs at all 3 fixed sites individually, for the 3 fixed sites combined, and for sites where we used the movable paired plot configuration (Table 6) indicating that herbivore offtake did occur at detectable levels in the Hayden Valley. We found no difference between biomass in the protected plots of pairs for “grazed” and “ungrazed” pairs at individual fixed sites, but for the combined fixed sites and for movable paired sites, the biomass in protected plots of grazed pairs tended to be lower than the biomass in protected plots of ungrazed pairs.

Using combined plots from fixed sites and paired plots, we then looked at mean UPO and mean biomass inside exclosures for our original 3 grazing classes (obvious, slight, and no grazing). For both the fixed site and paired plot configurations, significant differences occurred in mean UPO among grazing categories and the ranking of mean values increased as grazing intensity increased (Table 7). As in the 2-class tests, biomass in the protected plot of each pair was inversely related to apparent grazing intensity.

Did physical effects of cages influence offtake estimates? We did not identify any micro-climatic or chemical attributes of cages that would influence plant growth. Similar snow depths were measured inside and outside exclosures in the Hayden Valley on several occasions during mid and late winter, indicating exclosures did not increase deposition of snow. However, we did not visit exclosures during late spring to determine if a difference in snow melt rate existed.

Table 6. Biomass (g) of plots clipped inside exclosure cages and unadjusted percent offtake (UPO,negative values included) for pairs of plots with evidence of grazing and pairs without grazing for fixed sites and paired plot locations in the Hayden Valley during 1998, 1999, 2000 and results of Wilcoxon's rank-sum test comparing grazed to ungrazed pairs.

Site	Not grazed[a]		Grazed[b]				
Variable	n	Mean (SD)	n	Mean (SD)	Test[c]	Value	P
Mesic graminoid							
Biomass in cage	48	78.6 (22.9)	11	83.4 (26.1)	W	383	0.849
UPO	48	3.9 (25.1)	11	20.2 (19.3)	W	434	0.021
Silver sage							
Biomass in cage	40	47.8 (11.7)	20	52.3 (14.5)	W	688	0.890
UPO	40	-16.7 (53.3)	20	30.5 (25.6)	W	831	<0.001
Big sage							
Biomass in cage	23	24.5 (11.9)	33	28.7 (14.7)	W	1005	0.859
UPO	23	-4.8 (70.7)	33	33.7 (60.7)	W	1122	0.001
Fix sites combined							
Biomass in cage	111	56.3 (27.5)	64	45.5 (26.3)	Z	-2.76	0.003
UPO	111	-5.3 (48.6)	64	30.4 (46.4)	Z	5.65	<0.001
Paired plots combined							
Biomass in cage	57	59.4 (32.5)	109	48.4 (28.5)	Z	-2.18	0.015
UPO	57	11.1 (36.7)	109	43.3 (30.5)	Z	6.11	<0.001

[a] Not Grazed = Plot pairs without evidence of grazing in unprotected plots

[b] Not Grazed = Plot pairs with evidence of grazing in unprotected plots

[c] Wilcoxon's rank-sum tests. W indicates an exact test. The Z statistic was used when ties precluded exact tests.

Table 7. Biomass (g) of plots clipped inside exclosure cages and unadjusted percent offtake (UPO, negative values included) for pairs of plots using 3 levels of grazing for fixed sites and paired plot locations in the Hayden Valley during 1998, 1999, 2000.

Site	No grazing	Slight grazing	Obvious grazing		
Variable	n, Mean (SD)	n, Mean (SD)	n, Mean (SD)	K-W[a]	P
Fixed Sites					
Biomass in cage	111, 56.3 (27.5)	53, 47.5 (26.3)	11, 35.7 (25.3)	9.26	0.01
UPO	111, -5.3 (48.6)	53, 27.4 (34.5)	11, 44.7 (84.1)	37.49	<0.001
Paired Plots					
Biomass in cage	57, 59.4 (32.5)	66, 53.7 (31.4)	43, 40.4 (21.4)	9.22	0.01
UPO	57, 11.1 (36.7)	66, 33.5 (32.3)	43, 58.4 (19.9)	53.84	<0.001

[a] Kruskal-Wallis rank-sum test for >2 classes

Paired t-tests did not reveal differences in standing crop at the end of the growing season or after cages had been in place for a full year between vegetation inside and outside exclosures from a fenced area protected from grazing in the Bridger Mountains (Table 8). Mean biomass of standing crop inside exclosures was 0.8 g greater than outside exclosures for pairs during the growing season and 1.3 g less for plots inside exclosures when plots were re-sampled after an additional year. While not located within our study area, the location we used was at the same approximate elevation and was of the same vegetation type as the dominant cover type in the Hayden Valley. Results indicate exclosures do not have a measurable effect on production in high elevation Idaho fescue grasslands and, therefore, did not influence our estimates in the Hayden Valley. The small mean differences between biomass inside and outside exclosures and lack of a difference in biomass using NDVI as a surrogate when pairs were selected the first time in the Hayden Valley suggest our methodology for selecting matching plots provided pairs of similar biomass.

Does small mammal use of cages affect offtake estimates? We hypothesized that exclosures could influence small mammal activity and affect our estimates of offtake in 2 ways. Cages could serve as refugia for rodents, where higher use by small mammal inside exclosures would lead to underestimates of offtake by ungulates. Second, cages could either harbor rodents that fed outside or somehow restrict entry of rodents (unlikely given the mesh size of our cages) which would exacerbate rodent offtake outside cages and lead to overestimation of ungulate impacts.

Table 8. Mean weights (SD) and differences (g) of standing biomass clipped at the end of the growing season (post-growing) and at the end of a full year (1-year biomass) in ungrazed paired plots inside and outside exclosures. Plots were located in an area protected from grazing in the Bridger Mountains near Bozeman, MT, during 2000 and 2001.

		Inside	Outside			
Vegetation type	n	Mean (SD)	Mean (SD)	Diff.[a]	Paired-t	P
Post-growing	12	45.6 (14.7)	44.7 (14.3)	0.8	0.32	0.76
1-year biomass	11	20.1 (8.0)	21.4 (8.1)	-1.3	-1.17	0.27

[a] Mean difference between vegetation inside and outside cages (inside - outside)

We used 3 approaches to assess small mammal impacts on fixed site and paired plots: 1) comparison of the overall distribution of small mammal activity between protected and unprotected plots (chi-square) and also the overall distribution of activity within different vegetation types; 2) determination of the consistency of activity between protected and unprotected plots of each pair of plots; and 3) determination if pairs with high rodent activity (inside or outside) had different mean offtake than pairs without visible rodent activity or similar activity.

When we compared numbers of protected plots with moderate, slight, or no small mammal use to numbers of unprotected plots with moderate, slight, or no small mammal use by season for each cage configuration (Table 9), the only difference in overall distribution was between protected and unprotected plots at fixed sites during the growing season ($X^2 = 8.95$, $P = 0.011$). The difference was probably attributed to a higher numbers of "slight" use inside exclosures during this time period. Overall, the only instance when the amount of moderate activity occurred in greater than 10% of the plots was for unprotected plots of paired plots during the non-growing season (13.6%), but the overall distribution of activity was not significantly different between protected and unprotected plots.

Table 9. Total number of plots (unpaired) with none, slight, and moderate amounts of use by small mammals inside exclosures (protected) and outside exclosures (unprotected) for fixed sites and paired plot locations during the growing season and non-growing season during 1998, 1999, and 2000 in the Hayden Valley.

	Fixed sites				Paired plots			
	Growing		Non-growing		Growing		Non-growing	
Use	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
None	133	154	89	92	147	147	88	81
Slight	35	16	18	16	12	10	9	8
Moderate	7	5	13	12	7	9	6	14

Our fixed sites represented vegetation catenas and contained more than 1 cover type. We selected paired plots containing the same cover types as those within fixed sites and grouped them by vegetation types of fixed sites and by amount of small mammal activity (Table 10). Chi-square tests for differences in distribution of small mammal activity among these broad vegetation types were only significant ($X^2 = 12.92$, $P = 0.012$)

for fixed sites during the non-growing season. While highly insignificant, Chi-square tests for other distributions were unreliable due to cells with expected counts <5.

Table 10. Number of plot pairs with small mammal activity for fixed sites and paired plots (classified by fixed site vegetation classes) during the growing and non-growing seasons for 1998-2000 in the Hayden Valley .

	Fixed sites						Paired plots					
	Growing season			Non-growing			Growing season			Non-growing		
Use	Big	Silver	Mesic	Big	Silver	Mesic	Big	Silver	Mesic	Big	Silver	Mesic
None	42	35	42	23	21	31	33	18	27	17	8	22
Slight	10	21	13	4	12	5	8	3	1	5	1	1
Mod.	4	4	4	13	7	4	2	1	2	4	2	1

We then compared consistency of small mammal activity (same activity level for both plots within the pair) within pairs of plots. Consistency of activity was generally high, with 75% of all pairs having the same activity level in both plots. Of pairs with different activity levels, we hypothesized no net effect from small mammal activity would be represented by the same proportion of pairs with greater activity level inside exclosures as the proportion with greater activity level outside exclosures. We calculated hypothesized proportions by equally partitioning the proportion of pairs with different activity levels inside and outside exclosures between categories of more activity inside exclosures and more outside (Table 11), and used Chi-square tests of proportions to examine differences between observed and hypothesized equal proportions. We only found a significant deviation for 1 test, fixed sites during the growing season, with the difference due to higher than expected small mammal activity in protected plots of pairs.

Table 11. Number and percent of pairs of plots with the same small mammal activity within pairs, greater activity inside exclosures, lesser activity inside exclosures, and hypothesized proportions (Ho) when the number of pairs with greater activity inside equals the number with greater activity outside, at fixed sites and paired plot locations for both seasons during 1998-2000 in the Hayden Valley.

Site	Same in and out			Inside > outside			Inside < outside				
Season	n	(%)	Ho	n	(%)	Ho	n	(%)	Ho	$X^{2\ a}$	P
Fixed sites											
Growing	124	(70.8)	0.71	35	(20.0)	0.15	16	(9.1)	0.15	8.27	0.041
Non-growing	79	(65.8)	0.66	22	(18.3)	0.17	19	(15.8)	0.17	0.26	0.967
Paired plots											
Growing	140	(84.3)	0.84	13	(7.8)	0.08	13	(7.8)	0.08	0.001	0.999
Non-growing	79	(76.7)	0.77	8	(7.8)	0.12	16	(15.5)	0.12	3.01	0.390

[a] Chi-square test of proportions for observed use and hypothesized use within pairs of plots

The underlying dynamics of grazing and offtake of vegetation by ungulates and small mammals may depend on many factors. Ungulates may forage in an area after use by small mammals, but small mammals may not use an area after ungulates have foraged there, which may in turn be influenced by the amount of use. Vegetation type and associated interactions may further compound these dynamics. Differences in observed activity between protected and unprotected plots occurred as well as possible differences in distribution of small mammal use within vegetation types, but in addition to differences in observed use, a pertinent question is whether there is a measurable influence of small mammal activity on estimates of offtake.

Measurable influences of small mammal activity on offtake estimates should be evident by the following 2 conditions: 1) greater small mammal use of unprotected plots outside exclosures will result in higher UPO than pairs without small mammal utilization or similar activity; or 2) greater use of protected plots inside exclosures will result in lower UPO than pairs without small mammal utilization or similar activity. In Table 12, we present mean UPO for the 3 instances when pairs have: 1) a greater amount of small mammal activity in the unprotected plot; 2) when similar amount of activity is evident; and 3) when more activity occurs in the plot inside the exclosure. We found significant differences in rankings for UPO of residual growth at fixed sites and standing crop of paired plots, while standing crop of fixed sites was just above the 0.05 point level of significance. Mean values for these instances occurred in the expected order from highest to lowest under conditions of a measurable influence of small mammal use on UPO. Confounding this interpretation were negative values under conditions of greater small mammal use outside exclosures for residual vegetation of paired plots and new growth of fixed sites, indicating greater vegetative biomass in plots used by small mammals. While not significantly different in rankings, mean UPO of these 2 instances was less for pairs receiving more use in unprotected plots than plots without or with similar small mammal use. The exceptionally high standard deviation makes it risky to

Table 12. Mean percent unadjusted offtake (SD) of plot pairs with greater small mammal activity in plot outside exclosure, same amount of activity for both plots, and greater small mammal activity inside exclosure for fixed sites and paired plot locations during 1998-2000 in the Hayden Valley.

Site	Greater outside	Same	Greater inside		
Season	n, Mean (SD)	n, Mean (SD)	n, Mean (SD)	K-W [a]	P
Fixed sites					
New growth	19, -27.5 (143.1)	79, -11.8 (59.5)	22, -107.2 (268.7)	2.55	0.279
Residual	19, 26.1 (67.9)	79, 11.1 (78.5)	22, -57.7 (137.0)	11.05	0.004
Standing crop	16, 30.0 (29.1)	124, 8.2 (51.0)	35, -4.2 (54.7)	5.97	0.051
Paired plots					
New growth	16, 30.1 (32.9)	79, 11.9 (49.2)	8, 6.0 (49.3)	3.12	0.210
Residual	16, -2.0 (175.0)	79, 31.4 (58.5)	8, 27.0 (58.6)	0.38	0.829
Standing crop	13, 55.2 (21.6)	140, 31.1 (34.9)	13, 21.7 (51.1)	7.62	0.022

[a] Kruskal-Wallis rank-sum test for >2 classes.

place a numeric value on offtake attributable to small mammals. However, the magnitude of differences in UPO for the 3 categories of use would suggest offtake by small mammals inside exclosures has a greater influence on reducing offtake estimates than use of unprotected plots outside has on increasing estimates.

At fixed sites during the growing season, the overall distribution of small mammal activity inside exclosures was different than in unprotected plots outside (Table 9 and text), and consistency of use between protected and unprotected plots was different than expected (Table 11). Both results were due to greater use of protected plots inside exclosures by small mammals. Near-significant differences in mean UPO and a ranking consistent with measurable effects also occurred for fixed sites in the growing season. These data support our first hypothesis of the ability of exclosures to serve as refugia for small mammals with the potential of underestimating ungulate offtake, but this was 1 instance from multiple situations in our data supporting this conclusion. Assuming small mammal use in unprotected plots cancels use in protected plots, the net percent of plots potentially decreasing UPO from fixed plots during the growing season becomes relatively small (12%). Overall, offtake by small mammals using exclosures should probably be looked at on a case by case basis. While the magnitude of the influence in the case of our data may be small, offtake by small mammals could conceivably bias estimates in other situations.

We acknowledge small mammal use has the potential to decrease UPO of standing crop by ungulates at fixed sites, but making an absolute adjustment due to small mammal use is probably not possible given the high standard deviations we observed. However, truncating negative values at zero and using an “**Adjusted Percent Offtake”**

(**APO**) instead of UPO eliminates instances of greater biomass outside exclosures due to a greater amount of small mammal offtake inside exclosures and also corrects for paired plots in which actual vegetation production in the unprotected paired plot is greater than inside the exclosure. Both instances of higher biomass outside exclosures decreases offtake estimates for UPO, making APO a more conservative in addition to more accurate estimate.]

Offtake and Productivity Comparisons at Fixed Sites -- We calculated **"Adjusted Grams Offtake"** (**AGO** = biomass inside exclosure – biomass outside exclosure, with negative values truncated at zero) and used it for estimating vegetation offtake for the same reason reasons we decided to use APO instead of UPO. In addition to accounting for small mammal use and less productivity of vegetation within exclosures, truncating values at zero for APO and AGO further reduced the small amount of skewness in our data. The low skew made it unnecessary to use an arcsine transformation prior to conducting parametric tests.

For estimates of relative productivity of vegetation types, we used biomass within exclosures from each clipping period. The post-growing season clip provided data for comparisons of productivity among vegetation types for the growing season and new growth in the spring clip provided a means of comparing early spring growth among types.

For standing crop (fall clip) at fixed cage sites, APO of the big sage site was significantly greater (approximately twice the rate measured at the other 2 sites), while AGO remained about the same among sites (Table 13). Both APO and AGO were not significantly different among years. Significant interaction was not detected between site and year. Biomass of standing crop within exclosures differed among sites, averaging 27.0g/0.33m^2 for the big sage site, 49.30g/0.33m^2 for the silver sage site, and 79.50g/0.33m^2 for the mesic graminoid site. Overall production for the 3 sites varied among years, but sites did not vary in a similar pattern among years as indicated by the significant interaction between year and site. The greatest estimated biomass for the big sage site was in 1999, the same year with the lowest productivity for the silver sage and mesic graminoid sites (Appendix A, Table 43). Greatest estimates for the silver sage and mesic graminoid sites were in 2000 which was the second highest for the big sage site.

Table 13 provides summary statistics and results of ANOVA tests for 2 independent variables (site, year, and site x year interaction) tested on 3 vegetation parameters (APO, AGO, and standing biomass within exclosure) for data collected at the end of the growing season. Significant differences (based on 95% simultaneous confidence intervals derived using the Tukey method) among category means are indicated by different lower case letters. The same letter adjacent to multiple categories indicates membership in a group whose means are not significantly different (*i.e.* In the test of differences in APO among sites, the big sage site [followed by 'a'] is significantly different from the silver sage and mesic graminoid sites [followed by 'b'] , but the silver sage and mesic graminoid sites are not significantly different [both followed by 'b']). The table layout and nomenclature presented in Table 13 has been followed in all subsequent tables displaying ANOVA results for tests of effects of independent variables on APO, AGO, and biomass within exclosures for fixed sites and paired plots.

Table 13. ANOVA results for site, year, and site by year interaction, and 95% simultaneous confidence intervals between means of sites and years for APO, AGO, and biomass inside exclosures of standing crop at the end of the growing season from fixed exclosure sites during 1998, 1999, and 2000 in the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter							
Variable					ANOVA results		
Category	N	Mean	(SD)	95% C.I.[a]	df	F-value	P-value
APO - standing crop							
Site					2, 166	14.05	<0.000
Big sage	56	36.2	(30.2)	a			
Silver sage	60	19.2	(21.5)	b			
Mesic gram.	59	14.4	(14.6)	b			
Year					2, 166	0.72	0.49
1998	59	20.1	(24.6)	a			
1999	59	24.3	(22.5)	a			
2000	57	24.7	(26.6)	a			
Interaction					4, 166	0.10	0.98
AGO - standing crop							
Site					2, 166	0.14	0.87
Big sage	56	11.9	(12.7)	a			
Silver sage	60	10.8	(13.8)	a			
Mesic gram.	59	11.8	(13.7)	a			
Year					2, 166	1.65	0.20
1998	59	9.7	(12.2)	a			
1999	59	10.9	(10.6)	a			
2000	57	14.1	(16.6)	a			
Interaction					4, 166	0.83	0.51
Biomass of standing crop in cage							
Site					2, 166	151.18	<0.000
Big sage	56	27.0	(13.7)	a			
Silver sage	60	49.3	(12.8)	b			
Mesic gram.	59	79.5	(23.4)	c			
Year					2, 166	8.22	<0.000
1998	59	51.1	(26.7)	a b			
1999	59	47.1	(19.2)	b			
2000	57	59.1	(34.0)	a			
Interaction					4, 166	4.77	0.001

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

APO of new growth in the spring was similar for the big sage and silver sage site but significantly lower for the mesic graminoid site (Table 14). Measured in grams

(AGO), offtake of the big sage site was 2 or more times greater than other sites. Productivity of new growth was similar for the big sage and mesic graminoid site but lower for the silver sage site. Differences between 1999 and 2000 and interactions between sites and years were not detected for APO, AGO, or productivity of new growth at the fixed sites.

For over-winter residual vegetation, APO was not different among sites, but offtake of the mesic graminoid site was over twice the amount of the other sites when measured in grams (Table 15). Amount of residual vegetation in cages was significantly different at each site, with 7.7g / 0.33 m^2 at the big sage site, 25.7g / 0.33 m^2 at the silver sage site, and 36.4g / 0.33 m^2 at the mesic graminoid site. Amounts of residual vegetation, APO, and AGO were not significantly different among years. Lack of significant site by year interaction terms indicated consistency of estimates among years.

Regressions from the closest time periods (Table 4) were applied to radiometer readings taken within exclosures and unprotected plots selected for clipping outside exclosures in fall (*i.e.* the regression from the 16-23 August 1998 period was applied to fixed site radiometer readings taken on 10-12 August 1998; the 23 July 1999 regression was applied to readings from 1-2 August 1999; and the regression from the 29 July 2000 to 2 August 2000 period was applied to readings taken between 25-27 July 2000 at fixed sites).

Table 14. ANOVA results for site, year, and site by year interaction, and 95% simultaneous confidence intervals between means of sites and years for APO, AGO, and biomass inside exclosures of spring new growth from fixed exclosure sites during 1999 and 2000 in the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter							
Variable					ANOVA results		
Category	N	Mean	(SD)	95% C.I.[a]	df	F-value	P-value
APO - spring new growth							
Site					2, 114	9.11	<0.000
Big sage	40	29.3	(24.6)	a			
Silver sage	40	20.2	(24.0)	a			
Mesic gram.	40	8.5	(16.0)	b			
Year					1, 114	2.33	0.13
1999	60	22.4	(23.6)	a			
2000	60	16.3	(22.9)	a			
Interaction					2, 114	0.26	0.77
AGO - spring new growth							
Site					2, 114	10.62	<0.000
Big sage	40	4.0	(4.4)	a			
Silver sage	40	1.4	(2.0)	b			
Mesic gram.	40	1.1	(2.1)	b			
Year					1, 114	0.01	0.92
1999	60	2.2	(2.9)	a			
2000	60	2.1	(3.6)	a			
Interaction					2, 114	0.80	0.45
Biomass of new growth in cage							
Site					2, 114	17.66	<0.000
Big sage	40	11.0	(5.0)	a			
Silver sage	40	5.7	(2.5)	b			
Mesic gram.	40	12.8	(7.8)	a			
Year					1, 114	1.22	0.27
1999	60	9.3	(7.4)	a			
2000	60	10.4	(4.9)	a			
Interaction					2, 114	0.70	0.500

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

The mean biomass of plots inside exclosures estimated from radiometer readings during mid-summer was within 4.5 g of mean clipped weights in fall for each estimate except the big sage site during 2000 (Table 16). However, estimates using the radiometer were for current year's growth while fall clipping estimates of standing crop included previous year's standing litter. A direct comparison of estimates would require a small reduction in estimates of standing crop, but results suggest accurate estimates using the radiometer. The influence of previous year's standing litter would be the same between protected and unprotected plots when radiometer readings were taken each year, so we treated estimates from radiometer readings similar to clipped data in comparisons of productivity, APO, and AGO.

Table 15. ANOVA results for site, year, and site by year interaction, and 95% simultaneous confidence intervals between means of sites and years for APO, AGO, and biomass inside exclosures of over-winter residual vegetation from fixed exclosure sites during 1999 and 2000 in the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter Variable Category	N	Mean	(SD)	95% C.I.[a]	ANOVA results df	F-value	P-value
APO - residual vegetation							
Site					2, 114	0.62	0.54
Big sage	40	32.4	(37.4)	a			
Silver sage	40	28.1	(29.9)	a			
Mesic gram.	40	36.5	(32.1)	a			
Year					1, 114	0.51	0.48
1999	60	30.1	(31.0)	a			
2000	60	34.5	(35.4)	a			
Interaction					2, 114	0.01	0.99
AGO - residual vegetation							
Site					2, 114	9.87	<0.000
Big sage	40	3.6	(7.1)	a			
Silver sage	40	7.9	(9.3)	a			
Mesic gram.	40	16.4	(19.2)	b			
Year					1, 114	0.13	0.72
1999	60	8.9	(11.8)	a			
2000	60	9.7	(15.9)	a			
Interaction					2, 114	0.15	0.86
Biomass of residual vegetation in cage							
Site					2, 114	44.22	<0.000
Big sage	40	7.7	(8.2)	a			
Silver sage	40	25.7	(10.7)	b			
Mesic gram.	40	36.4	(19.8)	c			
Year					1, 114	2.75	0.10
1999	60	25.3	(17.4)	a			
2000	60	21.2	(18.8)	a			
Interaction					2, 114	0.58	0.56

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Table 16. Mean estimated biomass ($g/0.33m^2$) inside exclosures from portable multispectral radiometer (MSR) on ~August 1 and standing crop clipped in fall (Clip) at fixed sites in the Hayden Valley during 1998, 1999, 2000 .

	1998		1999		2000	
Site	MSR	Clip	MSR	Clip	MSR	Clip
Big sage	23.4	22.9 (14.6)	27.5	31.7 (13.2)	38.2	26.1 (12.0)
Silver sage	53.6	51.7 (13.2)	40.9	42.5 (9.0)	52.8	53.6 (13.2)
Mesic gram.	77.8	77.3 (16.5)	63.7	68.2 (12.7)	91.9	92.5 (30.5)

ANOVA tests for biomass inside cages using mid-summer estimates from the portable radiometer were similar to results from clipped standing crop in fall. The greatest biomass was at the mesic graminoid site followed by the silver sage site and lastly the big sage site (Table 17) with significant differences between all sites. Ranking of years was the same and estimated amounts were similar, but a significant difference was detected among all years for mid-summer estimates and only a difference between 1999 and 2000 for standing crop in fall.

