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WINTER HABITAT USE BY LARGE UNGULATES FOLLOWING FIRE IN NORTHERN YELLOWSTONE NATIONAL PARK[1]

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Abstract. The effect of fire and habitat heterogeneity on winter foraging by ungulates was studied in northern Yellowstone National Park (YNP). Grazing was monitored at 15 study sites for 14 wk during the winters of 1991 and 1992. The location and intensity of grazing activity within each site were recorded on topographic maps and digitized into a geographic information system. Maps of grazing intensity were compared to map layers of grassland habitat type, elevation, slope, aspect, annual precipitation, and the spatial pattern of fires that occurred in 1988. Burned areas were used by ungulates more often than expected based on their availability, especially during mid- to late winter, but the spatial pattern of burned areas (i.e., fragmented or clumped) was not related to grazing intensity. Ungulate grazing, as measured by minimum cumulative grazing intensity (MCGI), was greatest at low-elevation drier sites across the northern range and on steep southerly slopes. The influence of environmental characteristics on MCGI was evaluated at four spatial scales (1, 9, 81, and 255 ha). Grazing intensity was best predicted by environmental heterogeneity, especially the presence of burned areas, and topography (slope and aspect), at broader scales (81 and 255 ha) rather than on a per-hectare basis. The explanatory power of broad-scale features suggests that wintering ungulates in YNP respond strongly to coarse-grained variation in these landscapes. Interpreting or predicting ungulate grazing at a specific location requires understanding of environmental heterogeneity in the surrounding landscape.

Key words: Bison bison; Cervus elaphus; *fire; landscape ecology; northern Rocky Mountains; scale; winter foraging; Yellowstone National Park.*

INTRODUCTION

Spatial and temporal variation in habitat use and foraging are important manifestations of environmental heterogeneity for large ungulates because these animals may be strongly influenced by heterogeneity at the landscape scale (McNaughton 1985, McNaughton et al. 1988, Senft et al. 1987). Understanding the relationship between environmental heterogeneity at multiple scales and organism function remains a high priority for ecology (Lubchenco et al. 1991). However, evaluating the relative importance of local and landscape-scale influences on ungulates is challenging because it is difficult to manipulate the environment at broad spatial scales (Turner et al. 1989). Natural events (e.g., fires, storms, droughts) provide valuable opportunities to study ungulate responses to landscape heterogeneity. The 1988 fires in Yellowstone National Park (YNP), unusual in both scale and heterogeneity (Christensen et al. 1989, Knight and Wallace 1989, Singer et al. 1989), created an opportunity to study the relationship between broad-scale environmental heterogeneity and ungulate habitat use.

We present a 2-yr landscape-scale study of winter habitat use by large ungulates in northern YNP to address several questions. First, we asked whether ungulates preferentially use burned areas in the landscape for feeding. We then expand our analysis to incorporate environmental heterogeneity in a broader sense, addressing questions of whether ungulates preferentially use particular habitats or landscape positions for feeding, whether the geographic pattern of habitat use changes through the winter, and whether the use of burned areas is influenced by the spatial pattern of burning. Finally, we analyze our environmental data at four spatial scales to explore the scale(s) at which most of the variation in cumulative grazing intensity is explained.

We focus on elk and bison because these are among the most numerous ungulates in the area (Houston 1982), and we have chosen to examine winter foraging for several reasons. Winter range conditions appear to be the primary determinant of ungulate survival and reproduction in Yellowstone, and winter use of vege-

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tation by ungulates appears to be intense in some areas. Ungulates make distinct foraging choices in winter as in the rest of the year, and burn patterns may influence those choices. In addition, activities of animals can be readily monitored in winter.