APO and AGO of mid-summer estimates were significantly greater for the big sage site and for 2000, with no significant difference in APO or AGO between the silver sage and mesic graminoid sites or between 1998 and 1999 (Table 17). An estimated APO over twice as great at the big sage site in 2000 than 1998 or 1999 (Appendix A, Table 43) accounted for the difference among years and the significant interaction term between sites and years for APO and AGO of mid-summer estimates.

Results of clipped plots and estimates from the portable radiometer produced 4 seasonal estimates of APO we presented in the previous results of ANOVA tests: 1) mid-summer estimates using the portable radiometer; 2) fall estimates from clipped biomass standing crop; 3) winter estimates from clipped biomass of residual vegetation; and 4) early spring estimates from clipped amounts of new growth (Fig. 2). Overall trends in APO throughout the study between mid-summer 1998 and fall 2000 indicated higher

Table 17. ANOVA results for site, year, and site by year interaction, and 95% simultaneous confidence intervals between means of sites and years for APO, AGO, and biomass inside exclosures of estimates from portable radiometer on ~August 1 from fixed exclosure sites during 1998, 1999, and 2000 in the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter Variable Category	N	Mean	(SD)	95% C.I.[a]	ANOVA results df	 F-value	 P-value
APO - mid-summer							
Site					2, 171	107.14	<0.000
Big sage	60	41.3	(32.0)	a			
Silver sage	60	7.7	(9.6)	b			
Mesic gram.	60	5.5	(6.9)	b			
Year					2, 171	36.07	<0.000
1998	60	11.7	(19.5)	a			
1999	60	11.2	(15.7)	a			
2000	60	31.6	(32.9)	b			
Interaction					4, 171	15.21	<0.000
AGO - mid-summer							
Site					2, 171	45.68	<0.000
Big sage	60	14.5	(13.4)	a			
Silver sage	60	4.2	(5.2)	b			
Mesic gram.	60	4.6	(5.7)	b			
Year					2, 171	47.70	<0.000
1998	60	4.4	(6.6)	a			
1999	60	4.1	(5.8)	a			
2000	60	14.7	(12.6)	b			
Interaction					4, 171	10.91	<0.000
Mid-summer biomass in cage							
Site					2, 171	424.00	<0.000
Big sage	60	29.7	(12.9)	a			
Silver sage	60	49.1	(9.2)	b			
Mesic gram.	60	77.8	(14.0)	c			
Year					2, 171	51.92	<0.000
1998	60	51.6	(24.5)	a			
1999	60	44.0	(17.0)	b			
2000	60	60.9	(24.6)	c			
Interaction					4, 171	11.10	<0.000

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

offtake at the big sage site for all seasons except winter when APO was highest at the mesic graminoid site. However, APO of the mesic graminoid site was the lowest in all other periods except mid-summer 1998 when it was almost the same (4.3%) as the silver sage site (3.6%). APO of the silver sage site was generally intermediate to the big sage and mesic graminoid site except during winter when it was slightly lower than the others.

Offtake and productivity comparisons from paired plots -- Placement of 30 paired plots in the West Alum area during the second and third years of the study in addition to 50 in the Crater Hills created unequal sample sizes among years, areas, and cover types. Destruction of exclosures by bison further contributed to unequal sample sizes and unbalanced designs. Although visual observations indicated consistent grazing among areas and years (the proportion of unprotected plots with observed grazing was not significantly different [$X^2 = 2.41$, $P = 0.12$] between the Crater Hills and West Alum areas, and a difference was not detected among the 3 years of the study [$X^2 = 0.97$, $P = 0.62$]), the unbalanced samples had the potential to produce both type I and type II errors in tests of productivity and offtake. To minimize this potential, we sub-sampled plot pairs to provide balanced designs to test for site and year differences on productivity and offtake prior to looking at influences of vegetation types.

To test for a site influence on offtake and biomass estimates, we accounted for possible year influences and matched equal numbers of plot pairs from the same years and cover types from West Alum with plots from Crater Hills. Pairs were randomly selected when the number of pairs from one area exceeded the number at the other area. Statistical analysis was limited to pairs from 2 out of 3 fall clippings (1999, 2000) and 1 spring clipping (2000), the sampling periods when we had exclosures in both the Crater Hills and West Alum areas, and to the cover types for which we had suitable samples.

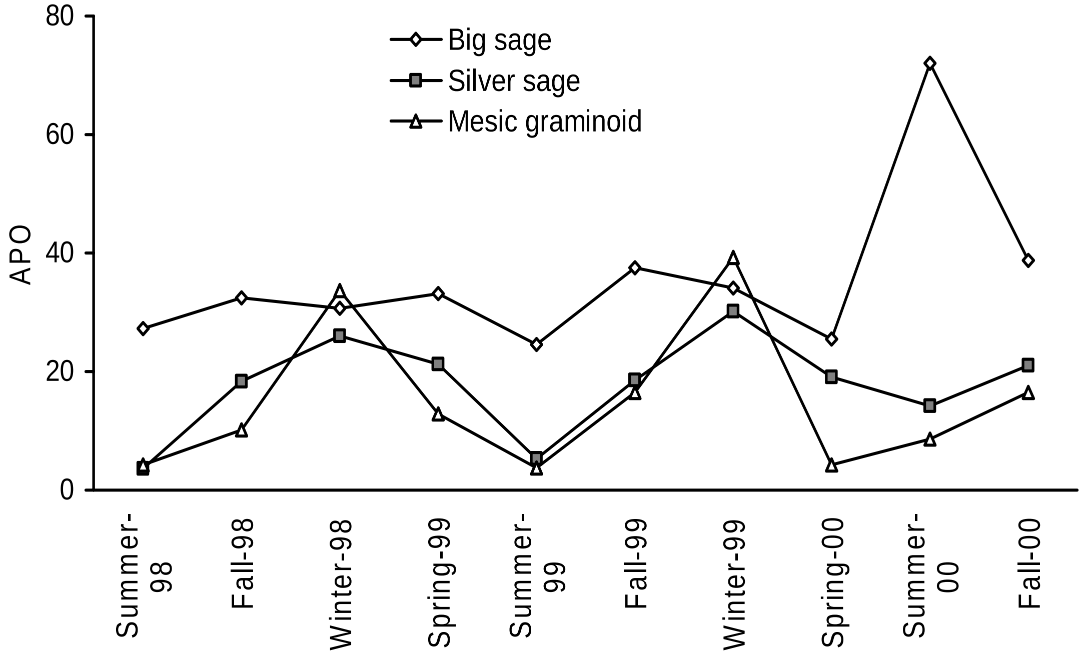


Fig.2. Seasonally adjusted percent offtake (APO) at fixed sites from Summer 1998 to Fall 2000 in the Hayden Valley.

Mean biomasses of fall standing crop and spring new growth were slightly greater in the West Alum area than in the Crater Hills area, but estimates of percentage offtake were similar in both areas. When we tested for differences between areas, all tests of APO, AGO, and biomass inside exclosures for standing crop, spring new growth, and spring residual biomass indicated no significant differences occurred (Appendix A, Table 44). Therefore, we combined pairs from the Crater Hills and West Alum areas for further tests.

Equal numbers of pairs from the same cover types were matched across years to determine if mean values differed among years. Destruction of exclosures by bison precluded tests of all cover types in all years, but surviving cages covered the range of productivity and species composition in available cover types and allowed us to test for differences among years. We had sufficient sample units to support tests among years for the *Arca/Dece*, *Artr/Feid*, *Artr/Feid – Dain* phase, *Dece/Carex*, and *Posa* cover types for vegetation clipped in fall. The same cover types, with the addition of the *Dece* type, were used to compare differences among years for spring vegetation. Results of 2-factor ANOVA for APO, AGO and biomass inside exclosures using models that included year, cover type, and interaction between year and cover type indicated differences among cover types but did not indicate differences among years in any tests. (Appendix A, Tables 45 and 46). Values of APO, AGO, and biomass inside cages by year are presented in Appendix A, Tables 47 and 48.

For fall standing crop (Appendix A, Table 45), differences among cover types were detected for APO and biomass inside exclosures but not for AGO. There was not a significant year by cover type interaction for APO, AGO, or biomass in cage for standing crop. Significant differences among cover types were also noted for APO and AGO for spring live vegetation but not for spring live biomass within exclosures. As with standing crop, significant year by cover type interaction were not detected for any parameter of spring new growth. For residual vegetation, differences among cover types occurred in biomass inside cages but not for AGO, and year by cover type interactions were not evident in both instances. APO of residual vegetation also differed among cover types. We detected a significant year by cover type interaction for APO indicating that although differences did not exist between years, differences among cover types may have been inconsistent between years.

Due to the lack of significant differences among years and sites for paired plots, the low range of variability in annual means (46.4 to 49.9 g/ 0.33m^2 over 3 years), and indications of significant differences among cover types in tests using a reduced but balanced number of cover types, we combined paired plots from all years and both sites for analysis of differences among vegetation types. Results of ANOVA tests indicated significant differences among cover types for vegetation parameters, but 95% simultaneous confidence intervals contained a large amount of overlap among types and seldom indicated a particular cover type was unique from all others. However, comparisons among groups of cover types with different means (indicated by different letters in tables) indicated relative trends among cover types.

APO of standing crop in fall averaged 32.6% over all cover types but differed significantly among cover types (Table 18). Greater percentages of offtake were generally seen in the upland types with the greatest amount in ridge top vegetation (54.7%). Lowest percentages of offtake (<20%) were in the moistest types (wet sedge and *Dece/Carex*). AGO was not different among cover types, averaging 17.6 g (per 0.33 m^2) across all types with a range of 11.8 g for the Feid/Agca type to 30.3 g for the *Artr/Agca* type. As expected, biomass of standing crop in cages was significantly different among cover types, with the greatest amounts in wetter types and the least amounts on hillsides and ridgetops.

Mean APO's of spring new growth (Table 19) and overwinter residual vegetation (Table 20) were highly variable among types. Our tests detected some significant differences among types, but large standard deviations and small sample sizes for several cover types may have obscured other differences. In general, cover type ranking from highest to lowest for APO for spring new growth was similar to APO for overwinter residual vegetation. The 4 cover types with greatest APO for overwinter residual vegetation (45-78% APO) and new spring growth (37-43% APO) were *Posa*, *Feid/Dece*, *Artr/Feid*, and *Feid/Agca*. The cover types with the least APO were *Carex* (16%) for overwinter residual vegetation and *Dece* (5%) for new spring growth.

When measured in grams offtake, ranking of means appeared quite different between AGO of residual vegetation and AGO of spring new growth. Amounts of AGO for spring new growth ranged from 1.7 g (per 0.33 m^2) in the *Dece* type to 15.6 g in the *Artr/Feid* type, and 4.1 g in the *Feid/Agca* type to 13.8 g in the *Feid/Dece* type for residual vegetation. Obvious breaks in the progression from lowest to highest were not seen for either measurement. Although ANOVA tests indicated significant differences among cover types for AGO of spring new growth, 95% simultaneous confidence intervals did not identify any differences between pairs of cover types. ANOVA tests for AGO for residual vegetation indicated there were no significant differences among cover types.

Biomass of spring new growth in exclosures (Table 19) ranged from19.7 g (per 0.33 m^2) in the Feid/Agca type to 52.4 g in the wet *Carex* type. Mean biomass of residual vegetation varied from ~ 9 g/0.33 m^2 (*Posa* and *Feid/Agca* types) to 38 g/0.33 m^2 (*Arca/Dece* type).

Table 18. ANOVA results and 95% simultaneous confidence intervals between means of cover types for APO, AGO, and biomass inside exclosures of standing crop at the end of the growing season for all paired plots during 1998, 1999, and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter				ANOVA results		
Cover type	N	Mean (SD)	95% C.I.[a]	df	F-value	P-value
APO - standing crop				12, 152	4.06	<0.000
Posa	26	54.7 (20.5)	a			
Artr/Agca	8	52.4 (16.7)	a b			
Arca/Feid	6	47.7 (10.8)	a b c			
Artr/Feid	32	44.3 (29.1)	a b c d			
Feid/Agca	14	33.9 (30.1)	a b c d			
Feid/Dece	7	33.3 (22.3)	a b c d			
Caca	5	29.3 (19.6)	a b c d			
Pofr/Dece	4	27.1 (30.8)	a b c d			
Artr/Feid-Dain	11	27.0 (24.6)	a b c d			
Arca/Dece	22	26.8 (22.0)	b c d			
Dece	8	25.3 (18.8)	a b c d			
Carex	7	18.1 (17.9)	b c d			
Dece/Carex	15	16.8 (15.3)	c			
AGO - standing crop				12, 152	1.07	
Artr/Agca	8	30.3 (16.9)	a			
Caca	5	27.8 (20.9)	a			
Carex	7	22.4 (24.1)	a			
Arca/Feid	6	19.0 (9.6)	a			
Arca/Dece	22	18.7 (17.6)	a			
Artr/Feid	32	17.1 (16.2)	a			
Pofr/Dece	4	17.1 (18.9)	a			
Dece/Carex	15	16.9 (16.9)	a			
Posa	26	16.4 (8.3)	a			
Dece	8	16.3 (12.8)	a			
Feid/Dece	7	13.9 (8.7)	a			
ArTr/Feid-Dain	11	12.9 (13.7)	a			
Feid/Agca	14	11.8 (11.6)	a			
Biomass of standing crop in cage				12, 152	22.30	<0.000
Carex	7	110.5 (22.4)	a			
Dece/Carex	15	94.4 (28.6)	a b			
Caca	5	85.9 (25.3)	a b c			
Arca/Dece	22	66.7 (19.3)	c d			
Pofr/Dece	4	64.6 (10.5)	b c d e			
Dece	8	62.8 (15.7)	c d e f			
Artr/Agca	8	55.0 (20.8)	c d e f g			
Feid/Dece	7	43.8 (21.8)	d e f g			
Artr/Feid-Dain	11	43.2 (13.3)	d e f g			
Arca/Feid	6	41.5 (25.6)	d e f g			
Artr/Feid	32	33.8 (18.5)	e g			
Posa	26	29.8 (12.4)	g			
Feid/Agca	14	28.9 (13.0)	e g			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Table 19. ANOVA results and 95% simultaneous confidence intervals between means of cover types for APO, AGO, and biomass inside exclosures of spring new growth for all paired plots during 1999 and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter				ANOVA results		
Cover type	N	Mean (SD)	95% C.I.[a]	df	F-value	P-value
APO - spring new growth				12, 89	3.25	<0.000
Feid/Dece	2	42.9 (31.1)	a b			
Artr/Feid	18	39.8 (19.1)	a			
Feid/Agca	10	37.1 (26.5)	a b			
Posa	16	37.0 (17.3)	a			
Caca	2	24.4 (34.5)	a b			
Artr/Agca	5	22.3 (32.2)	a b			
Carex	4	17.4 (20.9)	a b			
Arca/Feid	3	17.4 (29.8)	a b			
Dece/Carex	13	17.0 (15.7)	a b			
Arca/Dece	11	14.8 (12.1)	a b			
Artr/Feid-Dain	8	13.6 (13.0)	a b			
Pofr/Dece	3	12.4 (21.4)	a b			
Dece	7	5.2 (13.9)	b			
AGO - spring new growth				12, 89	1.92	0.04
Artr/Feid	18	15.6 (10.0)	a			
Carex	4	13.5 (20.5)	a			
Artr/Agca	5	13.2 (23.6)	a			
Posa	16	12.5 (8.6)	a			
Caca	2	11.2 (15.8)	a			
Feid/Dece	2	10.6 (8.6)	a			
Feid/Agca	10	8.8 (9.5)	a			
Dece/Carex	13	6.4 (5.3)	a			
Pofr/Dece	3	5.9 (10.2)	a			
Arca/Feid	3	5.6 (9.5)	a			
Arca/Dece	11	4.4 (3.9)	a			
Artr/Feid-Dain	8	3.1 (3.5)	a			
Dece	7	1.7 (4.5)	a			
Biomass of spring new growth in cage				12, 89	2.81	0.003
Carex	4	52.4 (31.3)	a			
Artr/Agca	5	45.7 (20.1)	a b			
Arca/Feid	3	40.2 (14.3)	a b c			
Dece/Carex	13	38.9 (17.3)	a b c			
Artr/Feid	18	36.0 (12.0)	a b c			
Pofr/Dece	3	33.3 (14.2)	a b c			
Posa	16	32.6 (10.2)	a b c			
Caca	2	29.4 (23.2)	a b c			
Arca/Dece	11	29.0 (8.4)	a b c			
Dece	7	28.0 (9.8)	a b c			
Feid/Dece	2	23.6 (2.9)	a b c			
Artr/Feid-Dain	8	21.1 (10.5)	b c			
Feid/Agca	10	19.7 (13.5)	c			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Table 20. ANOVA results and 95% simultaneous confidence intervals between means of cover types for APO, AGO, and biomass inside exclosures of residual vegetation (biomass persisting over winter from the previous growing season) for all paired plots during 1999 and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. AGO and biomass are

Parameter				ANOVA results		
Cover type	N	Mean (SD)	95% C.I.[a]	df	F-value	P-value
APO - residual vegetation				12, 89	3.17	<0.000
Posa	16	78.4 (17.5)	a			
Feid/Dece	2	57.0 (12.9)	a b			
Artr/Feid	18	54.6 (35.0)	a b			
Feid/Agca	10	44.7 (36.0)	a b			
Artr/Agca	5	43.4 (35.1)	a b			
Arca/Feid	3	39.6 (37.7)	a b			
Dece/Carex	13	33.7 (32.2)	b			
Arca/Dece	11	30.3 (27.4)	b			
Caca	2	29.5 (36.5)	a b			
Dece	7	27.4 (33.7)	b			
Artr/Feid-Dain	8	25.8 (27.4)	b			
Pofr/Dece	3	21.0 (36.4)	a b			
Carex	4	13.7 (15.8)	b			
AGO - residual vegetation				12, 89	0.70	0.75
Feid/Dece	2	13.8 (13.7)	a			
Artr/Agca	5	12.5 (14.1)	a			
Artr/Feid	18	11.1 (10.7)	a			
Dece/Carex	13	11.1 (12.2)	a			
Arca/Dece	11	9.5 (10.3)	a			
Caca	2	9.1 (11.4)	a			
Artr/Feid-Dain	8	8.4 (11.7)	a			
Arca/Feid	3	8.1 (7.1)	a			
Posa	16	7.4 (4.3)	a			
Pofr/Dece	3	7.0 (12.1)	a			
Dece	7	4.7 (5.6)	a			
Carex	4	4.4 (6.0)	a			
Feid/Agca	10	4.1 (3.8)	a			
Biomass of residual vegetation in cage				12, 89	3.18	<0.000
Arca/Dece	11	38.0 (30.3)	a			
Caca	2	29.4 (2.2)	a b			
Dece/Carex	13	27.4 (16.3)	a b			
Artr/Feid-Dain	8	26.7 (12.3)	a b			
Artr/Agca	5	24.8 (8.7)	a b			
Arca/Feid	3	23.1 (7.9)	a b			
Pofr/Dece	3	22.9 (11.3)	a b			
Dece	7	22.4 (14.8)	a b			
Feid/Dece	2	22.1 (19.0)	a b			
Carex	4	19.5 (17.8)	a b			
Artr/Feid	18	17.2 (11.1)	b			
Posa	16	9.0 (4.5)	b			
Feid/Agca	10	8.5 (6.1)	b			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Combining cover types into cover groups and understory groups produced similar but more distinct trends than results by individual cover types. Overall, APO of drier vegetation was usually greater than wetter vegetation and significant differences were not detected for AGO. Productivity of wetter types was higher, as expected.

For APO of standing crop in fall by cover groups, the dry grass group was not significantly different than the dry shrub group, but was different than all other groups (Table 21). The dry shrub group was similar to the intermediate grass group and the dry grass group, but differed from the moist shrub and moist / wet understory groups. No difference was detected between the intermediate grass group and groups other than the dry grass group. Combining cover types by understory groups instead of cover groups produced less overlap among categories. *Posa* (Sandberg bluegrass) and *Feid* (Idaho fescue) were each significantly different from all others, while *Dece* (tufted hairgrass) and wet *Carex* were not different from each other (Table 22).

Significant differences for AGO in the fall were not detected among cover groups or understory groups (Tables 21 and 22). Grouping cover types by dominant graminoid understory produced mean values over a narrower range (16.4g – 19.2g) than grouping by cover groups (12.5g – 19.4g). The opposite was true for APO, with understory groups encompassing a slightly wider range (17.2% - 54.7%) than cover groups (20.8% - 54.7%).

Similar results were noted for biomass of standing crop in exclosures. The 2 wettest categories, groups containing cover types dominated by wet sedge species and *Dece* (tufted hairgrass) were significantly different from each other and from groups with understories dominated by *Feid* (Idaho fescue) and *Posa* (Sandberg bluegrass). The

Idaho fescue and Sandberg bluegrass groups did not have significantly different standing crops at the end of the growing season (Table 22).

APO of spring new growth ranged from 14.3 (per 0.33 m^2) for the moist shrub group to 38.0 for the intermediate grass group (Table 23). The dry shrub group (29.1% APO), was not different from any of the other groups. The intermediate grass and dry understory groups were similar to each other but different from the moist / wet grass and moist shrub groups which were also not significantly different from each other.

Table 21. ANOVA results and 95% simultaneous confidence intervals between means of cover groups for APO, AGO, and biomass inside exclosures of standing crop at the end of the growing season for all paired plots during 1998, 1999, and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter				ANOVA results		
Cover group	N	Mean (SD)	95% C.I.[a]	df	F-value	P-value
APO - standing crop				4, 160	10.07	<0.000
Dry grass	26	54.7 (20.5)	a			
Dry shrub	57	42.5 (26.2)	a b			
Intermediate grass	21	33.7 (27.2)	b c			
Moist shrub	26	26.8 (22.8)	c			
Moist / wet grass	35	20.8 (17.2)	c			
AGO - standing crop				4, 160	0.82	0.51
Moist / wet grass	35	19.4 (18.0)	a			
Moist shrub	26	18.5 (17.4)	a			
Dry shrub	57	18.3 (15.8)	a			
Dry grass	26	16.4 (8.3)	a			
Intermediate grass	21	12.5 (10.5)	a			
Biomass of standing crop in cage				4, 160	48.60	<0.000
Moist / wet grass	35	89.2 (28.7)	a			
Moist shrub	26	66.4 (18.1)	b			
Dry shrub	57	39.4 (19.7)	c			
Intermediate grass	21	33.9 (17.5)	c			
Dry grass	26	29.8 (12.4)	c			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Table 22. ANOVA results and 95% simultaneous confidence intervals between means of understory groups for APO, AGO, and biomass inside exclosures of standing crop at the end of the growing season for all paired plots during 1998, 1999, and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter				ANOVA results		
Grass type	N	Mean (SD)	95% C.I.[a]	df	F-value	P-value
APO - standing crop				3, 161	13.19	<0.000
Posa	26	54.7 (20.5)	a			
Feid	78	40.1 (26.6)	b			
Dece	39	26.8 (21.2)	c			
Wet carex	22	17.2 (15.8)	c			
AGO - standing crop				3, 161	0.32	0.81
Dece	39	19.2 (16.9)	a			
Wet carex	22	18.7 (19.1)	a			
Feid	78	16.8 (14.8)	a			
Posa	26	16.4 (8.3)	a			
Biomass of standing crop in cage				3, 161	75.98	<0.000
Wet carex	22	99.5 (27.4)	a			
Dece	39	68.2 (19.4)	b			
Feid	78	37.9 (19.2)	c			
Posa	26	29.8 (12.4)	c			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

When we combined cover types by graminoid understory (Table 24), APO of spring new growth for *Dece* (tufted hairgrass) was lowest (12.4%), followed by wet *Carex* (17.1%), *Feid* (Idaho fescue) (31.4%), and *Posa* (Sandberg bluegrass) was highest (37.0%). The APO for *Dece* was significantly lower than that for *Posa*.

The mean AGO for spring new growth by cover groups varied from 4.8 g (per 0.33 m^2) for the moist shrub group to 12.5 g for the dry grass group. No significant differences among cover groups were detected (Table 23). Mean AGO for spring growth for groups based on graminoid understory ranged from 4.4 g for *Dece* to 12.5 g for *Posa*. We did not find any significant differences in pair-wise comparisons of AGO in new growth in spring for understory groups.

Table 23. ANOVA results and 95% simultaneous confidence intervals between means of cover groups for APO, AGO, and biomass inside exclosures of spring new growth and over-winter residual vegetation for all paired plots during 1999 and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter				ANOVA results		
Cover group	N	Mean (SD)	95% C.I.[a]	df	F-value	P-value
APO - spring new growth				4, 97	5.71	<0.000
Intermediate grass	12	38.0 (25.9)	a			
Dry grass	16	37.0 (17.3)	a			
Dry shrub	34	29.1 (23.3)	a b			
Moist / wet grass	26	14.5 (17.4)	b			
Moist shrub	14	14.3 (13.6)	b			
AGO - spring new growth				4, 97	1.96	0.11
Dry grass	16	12.5 (8.6)	a			
Dry shrub	34	11.4 (12.5)	a			
Intermediate grass	12	9.1 (9.0)	a			
Moist / wet grass	26	6.6 (9.7)	a			
Moist shrub	14	4.8 (5.3)	a			
Biomass of spring new growth in cage				4, 97	2.97	0.02
Moist / wet grass	26	37.3 (19.3)	a			
Dry shrub	34	34.3 (15.0)	a			
Dry grass	16	32.6 (10.2)	a b			
Moist shrub	14	29.9 (9.4)	a b			
Intermediate grass	12	20.3 (12.3)	b			
APO - residual vegetation				4, 97	7.87	<0.000
Dry grass	16	78.4 (17.5)	a			
Intermediate grass	12	46.7 (33.1)	a b			
Dry shrub	34	44.8 (34.2)	b			
Moist / wet grass	26	28.6 (30.0)	b			
Moist shrub	14	28.3 (28.2)	b			
AGO - residual vegetation				4, 97	0.69	0.6
Dry shrub	34	10.4 (10.9)	a			
Moist shrub	14	9.0 (10.2)	a			
Moist / wet grass	26	8.2 (9.9)	a			
Dry grass	16	7.4 (4.3)	a			
Intermediate grass	12	5.7 (6.6)	a			
Biomass of residual vegetation in cage				4, 97	7.57	<0.000
Moist shrub	14	34.7 (27.7)	a			
Moist / wet grass	26	25.0 (15.1)	a b			
Dry shrub	34	21.1 (11.2)	b c			
Intermediate grass	12	10.8 (9.5)	b c			
Dry grass	16	9.0 (4.5)	c			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Biomass of spring new growth in exclosures was significantly different for cover groups and understory groups, and similar trends were noted for each method of grouping cover types. However, relative rankings of cover types or understory groups were not dependent solely on moisture availability as might be expected. For understory groups, mean biomass of the wettest type (wet *Carex*) was greatest, but biomass of the second wettest (*Dece*) was least, with a significant difference among them indicating possible differences in early spring growth rates. *Posa*, the driest type, ranked second and was not different than wet *Carex* or *Feid* which ranked third. A similar trend was noted for cover groups, where the moist / wet grass group, which contained cover types dominated by both wet *Carex* and tufted hairgrass, had the greatest mean biomass of new spring growth and the moist shrub type (with an understory of tufted hairgrass) was second lowest. The difference between the 2 was not significant, possibly due to the presence of tufted hairgrass in the understory of both cover groups.

Similar trends were also noted in offtake of spring residual vegetation when we combined cover types into cover groups and understory groups (Tables 23 and 24). APO of residual biomass for the *Posa* understory group (78.4%) was greater than that for other understory groups. We did not detect differences among the 3 other understory groups, which had APO's ranging from 28.1% to 45.3%. For cover groups, APO of the dry grass cover group (78.4%) was greater than that for all other types except the intermediate grass group (46.7%), which was not different than any other cover groups (ranging from 28.3% to 44.8%).

Table 24. ANOVA results and 95% simultaneous confidence intervals between means of understory groups for APO, AGO, and biomass inside exclosures of spring new growth and over-winter residual vegetation for all paired plots during 1999 and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. AGO and biomass are grams / 0.33m2.

Parameter				ANOVA results		
Grass type	N	Mean (SD)	95% C.I.[a]	df	F-value	P-value
APO - spring new growth				3, 98	7.18	<0.000
PoSa	16	37.0 (17.3)	a			
FeId	46	31.4 (24.0)	a b			
Wet carex	17	17.1 (16.3)	b c			
DeCe	23	12.4 (15.7)	c			
AGO - spring new growth				3, 98	2.82	0.04
PoSa	16	12.5 (8.6)	a			
FeId	46	10.8 (11.7)	a			
Wet carex	17	8.0 (10.5)	a			
DeCe	23	4.4 (6.3)	a			
Biomass of spring new growth in cage				3, 98	2.92	0.04
Wet carex	17	42.0 (21.0)	a			
PoSa	16	32.6 (10.2)	a b			
FeId	46	30.6 (15.5)	b			
DeCe	23	29.3 (10.2)	b			
APO - residual vegetation				3, 98	10.58	<0.000
PoSa	16	78.4 (17.5)	a			
FeId	46	45.3 (33.6)	b			
Wet carex	17	29.0 (30.0)	b			
DeCe	23	28.1 (29.0)	b			
AGO - residual vegetation				3, 98	0.28	0.84
Wet carex	17	9.6 (11.2)	a			
FeId	46	9.2 (10.1)	a			
DeDe	23	7.7 (9.0)	a			
PoSa	16	7.4 (4.3)	a			
Biomass of residual vegetation in cage				3, 98	7.24	<0.000
DeCe	23	30.5 (23.4)	a			
Wet carex	17	25.6 (16.4)	a b			
FeId	46	18.4 (11.6)	b c			
PoSa	16	9.0 (4.5)	c			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

We were unable to identify any significant differences in AGO among cover groups or understory groups. AGO ranged from 5.7 g in the intermediate grass group to

10.4 g in the dry shrub group, and 7.4 g in the *Posa* understory group to 9.6 g in the wet *Carex* understory group.

Drier cover and understory groups generally had less residual biomass in spring inside exclosure cages than more mesic cover and understory groups (Tables 23 and 24). Residual vegetation on ridge tops, generally with understories dominated by Idaho fescue or Sandberg bluegrass, was lowest with the greatest amount of residual vegetation found in communities with understories dominated by wet sedges or tufted hairgrass. For both cover groups and understory groups, categories containing wet sedges had the greatest mean biomass of standing crop in fall, but were second to communities with understories dominated by tufted hairgrass in spring.

Of the 10 paired plots placed within non-native clover during the summer of 2000, 6 cages were destroyed and not clipped. Mean biomass of standing crop inside cages of the remaining 4 and for 1 cage placed the summer of 1999 was 60.6 g (SD=19.0). APO (59.2%, SD=36.0) and AGO (38.2 g, SD=30.0) of non-native clover were greater than any other cover group.

Forage availability at the start of winter and intrinsic loss -- We estimated forage availability at the start of winter from standing biomass clipped at the end of the growing season in plots unprotected from growing season grazing (*i.e.* uncaged plots) At our 3 fixed sites, available biomass varied significantly among sites, with values ranging from 17.4 g (per 0.33 m^2) at the big sage site to 72.8 g at the mesic graminoid site (Table 25). Forage availability was significantly lower in 1999 (38.2 g) than 1998 (49.0 g) or 2000 (51.7 g). The difference between 1998 and 2000 was not significant.

Table 25. ANOVA results and 95% simultaneous confidence intervals between means for available winter forage during 1998, 1999, and 2000 at fixed sites in the Hayden Valley. Mean biomass values are grams / 0.33m^2.

Variable Category	N	Mean (SD)	95% C.I.[a]	ANOVA results df	 F-value	 P-value
Site				2, 166	125.70	<0.000
Big sage	56	17.4 (9.6)	a			
Silver sage	60	46.9 (21.6)	b			
Mesic gram.	59	72.8 (24.1)	c			
Year				2, 166	8.64	<0.000
1998	59	49.0 (30.8)	a			
1999	59	38.2 (21.7)	b			
2000	57	51.7 (34.5)	a			
Interaction				4, 166	3.06	0.02

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

We also detected differences in forage availability at the start of winter among vegetation classes in uncaged plots we sampled in the Crater Hills and West Alum areas. We found significant differences among cover types, cover groups, and understory groups, with the greatest mean biomass occurring in the moistest vegetative types and the least amount occurring on ridge tops (Table 26). By cover type, *Carex* (91.9g/ 0.33 m^2) was significantly different than all cover types except *Carex/Dece* (81.8g), which was different than all cover types except *Caca* (59.1g) and carex. Over all categorization systems (cover type, cover group, and understory group), biomass available per unit area for herbivores in winter was low in categories with understories dominated by Idaho fescue or Sandberg bluegrass and high in categories with understories dominated by mesic graminoids.

Table 26. ANOVA results and 95% simultaneous confidence intervals between means for cover types, cover groups, and grass types of available winter forage for all paired plots during 1998, 1999, and 2000 in the Crater Hills and West Alum areas of the Hayden Valley. Mean biomass values are grams / 0.33m2.

Grouping Category	N	Mean (SD)	95% C.I.[a]	ANOVA results df	 F-value	 P-value
Cover types				12, 152	31.79	<0.000
Carex	7	91.9 (17.2)	a			
Dece/Carex	15	81.8 (25.2)	a b			
Caca	5	59.1 (13.8)	b c			
Arca/Dece	22	48.7 (19.9)	c			
Pofr/Dece	4	47.5 (22.9)	c d			
Dece	8	47.0 (13.6)	c d			
Feid/Dece	7	36.1 (24.0)	c d e			
Artr/Feid-Dain	11	31.8 (11.8)	c d e f			
Artr/Agca	8	24.7 (10.1)	d e f			
Arca/Feid	6	22.5 (17.5)	d e f			
Artr/Feid	32	17.8 (11.6)	e f			
Feid/Agca	14	17.8 (8.6)	e f			
Posa	26	13.4 (8.4)	f			
Cover groups				4, 160	63.05	<0.000
Moist / wet grass	35	72.6 (25.8)	a			
Moist shrub	26	48.5 (19.9)	b			
Intermediate grass	21	23.9 (17.3)	c			
Dry shrub	57	21.9 (13.0)	c			
Dry grass	26	13.4 (8.4)	c			
Grass types				3, 161	114.79	<0.000
Wet carex	22	85.0 (23.0)	a			
Dece	39	49.5 (18.1)	b			
Feid	78	22.5 (14.2)	c			
Posa	26	13.4 (8.4)	c			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

We used data for fall standing crop and residual vegetation measured in spring collected in plots protected from grazing (Tables 25 and 26) to estimate over winter disappearance of vegetative biomass at fixed sites (Table 27). Minimum and maximum estimated losses by weight during each of the 2 winters in which we collected data were greatest for the mesic graminoid site followed by the silver sage and big sage sites (Table

27). Percentage loss varied among sites and years, with minimum losses ranging from 31.1 – 54.6% and maximum losses ranging from 45.0 – 63.9%.

Our technique (comparing weight of residual vegetation clipped in spring from plots protected from ungulate foraging over winter with standing biomass at nearby plots in comparable vegetation clipped the preceding fall) presumably eliminated ungulate herbivory as a factor in over winter loss of biomass in exclosures. Some of the over winter loss may be attributable to small mammal use within exclosures (Table 12), but small mammals are unlikely to be responsible for all of the difference between fall standing crop and spring residual vegetation. For our fixed sites, the mesic graminoid site had the least amount of small mammal use during winter (Table 10) but the greatest over winter loss each year and the most consistent percent difference between years. In contrast, the big sage site had the greatest amount of small mammal use of the 3 sites and the least difference in biomass, but the highest variability in percent difference between years. We were unable to allocate biomass loss over winter among small mammals, decomposition, and mechanical losses from wind and snow compaction, but we did demonstrate that it was substantial in fixed sites, and is probably substantial in paired plots covering a wide array of cover types.

Overall Estimates of Herbaceous Production and Offtake

Mean estimates of herbaceous production (kg/ha) extrapolated from plots clipped at the end of the growing season during 1998 through 20001 at fixed sites and paired plots produced estimates similar to those reported in the literature (Table 28). Estimates using plots from fixed sites were 16-26% lower than comparable vegetation types from

Table 27. Estimated minimum and maximum amounts (g / 0.33m^2 and percent) of vegetation lost during winter from factors other than ungulate grazing at fixed sites in the Hayden Valley during winters of 1998-99 and 1999-00.

	Fall 98 - Spring 99				Fall 99 - Spring 00			
	Grams		Percent		Grams		Percent	
Site	Min.[a]	Max.[a]	Min.	Max.	Min.[a]	Max.[a]	Min.	Max.
Big sage	5.1	6.7 *	33.6	44.1	10.4 *	12.2 *	54.6	63.9
Silver sage	26.2 *	27.0 *	48.3	49.8	11.5 *	12.8 *	31.1	34.6
Mesic gram.	32.7 *	35.5 *	43.1	46.8	23.9 *	26.6 *	40.5	45.0

[a] Asterisk denotes significant difference at the 0.05 level for t-tests comparing mean biomass outside exclosures in fall and inside exclosures in spring. Minimum estimate is based on residual vegetation + 25% of live graminoids in exclosure, maximum is

paired plots in the Crater Hills and West Alum areas, but both were within published ranges. The greatest discrepancy between our estimates and reported estimates was for the Feid/Agca type, referred to as one of the most productive grassland types by Mueggler and Stewart (1980). Our estimates were much lower than estimates reported by Mueggler and Stewart (1980). The lower productivity we found may have been due to the microclimate at our sites (a short growing season accentuated by persistent snow drifts at the topographic position of these sites that retards growth initiation) and/or the high level of small mammal activity we observed in this cover type in the Hayden Valley.

We used data from fixed sites and paired plots, averaged over 3 years, to calculate rough estimates of total herbaceous biomass available to ungulates, herbaceous biomass removed by ungulates, and percent of available herbaceous biomass removed by ungulates for the Crater Hills and West Alum areas and for the entire Hayden Valley. Grazed loop data provided another estimate of percent offtake by ungulates (Table 29). Production estimates were 8,900 to 12,000 metric tons for the Hayden Valley with an estimated 2,800 to 4,200 metric tons removed by ungulates during the growing season.

Table 28. Measured production by cover type from paired plots and fixed sites in the Hayden Valley during 1998, 1999, 2000 and production estimates reported in literature for vegetation similar types.

Method	Production		Estimates from literature		
Cover type	kg/ha	SD	kg/ha	Source[1]	Notes
Paired plots					
Artr/Feid	1014	555	682 - 1728	1,2	
Arca/Feid	1245	768	1344 - 1680	1	Estimated range
Artr/Feid-Dain	1296	399	682 - 1728	1	Included in ArTr/FeId
Artr/Agca	1650	624	682 - 1728	1,2	similar to *Geranium* phase of ArTr/FeId
Pofr/Dece	1938	315			
Arca/Dece	2001	579			
Feid/Agca	867	390	1194 - 1672	1	
Posa	894	372	782 - 1440	1	Included in FeId/AgSm
Feid/Dece	1314	654	1344 - 1680	1	Estimated range
Caca	2577	759			
Dece	1884	471	560 - 3360	3	
Dece/Carex	2832	858	2906	1	Results of 1 stand
Wet Carex	3315	672			
Clover	1818	570	na		
Fixed sites					
Big sage	810	411	682 - 1728	1,2	
Silver sage	1479	384			
Mesic graminoid	2385	702	2906	1	Results of 1 stand

[1] 1=Mueggler and Stewart (1980), 2=Wilbert (1963), 3=Kovalchik (1987)

Table 29. Estimates of total herbaceous production (metric tons) and offtake (metric tons, percent) from fixed site plots and paired plots extrapolated to the Crater Hills and West Alum areas and across the entire Hayden Valley (Crater Hills and West Alum x 9.08) and estimates of total offtake (%) from fixed and paired plots (consumption/production) and from grazed loop data. Estimates from paired plots and fixed sites are combined 1998-2000, grazed loop are 1999-2000, entire Hayden Valley estimates are scaled estimates (x 9.08) from Crater Hills and West Alum estimates.

Location Method	Production (t)	Offtake (t)	Offtake (%)
Crater Hills and West Alum			
Paired plots	1311	462	35.2
Fixed sites	985	308	31.2
Grazed loop	na	na	23.1
Entire Hayden Valley			
Paired plots	11908	4190	35.2
Fixed sites	8941	2793	31.2
Grazed loop	na	na	23.1

Estimates of total offtake by weight using fixed site data were also lower than estimates from paired plots. However, estimated percent offtake developed from fixed site data (31.2%) was only slightly lower than estimates developed using paired plots (35.2%). In comparison, estimated percent offtake from grazed loop surveys was 23.7%.

Grazed loop surveys consistently underestimated percent offtake in relation to estimates using exclosures. In addition to lower combined estimates for the Crater Hills and West Alum areas, grazed loop estimates at fixed sites and the Crater Hills and West Alum areas separately in 1999 and 2000 (Appendix A, Table 49) ranged from 36.8% (big sage site, 1999) to 84.8% (mesic graminoid site, 1999) of estimated offtake from exclosures. Regression analysis produced a moderate linear relationship ($P = 0.01$; $R^2 = 0.69$) between the 2 measures of offtake:

$$\text{APO Using Exclosures} = 7.07 + 1.38 \times \text{Grazed Loop Estimate}$$

Vegetative regrowth subsequent to grazing was not included in all estimates from fixed sites and paired plots due to the use of season-long exclosures. The amount of regrowth from 16 plots clipped in 4 different cover types at approximately peak standing crop on July 14th and again on September 9th of 2000 ranged from 3.6% in a wet *Carex* type to 29.7% in an *Arca/Dece* type (Appendix A, Table 50). Based on visual observations adjacent to plots and height measurements taken at 16-day intervals, grazing of plots did not occur between the 2 sample periods. A regression predicting biomass (g) of regrowth using all 16 plots was highly insignificant ($P = 0.94$; $R^2 < 0.00$). However, regression analysis using just the 10 plots containing tufted hairgrass as the dominant grass indicated a moderate relationship ($P < 0.00$; $R^2 = 0.69$) between regrowth and initial biomass (g) for this vegetation type:

Regrowth Biomass = 25.97 – 0.1429 x Initial Biomass

Surveys and Indices of Animal Use

Use vs. availability from grazed loop surveys -- We used 4 grazed loop surveys (Crater Hills 1999, 2000 and West Alum 1999, 2000) to measure grazing distribution over common cover types in the Hayden Valley. Overall, the highest percentage of observed grazing from combined totals of the 4 surveys occurred in the *Posa*, *Artr/Posa*, and *Arca/Feid* cover types, while the highest percentage of level 2 grazing (moderate to heavy) occurred in the *Posa*, *Artr/Agca*, and *Arca/Feid* cover types (Table 30). We did not include the sage/dry *Carex* cover type, cover types from the non-vegetated group, and cover types from the forb or thermally influenced plant groups (see Appendix B for detailed descriptions) in statistical analyses because of their rarity in the Hayden Valley.

We had too few cover types with adequate samples (Tables 2 and 30) to support Chi-square analysis by cover type so we only tested for differences in grazing intensity among cover groups and understory groups.

For cover groups, Chi-square analysis of the distribution of "hits" with evidence of grazing (level 1 + level 2) indicated significant differences (X^2 = 34.69, P < 0.00) among the 4 surveys. When years were pooled, sites (Crater Hills vs. West Alum) also produced significant differences (X^2 = 29.48, P < 0.00) in grazing distribution. However, the distribution was not different between years for either the Crater Hills (X^2 = 4.38, P = 0.36) or West Alum areas (X^2 = 0.79, P = 0.94) individually, and combining sites within years and comparing distributions between years also did not produce significant differences (X^2 = 4.25, P = 0.37). These results were probably due to differences in availability of cover groups between the Crater Hills and West Alum areas (X^2 = 76.08, P < 0.00) and suggest the 4 surveys could be combined without biasing results from the influence of sites or years.

Similar results were obtained for understory groups when we combined level 1 and level 2 grazing. When we looked at only moderate to heavy grazing (level 2), distribution of grazed locations was not different among the 4 surveys by cover groups (X^2 = 17.05, P = 0.15) or understory groups (X^2 = 15.39, P = 0.08), indicating surveys could also be combined if we only examined the distribution of moderate to heavy grazing (level 2) among vegetation categories.

When we looked at the distribution of grazing among cover groups, we found similar trends in selection and avoidance in individual surveys, pooled surveys, analyses based on any evidence of grazing (levels 1 and 2) versus no grazing, and analyses based only on moderate to heavy grazing (level 2) versus no grazing (Table 31). Patterns were more pronounced for tests involving pooled surveys and level 2 grazing, but bison tended to graze disproportionately more in plots sampled in the dry shrub group and disproportionately less in plots sampled in the moist and wet graminoid group.

Selection and avoidance of vegetation types was also pronounced for understory groups (Table 32). The *Feid* group (Idaho fescue dominant in understory) and *Posa* group (Sandberg bluegrass dominant) tended to be used more than expected, and the *Dece* (tufted hairgrass dominant in understory) and wet *Carex* groups were used less than expected.

Table 30. Number of "grazed loops" by grazing level in each cover type for the Crater Hills (CH) and West Alum (WA) areas during 1999 and 2000, sample size in each type (N), percent total grazed (level 1 + level 2 / total available), and percent level 2 grazing

Cover group	CH 1999			WA 1999			CH 2000			WA 2000			total	Combined %	
Cover type	none	level 1	level 2	none	level 1	level 2	none	level 1	level 2	none	level 1	level 2	N	grazed	level 2
Dry shrub group															
Artr/Feid*	86	50	33	11	16	13	53	91	51	13	26	13	456	64.3	24.1
Arca/Feid	18	23	7	14	17	12	24	29	18	19	31	23	235	68.1	25.5
Artr/Feid-Dain	22	4	0	0	0	0	13	1	0	0	0	0	40	12.5	0.0
Arca/Feid-Dain	3	2	0	0	0	0	5	0	0	0	0	0	10	20.0	0.0
Artr/Agca	3	0	1	0	0	1	12	12	15	1	1	2	48	66.7	39.6
Artr/Posa	2	5	0	0	0	0	2	7	2	6	9	8	41	75.6	24.4
Sage/dry carex	4	1	0	0	0	0	0	0	0	0	0	0	5	20.0	0.0
Moist shrub group															
Pofr/Dece	5	0	0	0	0	0	0	1	0	0	0	0	6	16.7	0.0
Arca/Dece	76	22	7	12	7	7	59	24	16	9	13	7	259	39.8	14.3
Wet shrub group															
Salix/Carex	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0
Dry grass group															
Posa	1	2	6	1	1	5	5	8	7	4	5	6	51	78.4	47.1
Intermediate graminoid group															
Feid/Agca	10	10	3	5	4	3	19	22	11	9	6	2	104	58.7	18.3
Feid/Dece	15	6	1	9	4	5	19	19	6	7	20	4	115	56.5	13.9
Moist and wet graminoid group															
Caca	1	0	0	0	1	0	4	0	0	2	4	1	13	46.2	7.7
Dece	14	7	0	22	11	7	25	15	4	26	17	5	153	43.1	10.5
Dece/Carex	17	6	1	6	2	1	9	5	1	20	13	4	85	38.8	8.2
Wet carex	14	3	0	0	1	0	8	5	2	5	3	0	41	34.1	4.9
Forb or thermally influenced plant group															
Clover	0	0	0	0	0	0	0	0	1	0	0	0	1	100.0	100.0
Misc. Forb	0	0	0	0	1	1	1	2	0	0	0	0	5	80.0	20.0
Thermal Veg.	0	0	0	1	0	0	0	0	0	0	0	0	1	0.0	0.0
Non-vegetated group															
Eros / Dis.	4	3	0	1	0	0	9	0	0	1	0	0	18	16.7	0.0
Thermal gnd.	0	0	0	1	0	0	0	0	0	0	0	0	1	0.0	0.0

* See Appendix B for type descriptions.

Table 31. Results of Chi-square tests of use vs. availability (significant differences at alpha levels of 0.05 and 0.10 are presented) for 2 categories of grazing intensity distributed among 5 cover groups for surveys conducted in the Crater Hills (CH) and West Alum (WA) areas during 1999 and 2000. o = no significant deviation from expected; (-) = grazed less than expected; (+) = grazed more than expected.

Grazing level	CH 1999		CH 2000		WA 1999		WA 2000		All
Cover group	0.05	0.10	0.05	0.10	0.05	0.10	0.05	0.10	0.05
Presence of grazing *									
Dry shrub	o	(+)	o	(+)	o	o	o	o	(+)
Moist shrub	o	o	(-)	(-)	o	o	o	o	(-)
Dry grass	o	o	o	o	o	o	o	o	o
Intermediate gram.	o	o	o	o	o	o	o	o	o
Moist and wet gram.	o	o	o	o	o	o	o	o	(-)
Level 2 grazing *									
Dry shrub	(+)	(+)	o	(+)	o	o	(+)	(+)	(+)
Moist shrub	o	o	o	o	o	o	o	o	o
Dry grass	o	o	o	o	o	o	o	o	(+)
Intermediate gram.	o	o	o	o	o	o	o	o	o
Moist and wet gram.	(-)	(-)	(-)	(-)	o	(-)	(-)	(-)	(-)

[*] "Presence of Grazing" is a combination of grazing level 1 and 2. "Level 2 Grazing" includes only hits with evidence of moderate to heavy grazing (vegetation in plot clipped to a height of < 7mm).

Table 32. Results of Chi-square tests of use vs. availability (significant differences at alpha levels of 0.05 and 0.10 are presented) for 2 categories of grazing intensity distributed among 4 graminoid understory groups for surveys conducted in the Crater Hills (CH) and West Alum (WA) areas during 1999 and 2000. o = no significant deviation from expected; (-) = grazed less than expected; (+) = grazed more than expected.