The relationships between ungulates and habitat have been studied in Yellowstone (e.g., Meagher 1971, 1973, Barmore 1980, Houston 1982), other parts of the northern Rockies (e.g., Constan 1972, Singer 1979, Green and Bear 1990), and the boreal forest (Cairns and Telfer 1980). Some habitats, while not abundant, may be highly desirable (e.g., upland grasslands; Cairns and Telfer 1980). Winter diet composition and quality have also been extensively studied for elk (e.g., Kufeld 1972, Hobbs et al. 1981) and bison (Reynolds et al. 1978, Krueger 1986). Elk are generalists, using a variety of habitats to obtain a relatively stable diet quality (Hobbs et al. 1981). Bison are less selective feeders, eating grasses and sedges in similar proportions to their abundance (Reynolds et al. 1978, Krueger 1986). However, the effects of large-scale fire on habitat use patterns during winter, when forage may be inaccessible due to snow conditions, are not well understood. Prior to the 1988 fires, three variables—winter severity, summer herbaceous biomass, and population size—accounted for most of the year-to-year variance in per capita growth rates for both elk and bison (Merrill and Boyce 1991).

Fires that occur late in the growing season eliminate forage in burned areas, reducing the availability of forage for the following winter. However, fire may stimulate primary productivity in subsequent years, resulting in improved forage quantity, quality, and/or palatability (Hobbs and Spowart 1984, Coppock and Detling 1986). In addition, some shrubs (e.g., *Artemisia tridentata*) can only become reestablished in burned areas through seedling production (Harniss and Murray 1973, Gruell 1980, Griffin and Friedel 1984, West and Hassan 1985, Noste and Bushey 1987). Therefore, forage availability is likely to increase in these areas because the growth of forbs and grasses will be enhanced in the absence of shrubs (Harniss and Murray 1973, Griffin and Friedel 1984, West and Hassan 1985). Other field studies we conducted demonstrated increased quantities of winter forage in burned areas of northern YNP but no differences in quality (measured by crude protein, acid detergent fiber, and neutral detergent fiber content) between burned and unburned forage (Wallace et al., *in press*). With increased forage availability and decreased dead tissue (either woody tissue or litter), foraging efficiency may increase in burned areas and remain high for some period of time following the fires (Wilms et al. 1981, Hobbs and Spowart 1984). Boyce and Merrill (1991) hypothesized that the fire-enhanced forage base should enhance recruitment and population size for several years following the 1988 fires, but the extent to which the ungulates would use burned areas is not known.

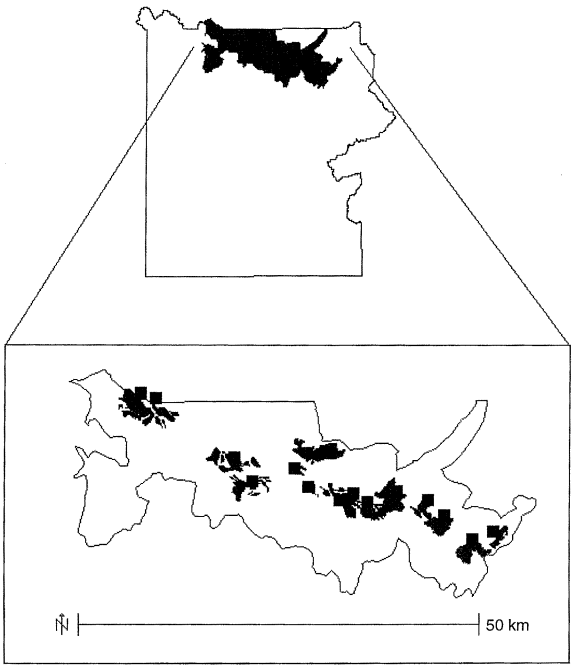

FIG. 1. Map of the 77 020-ha northern range study area with the viewing areas shaded and the fixed viewing positions indicated by ■. The viewing areas encompass a total of 7518 ha.

STUDY AREA

Yellowstone National Park (YNP) encompasses 9000 km^2 in the northwest corner of Wyoming and adjacent parts of Montana and Idaho. Elevations in the park range from 1500 to >3000 m, and much of the area is covered by Quaternary volcanic deposits that underwent at least three extensive glaciations (Houston 1982). General descriptions can be found for park geology (Keefer 1972); and for physiography, soils, and vegetation (Meagher 1973, Barmore 1980, Houston 1982, Despain 1991). The climate of YNP is characterized by long, cold winters and short, cool summers (Dirks and Martner 1982). Our study focused on the northern 20% of the park, which is primarily a lower elevation grassland or sagebrush steppe (Fig. 1). Northern Yellowstone elk and bison migrate seasonally between a high-elevation summer range and this lower elevation winter range (Craighead et al. 1972, Barmore 1980, Houston 1982).