Grazing level	CH 1999		CH 2000		WA 1999		WA 2000		All
Grass type	0.05	0.10	0.05	0.10	0.05	0.10	0.05	0.10	0.05
Presence of grazing [a]									
Feid	o	o	(+)	(+)	o	o	o	o	(+)
Posa	o	o	o	o	o	o	o	o	o
Dece	o	(-)	(-)	(-)	o	o	o	o	(-)
Wet carex	o	o	o	(-)	(-)	(-)	o	o	(-)
Level 2 grazing [a]									
Feid	o	o	(+)	(+)	o	o	o	o	(+)
Posa	o	o	o	o	o	o	o	o	(+)
Dece	(-)	(-)	(-)	(-)	o	o	o	o	(-)
Wet carex	(-)	(-)	(-)	(-)	(-)	(-)	o	o	(-)

[a] "Presence of Grazing" is a combination of grazing level 1 and 2. "Level 2 Grazing" includes only hits with evidence of moderate to heavy grazing (vegetation in plot clipped to a height of < 7mm).

Observational surveys and fecal counts -- When we began this study, we believed both bison and elk would contribute significantly to forage utilization in the Hayden Valley. Fecal counts and animal surveys indicated bison were the dominant ungulates using the Hayden Valley and that elk were not abundant, at least in open plant communities. Bison feces comprised 91.6% of ungulate fecal piles from all fecal counts (Table 33). The lowest proportion of bison feces (73%) was encountered in 45x45m grids used for radiometer sampling and the highest proportion, 98%, occurred near paired exclosures during summer. For animal surveys, 95.6% of observations were bison. Proportions ranged from 92.8% in aerial surveys to 99.9% in surveys with the laser rangefinder. Incidental elk sightings, recorded during surveys or en route to sampling sites, were generally higher in fall and spring than in summer. We also saw 1 moose and 3 mule deer in the Hayden Valley during the project but did not include them due to their infrequent occurrence.

Table 33. Percent (N) of bison, elk, and feces of bison and elk from fecal surveys and observations adjacent to paired plots, within boundaries of fixed sites, within grids sampled ith the portable radiometer, from feeding location surveys in the Crater Hills and West Alum areas, and from complete coverage aerial surveys during 1998-2000 in Hayden Valley.

Type Location	Bison		Elk	
Fecal counts				
Summer 2000 within 5m of paired cages	98.0	(99)	2.0	(2)
Winter 2000 within 5m of paired cages	87.0	(134)	13.0	(20)
Summer 1998-2000 total of fixed sites	93.5	(4477)	6.5	(312)
Winter 1999-2000 total of fixed sites	90.9	(3279)	9.1	(327)
Summer 1998-2000 totals of grids	73.1	(242)	26.9	(89)
Animal surveys				
Summer 1998-2000 total of fixed sites	99.8	(500)	0.2	(1)
Summer 1999-2000 bison feeding surveys	99.9	(4765)	0.1	(4)
Summer 1999-2000 aerial surveys	92.8	(7375)	7.2	(573)

At the big sage site, densities of bison and elk feces were greater in the xeric portion (*Artr/Feid* and *Artr/Feid-Dain*) than the mesic inclusion (*Arca/Dece*) but were not statistically significant (Table 34). For the mesic graminoid site, mean density of bison feces was greater in the mesic portion (*Dece/Carex* and wet carex) than the xeric portion (*Arca/Dece*) but elk feces were higher in the xeric portion. Due to the lack of statistically significance in fecal densities between vegetative types, we ignored vegetative inclusions that would result in highly convoluted shapes of the big sage and mesic graminoid sites and used overall perimeters and combined fecal densities for analysis of differences in fecal densities among sites.

Table 34. Mean bison and elk fecal density (n/ha) of xeric and mesic portions of big sage and mesic graminoid fixed sites for growing and non-growing seasons in the Hayden Valley during 1998, 1999, 2000, and results of Wilcoxon's test comparing mean values.

Site	Xeric portion		Mesic portion				
Variable	n	Mean (SD)	n	Mean (SD)	Test[a]	Value	P
Big sage							
Bison fecal density	5	283.9 (139.0)	5	180.8 (161.1)	V	15	0.06
Elk fecal density	5	33.2 (28.7)	5	19.0 (19.1)	Z	1.77	0.08
Mesic graminoid							
Bison fecal density	5	356.0 (171.9)	5	511.6 (472.1)	V	9	0.81
Elk fecal density	5	36.0 (41.1)	5	19.5 (14.7)	V	11	0.44

[a] Wilcoxon's signed-rank test used because of nonnormality of data. Z used when ties make exact test impossible.

Bison fecal densities were quite variable among sites and seasons, and both the highest (879.6/ha in the mesic graminoid site) and lowest (63.9/ha in the silver sage site) densities occurred during the non-growing season of 1999-2000 (Appendix A, Table 51). Although differences in mean values among sites differed by a factor of almost 3, sample variability and small sample sizes obscured any significant differences among sites and between the growing and non-growing seasons (Table 35).

Table 35. ANOVA results for site, season and site by season interaction, and 95% simultaneous confidence intervals between means of sites and seasons for bison and elk fecal density (n/ha) at fixed exclosure sites during growing and non-growing seasons of 1998, 1999, and 2000 in the Hayden Valley, and ANOVA results for density of bison observed between fixed sites during the growing seasons of 1998, 1999, and 2000.

Parameter Variable Category	N	Mean	(SD)	95% C.I.[a]	ANOVA results df	 F-value	 P-value
Bison fecal density							
Site					2, 9	3.11	0.09
Big sage	5	250.8	(144.9)	a			
Silver sage	5	154.1	(66.9)	a			
Mesic gram.	5	439.3	(284.5)	a			
Season					1, 9	0.13	0.73
Growing	9	267.4	(152.3)	a			
Non-growing	6	302.4	(298.7)	a			
Interaction					2, 9	1.73	0.23
Elk fecal density							
Site					2, 9	1.61	0.25
Big sage	5	28.7	(25.5)	a			
Silver sage	5	6.2	(7.5)	a			
Mesic gram.	5	27.2	(26.6)	a			
Season					1, 9	0.38	0.55
Growing	9	17.8	(24.5)	a			
Non-growing	6	25.0	(21.2)	a			
Interaction					2, 9	1.09	0.38
Bison observation density							
Site					2, 6	0.46	0.65
Big sage	5	11.4	(12.1)	a			
Silver sage	5	39.3	(61.4)	a			
Mesic gram.	5	17.6	(16.5)	a			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Density of elk feces was also variable, ranging from 0/ha at the big sage site during the 1999 growing season to 71.1/ha at the mesic graminoid site during the 2000 growing season (Appendix A, Table 51). As with bison, significant differences among sites or seasons were not detected (Table 35).

We observed a total of 500 bison and 1 elk during the 259 times we surveyed the fixed sites over 3 growing seasons, so we did not calculate density of elk observations within sites. The greatest mean density of bison (39.3/ha) occurred at the silver sage site and the lowest density (11.4/ha) was at the big sage site (Table 35). Mean differences among sites were not significant.

Regression analysis predicting APO and AGO of standing crop during the growing season using fecal and observed animal densities at fixed cage sites did not produce any strong ($R^2 \geq 0.70$) associations (Table 36). Bison and elk fecal densities produced weak ($0.20 \leq R^2 < 0.50$) and moderate ($0.50 \leq R^2 < 0.70$) associations, respectively, for predicting AGO of standing crop, but no association ($R^2 < 0.20$) was detected for APO of standing crop. Although R^2 values were <0.20 for both regressions, density of observed bison produced negative coefficients for predicting APO and AGO of standing crop, suggesting a negative association between observed numbers of bison and offtake of standing crop.

Non-growing season regressions produced the strongest associations of the 3 time periods tested. Overall, bison fecal density was negatively associated with offtake of spring new growth, indicating lower offtake where bison fecal densities were higher, but positively associated with offtake of residual vegetation. Bison fecal density had a moderate negative association with APO for spring new growth, and a weak negative association with AGO for spring new growth. Bison fecal density was strongly and positively associated with APO of spring residual biomass and was moderately and positively with AGO for spring residual biomass. In contrast, regressions of elk fecal density with vegetation parameters indicated weak and moderate positive associations with APO and AGO of spring new growth and no positive associations with spring residual offtake.

Table 36. Regression coefficients, multiple R^2, and test conclusions of bison fecal density, elk fecal density, and density of observed animals for predicting APO and AGO during the growing season, non-growing season, and yearlong at fixed sites during 1998, 1999, 2000 in the Hayden Valley.

Season Response	Predictor	R^2	Coefficient	Conclusion[1]
Growing				
Standing crop APO	Bison fecal density	0.04	0.01	No assoc.
	Elk fecal density	<0.00	< 0.01	No assoc.
	Density of obs. Bison	0.06	-0.07	No assoc.
Standing crop AGO	Bison fecal density	0.40	0.01	Weak pos. assoc.
	Elk fecal density	0.54	0.08	Mod. pos. assoc.
	Density of obs. Bison	0.02	-0.01	No assoc.
Non-growing				
Spring new growth APO	Bison fecal density	0.55	-0.03	Mod. neg. assoc.
	Elk fecal density	0.33	0.27	Weak pos. assoc.
Spring new growth AGO	Bison fecal density	0.21	< -0.00	Weak neg. assoc
	Elk fecal density	0.62	0.05	Mod. pos. assoc.
Spring residual APO	Bison fecal density	0.70	0.01	Strong pos. assoc.
	Elk fecal density	0.03	0.04	No assoc.
Spring residual AGO	Bison fecal density	0.61	0.02	Mod. pos. assoc.
	Elk fecal density	0.15	-0.11	No assoc.
Spring combined APO	Bison fecal density	0.23	< 0.01	Weak pos. assoc.
	Elk fecal density	0.40	0.17	Weak pos. assoc.
Spring combined AGO	Bison fecal density	0.67	0.01	Mod. pos. assoc.
	Elk fecal density	0.05	-0.05	No assoc.
Yearlong				
Yearlong APO	Bison fecal density	0.07	0.01	No assoc.
	Elk fecal density	0.05	0.10	No assoc.
Yearlong AGO	Bison fecal density	0.57	0.01	Mod. pos. assoc.
	Elk fecal density	0.06	0.04	No assoc.

[1] $R^2<0.20$=No association, $0.20\leq R^2<0.50$=Weak association, $0.50\leq R^2<0.70$=Moderate association, $R^2\geq 0.70$=Strong association

Associations between fecal densities and offtake were generally reduced when we combined offtake of spring new growth and residual vegetation into a single response variable. Weak positive associations with APO for both bison and elk fecal densities were concluded, with moderate and no association to AGO for bison and elk fecal densities, respectively. For yearlong offtake, we concluded a moderate positive association between AGO and bison fecal density and no association for other yearlong regressions.

Occurrence of repeat grazing -- Of the 3 fixed cage sites, the big sage site had the greatest occurrences of ungulate grazing and repeat grazing during the 3 years of this study (Table 37). When we located unprotected plots at fixed sites prior to clipping standing crop in fall and revisited the same locations during subsequent years of the study, locations in the big sage site had the highest proportion of observed grazing in any 1 year (54.2%), followed by the silver sage site (35.0%) and mesic graminoid site (24.2%). Overall proportions of observed grazing in any 1 year at locations across the 3 fixed sites were significantly different. Pairwise comparisons indicated the big sage site had significantly higher values than the other 2 sites. The same pattern was evident for observed grazing at locations over 2 and 3 consecutive years. At the big sage site, 20% of locations were grazed 3 years in a row. We did not observe grazing at specific locations over 3 consecutive years in the silver sage or mesic graminoid sites. The silver sage site had the highest proportion of grazed locations in 2 out of 3 years, but differences in proportions among sites were not statistically different.

Table 37. Percent unprotected plots (of N) with visual signs of ungulate or small mammal grazing, overall tests for simultaneous differences in similarity of proportions, and paired comparisons (s=significant, P<0.05; n=not significant, P>0.05) when overall results indicated significance for grazing observed during any year, 2 consecutive years, 3 consecutive years, and 2 out of 3 years for 1998, 1999, and 2000 at fixed sites in the Hayden Valley.

Grazing source				Overall		Big v.	Big v.	Mesic v.
Occurrence	Big sage	Silver sage	Mesic	X^2	P	silver	mesic	silver
Ungulates								
Any 1 year	54.2 (120)	35.0 (120)	24.2 (120)	23.56	<0.00	s	s	n
2 years in a row	35.0 (60)	11.7 (60)	3.3 (60)	23.28	<0.00	s	s	n*
3 years in a row	20.0 (20)	0 (20)	0 (20)	*	0.03	n*	n*	--
2 of 3 years	15.0 (20)	35.0 (20)	10.0(20)	*	0.19	--	--	--
Small mammals								
Any 1 year	18.3 (120)	13.3 (120)	8.3 (120)	5.19	0.07	--	--	--
2 years in a row	8.3 (60)	1.7 (60)	1.7 (60)	*	0.22	--	--	--
3 years in a row	5.0 (20)	0 (20)	0 (20)	*	>0.99	--	--	--
2 of 3 years	0 (20)	0 (20)	5.0 (20)	*	>0.99	--	--	--

* Fisher's exact test used with expected counts <5

When we grouped cover types at paired plots in the Crater Hills and West Alum areas by graminoid understory types, significant differences in proportions of ungulate grazing and repeat grazing were detected. Higher proportions of locations were grazed in *Posa* and *Feid* types than in *Dece* and wet *Carex* types across all categories (Table 38). Significant differences were found in overall proportions of grazing across all understory groups for any year, 2 consecutive years, and 3 consecutive years, but a difference was not detected for grazing at locations 2 out of 3 years. Pairwise comparisons produced the same pattern of results for categories of any year and 2 consecutive years; *Posa* vs. *Feid* and *Dece* vs. wet *Carex* were not different, while all other pairs were statistically different. For pairwise comparisons of grazing over 3 consecutive years, *Posa* vs. *Dece* and *Pos*a vs. wet *Carex* were the only pairs producing significant differences.

Occurrence of visible small mammal activity was higher at the big sage fixed site than at the silver sage or mesic graminoid sites ($P = 0.07$). We detected very low levels of repeated use of a plot over 2 or more years by small mammals at all 3 sites and no difference among sites in repeated use (Table 37). For paired plot locations in the Crater Hills and West Alum areas categorized by graminoid understory, occurrence of visible small mammal activity was lower in the wet *Carex* than in the *Feid*, *Posa*, or *Dec*e understory groups ($P < 0.05$) (Table 38). Although visible use at the same plot in 2 or 3 consecutive years was low for all understory groups, visible activity in the *Feid*, *Posa*, and *Dece* groups was about as likely to occur in alternate years (*i.e.* 2 out of the 3 years) as in any 1 year.

Ungulate damage to trees along forest margin -- Of 1,343 trees in all size classes we sampled along forest margins, 91.4% had evidence of ungulate scraping (28.1% were dead with evidence of scraping, 35.7% were girdled by scraping over greater than 50% of the circumference, 18.2% were girdled from 20 – 50% of the circumference, and 9.4% were scraped but girdled less than 20% of the circumference). Damage extent and frequency varied among size classes ($X^2 = 17.24$, $P = 0.03$).

We did not detect significant differences among size classes for proportions of trees with none to minor damage (Table 39). Sapling, pole, and mature classes did differ in the occurrence of moderate (20-50% girdling) and severe (>50% girdling but still alive) damage and in the proportion of trees that were dead. Mature trees had the highest proportion of moderate damage (21% of trees examined); the pole-size class had the

Table 38. Percent unprotected plots (of N) with visual signs of ungulate or small mammal grazing, overall tests for simultaneous differences in similarity of proportions, and paired comparisons (s=significant, P<0.05; n=not significant, P>0.05) when overall results indicated significance for grazing observed during any year, 2 consecutive years, 3 consecutive years, and 2 out of 3 years for 1998, 1999, and 2000 at paired plots in Crater Hills and West Alum areas.

Grazing source					Overall		PoSa	PoSa	PoSa	Feld v.	Feld v.	DeCe
Occurrence	PoSa	Feld	DeCe	Wet carex	X^2	P	Feld	DeCe	carex	DeCe	carex	carex
Ungulates												
Any year	83.6 (61)	72.2 (180)	45.9 (98)	32.7 (52)	49.86	<0.00	n	s	s	s	s	n
2 years in a row	76.9 (26)	57.1 (84)	23.5 (51)	11.1 (18)	33.41	<0.00	n	s	s	s	s	n*
3 years in a row	85.7 (7)	39.1 (23)	25.0 (16)	0 (4)	*	0.02	n*	s*	s*	n*	n*	n*
2 of 3 years	0 (7)	21.7 (23)	18.8 (16)	0 (4)	*	0.62	--	--	--	--	--	--
Small mammals												
Any year	21.3 (61)	21.9 (178)	16.3 (98)	0 (52)	14.15	<0.00	n	n	s	n	s	s
2 years in a row	3.8 (26)	7.1 (84)	3.9 (51)	0 (18)	*	0.84	--	--	--	--	--	--
3 years in a row	0 (7)	0 (23)	0 (16)	0 (4)	*	>0.99	--	--	--	--	--	--
2 of 3 years	14.3 (7)	17.4 (23)	12.5 (16)	0 (4)	*	>0.99	--	--	--	--	--	--

* Fisher's exact test used with expected counts <5

highest percentage of severe damage (42% of trees examined); and the sapling class had the highest percentage of dead trees (44%). This pattern suggested that larger trees may be less vulnerable to ungulate damage than smaller trees and, possibly, that the rate at which trees are being damaged had increased in recent years (*e.g.* More trees may have survived through the sapling and pole stages to reach maturity in the past). Without data from other points in time, however, statements on rates of change are only speculation.

Table 39. Percent (N) trees in each size class (sapling = 2-4" dbh, pole timber = 4-8" dbh, mature = >8" dbh) with evidence of ungulate scraping (% circumference girdled), overall tests for simultaneous difference in proportions, and paired comparisons (s=significant, P<0.05; n=not significant, P>0.05) when overall results indicated significance differences, for trees along the forest margin in the Hayden Valley during 2000.

Circumference girdled (%)	Sapling	Pole timber	Mature	Overall X^2	Overall P	Sap. v. pole	Sap. v. mature	Pole v. mature
None	10.0 (27)	6.2 (21)	9.1 (67)	3.41	0.18	--	--	--
<20	9.7 (26)	6.5 (22)	10.6 (78)	4.59	0.10	--	--	--
20 - 50	13.8 (37)	16.3 (55)	20.8 (153)	7.71	0.02	n	s	n
>50	22.7 (61)	41.7 (141)	37.6 (277)	26.42	<0.00	s	s	n
Dead[1]	43.9 (118)	29.3 (99)	21.9 (161)	47.40	<0.00	s	s	s

[1] Dead trees with visual signs of scraping by ungulates

Plant Nutritional Analysis and Bison Food Habits

Bison food habits -- Results of microhistological analysis of bison feces indicated graminoids comprised >90% of bison diets during each time period with the exception of September 1998, when graminoids made up only 82.5% of the sample. Grasses comprised 54.6% of the diet over all sample periods with a range of 41.1% to 60.1% over the 9 time periods we sampled. Sedges and rushes averaged 37.1% of the diet and ranged from 25.2% to 50.2% in individual monthly samples (Fig.3). The September 1998 sample included 6.7% *Lupine* spp. and was the only sample containing >10% forbs. Dietary composition of shrubs was <0.05% in all of our samples.

Of individual taxonomic groups identified in feces, *Carex aquatilis* (13.2%) and *Poa* spp. (11.2%) had the highest average occurrence and were the only 2 taxa with an average frequency >10% (Table 41). However, amounts and relative ranking in the diet of both varied among time periods, with *Carex aquatilis* ranking as low as 7th in July, 1999 and *Poa* spp. ranking as low as 10th in September 2000. *Deschampsia cespitosa* had the most consistent frequency of occurrence of the 9 species/genera averaging >5% occurrence in feces over all sampling periods and varying only from 6 to 12% in individual monthly samples. Fecal nitrogen consistently declined through the growing season in each year.

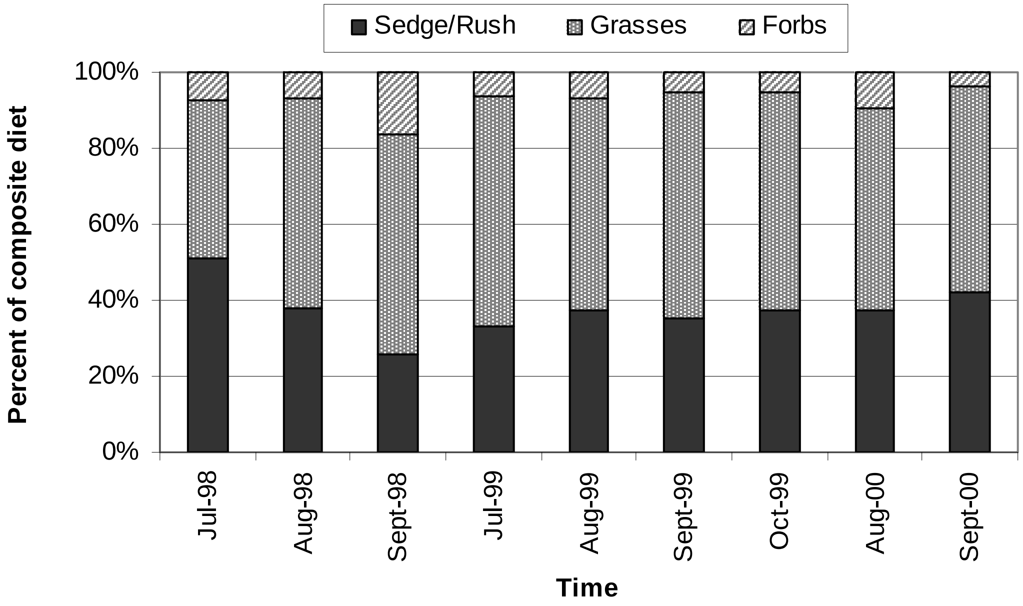


Fig.3. Frequency of occurrence of plant types in bison feces from the Hayden Valley during growing seasons of 1998, 1999, 2000.

Table 40. Percent botanical composition of bison diets from microhistological analysis of fecal samples and fecal nitrogen content (%) from 1998, 1999, 2000 in the Hayden Valley.

Category	1998			1999				2000		All dates	
Plants	July	Aug.	Sept.	July	Aug.	Sept.	Oct.	Aug.	Sept.	mean	SD
Sedges and rushes											
Carex aquatilis	13.4	16.3	9.9	5.6	16.7	15.8	12.6	14.5	14.1	13.2	3.5
Carex nebraskensis	6.3	5.9	2.8	7.2	3.4	3.3	8.3	2.8	6.2	5.1	2.1
Carex rostrata	10.4	6.1	8.6	8.6	6.1	5.0	6.5	10.9	9.1	7.9	2.1
Carex spp.	15.2	7.0	2.2	7.7	7.2	7.5	8.9	7.3	6.3	7.7	3.4
Eleocharis spp.	0.8	0	0	0	0	0	0	0	0	0.1	0.3
Eriophorum spp.	0	0	0	0	0.5	0	0	0	0	0.1	0.2
Juncus spp.	4.1	2.2	1.7	3.5	3.4	2.5	0.8	1.8	6.3	2.9	1.6
Scirpus spp.	0	0	0	0	0.2	0	0	0	0	0	0.1
Grasses											
Agropyron spp.	2.6	7.0	11.4	4.9	5.3	12.8	10.2	6.7	8.8	7.7	3.3
Agrostis spp.	8.4	7.7	7.1	15.5	8.8	7.5	7.9	8.1	6.6	8.6	2.7
Bouteloua spp.	0	0	0	0	0.8	0	0	0	0	0.1	0.3
Calamagrostis spp.	1.3	1.1	1.1	1.1	4.0	2.3	3.3	1.2	2.1	1.9	1.1
Danthonia intermedia	5.2	5.9	1.9	3.7	4.0	0.6	2.0	3.2	2.1	3.2	1.7
Deschampsia cespitosa	6.3	7.9	9.0	12.1	8.3	9.7	9.2	11.7	10.2	9.4	1.8
Festuca idahoensis	2.9	6.1	10.1	8.6	7.5	5.6	8.7	8.3	13.8	8.0	3.1
Phleum spp.	2.4	0.4	0.4	0.7	0.6	3.1	0.4	1.0	1.5	1.2	1.0
Poa spp.	9.6	15.1	12.9	10.0	11.8	12.2	13.2	9.1	5.7	11.1	2.8
Stipa spp.	0	0	0	0	0.5	0	0	0	0	0.1	0.2
Other Grass	2.4	3.9	3.4	3.5	4.3	3.9	2.2	3.8	2.9	3.4	0.7
Forbs											
Achillea spp.	0.6	0.6	1.2	1.1	0.5	1.2	2.0	0	0.1	0.8	0.6
Astragalus spp.	0.2	0.1	0.9	0	0	1.3	0	0.7	1.0	0.5	0.5
Fragaria spp.	0	0	0	0	0.2	0	0	0	0	0	0.1
Lupinus spp.	0.5	0.4	6.7	0	0	0	0.6	2.3	1.0	1.3	2.2
Phlox/Leptodactylon	0	0.9	2.8	0	1.1	0	0	1.6	0	0.7	1.0
Potentilla spp.	0	0	1.9	0	0	0	0	0	0	0.2	0.6
*Stellari*a spp.	0	0	0	0	0	0	0	1.6	0.6	0.2	0.5
Trifolium spp.	1.9	2.7	0.7	0	0	0	0.4	0.3	0	0.7	1.0
Composite	0	0	0	0	0.2	0	0	0	0	0	0.1
Other Forb	4.3	2.2	1.6	5.3	4.6	2.6	2.4	2.9	1.1	3.0	1.4
Shrubs											
Artemisia spp.	0.2	0	0	0	0	0	0	0	0.2	0	0.1
Betula spp. stem	0	0	0	0	0	0.4	0	0	0	0	0.1
Other Shrub	0	0	0.4	0	0	0	0	0	0	0	0.1
Moss and plant parts											
Moss	1.0	0.5	0.4	0.5	0	2.7	0.4	0.2	0.3	0.7	0.8
Flowers	0	0	0.9	0	0	0	0	0	0	0.1	0.3
Thorns	0	0	0	0.4	0	0	0	0	0	0.0	0.1
Fecal nitrogen	3.01	2.31	1.63	3.04	2.32	1.86	1.89	1.91	1.69	2.2	0.5

Plant nutritional content -- Crude protein (CP) of the 6 plant species we sampled in the summer of 2000 declined from July to mid-September with the exception of *Poa sandbergii* which had unexpectedly high protein values in September (Table 41). We noted seed bearing culms were the most common structures of *Poa sandbergii* during the September collection, and the high protein level and apparent increase at the end of the growing season may be a result of a large proportion of seeds in the sample.

The lowest CP occurred in *Danthonia intermedia* during the September 13th sample (5.91%). This was 1 of only 3 instances in which protein was below the 7% level considered adequate for maintenance of weight in non-lactating adult cattle. Level of CP for *Deschampsia cespitosa* was just below the 7% level (6.94%) during September, as was *Poa sandbergii* in August (6.62%). Total digestible nutrient (TDN) levels were greater than ~60%, a level considered adequate in cattle, in every sample.

The TDN:CP ratio was <8 for all samples in July, and increased to >8 for *Danthonia intermedia*, *Poa sandbergii*, and *Deschampsia cespitosa* in August, suggesting a deficiency of protein relative to energy for these species in August. *Festuca idahoensis* and *Poa sandbergii* were the only 2 species with a ratio below 8 in September, but the change in *Poa sandbergii* from >8 in August to <8 in September may have resulted from the large number of seeds in the sample.

Percentages of sodium (Na) and potassium (K) in *Carex nebraskensis* were much higher than amounts in other species. Levels of Na in *Carex nebraskensis* were twice those of any other samples in July, 3 times those of other samples in August, and 10 times greater than other samples in September, with the exception of the combined *Carex*

Table 41. Seasonal variation in crude protein (CP), total digestible nutrients (TDN), macro minerals, trace minerals, and forage index ratios for select plant species in the Hayden Valley during 2000. (All values based on dry weight). Percent diet includes July (the mean of diets estimated from fecal samples collected in 1998 and 1999), August (feces collected in August 2000), and September (feces collected in September 2000).

Date	Roughage (%)		Macro minerals (%)						Trace minerals (ppm)				Ratios		% Diet
Species[1]	CP	TDN	S	K	Na	Mg	Ca	P	Cu	Zn	Fe	Mn	TDN:CP	Ca:P	
July 5															
Feid	14.10	65.0	0.17	1.85	0.01	0.16	0.49	0.30	5	23	105	59	4.61	1.63	4.8
Dain	10.30	76.9	0.14	1.26	0.01	0.08	0.25	0.17	7	36	212	162	7.47	1.47	4.4
Posa	11.80	67.0	0.17	1.58	0.01	0.15	0.29	0.28	8	18	77	35	5.68	1.04	9.8
Dece	11.90	67.3	0.18	1.41	0.01	0.09	0.30	0.21	6	27	97	116	5.66	1.43	9.2
Cane	14.40	66.5	0.38	2.68	0.02	0.15	0.30	0.24	1	18	69	54	4.62	1.25	6.8
Carex spp.	13.20	69.6	0.35	1.95	0.01	0.14	0.49	0.23	29	34	129	248	5.27	2.13	19.0
August 19															
Feid	10.20	68.6	0.13	1.07	0.01	0.15	0.59	0.16	4	30	182	135	6.73	3.69	8.3
Dain	7.00	62.5	0.11	0.77	0.01	0.07	0.27	0.11	4	27	117	173	8.93	2.45	3.2
Posa	6.62	59.7	0.13	0.91	0.01	0.12	0.28	0.11	3	12	212	78	9.02	2.55	9.1
Dece	7.56	66.8	0.14	0.97	0.01	0.14	0.47	0.13	4	25	91	146	8.84	3.62	11.7
Cane	8.44	64.7	0.44	2.38	0.03	0.21	0.48	0.14	1	14	102	155	7.67	3.43	2.8
Carex spp.	9.19	69.1	0.20	1.04	0.01	0.21	0.62	0.15	15	33	102	216	7.52	4.13	25.4
September 13															
Feid	9.56	66.2	0.13	0.96	0.01	0.16	0.66	0.17	3	32	218	195	6.92	3.88	13.8
Dain	5.91	59.8	0.10	0.47	0.01	0.08	0.38	0.10	4	27	131	249	10.12	3.80	2.1
Posa	11.90	63.2	0.17	0.80	0.01	0.19	0.49	0.15	3	14	241	48	5.31	3.27	5.7
Dece	6.94	63.0	0.11	0.69	0.01	0.14	0.51	0.09	3	21	217	106	9.08	5.67	10.2
Cane	9.38	84.8	0.48	2.04	0.10	0.24	0.49	0.14	1	8	101	99	9.04	3.50	6.2
Carex spp.	7.94	64.6	0.30	1.40	0.04	0.16	0.62	0.16	3	24	193	378	8.14	3.88	23.2

[1] Carex spp. is combination of *Carex aquatilis* and *Carex rostrata*, other names are binomial representations of genus and species

aquatilis and *Carex rostrata* sample. Calcium (Ca) levels generally increased from July to September as expected, but Ca and phosphorus (P) concentrations were adequate in all samples and the Ca:P ratio remained below the level which can interfere with P metabolism in cattle.

For trace minerals, amounts of copper (Cu) were mostly below 8 ppm and amounts of zinc (Zn) were often below the 25-30 ppm concentrations reported to be adequate for bison (John Paterson, MT State University beef specialist, personal communication). Levels of sulfur (S) >0.21% in plants, as in the case of our *Carex* samples, and high levels of SO_4 in water >1000-1500 ppm may further interfere with utilization of Cu and Zn.

Remote sensing techniques for estimating productivity and offtake -- The following results using satellite imagery to estimate standing crop of herbaceous and possibly sagebrush biomass for the Hayden Valley and other portions of Yellowstone Park on different dates during the growing season are preliminary at this time. Final results will require completion of the cover type map and additional remote sensing and statistical analysis.

We applied regression results between clipped biomass and reflectance from the portable radiometer (Table 4) to radiometer readings taken within sampling grids and used kriging techniques to calculate current year's growth of herbaceous biomass in sample grids on 5 dates each during 1999 and 2000. Individual regressions of Table 4 were applied to corresponding grid samples taken during listed dates or within 2 days of listed dates for the 4 occurrences in 1999 and 5 in 2000. We sampled grids on days before and after August 6, 1999, but adverse weather conditions did not allow completion of field work for a separate regression at this time period. Therefore, we applied a regression extrapolated from the previous and successive time periods to the August 6, 1999 grid samples for the fifth estimate during 1999. We separated and discarded previous year's standing litter when we clipped vegetation used in conjunction with radiometer readings and thus we refer to estimates as current year's growth of herbaceous vegetation or simply "current herbaceous" rather than "standing crop" from exclosure data which was not sorted from previous year's standing litter.

Estimated biomass of current herbaceous within all grids was always within the estimated range from paired plots and from literature (Table 27). Smoothed curves of a low-productivity grid within the *Artr/Feid-Dain* phase cover type (Fig. 4) and from a wet carex meadow (Fig. 5) indicated similar phenological trends in biomass between grids each year but different trends between years. All grids in 2000 indicated a relatively steep decline in biomass during early August, similar to Figures 4 and 5. In comparison, all grids except 1 indicated a shallower decline during 1999. However, the grid with a steeper decline in biomass during 1999 was the only grid where we observed patches of vegetation grazed to approximately ground level during 1999 or 2000 and timing of observations correlated with the decline in vegetative biomass.

Results from the portable radiometer and clipped plots also indicated the potential to estimates biomass of sagebrush within grids using a combination of classification trees and a sagebrush specific regression. We have not attempted to apply those results to estimate sagebrush biomass at this time.

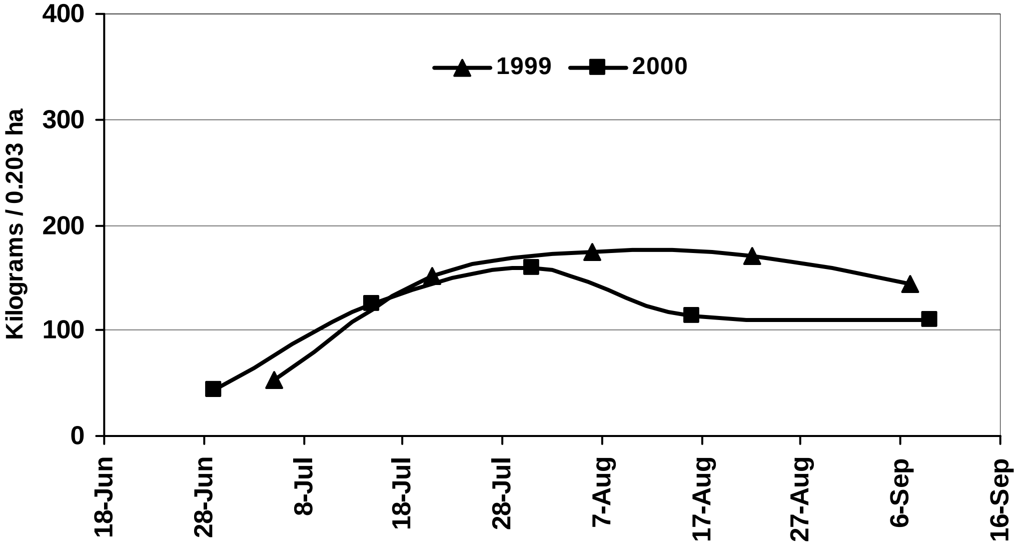


Fig.4. Estimated herbaceous biomass within a 45x45m (0.203 ha) sample grid of the *Artr/Feid-Dain* cover type in the Hayden Valley during 1999 and 2000.

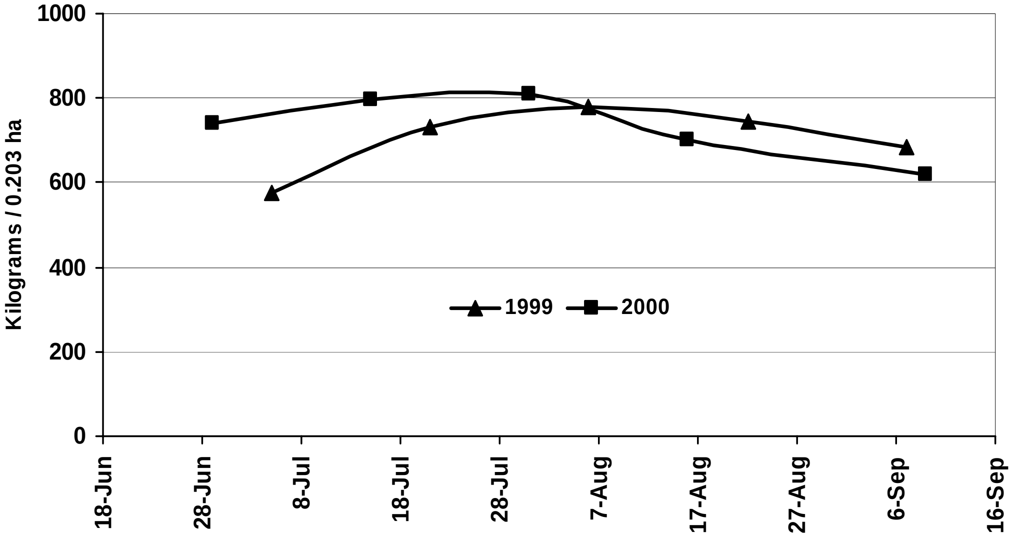


Fig. 5. Estimated herbaceous biomass within a 45x45m (0.203 ha) sample grid of the wet *Carex* meadow cover type in the Hayden Valley during 1999 and 2000.

Regression analysis indicated a strong linear relationship ($P < 0.00$; $R^2 = 0.98$; Fig. 6) between reflectance from satellite imagery and estimates of current herbaceous biomass within grids for a combined data set of satellite imagery encompassing 3 dates over 2 years (July 13 1999, September 15 1999, and July 15 2000) and corresponding grid estimates from data collected within 5 days of imagery acquisition. The 32 grid estimates used in the regression contained all 8 45x45m grids for each date and 8 30x30m grids from July 15, 2000. The following regression used the same predictors as those in the regression of biomass from reflectance of the portable radiometer (Table 4), the amount of light in red and NIR bands and an indicator variable for pixels containing the wet *Carex* cover type:

(A) Current Herbaceous Biomass (kg) = 203.50 – 2.38(Red) + 0.44(NIR) + 176.44(carex)

Addition of indicator variables controlling for atmospheric effects of non-atmospherically corrected imagery from 3 different dates were significant ($P < 0.00$) but only accounted for a slight increase in explanatory power (*i.e.* R^2 increased from 0.98 to 0.99) .

We applied Regression A without the “*Carex*” variable to all pixels within satellite scenes for the 3 dates of imagery, producing a pixel by pixel estimate of biomass extending >100km from the Hayden Valley to all areas within Yellowstone Park and beyond (Fig. 7). We were unable to include the “*Carex*” variable because we did not have a map that identified pixels with wet *Carex* cover groups for the area included in the images. Estimates for the Hayden Valley and for adjacent areas containing similar vegetation such as the Pelican Valley cannot be considered reliable until that time.

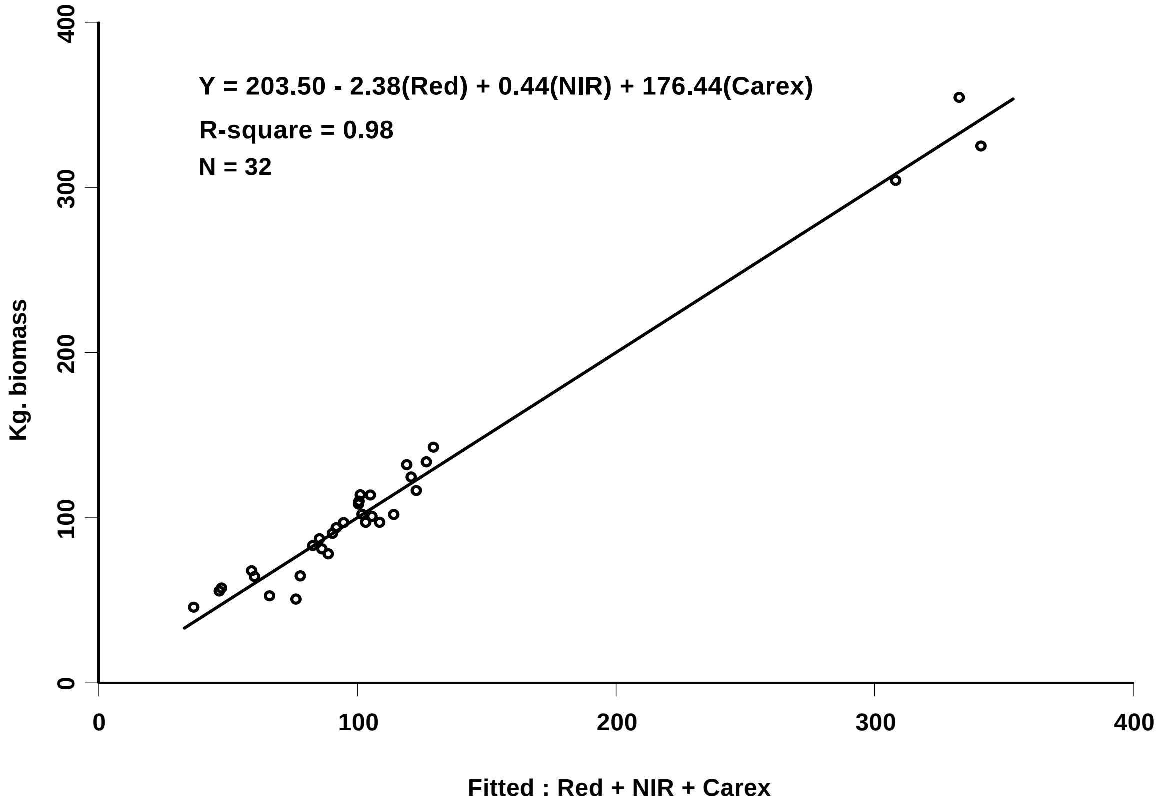


Fig. 6. Prediction of grid biomass from reflectance for 3 dates of Landsat imagery for the Hayden Valley during 1999 and 2000.

The process produced pixel by pixel estimates within expected ranges for the Hayden Valley (Table 28). Figure 7 gives a spatially explicit example of how MSR-based estimates of standing biomass can be used to identify areas with high or low productivity Pixels containing trees or water throughout the satellite scene seemed to “drop out” and form their own distinct categories. We currently have not compared estimates outside our study area to expected estimates within other cover types.

Estimated current herbaceous biomass (kg/ha) from pixels of satellite imagery within boundaries of the big sage and silver sage fixed sites on September 15, 1999 were very similar to estimates of standing crop outside exclosures from clipping estimates approximately 10 days later (Fig. 8 and 9). We did not compare the mesic graminoid site because the irregular boundary did not contain whole pixels of imagery to calculate a similar estimate as clip data. Considerably greater amounts of previous year's standing litter were observed at the silver sage site than the big sage site and accounting for it in clipping estimates (we have currently sorted but not yet weighed previous year's litter from 2000 as an estimate of the amount) will produce estimates of current herbaceous at fixed sites for a direct comparison to satellite estimates. Comparison between estimates

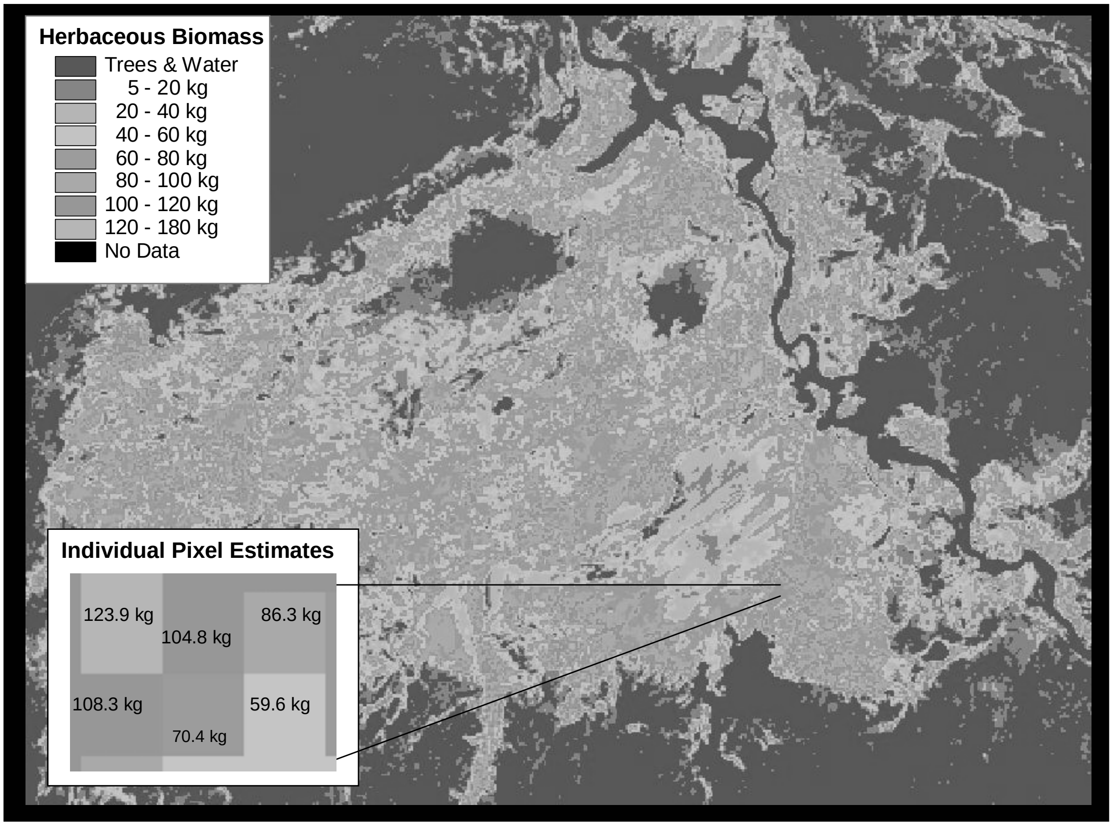


Fig. 7. Example of imagery regression (Fig.6) applied to all pixels within the scene of satellite imagery to produce estimates of herbaceous biomass within each ~30x30 m pixel

from satellite imagery and clipping will become closer at the silver sage site and farther apart at the big sage site. However, satellite estimates at the big sage site included the small area containing *Arca/Dece* within the overall boundary and adjusting for it will subsequently also decrease the satellite estimate for the big sage site. Confidence intervals of satellite estimates in Figures 8 and 9 only reflect the mean and standard deviation of pixels used in the estimate. Incorporation of all sources of error in estimates is an issue we still need to resolve.

Pixel values from the September 15, 1999 satellite scene were subtracted from the July 13, 1999 scene in a preliminary analysis testing this method for determining change in current herbaceous biomass and offtake. The 2 satellite scenes were not georeferenced to actual coordinates or registered to each other to assure the same locations on the ground were being used. Therefore, we did not use locations of areas we observed vegetation grazed to approximately ground level as a validation of the process. However, a random check of pixel differences indicated changes in biomass consistent with expected offtake and growth for this period. We also noted an area of the satellite scene interspersed with large increases and decreases in biomass, corresponding to center pivot fields and other agriculture areas outside Yellowstone Park to the southwest. Accuracy of biomass changes across both the distance and change in vegetation types these fields represent has not been checked, but the ability to detect changes suggests precise estimates from this method.

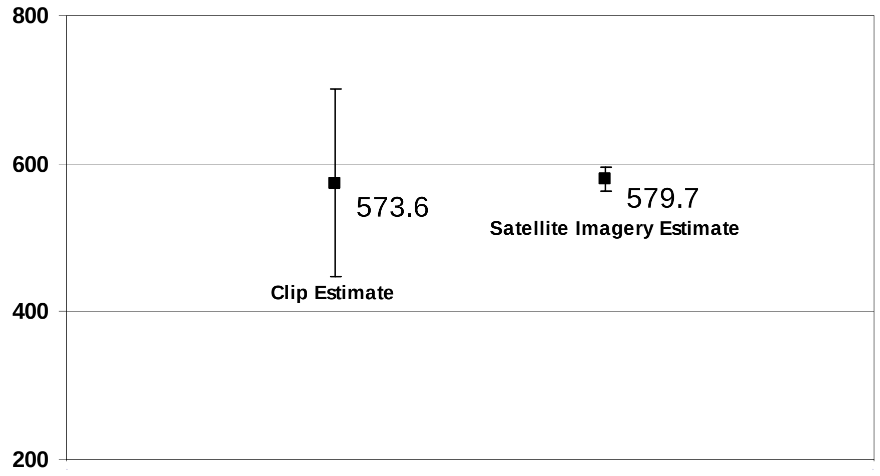


Fig. 8. Estimates of herbaceous biomass (kg / ha) at the big sage fixed site during fall 1999 from clipping data and mean of pixels (Fig. 7) within site boundary.

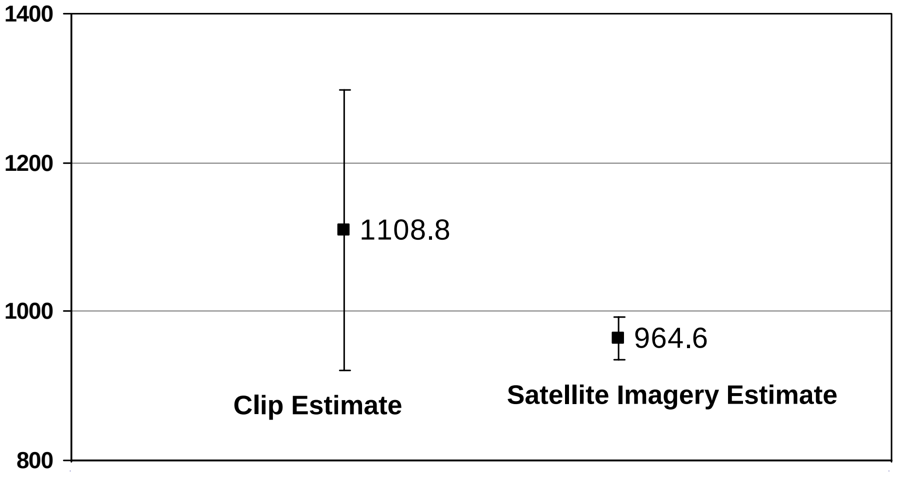


Fig. 9. Estimates of herbaceous biomass (kg / ha) at the silver sage fixed site during fall 1999 from clipping data and mean of pixels (Fig. 7) within site boundary.