The northern range extends ≈80 km down the Lamar, Yellowstone, and Gardner river drainages (Houston 1982). Approximately 83% of the winter range for elk is included within YNP (Houston 1982), and we focused solely on this winter range within park boundaries. The northern range comprises nearly 80 000 ha and has a warmer, drier climate than the rest of the park (Diaz 1979, Dirks and Martner 1982). Most soils derive from glacial till deposited during the Pinedale glaciation (Houston 1982), and tend to be higher in silt, clay, and organic matter than soils derived from rhy-

olite, the parent rock of most of YNP (Despain 1991). Grasslands cover most of the northern range and are dominated by big sagebrush (*Artemisia tridentata*), bluebunch wheatgrass (*Agropyron spicatum*), and Idaho fescue (*Festuca idahoensis*). More continuous forest occurs at high elevations and on north slopes (see detailed descriptions in Houston 1982 and Despain 1991). At lower elevations, the sagebrush grasslands are interspersed with coniferous forest, primarily Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.); aspen groves (*Populus tremuloides*); and riparian willow communities.

Natural fires have influenced plant succession on the winter range for a long time (Houston 1973). Tree-ring evidence suggests that 8–10 extensive fires occurred in the area during the last 300–400 yr, but no large fires have occurred previously in this century (Houston 1973). Approximately 34% of the winter range burned during the 1988 fires, including 22% of the grasslands (Despain et al. 1989). The vegetation has been dynamic during the past century (Houston 1982). Forest cover has increased, mostly on north slopes, and forests have recolonized burned areas, although aspen forests appear to have declined from 4–6 to 2–3% of the winter range (Houston 1982). Sagebrush increased in extent on many slopes and exposures. Willows and associated riparian vegetation have shown a net decrease (Chadde and Kay 1991). The production of herbaceous vegetation on the northern range during a 29-yr period (1935–1963) showed substantial annual fluctuations resulting from varied growing conditions, primarily precipitation (Houston 1982).

METHODS

Landscape heterogeneity

Spatial heterogeneity across the landscape was represented by a series of data layers obtained from the YNP geographic information system (GIS) GRASS (USA-CERL 1991). First, we aggregated the grassland habitat types defined by Despain (1991) into four classes (wet, moist, mesic, and dry; Table 1) that represent a gradient of moisture and net aboveground production (Wallace et al., *in press*). Second, we identified burned and unburned areas. Third, we used slope, aspect, and elevation maps from the YNP GIS and aggregated the numerous classes in each of these maps into fewer categories. Slopes were assigned to one of four categories: <3°, 3–15°, 15.1–30°, and >30°. Aspects also were grouped into four categories, approximating differences in moisture availability: flat (no aspect), northerly (north, northeast, and northwest), southerly (south, southeast, and southwest), and intermediate (east and west). Elevation was aggregated into five classes: <1864 m, 1865–1951 m, 1952–2164 m, 2165–2286 m, and >2286 m.

Field studies

Fifteen study areas were established across the northern range (Fig. 1) in January 1991 by using the vegetation classification generated with the GIS to assure that all habitats were represented in our sampling and by considering accessibility in winter. Each study area provided a view of several hundred hectares of the northern range (Table 2) from a fixed position of relatively high elevation. These study areas encompass a total of 7514 ha (≈10% of the northern range) and will be referred to as viewing areas. The boundaries of each viewing area were recorded on 7.5′ topographic maps and digitized in the GIS. Only areas that could be seen clearly (i.e., not obstructed by rocks, trees, or other features) were included within the boundaries.

Each viewing area was visited at 2-wk intervals from mid-January through snow melt in late March or early April (Table 3) by hiking or skiing to the fixed viewing position. Each area was visited a minimum of six times in 1991 and 1992. Sites at higher elevations with more persistent snowpacks were visited seven times, but snow had melted earlier at some low-elevation sites due to mild winter conditions. Each visit entailed carefully scanning the viewing area with a Celestron SS80

TABLE 1. Habitat categories used in this study and their common species. The habitat maps were created by aggregating Despain's (1991) habitat types (i.e., potential natural vegetation) into the four grassland classes. We attempted to sample each habitat type, both burned (B) and unburned (U), roughly in proportion to its availability.