DISCUSSION

1. Bison Seasonal Forage Use Patterns in the Hayden Valley.

Olexa and Gogan (in prep.) utilized radio-collared bison to determine movement patterns and broad habitat preference by season for all sub-populations associated with the Yellowstone bison herd. We focused on habitat use and foraging patterns for bison using one important bison range within YNP, the Hayden Valley. We examined habitat selection by bison from 2 perspectives: 1) bison selection at the plant community level (using multiple definitions of community, *e.g.* habitat type, dominant species, moisture regime, and plant physiognomy); and 2) dietary selection (by plant species/genus, taxonomic group, and forage quality/quantity). A wide array of data, collected from observation of unmarked bison, fecal counts, microhistological analysis of fecal samples, chemical analysis of vegetation, examination of vegetation for evidence of grazing and rubbing, MSR results, and clipping (in feeding exclusion cages and sites exposed to bison foraging), were used to address this objective. Where possible, we have attempted to go beyond description to explain why bison in the Hayden Valley have adopted the habitat use patterns we observed.

Delineation of habitat categories -- Categorizing vegetation has been a recurring theme in ecology for >100 years (Oosting 1956, Crow and Gustafson 1997). Most ecologists acknowledge that plant species composition and structure vary over a continuum in time and space rather than segregate into discrete units, but most also recognize that this continuum can be divided into units with “similar” characteristics for investigating aspects of plant and/or animal ecology and for practical applications such as mapping. In our study, we constructed units based on potential importance to bison (*i.e.* Which vegetation characteristics might be important enough to bison to drive them to discriminate among units?) modified by mapping constraints (*i.e.* Which vegetation characteristics can be reliably used to identify units?). The multi-level, semi-hierarchal categorization we developed (units based on dominant plant species nested within plant growth form/moisture regime categories) allowed us to identify units by direct observation or, potentially, indirectly through satellite imagery. The system also allowed us to recombine units to test different hypotheses that might explain bison habitat use patterns.

Previous attempts to classify vegetation in the Hayden Valley were either too general to be useful in explaining bison habitat preference (Despain 1990), developed to explain distribution of other animal species (Graham 1978), or developed to describe vegetation at the state or regional level (Mueggler and Stewart 1980, Hansen *et al.* 1995). Our system will facilitate mapping based on remote imagery (using a combination of LANDSAT and IKONOS imagery) and can be easily employed by personnel in the field. The comprehensive key we developed (Appendix B) requires field personnel to use <20 plant species to identify vegetation units.

Bison use of vegetation categories -- The 3-tiered vegetation classification scheme we developed allowed us to examine many aspects of forage use by bison in the Hayden Valley. As the largest block of gentle terrain dominated by the grassland and shrubland vegetation preferred by bison (Meagher 1973, Reynolds *et al.* 1982) in the central area of YNP, the importance of the Hayden Valley to bison is not surprising.

Within the Hayden Valley, however, we found that bison displayed a complex pattern of habitat selection. While this high elevation, non-forested valley has been frequently mapped as a single vegetation unit (Mattson and Despain 1985), we identified a minimum of 17 vegetation communities and demonstrated that bison differentially utilized (and presumably recognized) many of these communities.

We used a point-intercept technique to determine the proportion of different vegetation categorization units in 2 representative areas (the West Alum and Crater Hills blocks) of the study area. Only 3 of the 22 cover types we identified comprised >10% of the 1,668 points measured: *Artr/Feid* (27%); *Arca/Dece* (15%); and *Arca/Feid* (14%). When vegetation was categorized by cover group (based on plant structure and moisture regime), the dry shrub group was the most abundant category (49% of 1,668 points). Other common types included the moist graminoid group (17%), the moist shrub group (16%), and the intermediate graminoid group (13%). When only dominant graminoids were considered, Idaho fescue (*Festuca idahoensis*) was dominant or co-dominant at 57% of the points we sampled. Tufted hairgrass (*Deschampsia cespitosa*) (37% of points), Bearded wheatgrass (*Agropyron caninum*) (9%), Sandberg bluegrass (*Poa sandbergii*) (5 %), and Timber oatgrass (*Danthonia intermedia*)(3%) were also common dominants. Several sedge species (*Carex* spp.) were common in wet sites (dominant or co-dominant at 7% of points).

Grazed loop surveys indicated that the highest frequencies of grazing occurred in the *Posa* (78% of 51 plots sampled were grazed), *Artr/Posa* (76% of 41 plots), and *Arca/Feid* (68% of 235 plots) cover types. We did not test use versus availability by cover type because of small sample sizes for several cover types, but the *Arca/Feid* type was the only 1 of the 3 top types that comprised >10% of the points sampled.

When use was contrasted with availability for cover groups, bison selected the dry shrub and dry graminoid cover groups and avoided moist shrub and moist graminoid types, at least during summer. Data from paired cages also suggested a summer preference for dry plant communities in that bison removed a larger percentage of standing biomass from dry graminoid and shrub types than from wetter types during summer. As with point-intercept data, preferred cover types and cover groups had understories dominated by native xeric bluegrasses (such as *Poa sandbergii*), Idaho fescue, and bearded wheatgrass.

When we examined offtake of vegetation at the catena scale (*i.e.* landscape units comprised of several habitat types that occur repeatedly in a predictable sequence) via our fixed cage arrays, we again found the highest summer offtake in a dry, upland community complex (big sage site). In contrast, bison fecal counts within the fixed cage sites were highest in the mesic graminoid site. This may have been an artifact of differing habitat use in the non-growing season or simply an indication that fecal counts were not highly correlated with forage offtake.

Data collected from randomly placed paired cages and from randomly selected plots in fixed cage sites allowed us to estimate the relative intensity of utilization of plant communities by bison during spring. Although estimated percentage offtake in spring derived from paired cages was highly variable (and subsequent statistical tests ambiguous), cages clipped in dry communities, especially those with Idaho fescue or Sandberg bluegrass understories, tended to have the greatest percent offtake and wetter communities the lowest percent offtake. Spring offtake at the fixed cage sites was lower than at paired cage sites, but the mesic grassland site had much lower estimated percent offtake than the drier big sage and silver sage sites.

Our estimates of over-winter offtake from paired and fixed caged sites were possibly influenced by small mammal activity and/or mechanical and biological degradation of residual vegetation, but relative differences between residual vegetation measured inside and outside exclosure cages again indicated much higher proportionate removal of standing vegetation in dry communities than in wetter communities in randomly paired sites. Clips of residual vegetation at our fixed sites indicated much lower offtake through the non-growing season than we measured at paired cages and no difference in percent offtake among the 3 catenas (big sage, silver sage, mesic graminoid) we sampled.

When we compared offtake only in terms of biomass removed per unit area, bison were able to harvest the same or greater amounts of biomass by taking a relatively low percentage of the standing herbaceous vegetation in many mesic communities as they harvested by taking 50% or more of the standing herbaceous biomass in dry communities. Although we measured high percent offtake and grams offtake in some plant communities, several mesic communities yielded more plant biomass per unit area for bison than the apparently favored dry graminoid communities in spring, summer, and over winter.

The overall picture that emerged from our line-intercept and clipping results was bison selection for sites with relatively low productivity of herbaceous vegetation. The big sage, Idaho fescue, and Sandberg bluegrass communities which had greater than expected grazing intensity produced <25% of the biomass produced in sedge and mesic graminoid communities that were utilized much less heavily. This pattern does not appear logical for a species classified as a “bulk feeder” (Reynolds *et al.* 1982). Assuming forage access and quality are similar, a large ruminant such as a bison could theoretically forage more efficiently in a highly productive sedge community than in a low productivity Sandberg bluegrass community.

Microhistological analysis of plant epidermal fragments from fecal samples indicated a different feeding strategy. Graminoids made up >90% of the overall summer and early fall diets for bison in the Hayden Valley during 1998 – 2000. This was expected (Meagher 1973, Reynolds *et al.* 1982). The graminoid taxa dominant in the summer – early fall diet were not expected based on data we collected from the point-intercept surveys and from clipped plots. Fecal analysis indicated that 49% of the overall summer – early fall diet was comprised of mesic grasses and graminoids (sedges, rushes, etc.) associated with the wet sites bison apparently utilized at low intensities. Of grasses abundant in the favored dry plant communities we identified from point-intercept surveys and clipping, only native bluegrass (probably mostly *Poa sandbergii*) contributed >10% (overall monthly mean = 11.1%) to the overall diet. Idaho fescue, the dominant grass in several dry plant communities apparently favored by bison comprised 8% of the overall summer – early fall diet while tufted hairgrass (*Deschampsia cespitosa*), a dominant graminoid in several communities apparently avoided by bison, made up >9% of the overall summer – early fall diet.

Analyses of nutritional value of 6 common herbaceous taxa indicated that all of the taxa maintained the 7% crude protein level commonly identified as necessary for “maintenance” in cattle (Weinmann 1955) during summer and early fall except timber oatgrass (*Danthonia intermedia*). Even this species maintained a minimum crude protein in fall of nearly 6%, a value reported to be close to maintenance for adult white-tailed deer (*Odocoileus virginianus*) (Verme and Ullrey 1984) and presumably more than adequate for adult bison.

Levels of other macro nutrients, micro nutrients, and digestible energy were reasonable in all of the 6 taxa. Crude protein, total digestible nutrients, and fecal nitrogen declined from July to September in all taxa, but this was an expected consequence of vegetation senescence. Similarly, calcium to phosphorus ratios and ratios of digestible energy to protein increased as plants matured and senesced. Timber oatgrass, the species least frequently ingested of the 6 taxa tested, did have total digestible nutrients to protein (10:1 rather than the 8:1 ratio regarded as a threshold for poor forage quality) and calcium to phosphorus ratios (~4:1 rather than the desired 1 to 2:1) that were undesirable by September, but taxa that were frequently eaten had similar ratios.

Despite superficially contradictory results, our data indicate that bison exhibit a biologically rational grazing strategy in the Hayden Valley. We believe that bison in the Hayden Valley select grasses in dry plant communities until they cannot efficiently harvest them (apparently the threshold for offtake on low growing species such as Sandberg’s bluegrass and Idaho fescue is 50-60% during summer). Searches for ungrazed patches or grazed patches with regrowth in favored xeric plant communities drive bison herds to move back and forth across the Hayden Valley during summer and fall. Bison utilize mesic communities adjacent to dry shrub and grass stands throughout the summer and ingest substantial amounts of forage from these moist communities, but they avoid heavy utilization of mesic communities until the easily harvested forage in dry communities is exhausted.

Based on our chemical analyses, Sandberg bluegrass and Idaho fescue, dominants in several of the xeric plant communities favored by bison, had reasonable nutritional values but were not outstanding compared to graminoid species abundant in mesic communities. For example, Idaho fescue is generally acknowledged to be a very desirable forage plant while Sandberg bluegrass, a species ranked higher in bison diets than Idaho fescue, is regarded as good but not outstanding (Mueggler and Stewart 1980) and of comparable forage quality to timber oatgrass and tufted hairgrass, species dominant in several mesic plant communities that bison evidently avoided in summer. The attraction of grasses associated with dry plant communities to bison in the Hayden Valley may be due to some combination of characteristics which we did not discover (perhaps these species are simply better tasting than the mesic graminoids), or use of dry plant communities in preference to mesic communities may be an artifact of the problems heavy animals such as bison have in foraging on wet soils. Bison may make less use of wet sites simply because they become stuck in the mud.

2. Determine long and short term effects of ungulate foraging on vegetation in the Hayden Valley

Three years of field research is a generous time span for a funded study but is far too short to track long-term changes due to grazing in the Hayden Valley. We had hoped that photographic or LANDSAT imagery would allow us to address some aspects of change, such as erosion, but we did not locate appropriate imagery in our preliminary searches and were forced to abandon attempts to locate this material due to time constraints. We did determine that bison were responsible for >90% of large herbivore activity in the Hayden Valley (based on fecal counts and observation) at the time of our study. Elk impacts were low (<10% of fecal counts and observations) throughout the Hayden Valley, but elk were more common in the western portion of the valley than the eastern portion, and potential impacts from elk were more likely along the forested margins of the valley than in the central grass/shrublands.

Incidental observations indicated that bison were responsible for erosion along trails and in wallows, but we were not able to determine if erosion was increasing. Bison were capable of creating an unvegetated wallow at a site that supported apparently average vegetation density in 1 to a few days. Subtle patterns in vegetation species composition, plant distribution, and/or terrain micro-physiognomy suggested that wallows were frequently created and re-vegetated, but we were unable to develop techniques for measuring either the extent of land disturbed by wallows or the rate of succession in re-vegetation of wallows. The high level of damage to trees on the margin of the Hayden Valley (91% of trees damaged and 28% dead along the valley margin) demonstrated that ungulates, probably bison, were effective in slowing invasion of the shrub and grasslands by trees or, perhaps, extending grassland into the forest margin.

Short-term impacts were more easily determined. Bison removed significant proportions of spring, summer-fall, and residual winter biomass from the herbaceous component of several grass and shrub communities in the Hayden Valley. The data we collected from paired cages randomly assigned and semi-randomly distributed in the Crater Hills and West Alum Creek areas of the Hayden Valley indicated that bison utilized ~25% of new growth in spring (May to early June) over all cover types. We did not detect differences between the 2 years sampled, 1999 and 2000. Dry and intermediate moisture plant communities were utilized twice as heavily as mesic communities (38% estimated removal versus 14%). The average offtake for spring growth over 2 years at the dry big sage fixed site was 29%, compared to 8% at the mesic graminoid site.

Our data from paired cages indicated that bison removed 36% of standing biomass (across all common cover types) from June through September. We were unable to detect differences among the 3 growing seasons (1998, 1999, and 2000) we monitored. Over these 3 years, mean percent offtake among cover types varied from >50% (*Posa* and *Artr/Cana*) to <20% (*Carex* and *Dece/Carex*). Plant communities with the lowest productivity (xeric grass and shrub types) tended to experience higher utilization than more productive, mesic plant communities. Data from clipping at fixed sites supported this pattern. Percent forage offtake at the driest site (big sage) averaged 36% over 3 growing seasons versus 14% offtake for the mesic graminoid site.

Changes in residual vegetation over winter were likely influenced by factors other than bison grazing (*i.e.* small mammal activity, mechanical degradation from snow, and/or activity of bacteria and fungi), but, over all cover types, 45% of residual vegetation disappeared over winter in the 2 winters (1999 and 2000) we sampled. Dry grass types lost 76% of residual vegetation, nearly 3 times the loss recorded for wet graminoid and shrub types (28% disappearance). Disappearance of vegetation over winter was similar (~30%) for all 3 fixed cage sites.

The extent of utilization of the herbaceous standing biomass during the growing season in most plant communities was <50%. This would indicate light to moderate stocking rates were the Hayden Valley being managed for livestock using traditional, conservative pasture management guidelines (*i.e.* "take half, leave half") (Stoddart and Smith 1955). Frank and McNaughton (1993) have demonstrated that grazing can stimulate production in graminoids in the Yellowstone ecosystem which could mean that offtake of >50% is acceptable in graminoid-dominated plant communities in YNP. However, if bison regraze the same plants during a single grazing season or consistently return to the same plants during consecutive seasons, 50% offtake in the heart of the growing season combined with >30% utilization in early spring, and possibly >70% utilization of residual standing vegetation over winter (offtake we calculated in paired cage studies in some communities favored by bison) may be more than some dry plant communities can withstand over long periods of time. In plant communities with understories dominated by Sandberg bluegrass and Idaho fescue, species indicative of xeric plant communities favored by bison, 62% of 110 plots we followed for 2 years were grazed by bison in both years, and 50% of 30 plots we followed for 3 years were grazed by bison in all 3 years.

The abundance of timber oatgrass, a species that was consistently low in bison diets, in plant stands that met microclimate, soil, and slope characteristics typical of conditions expected for Idaho fescue stands may indicate that past use of these areas by bison has already led to decreases in graminoids favored by bison. With no data to trace changes at individual sites over long periods of time, we cannot verify any changes in graminoid or shrub communities in the Hayden Valley due to bison herbivory, but this is definitely a situation worth monitoring.

3. Determine efficacy of vegetation monitoring approaches

We used several approaches to monitoring vegetation status and/or use of vegetation by large herbivores. All of the approaches could be incorporated into a viable monitoring program, but each approach had disadvantages as well as advantages. The "gold standard" for monitoring vegetation biomass and biomass utilization is the grazing exclosure approach. In this approach, herbivores of concern are excluded from grazing some plots and allowed access to others. Differences between plots open to grazing/browsing and those from which grazing/browsing is excluded provide the most defensible estimates of production within a plant community over the exclosure period and of utilization of biomass by herbivores during the same period. This approach, however, requires extensive and intensive allocation of resources to provide accurate estimates of trends in vegetation production at large scales (A team of 2 people required 0.5 to 3 hours to clip and sort photosynthesizing from non-photosynthesizing biomass for a single 0.33-m^2 plot); it cannot account for production stimulated by grazing (McNaughton and Frank 1993) without labor intensive movement of cages within the growing season; it is potentially subject to biases due to the presence of cages (attraction of small mammals, changes in microclimate within cages, leaching of chemicals from cage materials into soil, etc.) (Litvaitis *et al.* 1994); it cannot accurately detect very light grazing; and results are almost always based on sample sizes that are smaller than desirable and distributed less than ideally.

We tested several factors that may have influenced results of our clipping/caging techniques in the Hayden Valley and found that bison herbivory was sufficiently intense to be consistently detectable in favored plant communities using relatively low sample sizes. Cage effects, if present, were small compared to herbivore effects. Small mammal activity and mechanical and biological degradation of standing vegetation probably did influence our estimates of standing biomass and offtake in some plant communities, but effects from these sources were small compared to effects attributable to bison (with the possible exception of over winter loss of standing biomass to mechanical or biological degradation). Estimates of standing crop were consistent with published estimates for biomass in similar plant communities in other areas indicating that our samples were reasonably adequate and our clipping protocol was appropriate, but we did not determine the contribution of individual plant species to total biomass. Without information on species composition, we could not follow major changes in community makeup that might occur with long term over grazing. Estimating canopy coverage by species would have added 20 - 30 minutes per plot and would require personnel able to identify most species present in the Hayden Valley. Adding this approach to biomass estimation at the plot level would provide only marginally reliable information on the proportionate contribution of each species to standing biomass. Collecting information on biomass by species would have added 1 to 3 hours to each plot sampled. Overall time per plot for biomass estimation by plot or by species could be reduced by double sampling (i.e. clipping a few calibration plots and estimating biomass at other plots), but this would also reduce accuracy of estimates and increase the vulnerability of estimates to errors due to poorly trained or motivated personnel.

The point-intercept approach we used in sampling vegetation in the Crater Hills and West Alum blocks with the grazing loop was inexpensive, quick, and allowed us to cover large areas in a short period of time. When data were collected by personnel who were very familiar with the plants species and growth characteristics of the Hayden Valley, the results of this approach were generally in agreement with results from clipping (*i.e.* both techniques indicated bison favored dry plant communities). By randomizing starting points for transects and the distance between individual sample points along transects, we were able to develop estimates of proportions of different habitat categories in areas we sampled and relative intensity of grazing within habitat categories. The estimates of biomass offtake produced using this technique were lower than that those calculated based on clipped plots. This approach did not provide estimates of standing biomass or species composition at individual sample points, and, because this technique called for quick judgments on plant community and intensity of grazing, results could be very subjective, especially with poorly trained or motivated personnel.

A portable MSR unit (Pearson et al. 1976) produced accurate estimates of standing biomass during the growing season with minimal investment of time and labor in clipping plots. When used with calibration clips within a few days of the MSR estimation, our regressions accounted for 84 - 97% of the variability in biomass in vegetation plots (with the inclusion of a classification variable to identify wet sites). When the presence or absence of sagebrush at a sampling point was included as an additional classification variable, we were able to empirically estimate both herbaceous and shrub green biomass (Olenicki and Irby unpubl.) at each point with >80% accuracy.

The portable radiometer would allow personnel involved in a monitoring program to spend 1 day calibrating the MSR unit to clipped plots and, because each radiometer sample takes <30 seconds, then sample vegetation as fast as a person could walk for the next week. Instead of sampling 10 to 20 plots per day using a 2-person team, 1 person could estimate biomass at hundreds or thousands of points per day (with sample numbers limited primarily by distance between sampling points).

Although we believe that results are more reliable if calibration plots are clipped within a few days of MSR sample plots, our data suggest that 1 set of calibration plots may provide useful data for biomass estimation over a full growing season or, perhaps, over several years . We used data from 12 sampling periods to come up with a single regression that explained 81% of the variation in biomass variability within clipped calibration plots.

We also tested biomass estimation from satellite imagery. This process involved a double-sampling procedure. A regression formula was developed from the relationship between biomass clipped in 0.75-m^2 plots and reflectance measured at the same plots using a ground-based radiometer. This regression was then used to convert samples of reflectance obtained from the ground-based radiometer in a 45 x 45-m plot to an estimate of biomass in the 45 x 45-m plot. Biomass estimates in 10 or more 45 x 45-m plots were then used to create a regression formula that utilized reflectance values in pixels representing those plots taken from LANDSAT imagery to estimate the relationship between reflectance in a pixel and standing biomass on the ground. Although we were unable to satisfy all the theoretical considerations in developing error terms around estimates, we derived empirical formulae that would explain 83 to 96% of the variability between reflectance and herbaceous biomass estimates – when the moisture (wet vs. dry) and shrub status (presence vs. absence and sage vs. other shrub species) of the pixel was known. This suggests that 1 or 2 days of calibration clipping and measurement of reflectance in 45 x 45-m plots would allow monitoring of standing biomass for the entire Hayden Valley (or for all open vegetation in YNP if imagery were obtained) at a given point in time. Use of fixed reflectance sites (water surfaces, unvegetated soil, roads, empty parking lots, etc.) in calibrations may allow extension of pixel by pixel biomass estimates in herbaceous and shrub communities back in time through the first LANDSAT imagery from the 1970s. This would require geo-referencing of pixels in different images and an accurate map of cover types in the Hayden Valley.

The ability of all monitoring approaches to detect changes in vegetation would be improved if an accurate, spatially explicit habitat map of the Hayden Valley were available. We were unable to complete such a map, but we strongly recommend that YNP provide funding for completion of this map. We believe that high resolution IKONOS satellite imagery from Space Imaging will provide a reliable means of categorizing grass and shrub communities in the Hayden Valley at a very fine scale. First available in 2000, this imagery provides 4m multispectral and 1m panchromatic data. We did preliminary work on identifying reflectance characteristics of vegetation types we defined in the Hayden Valley, and a combination of the panchromatic data (for distinguishing grassland from sites with shrub presence) and reflectance is 1 or more bands will allow a pixel by pixel categorization of vegetation cover types at the 4-m scale with accuracy in excess of 80% on most types.

4. Estimate annual production and standing crop available during non-growing seasons for herbaceous and shrub layers in major habitat types in the Hayden Valley.

Frank and McNaughton (1993) demonstrated that standing biomass protected from grazing by enclosures does not provide a true estimate of herbaceous plant annual productivity in YNP because herbivory can stimulate biomass production. The data used to estimate the extent of production stimulus by grazing were collected using intensive measurements at a few small sites scattered over the northern range of YNP (Frank 1990) This approach is not realistic for obtaining large scale estimates of herbaceous productivity. Sampling sufficient sites to obtain valid, community-level estimates of plant productivity when exclosure cages must be moved and resampled several times during a growing season is highly unlikely to impossible, given restraints on equipment, time, and personnel available for plant monitoring in YNP. Data from Frank (1990) suggest that sites protected from grazing for the entire growing season might produce 10% less biomass, on average, than sites exposed to grazing, but given variability in productivity among sample sites, we doubt that this small a difference is realistically detectable. As an alternative, exclosures set up at the beginning of the growing season and clipped at the end of the growing season should give reasonable production estimates in most plant communities.

Estimates of productivity obtained from exclosures can also be biased by cage effects. Our tests (differential small mammal activity in or out of cages; microclimatic effects of cages on plant growth or decomposition) indicated that any biases due to cage effects were likely to be small in plant communities of the Hayden Valley.

Exclosure data we collected indicated herbaceous productivity in the Hayden Valley varied from <900 kg/ha in dry graminoid communities (Feid/Agca: 874 kg/ha; *Posa*: 894 kg/ha) to >3,300 kg/ha in wet *Carex* communities. Most values for individual plant communities in each year fell within ranges estimated for other areas in the Northern Plains or Rocky Mountains (Wilbert 1963, Mueggler and Stewart 1980, Kovalchik 1987).