Habitat type	Common species	Burned/ unburned	Percent of grasslands: Viewing areas	Percent of grasslands: Northern range
Wet grassland	*Poa pratensis, Phleum pratense, Agropyron caninum, Deschampsia caespitosa, Carex* spp., *Calamagrostis* spp.	B	0.8	0.6
		U	8.2	12.8
Moist grassland	*Artemisia tridentata, Phleum pratensis, Bromus carinatus, Agropyron caninum, Geranium viscoscisimum, Potentilla* spp., *Carex* spp.	B	6.0	18.2
		U	48.4	51.7
Mesic grassland	*Artemesia tridentata, Agropyron caninum, Agropyron spicatum, Bromus* spp., *Potentilla* spp., *Stipa* spp.	B	9.2	5.7
		U	21.8	19.3
Dry grassland	*Artemisia tridentata, Agropyron spicatum, Koeleria cristata, Festuca idahoensis, Chrysopsis villosa, Stipa comata, Danthonia* spp., *Poa* spp., *Sedum* spp.	B	0.7	0.7
		U	0.6	0.8

TABLE 2. Area (ha) in each grassland category (dry, mesic, moist, and wet; see Table 1) for the 15 viewing areas used to assess landscape-level patterns of habitat utilization during the winter.

Viewing area	Burned				Unburned				Other	Total area
	Dry	Mesic	Moist	Wet	Dry	Mesic	Moist	Wet		
Soda Butte	0	0	0	0	0	16	160	62	16	254
Cliff	0	67	16	18	0	227	44	228	13	613
Lamar	0	32	38	0	0	82	102	225	6	485
Jasper	0	11	91	19	0	6	112	74	0	313
Slough Creek	0	14	3	7	0	250	372	173	15	834
Specimen	0	23	2	0	0	36	394	0	22	477
Junction South	3	44	28	0	3	34	84	0	15	211
Junction Northeast	0	0	0	0	0	105	111	0	4	220
Junction Northwest	12	64	28	0	4	73	15	0	1	197
Yancy	0	43	34	10	0	6	12	2	24	131
Hellroaring	0	50	328	26	0	146	571	4	19	1144
Frog Rock	2	92	85	0	25	185	147	6	37	579
Blacktail	0	291	82	0	59	153	67	4	22	678
McMinn	0	0	0	0	245	472	0	0	18	735
Quarry	0	0	0	0	351	290	0	0	2	643
Total	17	731	735	80	687	2081	2191	778	214	7514

spotting scope (Celestron International, Torrance, California, USA) to observe evidence of ungulate foraging activity in the snow pack. Elk paw through the snow to locate suitable forage, feed in this "crater" of ≈0.5 m^2 with their forefeet stationary, then move and repeat the process. Bison use their heads to move snow and locate forage, hence "tilling" the snow within their foraging location. Presence and location of feeding areas used by elk and bison remain easily detectable until the craters or tilled areas are completely covered by new snow or until the snow melts. To identify spatial locations of winter foraging and intensity of use, we defined a feeding patch to be a contiguous area within which animals have grazed with the same level of intensity. Grazing intensity was measured as a percentage in 20% increments of area cratered or tilled.

During each visit to a viewing area, the locations and sizes of ungulate feeding patches and the percentage of the area cratered or tilled were recorded on 7.5′ topographic maps at a minimum resolution of 1 ha. That is, a feeding patch had to be ≥1 ha in size to be mapped. Locations for which data could not be obtained within the viewing area (e.g., because of sun angle, blowing snow, or snow melt) were also mapped. Thus, our habitat-use maps contained a total of seven categories: (1) no feeding activity, (2) 1–20% of area cratered, (3) 21–40%, (4) 41–60%, (5) 61–80%, (6) 81–100%, and (7) no data.

TABLE 3. Dates during which field data were collected for all viewing areas during each winter.

Time period	1991	1992
1	14–16 January	7–10 January
2	30 January–1 February	20–24 January
3	13–15 February	2–5 February
4	28 February–2 March	18–26 February
5	12–14 March	4–7 March
6	24–27 March	22–26 March
7	8–12 April	

Feeding patch maps for each time period and viewing area were digitized in GRASS, and polygons were converted to a grid-cell format with a resolution of 1 ha for analysis. In addition, several aggregate maps were created. First, a frequency map was created in which presence of grazing, regardless of intensity, was summed over the time series for each grid cell. To make a conservative estimate of frequency of use, a value of 0 (no use) was assumed if data were not available for a time period. Thus, the resulting map contained values that ranged from 0 (never used) to 7 (used during each time period). Second, an aggregate map was created that represented the minimum cumulative grazing intensity (MCGI) observed on each grid cell over the study period. The MCGI map was created in GRASS by summing the layers representing the feeding patches for each time period. Each of the grazing intensity categories is represented in the GIS by an integer from 0 to 5 (grazing intensity/20), and thus the MCGI map could potentially range from 0 (no feeding) to 35 (maximum feeding activity during each time period) for an entire winter. MCGI maps were also produced for early, mid-, and late winter periods in 1991 and early and late winter 1992 (see factor analysis of grazing intensity in *Results* for further information). Map cells where data was not available for one or more time periods were not included in the MCGI maps.

Data analysis: patterns of habitat use

Chi-square analysis was used to examine the null hypothesis that burned areas were used at each time period in proportion to their availability in the landscape. Frequency maps containing only grazed and ungrazed sites for each time period were overlaid on a map showing burned and unburned sites to generate a 2 × 2 contingency table.

To address the question whether ungulates preferentially use particular habitats or positions in the landscape for feeding, we tested for relationships between grazing intensity and six environmental parameters (grassland habitat type, burn status, slope, aspect, elevation, and mean annual precipitation). Spatially explicit data for habitat and environmental conditions were available at the resolution of 1 ha from data stored in the GIS. Maps of grazing intensity were constructed for each of the six or seven time periods listed in Table 3. Using the GIS data layers, we extracted information from all 1-ha cells. Cells for which either grazing or environmental data were missing were excluded from this analysis. The resulting data set contained time-specific information on grazing intensity and a multivariate description of the environment for each pixel that had complete data. Correlation analysis was performed between MCGI over the entire winter and each of the six environmental parameters on a per-hectare basis.

Factor analysis was used to identify the covariance structure of the environmental data and to reduce the data to a smaller number of "factors." These factors represent interpretable, independent descriptors of the variation within the environmental data set that could be used in subsequent statistical analyses (Johnson and Wichern 1988). The factor analysis used a principal components solution and varimax rotation method (SAS 1987). Because these factors are uncorrelated, the factor scores were later used in regression analyses of grazing intensity. Scoring coefficients were used in combination with maps of environmental parameters to produce maps of environmental factor scores.

The grazing intensity data were reduced from six or seven separate time periods to several grazing factors for each year by using the same factor analysis methods. These grazing factors were used to test for temporal and geographic trends in habitat use. Previous researchers (Barmore 1980, Houston 1982) have noted that ungulates abandon high-elevation, eastern portions of the northern range as winter progresses. We tested for this shift in the spatial location of habitat use by measuring correlations between the grazing factor scores for each cell and the UTMGS (Universal Transverse Mercator Grid System) easting for the fixed viewing position of each viewing area.

To examine whether the spatial extent (i.e., total area) of foraging areas remained the same or constant through the winter, we calculated the proportion of the viewing areas used during each time period, regardless of intensity of use. The total number of grid cells used was divided by the total number of grid cells for which data were available (i.e., we excluded sites with no data) for each time period to obtain this proportion.

The analyses described above use data from all viewing areas. To examine the null hypothesis that the use of habitats by ungulates is not affected by the spatial arrangement of burning, an analysis of variance was done to test for the effect of the proportion of area burned and the burn pattern for the six viewing areas in which >30% of the area was burned. Each viewing area represented one sample in this analysis, and an index of contagion (O'Neill et al. 1988) was computed for each area. A high value of contagion indicates a clumped pattern of burning, and a low value of contagion indicates a more fragmented or dissected pattern.