Overall, our exclosure cage data indicated that herbaceous plant productivity in the Hayden Valley (~250 km^2) during the 1998-2000 growing seasons varied from 8,900 to 12,000 metric tons. Comparisons of plots protected by cages with adjacent sites open to grazing indicated that large mammals removed 2,800 to 4,200 metric tons per growing season over the same 3 years. Assuming an average bison weight of 500 kg (Reynolds *et al.* 1982) and an average intake of 2% body weight (dry weight of forage) over a 150-day growing season (May through September in the Hayden Valley), approximately 2,300 bison would be required to utilize 3,500 metric tons of forage. During 1998-2000, the central bison herd averaged around 2,000 individuals. This suggests that our offtake estimates were reasonable; and, because offtake and standing biomass were based on the same methodology, our estimates of herbaceous productivity were probably reasonable.

We were unable to utilize reflectance values from satellite imagery to estimate community productivity or overall productivity for the Hayden Valley. Our preliminary data indicate that regressions derived from the 2-stage sampling scheme we used accurately predict standing biomass at the pixel level. This provides a useful device for explicit spatial mapping of standing biomass in graminoid and shrub communities of the Hayden Valley (see Fig. 9), but it does not yield estimates of productivity in a system where herbivores remove >25% of the annual production over the course of the growing season. With geo-referenced pixels and an accurate map of plant community distribution, satellite imagery does have the potential to answer many questions about bison use of plants. Geo-referencing will allow direct comparison of pixels from one month to another and in the same months over different years to track consistency of plant growth/utilization over time. It would also allow personnel monitoring vegetation to construct a series of pixel-sized exclosures to track changes in biomass in the absence of herbivory by large mammals over time. An accurate vegetation map, a very feasible product that could be developed from IKONOS imagery, would allow researchers (or monitoring personnel) to track changes in standing biomass and phenology in specific plant communities over time. We strongly urge YNP to complete the vegetation map of the Hayden Valley and to devote resources to LANDSAT imagery interpretation.

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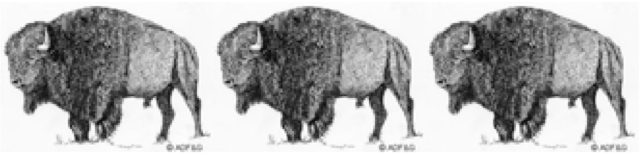

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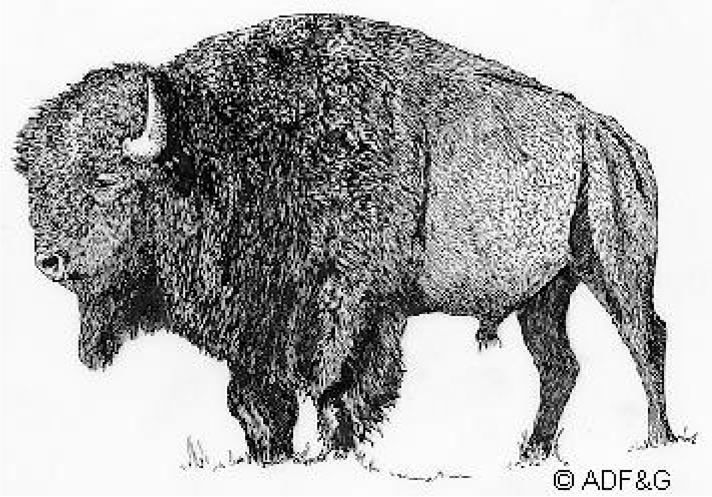

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APPENDIX A

TABLES 42 - 51

Table 42. Mean weight (grams / $0.33m^2$) and percent of total new growth of forbs and graminoids clipped at fixed sites prior to placement of exclosures during May 1998 in the Hayden Valley.

	Forbs		Graminoids	
Site	Weight	Percent	Weight	Percent
Big sage	1.8	38.5	2.9	61.5
Silver sage	1.4	26.6	3.8	73.4
Mesic gram.	1.4	14.2	8.6	85.8

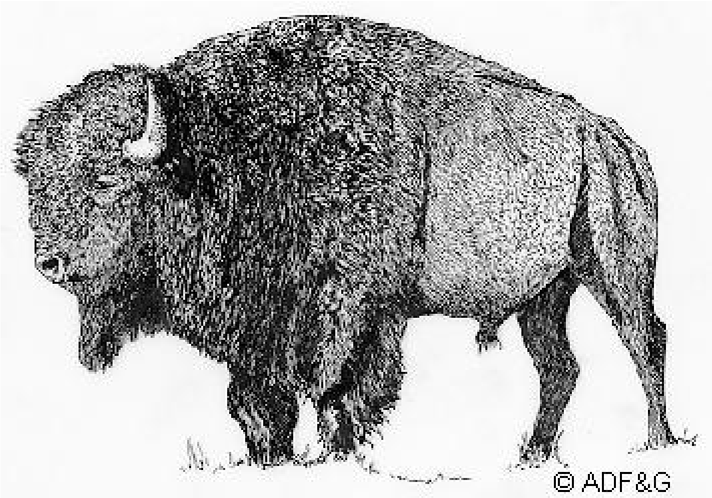


Table 43. Means and standard deviations (SD) for adjusted percent offtake (APO), adjusted grams offtake (AGO), and biomass production inside exclosure (Bio.), by year, for all seasons at fixed exclosure sites during 1998, 1999, 2000 in the Hayden Valley. Mid-summer numbers are means of estimated biomass from the portable radiometer and standard deviations are therefore not included.

Parameter	1998				1999				2000			
Site	n	APO (SD)	AGO (SD)	Bio. (SD)	n	APO (SD)	AGO (SD)	Bio. (SD)	n	APO (SD)	AGO (SD)	Bio. (SD)
Standing crop												
Mesic gram.	20	10.2 (12.2)	8.0 (9.8)	77.3 (16.5)	19	16.5 (15.2)	10.5 (9.0)	68.2 (12.7)	20	16.5 (15.9)	17.0 (18.9)	92.5 (30.5)
Silver sage	20	18.3 (22.2)	11.1 (14.1)	51.7 (13.2)	20	18.5 (18.2)	8.5 (9.2)	42.5 (9.0)	20	21.0 (24.7)	12.8 (17.3)	53.6 (13.2)
Big sage	19	32.4 (31.6)	9.9 (12.8)	22.9 (14.6)	20	37.5 (26.7)	13.7 (12.8)	31.7 (13.2)	17	38.8 (33.9)	12.1 (12.8)	26.1 (12.0)
Spring new growth												
Mesic gram.		---	---	---	20	12.8 (19.9)	1.6 (2.6)	13.0 (10.4)	20	4.2 (9.3)	0.6 (1.4)	12.6 (3.8)
Silver sage		---	---	---	20	21.2 (23.2)	1.1 (1.5)	4.4 (2.0)	20	19.1 (25.5)	1.7 (2.4)	7.0 (2.4)
Big sage		---	---	---	20	33.2 (24.0)	3.8 (3.7)	10.4 (4.0)	20	25.5 (25.2)	4.1 (5.1)	11.6 (5.9)
Residual												
Mesic gram.		---	---	---	20	33.7 (30.8)	15.1 (15.1)	40.4 (14.4)	20	39.3 (33.9)	17.7 (23.0)	32.4 (23.8)
Silver sage		---	---	---	20	26.0 (23.4)	7.6 (7.8)	27.2 (9.9)	20	30.2 (35.8)	8.2 (10.7)	24.2 (11.5)
Big sage		---	---	---	20	30.7 (38.1)	3.9 (8.4)	8.5 (9.9)	20	34.1 (37.6)	3.3 (5.7)	6.9 (6.2)
Mid-summer												
Mesic gram.	20	4.3	3.4	77.8	20	3.7	2.1	63.7	20	8.6	8.1	91.9
Silver sage	20	3.6	2.2	53.6	20	5.3	2.5	40.9	20	14.2	7.9	52.8
Big sage	20	27.3	7.8	23.4	20	24.6	7.7	27.5	20	72.0	28.1	38.2

Table 44. Results of ANOVA comparing mean values of APO, AGO, and biomass inside exclosure of paired plots between Crater Hills and West Alum sites for standing crop at the end of the growing season, new growth in the spring, and over-winter residual vegetation using equal sample sizes from each site during 1999 and 2000 in the Hayden Valley.

Parameter Variable Category	N	Mean	(SD)	95% C.I.[a]	ANOVA results df	 F-value	 P-value
APO - standing crop							
Site					1, 52	0.002	0.96
Crater Hills	27	36.5	(28.8)	a			
West Alum	27	36.9	(27.8)	a			
AGO - standing crop							
Site					1, 52	0.91	0.35
Crater Hills	27	13.9	(11.2)	a			
West Alum	27	17.5	(16.3)	a			
Biomass of standing crop in cage							
Site					1, 52	0.31	0.58
Crater Hills	27	47.8	(27.9)	a			
West Alum	27	52.6	(35.5)	a			
APO - spring new growth							
Site					1, 22	0.04	0.85
Crater Hills	12	31.9	(20.4)	a			
West Alum	12	30.2	(24.4)	a			
AGO - spring new growth							
Site					1, 22	0.07	0.79
Crater Hills	12	9.8	(7.0)	a			
West Alum	12	10.9	(11.9)	a			
Biomass of new growth in cage							
Site					1, 22	2.40	0.14
Crater Hills	12	27.0	(11.3)	a			
West Alum	12	35.7	(15.7)	a			
APO - residual vegetation							
Site					1, 22	0.05	0.83
Crater Hills	12	57.8	(33.2)	a			
West Alum	12	60.8	(33.6)	a			
AGO - residual vegetation							
Site					1, 22	0.97	0.34
Crater Hills	12	12.2	(10.7)	a			
West Alum	12	8.5	(7.9)	a			
Biomass of residual vegetation in cage (g/0.33m^2)							
Site					1, 22	1.46	0.24
Crater Hills	12	20.6	(19.0)	a			
West Alum	12	13.3	(8.4)	a			

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Table 45. Results of ANOVA comparing mean values of APO, AGO, and biomass inside exclosure of paired plots between years, cover types, and interaction of year and cover type for standing crop at the end of the growing season using equal sample sizes each year during 1998, 1999 and 2000 in the Hayden Valley.

Parameter Variable Category	N	Mean	(SD)	95% C.I.[a]	ANOVA results df	 F-value	 P-value
APO - standing crop							
Year					2, 69	1.16	0.32
1998	28	32.3	(30.3)	a			
1999	28	36.4	(28.6)	a			
2000	28	42.1	(22.4)	a			
Cover type	28				4, 69	6.42	<0.000
Interaction					8, 69	0.95	0.49
AGO - standing crop							
Year					2, 69	0.24	0.79
1998	28	15.4	(16.2)	a			
1999	28	17.2	(16.2)	a			
2000	28	18.2	(13.5)	a			
Cover type	28				4, 69	0.33	0.86
Interaction					8, 69	1.54	0.16
Biomass of standing crop in cage							
Year					2, 69	0.32	0.73
1998	28	46.4	(23.3)	a			
1999	28	49.9	(24.0)	a			
2000	28	49.1	(32.9)	a			
Cover type	28				4, 69	28.82	<0.000
Interaction					8, 69	1.68	0.12

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Table 46. Results of ANOVA comparing mean values of APO, AGO, and biomass inside exclosure of paired plots between years, cover types, and interaction of year and cover type for new growth in the spring and over-winter residual vegetation using equal sample sizes each year during 1999 and 2000 in the Hayden Valley.

Parameter Variable Category	N	Mean	(SD)	95% C.I.[a]	ANOVA results df	F-value	P-value
APO - spring new growth							
Year					1, 36	0.09	0.77
1999	24	23.1	(20.0)	a			
2000	24	24.7	(20.9)	a			
Cover type	24				5, 36	3.84	0.007
Interaction					5, 36	0.37	0.86
AGO - spring new growth							
Year					1, 36	0.11	0.74
1999	24	8.7	(9.7)	a			
2000	24	8.0	(8.1)	a			
Cover type	24				5, 36	4.11	0.005
Interaction					5, 36	0.32	0.90
Biomass of new growth in cage							
Year					1, 36	0.04	0.85
1999	24	31.2	(13.6)	a			
2000	24	30.6	(9.6)	a			
Cover type	24				5, 36	1.42	0.24
Interaction					5, 36	1.48	0.22
APO - residual vegetation							
Year					1, 36	0.06	0.81
1999	24	44.0	(32.2)	a			
2000	24	45.9	(34.7)	a			
Cover type	24				5, 36	4.04	0.005
Interaction					5, 36	2.99	0.02
AGO - residual vegetation							
Year					1, 36	0.63	0.43
1999	24	9.2	(9.8)	a			
2000	24	7.3	(7.0)	a			
Cover type	24				5, 36	0.73	0.60
Interaction					5, 36	1.41	0.24
Biomass of residual vegetation in cage							
Year					1, 36	0.86	0.36
1999	24	23.7	(23.1)	a			
2000	24	18.9	(14.4)	a			
Cover type	24				5, 36	3.30	0.01
Interaction					5, 36	0.20	0.96

[a] 95% simultaneous confidence intervals by the Tukey method. Means with different letters are significantly different.

Table 47. Means and standard deviations (SD) for adjusted percent offtake (APO), adjusted grams offtake (AGO), and biomass production inside exclosures (Bio.), for fall standing crop at paired exclosures during 1998, 1999, 2000 in the Hayden Valley.

	1998				1999				2000			
Cover type	n	APO (SD)	AGO (SD)	Bio. (SD)	n	APO (SD)	AGO (SD)	Bio. (SD)	n	APO (SD)	AGO (SD)	Bio. (SD)
ArCa/DeCa	7	21.5 (23.3)	13.2 (14.2)	59.6 (4.9)	8	33.2 (23.4)	25.8 (20.6)	70.6 (20.9)	7	24.7 (20.0)	16.2 (16.5)	69.4 (26.2)
ArCa/FeId	2	41.2 (5.6)	20.2 (18.3)	52.4 (51.4)	3	53.9 (12.7)	18.0 (7.7)	32.6 (8.0)	1	42.2 (NA)	19.6 (NA)	46.4 (NA)
ArTr/AgCa	3	53.3 (14.3)	37.0 (17.1)	68.4 (20.0)	4	47.4 (19.6)	21.2 (15.1)	41.9 (17.0)	1	69.4 (NA)	46.8 (NA)	67.4 (NA)
ArTr/FeId	9	30.5 (36.2)	16.9 (24.1)	37.1 (27.6)	15	50.5 (26.2)	18.8 (14.3)	36.0 (14.0)	8	48.2 (22.9)	14.1 (9.0)	26.0 (12.6)
ArTr/FeId-DaIn	3	18.6 (13.1)	6.5 (5.0)	35.3 (5.7)	4	5.0 (7.6)	2.5 (4.1)	41.8 (8.2)	4	55.3 (7.3)	28.0 (10.3)	50.5 (19.1)
CaCa	2	41.8 (11.1)	46.1 (7.5)	111.8 (11.8)	3	21.0 (21.1)	15.6 (16.9)	68.7 (9.5)	0	NA	NA	NA
carex	1	21.8 (NA)	23.0 (NA)	105.3 (NA)	1	42.0 (NA)	61.6 (NA)	146.6 (NA)	5	12.5 (17.2)	14.4 (20.2)	104.3 (19.3)
DeCe/Carex	3	15.1 (5.4)	12.3 (5.5)	80.3 (11.4)	4	6.9 (10.5)	5.9 (9.0)	79.3 (14.3)	8	22.4 (17.9)	24.2 (19.8)	107.3 (33.3)
DeCa	3	13.1 (9.1)	6.9 (4.5)	53.8 (5.6)	4	30.9 (22.7)	19.1 (13.0)	63.9 (17.3)	1	39.4 (NA)	33.7 (NA)	85.3 (NA)
FeId/DeCa	3	24.1 (12.7)	16.5 (10.8)	62.5 (22.5)	4	40.2 (27.2)	11.9 (8.0)	29.9 (3.0)	0	NA	NA	NA
FeId/AgCa	1	0 (NA)	0 (NA)	15.3 (NA)	5	60.0 (18.9)	21.2 (9.6)	34.6 (8.7)	8	21.8 (25.7)	7.4 (9.5)	27.0 (14.7)
PoFr/DeCa	2	2.0 (0.9)	1.4 (0.9)	65.5 (17.5)	1	65.1 (NA)	39.4 (NA)	60.6 (NA)	1	39.2 (NA)	26.1 (NA)	66.7 (NA)
PoSa	7	57.8 (25.1)	20.7 (9.9)	36.3 (16.7)	7	56.4 (18.4)	15.0 (4.7)	26.8 (4.7)	12	51.9 (20.3)	14.8 (8.7)	27.8 (12.1)

Table 48. Means and standard deviations (SD) for adjusted percent offtake (APO), adjusted grams offtake (AGO), and biomass production inside exclosure (Bio.), for spring new growth and residual vegetation at paired exclosures during 1999, 2000 in the Hayden Valley.

Parameter	1999				2000			
Cover type	n	APO (SD)	AGO (SD)	Bio. (SD)	n	APO (SD)	AGO (SD)	Bio. (SD)
Spring new growth								
ArCa/DeCa	6	13.1 (13.4)	3.6 (3.7)	26.5 (5.7)	5	16.9 (11.5)	5.5 (4.2)	32.0 (10.7)
ArCa/FeId	2	0.2 (0.3)	0.1 (0.2)	44.3 (17.5)	1	51.8 (NA)	16.6 (NA)	32.0 (NA)
ArTr/AgCa	4	10.4 (20.8)	2.9 (5.8)	37.7 (10.7)	1	70.2 (NA)	54.4 (NA)	77.5 (NA)
ArTr/FeId	6	36.8 (23.5)	16.6 (13.9)	38.3 (18.6)	12	41.2 (17.5)	15.1 (8.1)	34.8 (7.8)
ArTr/FeId-DaIn	3	22.6 (4.8)	6.1 (3.3)	27.2 (15.9)	5	8.2 (13.7)	1.3 (2.3)	17.4 (4.5)
CaCa	1	0 (NA)	0 (NA)	13.0 (NA)	1	48.9 (NA)	22.4 (NA)	45.8 (NA)
carex	0	NA	NA	NA	4	17.4 (20.9)	13.5 (20.5)	52.4 (31.3)
DeCe/Carex	2	7.6 (10.8)	3.1 (4.3)	24.3 (22.6)	11	18.7 (16.3)	7.0 (5.4)	41.5 (16.0)
DeCa	4	0 ()	0 (0)	22.0 (7.5)	3	12.2 (21.2)	4.0 (6.8)	36.0 (6.1)
FeId/DeCa	2	42.9 (31.1)	10.6 (8.6)	23.6 (2.9)	0	NA	NA	NA
FeId/AgCa	1	60.8 (NA)	32.7 (NA)	53.7 (NA)	9	34.4 (26.7)	6.1 (4.8)	15.9 (6.6)
PoFr/DeCa	2	0 (0)	0 (0)	26.2 (10.1)	1	37.1 (NA)	17.6 (NA)	47.4 (NA)
PoSa	5	34.4 (19.2)	12.9 (7.8)	37.6 (7.3)	11	38.2 (17.2)	12.3 (9.3)	30.3 (10.7)
Residual vegetation								
ArCa/DeCa	6	45.1 (27.0)	12.4 (11.5)	38.6 (39.6)	5	12.4 (15.4)	6.1 (8.5)	37.2 (18.2)
ArCa/FeId	2	21.9 (31.0)	6.7 (9.4)	27.4 (4.3)	1	75.0 (NA)	11.0 (NA)	14.7 (NA)
ArTr/AgCa	4	30.6 (23.3)	6.6 (6.3)	21.6 (5.5)	1	94.8 (NA)	35.8 (NA)	37.7 (NA)
ArTr/FeId	6	41.5 (33.1)	8.1 (7.4)	17.9 (10.7)	12	61.1 (35.5)	12.6 (12.1)	16.9 (11.7)
ArTr/FeId-DaIn	3	21.1 (22.0)	4.4 (5.8)	22.1 (9.3)	5	28.5 (32.4)	10.8 (14.3)	29.4 (14.0)
CaCa	1	3.6 (NA)	1.0 (NA)	27.8 (NA)	1	55.3 (NA)	17.1 (NA)	30.9 (NA)
carex	0	NA	NA	NA	4	13.7 (15.8)	4.4 (6.0)	19.5 (17.8)
DeCe/Carex	2	69.2 (41.4)	23.0 (19.6)	30.1 (10.3)	11	27.2 (27.8)	9.0 (10.3)	26.9 (17.5)
DeCa	4	3.9 (7.5)	1.8 (3.6)	28.6 (17.1)	3	58.8 (27.1)	8.4 (6.2)	14.2 (6.3)
FeId/DeCa	2	57.0 (12.9)	13.8 (13.7)	22.1 (19.0)	0	NA	NA	NA
FeId/AgCa	1	63.0 (NA)	4.1 (NA)	6.5 (NA)	9	42.7 (37.6)	4.1 (4.0)	8.7 (6.4)
PoFr/DeCa	2	31.5 (44.6)	10.5 (14.8)	28.9 (6.1)	1	0 (NA)	0 (NA)	10.9 (NA)
PoSa	5	67.9 (23.8)	7.2 (6.1)	9.3 (6.3)	11	83.1 (12.4)	7.5 (3.5)	8.9 (3.8)

Table 49. Comparison between estimates of offtake (%) from grazed loop surveys and exclosures for the combined Crater Hills and West Alum areas and fixed sites for 1999 and 2000 in the Hayden Valley.

	1999		2000	
Location	Grazed loop	Exclosures	Grazed loop	Exclosures
Crater Hills and West Alum	18.0	36.4	27.3	42.1
Big sage fixed site	13.8	37.5	22.3	38.8
Silver sage fixed site	11.0	18.5	9.0	21.0
Mesic graminoid fixed site	14.0	16.5	8.0	16.5

Table 50. Biomass (g / 0.75m^2) of 16 plots clipped July 14, 2000 and amount of regrowth (g / 0.75m^2 and percent) clipped on September 9, 2000.

Cover type		Regrowth	
Location	July 14 biomass	Biomass	Percent
ArTr/FeId-DaIn phase			
Grid 1	48.5	5.4	11.2
Grid 1	34.5	3.7	10.8
Grid 2	45.7	8.8	19.2
Grid 2	73.1	16.4	22.5
ArCa/DeCe			
Grid 3	80.9	16.2	20.0
Grid 3	68.7	20.4	29.7
Grid 4	78.1	10.3	13.2
Grid 4	109.7	10.2	9.3
Grid 5	107.7	8.2	7.6
Grid 5	78.9	13.2	16.7
Grid 7	136.2	6.8	5.0
Grid 7	117.9	10.1	8.5
PoFr/DeCe			
Grid 6	136.2	6.8	5.0
Grid 6	117.9	10.1	8.5
Wet carex			
Grid 8	212.1	13.0	6.1
Grid 8	283.7	10.3	3.6

Table 51. Fecal density and density of observed animals (n/ha) for fixed exclosure sites during growing and non-growing seasons in the Hayden Valley for 1998, 1999, 2000.

Parameter	Big sage			Mesic graminoid			
Season	Xeric	Mesic	Combined	Xeric	Mesic	Combined	Silver sage
Bison fecal density							
Growing 1998	194.2	75.3	156.6	71.2	122.4	98.6	177.4
Non-growing 1998-99	265.5	142.9	226.5	400.0	300.0	346.5	123.3
Growing 1999	214.6	139.0	190.4	412.1	360.5	384.5	161.1
Non-growing 1999-00	217.0	83.1	174.7	362.1	1328.9	879.6	63.9
Growing 2000	528.1	463.6	506.0	534.8	446.1	487.3	244.8
Elk fecal density							
Growing 1998	5.8	0	4.0	4.5	1.3	2.8	0.7
Non-growing 1998-99	65.5	41.6	57.8	43.9	21.1	31.7	4.2
Growing 1999	0	0	0	13.6	17.1	15.5	2.4
Non-growing 1999-00	45.6	19.5	37.3	13.6	15.8	14.8	4.2
Growing 2000	49.1	33.8	44.2	104.5	42.1	71.1	19.4
Bison animal density							
Growing 1998	--	--	4.4	--	--	36.6	110.1
Growing 1999	--	--	25.3	--	--	8.5	7.6
Growing 2000	--	--	4.4	--	--	7.7	0.3

APPENDIX B

KEY AND DESCRIPTION OF COVER TYPES IN THE HAYDEN AND PELICAN VALLEYS

The following cover types are intended to represent common existing plant associations of the Hayden Valley and, based on brief surveys, the nearby Pelican Valley. The Hayden and Pelican Valleys are predominately shrub/grasslands that are influenced by numerous streams, seeps, and thermal areas and existing classification systems did not meet our needs to delineate all types of existing vegetation and at a minimum map unit of 0.01ha.

Grassland and shrubland habitat types defined by Mueggler and Stewart (1980), riparian and wetland habitat and cover types by Hansen et al. (1995), and local habitat and cover types described by Mattson and Despain (1985), Despain (1990), and Graham (1978) formed the basis for the following types. However, our intent is the delineation of existing vegetation rather than potential vegetation which habitat types often define. In many instances we have split their types into several types to reflect the presence of specific plant species. Quantities of indicator species may therefore differ between their system and ours, or may simply reflect overall differences in the Hayden Valley from other locals. Corresponding habitat or cover types by the previously mentioned authors are included in the following descriptions to provide references of plant species, additional descriptions, or to allow incorporation into their systems if desired. We refer to all vegetation types as cover types for consistency and to reflect current vegetation as the basis of classification even though nomenclature may be the same as habitat types by other authors.

Cover types of the Hayden Valley containing *Artemisia cana* were of particular interest in relation to other classification systems. Based on leaf morphology and life form, all *Artemisia cana* observed in Hayden Valley is the subspecies *viscidula* (mountain silver sagebrush) except possibly 1 isolated instance. In contrast to more xeric *Artemisia cana* var. *cana* (plains silver sagebrush), distribution of mountain silver sagebrush is generally limited to the west side of the continental divide, at elevations of ~2,000 to 2,700m in Wyoming, and characteristic of areas with seasonally high soil moisture or heavy, lingering snow pack. Mountain silver sagebrush was most often observed in association with the mesic indicator *Deschampsia cespitosa.* Other than Graham (1978), little mention of this association was made in other classification systems, possibly due to inclusion or sole existence of plains silver sagebrush in other classification systems. Subsequently, the *Arca/Dece* association may be somewhat limited to morphological and climatological conditions of the Hayden and Pelican Valleys. All following reference to *Artemisia cana* is for the subspecies *viscidula.*

The relatively large number of cover types and small minimum map unit we are using is a result of the scale of vegetation heterogeneity in the Hayden and Pelican Valleys, biological significance in relation to grazing ungulates, and our attempt to classify vegetation using satellite imagery. The ability to discern more vegetation types and smaller patches should provide better information concerning amounts and juxtaposition of vegetation available for grazing. Classification accuracy using satellite imagery could potentially be improved if the cover types we have defined have distinct differences in reflection properties to provide better separation of satellite data.

The following key and descriptions were constructed through general reconnaissance of the Hayden Valley and 119 plots in the Crater Hills and West Alum areas. Percent cover of the main indicator species, forbs, and other graminoids are summarized in Table 52.

Table 52. Mean percents of total vegetated cover, dominant graminoid species, co-dominant graminoid species, other graminoids present, and forbs for plots of graminoid dominated cover types in the Hayden Valley.

		Percent	Percent graminoids			Percent
Cover type	N	vegetated	Dominant	Co-dominant	Other	forbs
PoSa	24	46	22 PoSa	--	17	8
ArCa/FeId	3	63	32 FeId	--	13	19
ArCa/FeId-DaIn	3	40	4 DaIn	13 FeId	4	18
ArTr/AgCa	4	66	9 AgCa	20 FeId	22	15
ArTr/FeId	21	49	20 FeId	--	13	16
ArTr/FeId-DaIn	5	61	31 DaIn	12 FeId	6	12
FeId/AgCa	16	49	22 FeId	--	13	14
ArCa/DeCa	10	61	29 DeCe	--	15	16
PoFr/DeCa	1	80	50 DeCe	--	10	20
DeCe	6	58	31 DeCe	--	13	16
CaCa	1	90	65 CaCa	--	0	25
Carex	5	89	88 carex	--	0	1
DeCe/Carex	20	87	38 carex	20 DeCe	12	16

Key to Non-Forested Cover Types of the Hayden and Pelican Valleys

1. Well vegetated, herbaceous vegetation appearing stable and persistent……….……….....2

1. Little or no vegetation with >85-90% bare ground, often eroded or disturbed……….....…….22

   2. Thermally influenced vegetation, containing only salt tolerant species or species normally found in warmer climates…………………..…………..**Thermal Vegetation c.t.**

   2. Vegetation consisting of expected bioclimatic species, thermal influence not obvious…...3

3. Shrub species common and well represented………………………………………...……….4

3. Shrub species absent or of such small stature (generally <0.1m) and quantities to be inconsequential……………………………….………………………………………….14

   4. *Salix* or *Betula* well established and >0.5m in height……….....……….…***Salix* / *Carex* c.t.**

   4. *Artemisia cana, Artemisia tridentata,* or *Potentilla fruticosa* robust and well represented……………………………………………………………………………..5

5. *Potentilla fruticosa* well represented and comprising >20% of all shrub specie. *Artemisia cana* common, *Artemisia tridentata* rare. Herbaceous vegetation dominated by *Deschampsia cespitosa*………………………………..... ***Potentilla fruticosa* / *Deschampsia cespitosa* c.t.**

5. *Artemisia* spp. the dominant shrubs……………………………………………………..……….6

   6. *Artemisia tridentata* common and well represented. Scattered *Artemisia cana* may also be present but usually <20% of shrub cover (*Artemisia tridentata* types)……………..……10

   6. *Artemisia cana* var. *viscidula* common and well represented. *Artemisia tridentata* often widely scattered but usually <10% of shrub cover and appearing less robust than areas containing only *Artemisia tridentata* as the shrub species. Generally areas where seasonal soil moisture precludes *Artemisia tridentata* (*Artemisia cana* var. *viscidula* types)…………………………………………………………………….………………....7

7. Herbaceous vegetation almost entirely dry site *carex* spp……………***Artemisia* / dry *carex* c.t.**

7. Herbaceous vegetation containing mixed grasses…………………………………….…………8

   8. *Deschampsia cespitosa* well represented with a minimum of 15% and often close to 100% of the graminoid component. Moist *carex* spp. may also be present..…………… …………………………………………… ***Artemisia cana* / *Deschampsia cespitosa* c.t.**

   8. *Festuca idahoensis* common. If present, *Deschampsia cespitosa* low in stature and widely scattered………………………………………………….…….…………….……….. 9

9. *Danthonia intermedia* becoming common and widespread, usually >30% of the grass component……… ***Artemisia cana* / *Festuca idahoensis* – *Danthonia intermedia* phase c.t.**

9. If present, *Deschampsia cespitosa* and *Danthonia intermedia* less common than *Festuca idahoensis*…………………………………………..…… ***Artemisia cana* / *Festuca idahoensis* c.t.**

10. Herbaceous vegetation almost entirely dry site *carex* spp…………***Artemisia* / dry *carex* c.t.**

10. Herbaceous vegetation containing mixed grasses………………………………..……………..11

11. *Artemisia tridentata* low in stature (<45cm), *Poa sandbergii* common, upper slopes or ridge tops exclusively……………………….... ***Artemisia tridentata / Poa sandbergii* c.t.**

11. *Artemisia tridentata* generally robust, grasses other than *Poa sandbergii* most common, uplands and hillsides…………………………………………………………….12

12. *Festuca idahoensis* present, *Agropyron caninum* well represented with >15% of the grass component, *Geranium viscosissimum* often present. Frequently on north-facing slopes of higher productivity……………………...….. ***Artemisia tridentata / Agropyron caninum* c.t.**

12. *Festuca idahoensis* more common than *Agropyron caninum*……………………….……….13

13. *Danthonia intermedia* becoming common and widespread, usually >30% of the grass component……………………………………………………………………………… ……….***Artemisia tridentata / Festuca idahoensis – Danthonia intermedia* phase c.t.**

13. *Danthonia intermedia* less common than *Festuca idahoensis*……………………………… ……………………………………...…… ***Artemisia tridentata / Festuca idahoensis* c.t.**

14. Forbs more common than graminoids, comprising >65% of the canopy. *Senecio triangularis*, *Trifolium repens*, or *T. hybridum* often present (forb dominated cover types) ....………..….21

14. Grasslands and sedge meadows with graminoids dominant, shrubs absent (graminoid dominated cover types)…………………………………………………………..……..…..…15

15. *Poa sandbergii* common and often comprising >75% of the vegetation. Generally found only on ridge tops and exposed areas.. …………………**Ridge Top *Poa Sandbergii* c.t.**

15. *Poa sandbergii* generally absent, graminoids various…………………………………..16

16. *Festuca idahoensis* common, generally upland sites..……………………………………..…17

16. *Festuca idahoensis* not present, generally moist sites…………………….………………….18

17. *Festuca idahoensis* abundant, *Agropyron caninum* usually present, *Deschampsia cespitosa* absent. Vegetation often patchy and in clumps……………………………….… …………………………………………..***Festuca idahoensis / Agropyron caninum* c.t.**

17. *Festuca idahoensis* common, *Deschampsia cespitosa* present but often short in stature. Often on toe slopes……………..….***Festuca idahoensis / Deschampsia cespitosa* c.t.**

18. Vegetation often occurring in discrete patches, composed of 50% to 100% *Calamagrostis canadensis*……………………………………………………..***Calamagrostis canadensis* c.t.**

18. Wet site *carex* spp. and/or *Deschampsia cespitosa* common and abundant…………………19

19. Wet *Carex* meadows with 90-100% of the canopy coverage containing moist or wet site carex spp…………………………..……………………**Wet *Carex* Meadow c.t.**

19. Canopy coverage containing <90% carex, *Deschampsia cespitosa* often becoming common……………………………………………………………………………………...20

20. *Carex* and *Deschampsia cespitosa* both common and often equally abundant, with at least 10% of the canopy containing each spp…………...……. ***Deschampsia cespitosa* / Carex c.t.**

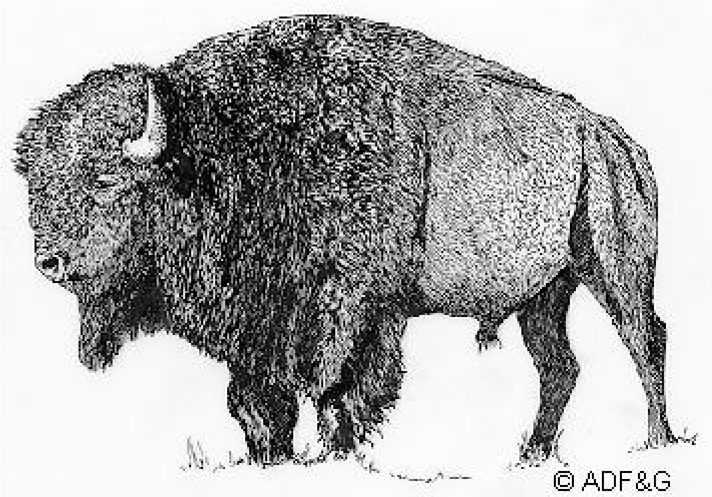
20. *Deschampsia cespitosa* with a canopy coverage of at least 15%, *carex* lacking or with a canopy cover <10%, forbs may also be common………………. ***Deschampsia cespitosa* c.t.**

21. Non-native clover (*Trifolium repens* and *T. hybridum*) with >15% canopy cover, often occurring in nearly pure stands…………………….……………….**Non-native Clover c.t.**

21. Clover not present or with <10% canopy cover………………....**Miscellaneous Forb c.t.**

22. Thermal influence obvious, often light colored soil………………………..**Thermal Ground c.t.**

22. Thermal influence not obvious, ground generally appearing highly eroded or disturbed…………..……………….…………………..………..**Erosive / Disturbed Ground c.t.**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Description of Cover Types

***Artemisia tridentata / Festuca idahoensis* (*Artr/Feid*)**

Artemisia tridentata is common and robust, ranging from ~5% cover upwards. *Artemisia cana* may also be present, but occupies <20% of the *Artemisia* component. *Festuca idahoensis* is obvious under ungrazed conditions. Other graminoids (including *Danthonia intermedia* and *Agropyron* spp.) may be present, but *Festuca idahoensis* is the dominant grass occurring in patches throughout the area. Generally found on moderate slopes from mid-slope to ridge top. This is one of the most common cover types in the Hayden. It is the same as the *Artr/Feid* type of Mueggler and Stewart (1980), Despain (1990), and Graham (1978).

***Artemisia cana / Festuca idahoensis* (*Arca/Feid*)**

Artemisia cana var. *viscidula* has replaced *Artemisia tridentata* as the dominant *Artemisia* sp., in areas where the soil is too wet, at least seasonally, for *Artemisia tridentata* roots to survive. It is usually found on lower and gentler slopes, often in a band between *Artr/Feid* on hillsides and *Feid/Dece* bottoms. *Artemisia tridentata*, if present, occupies <10% of the *Artemisia* component. *Festuca idahoensis* is obvious under ungrazed conditions. Other graminoids (including *Deschampsia cespitosa* at <10% cover) may be present, but *Festuca idahoensis* is the dominant grass occurring in patches throughout the area. This type was suggested but not differentiated by Mueggler and Stewart (1980). It was considered a distinct type by Despain (1990), and Graham (1978) and included all amounts of *Deschampsia cespitosa* rather than a limited amount as we have defined. Graham (1978) listed the *Arca/Feid* type as the most common in the

Hayden (27%) and Pelican (43%) Valleys. Hansen et al. (1995) considered the *Arca/Feid* type an incidental riparian type under certain locations and landforms that often intergraded with the *PoFr/Dece* type.

***Artemisia tridentata / Festuca idahoensis–Danthonia intermedia* phase (*Artr/Feid-Dain*)**

Danthonia intermedia is replacing *Festuca idahoensis* as the dominant graminoid, generally occurring as ~30% or greater of the graminoid component. It is usually present on flatter areas than *Artr/Feid* and *Artr/Agca* type. This type is included in the *Artr/Feid* type of Mueggler and Stewart (1980), Despain (1990), and Graham (1978).

***Artemisia cana / Festuca idahoensis- Danthonia intermedia* phase (*Arca/Feid-Dain*)**

Danthonia intermedia is replacing *Festuca idahoensis* as the dominant graminoid, generally occurring as ~30% or greater of the graminoid component. It is otherwise similar to *Arca/Feid*. Generally occurring in limited areas, it is not as common as the *Dain* Phase of *Artr/Feid*.

***Artemisia tridentata / Agropyron caninum* (*Artr/Agca*)**

Festuca idahoensis is common in this type, but *Agropyron caninum* has also become common, occupying at least 10-15% of the graminoid component. *Geranium viscosissimum* (sticky geranium) is often present. This type occurs on moderate slopes similar to the *Artr/Feid* type, but may be more prone to appear on damper north slopes. It is generally more productive than the *Artr/Feid* type. Mueggler and Stewart (1980) and

Despain (1990) classified this type as a sticky geranium phase of the *Artr/Feid* type, Graham (1978) included it in the *Artr/Feid* type. We classified it as *Artr/Agca* because *Agropyron caninum* was more commonly found than *Geranium viscosissimum.*

***Artemisia tridentata / Poa sandbergii (Artr/Posa*)**

This is a very limited type, generally occurring in only limited topographic positions of the Hayden Valley. It occurs on gentle semi-protected ridge tops where adjacent topography may moderate the wind and soils may be slightly deeper and less rocky than most ridge tops. *Artemisia tridentata* is short (generally <45cm) and widely scattered. *Poa* sandbergii, the common grass on ridge tops, is the most common graminoid. Very widely scattered *Festuca idahoensis* may also be present. This is a transition type between *Artr/Feid* and Ridge Top cover types and included as *Artr/Feid* by Mueggler and Stewart (1980), Despain (1990), and Graham (1978). We considered it a separate type because of the presence of *Artemisia tridentata* in conjunction with the understory of ridge top vegetation type.

***Artemisia* / Dry carex (Sage/dry *Carex*)**

This is a rare type, most likely occupying <1% of the Hayden Valley, that is probably a phase of *Artemisia tridentata* and *Artemisia cana* types. It may contain either or both *Artemisia* spp. with an understory almost exclusively containing dry site *Carex* spp.. It is often in a narrow band on gentle slopes between cover types containing *Deschampsia cespitosa* and *Festuca idahoensis* in the understory. We defined it as a separate type rather than phases of *Artemisia* types due to the distinctness of the understory and lack of either *Festuca idahoensis* or *Deschampsia cespitosa*. Similarities were not noted with other classification systems.

***Potentilla fruticosa / Deschampsia cespitosa* (*PoFr/Dece*)**

The *PoFr/Dece* type occurs where *Potentilla fruticosa* has become common, often in conjunction with *Artemisia cana,* and comprises at least 20% of the shrub canopy. The understory of *PoFr/Dece* is similar to *Arca/Dece*. This type is found on gentle slopes in the Hayden Valley and is of limited occurrence. Hansen et al. (1995) identify a habitat type by the same name and similar characteristics. Despain (1990) noted the existence of a *Potentilla fruticosa* type and suggested it be considered a separate type or at least a phase of the *Arca/Feid* type. Graham (1978) defined a *PoFr/Feid* type for the Hayden and Pelican Valleys similar to Mueggler and Stewart (1980), with *Deschampsia cespitosa* as the most dominant grass.

Artemisia cana / Deschampsia cespitosa (Arca/Dece)

This is a more mesic type than *Arca/Feid* as evident by the universal presence of *Deschampsia cespitosa*. It commonly occurs in lower areas and gentle slopes. *Artemisia cana* is common throughout. Similar to the *Arca/Feid* type, *Artemisia tridentata*, if present, occupies <10% of the *Artemisia* component. *Potentilla fruticosa* may be widely scattered but weakly represented in the canopy and comprising <10% of the shrub canopy. *Deschampsia cespitosa* is widespread and common, comprising at least 10% of graminoids and is often the only graminoid present. *Festuca idahoensis*, if present, is very limited in abundance. Due to the mesic nature of this type, similarities with types of

Mueggler and Stewart (1980) were not evident. Graham (1978) noted the common occurrence of *Deschampsia cespitosa* in an *Arca/Feid* type he and also Despain (1990) defined. Hansen et al. (1995) listed *Artemisia cana* as common in their *PoFr/Dece* type and noted the *Arca/Feid* type may be found adjacent to *PoFr/Dece* on slightly drier sites.

***Salix / Carex* (*Salix/Carex*)**

This is a very limited type found along streams or seeps, where *Salix* or *Betula* has become well established and is greater than 0.5m in height. Both species were occasionally found growing to a height matching surrounding herbaceous vegetation, but only taking on the appearance of a woody shrub in limited areas. Despain (1990) described a willow / sedge type and Graham (1978) noted a *Salix* spp. cover type. Mueggler and Stewart (1980) did not classify any types containing willow. Hansen et al. (1995) identified 16 types containing *Salix* in the overstory.

Ridge Top *Poa sandbergii* (*Posa*)

The *Posa* cover type occurs exclusively on wind swept ridge tops where soil has become thin and rocky and adequate soil moisture for plant growth is sporadic. *Poa sandbergii* is persistent, shrubs are lacking, very occasional *Festuca idahoensis* may be present. This type would be included in the *Feid/AgSm-AgDa* type of Graham (1978), based on some similarities in species with the habitat type of the same name by Mueggler and Stewart (1980). It would be an inclusion to the *Artr/Feid* type of Despain (1990).

***Festuca idahoensis / Agropyron caninum* (*Feid/Agca*)**

Occasionally present in patches on gentle slopes, the *Festuca idahoensis* type most often occurs on leeward slopes below ridge tops. These are areas receiving the deepest snow drifts during winter and the last to melt in spring. A large amount of bare ground and pocket gopher activity are common and often create a disturbed look. *Festuca idahoensis* is always present, *Agropyron caninum* common, this cover type often contains a high proportion of forbs. Vegetation is generally scattered in small patches throughout this cover type. The *Feid/Agca* type is similar to the habitat type of the same name by Mueggler and Stewart (1980), Despain (1990), and Graham (1978). However, pocket gopher disturbance and persistent snow drifts of many areas containing this type in the Hayden Valley have probably reduced productivity and existence of some plant species in comparison to other locales of the same habitat type.

***Festuca idahoensis / Deschampsia cespitosa* (*Feid/Dece*)**

The *Festuca idahoensis* / *Deschampsia cespitosa* type is frequently located between *Feid/Agca* and *Dece*/*Carex* types and can sometimes be thought of as a transitional type between the two. *Deschampsia cespitosa* and *Festuca idahoensis* are always present, with *Deschampsia cespitosa* widely scattered and usually of low stature. Forbs are often abundant. Often located on toe slopes, moisture from melting snow drifts upslope may increase moisture availability at the start of the growing season to allow the presence of *Deschampsia cespitosa*. The *Festuca idahoensis* / *Deschampsia cespitosa* type was also identified by Mueggler and Stewart (1980), Despain (1990), and Graham (1978).

***Calamagrostis canadensis* (*Caca*)**

This is a limited cover type usually occurring in isolated patches with *Calamagrostis canadensis* comprising at least 50% of the vegetative cover. *DeCa* and moist carex species may also be present. Graham (1978) included this type with his *Carex* spp. cover type, and although no mention of *Calamagrostis canadensis* was made, Despain (1990) probably did also. It was not mentioned by Mueggler and Stewart (1980), while Hansen et al. (1995) described it as a minor to incidental type at mid to high elevations.

***Deschampsia cespitosa* (*Dece*)**

Deschampsia cespitosa is always present with a minimum canopy coverage of 15%, this type usually forms a dense stand of individual tussocks with *Deschampsia cespitosa* as the clear dominant. *Carex* genera may be present but are less common than *Deschampsia cespitosa* and make up <10-15% of the canopy. Sites are too wet for *Festuca idahoensis.* This type is often found in gullies, small depressions, and adjacent to streams. Hansen et al. (1995) identified the *Deschampsia cespitosa* type as a minor habitat type at mid to high elevations. It would be included in the *Dece*/*Carex* type of Mueggler and Stewart (1980), Despain (1990), and Graham (1978).

***Deschampsia cespitosa/Carex* (*Dece*/*Carex*)**

Deschampsia cespitosa and moist *carex* genera are always present, often in equal abundance, but with a minimum of 10% of each. The increased amount of *Carex* differentiates this type from the *Dece* type. This type is found in similar sites as the *Dece* type and also adjacent to meadows containing almost pure stands of *Carex*. Mueggler and Stewart (1980), Despain (1990), and Graham (1978) all identified this type. It was not recognized by Hansen et al. (1995), but is probably a grouping of several of their more distinct types.

Wet *Carex* Meadows (Wet *Carex*)

Areas containing almost 100% moist *Carex* spp. make up the wet *Carex* meadow cover type. This includes small stands composed exclusively of *Carex nebrascensis* and larger meadows solely containing *Carex rostrata* and/or *Carex aquatilis*. A low growing forb component may be present in limited occurrences but mesic grasses are virtually non-existent. Despain (1990) and Graham (1978) described a similar wet *Carex* type, Mueggler and Stewart (1980) concentrated on upland vegetation and did not. Hansen et al. (1995) described species specific types rather than lumping them into 1 group.

Non-native Clover (Clover)

These are areas containing a minimum of 15%, and often nearly pure stands of *Trifolium repens* and *T. hybridum*. *Poa pratensis* is often present. All 3 of these species are listed as Priority III exotic species in Yellowstone Park. Graham (1978) considered it distinct enough to classify as a cover type. However, since this cover type is dominated by a non-native invasive species, it was not discussed in the context of an indicator of a habitat type by Despain (1990), Mueggler and Stewart (1980), or Hansen et al. (1995) and would probably be an inclusion of the adjoining cover type.

Miscellaneous Forb (Misc. Forb)

Somewhat disturbed sites on hillsides dominated by *Senecio triangularis*, considered a separate cover type by Hansen et al. (1995) are the most common areas contained in the miscellaneous forb cover type. Moist areas adjacent to streams and seeps may also be part of this cover type when they occur in areas greater than the minimum map unit. This cover type is generally found in limited small patches in the Hayden and Pelican Valleys. Mueggler and Stewart (1980), Despain (1990), and Graham (1978) did not classify forb dominated cover types and would probably classify these areas by co-existing graminoid species or as inclusions in adjoining types. Patches containing *Senecio triangularis* would probably be included in the *Arca/Feid* type if not defined in the miscellaneous forb cover type.

Thermal Vegetation (Thermal Veg.)

This cover type contains vegetation influenced by thermal activity. These areas are typically moist and adjacent to thermal features. Salt tolerant species are often the only plants present and may include species of warmer areas not commonly found at this elevation and climate. However, thermal activity has influenced many parts of the Hayden and Pelican Valleys and this cover type is strictly meant to classify areas where thermal activity has produced distinct differences from areas lacking of thermal influence. Despain (1990) discussed thermal communities and identified different vegetation zones based on temperature. Thermal influenced vegetation occurs in limited areas of the Hayden and Pelican Valleys and Graham (1978) did not specify them as a cover type. Due to the uniqueness of thermal areas, they were not discussed by Mueggler and Stewart (1980) or Hansen et al. (1995).

Erosive and Disturbed (*Eros/Dist*)

These are non-thermal areas where disturbance has prevented the establishment of persistent herbaceous vegetation. Scattered shrub species may be present but >85% of the understory is not vegetated. Included in this type are several areas in the Hayden Valley analogous to sand dunes containing widely scattered *Artemisia cana*, where wind erosion has prevented establishment of a herbaceous understory. Steep eroded banks and active bison wallows larger than 0.01ha are also included in this cover type.

Non-vegetated Thermally Influenced (Thermal Gnd.)

Adjacent to hot pots and other thermal features are areas containing little if any vegetation. Often light in color and heavily crusted, mineral content and hot temperatures of these areas may prevent establishment of plants.