Data analysis: spatial scale of ungulate foraging choices

Ungulate grazing intensity measured at the scale of 1 ha might be influenced by environmental variation at several scales. To test this hypothesis, multiple regression was used to explore the relationship between grazing intensity, as measured by MCGI at the scale of 1 ha, and environmental characteristics at scales ≥1 ha. Habitat information at several spatial scales was represented by maps of environmental factor scores.

First, the data were subsampled to remove the effect of spatial autocorrelation in MCGI. A semivariogram describing spatial variation in MCGI was examined to determine the appropriate spatial scale for sampling individual 1-ha cells (Palmer 1990), i.e., the distance at which 1-ha cells could be considered statistically independent. The first sill of this semivariogram occurred at a spatial resolution of 600 m, which we interpret to represent the extent of autocorrelation within viewing areas. Next, we subsampled the MCGI and environmental factor maps using a grid with points spaced at 600-m intervals. Grid points located within a viewing area and having a complete set of MCGI and environmental data were selected for analysis. To quantify the characterisitics of 1-ha cells and the surrounding landscape, environmental factor scores were measured at four spatial scales: 1, 9, 81, and 225 ha for each cell. At the 1-ha scale, the environmental factor scores were used directly from the appropriate 1-ha map cell on the environmental factor maps. To measure habitat at scales >1 ha, a square was centered on the sampling point (e.g., a 3 × 3 cell square for 9 ha) and the mean score of all cells in the square was calculated to represent habitat at a particular scale. Thus, a total of 12 variables described habitat variability due to (1) grassland habitat, precipitation, and elevation; (2) slope and aspect; and (3) burn status (three environmental factors × four scales).

Distance to cover habitat, which may influence ungulate feeding site selection (e.g., Grover and Thompson 1986), was also used in the regression. The GIS was used to generate a map layer containing the distance in metres to unburned patches of conifer and aspen forest for each 1-ha cell. Ungulates are not subject to hunting pressure within park boundaries, but cover habitat can provide sheltered resting areas during inclement weather and cold periods. Stepwise regression was used to select from the 13 habitat variables

TABLE 4. Ratio of observed to expected grazing use by elk and bison in burned and unburned areas through time on a per-grid-cell basis. All values shown differ at $P < 0.05$ (chi-square analysis) except where indicated by NS. See Table 3 for explanation of time periods.

Time period	1991		1992	
	Burned	Unburned	Burned	Unburned
1	NS	NS	0.93	1.02
2	1.12	0.95	0.97	1.01
3	1.04	0.98	NS	NS
4	1.15	0.95	0.97	1.01
5	1.22	0.92	1.05	0.98
6	0.88	1.05	1.06	0.97

those that were useful for explaining variation in MCGI. To be included in the model, a variable had to have values of $P < 0.10$ and $r^2 > 0.01$. Because grazing intensity varied with time during both winters, these analyses were conducted separately for the time periods corresponding to the grazing factors identified by the factor analysis described above.

RESULTS

Patterns of habitat use

Presence of grazing in burned areas.—Over the winter of 1991, burned areas were used more often than expected and unburned areas were used less often than expected if ungulates were using burned areas in proportion to their availability (Table 4). However, there were temporal trends in the use of burned areas. During the first time period (mid-January), burned areas were used in proportion to their availability (Table 4). During time periods two through five (late January through late March), burned areas were used more frequently than expected and unburned areas were used less frequently than expected. The difference in use was greatest in late March, when the ratio of observed to expected use of burned areas was 1.22. During the sixth time period, burned areas received less use than expected. Over the winter of 1992, burned areas were used less than expected or in proportion to their availability during early to midwinter, then used more than expected during late winter (Table 4). In most cases, deviations from 1.0 in the ratios of observed to expected use were greater during 1991 than in 1992.

Influence of environmental heterogeneity.—On a per-grid-cell basis, correlation analysis revealed that MCGI was significantly correlated with elevation, mean annual precipitation, and grassland habitat in both years of the study (Table 5). Habitat type had the strongest relationship with MCGI, with MCGI increasing in the drier habitats. MCGI also decreased with elevation, suggesting that ungulates used lower elevation, drier sites for feeding. MCGI was correlated with burning and slope in 1991, with grazing intensity being greater on burned sites and on steeper slopes.

Factor analysis of environmental variables and grazing intensity.—The factor analysis identified the covariance structure of the environmental variables and reduced the six parameters to three independent factors (Table 6). The first environmental factor (ENVFACT1) described a gradient in elevation, mean annual precipitation, and grassland production. Large positive scores for this factor represent cells of higher elevation, increased precipitation, and more moist grassland habitats. ENVFACT2 describes topographical variation in slope and aspect, with large positive scores representing cells having steeper slopes with southerly aspects. ENVFACT3 describes the burn status of cells, with large positive scores representing burned cells. Maps of the three environmental factors were produced using the GIS.

TABLE 5. Spearman rank correlation coefficients (r) between minimum cumulative grazing intensity (MCGI) over the entire winter and environmental variables on a per-grid-cell basis. The environmental variables are categorical. All significance levels are $P \leq 0.0001$. Footnotes show the values assigned to environmental variables based on quantitative data.

Variable	Correlation (r) with MCGI	
	1991 (n = 4048)	1992 (n = 2980)
Elevation*	−0.12	−0.08
Mean annual precipitation†	0.06	−0.12
Grassland habitat type‡	−0.22	−0.16
Slope§	0.17	NS
Aspect‖	NS	NS
Burn status¶	0.12	NS

* Elevation categories were 1: <1865 m, 2: 1865–1951 m, 3: 1952–2164 m, 4: 2165–2286 m, 5: >2286 m.

† Mean annual precipitation categories were 1: 30–36 cm, 2: 37–51 cm, 3: >51 cm.

‡ Moisture categories for grassland habitat were 1: dry, 2: mesic, 3: moist, 4: wet.

§ Slope categories were 1: <3°, 2: 3–15°, 3: 15.1–30°, 4: >30°.

‖ Aspect categories were 0: flat; 1: southeast, south or southwest; 2: east or west; 3: northeast, north or northwest.

¶ Burn status categories were 0: not burned, 1: burned.

A factor analysis of the grazing data was conducted for both winters. The time-specific grazing data were reduced to three factors for the winter of 1991 (Table 6). Factor GRAZE1 described grazing in late winter (time periods 4–6), GRAZE2 describes grazing in midwinter (time periods 2–3), and GRAZE3 describes grazing in early winter (time period 1). High positive scores represent cells with high values of grazing intensity during the specific time period. During the winter of 1992, the time-specific grazing data were reduced to two factors that described the late winter and early winter (Table 6).

Geographic trends in grazing.—The geographic location of grazing changed during the course of the 1991 winter but not during 1992. During 1991, grazing during mid- to late winter (factors GRAZE1 and GRAZE2) was negatively correlated with the UTM easting associated with each viewing area (Pearson correlation coefficients: GRAZE1, $r = -0.21$; GRAZE2, $r =$

TABLE 6. Factor analysis of environmental variables and 1991 and 1992 grazing intensity showing rotated factor patterns for all viewing areas. The factor associated with each variable is indicated by the loading in boldface type.

Variable	Environmental factors*		
	ENVFACT1	ENVFACT2	ENVFACT3
Elevation	**0.79329**	−0.07553	−0.39739
Precipitation	**0.75519**	0.14540	−0.33292
Grassland habitat	**0.75554**	−0.16048	0.37565
Slope	−0.17590	**0.80136**	−0.06485
Aspect	0.12645	**0.82517**	0.02376
Burn	−0.15537	−0.05884	**0.86938**
Proportion of total variance	0.414	0.312	0.274
	1991 grazing factors†		
Variable	GRAZE1	GRAZE2	GRAZE3
Time period 1	0.04371	−0.00224	**0.99145**
Time period 2	0.13421	**0.86361**	0.02029
Time period 3	0.29653	**0.82038**	−0.04740
Time period 4	**0.63450**	0.48677	0.14044
Time period 5	**0.79884**	0.27967	−0.08281
Time period 6	**0.88643**	0.08805	0.08410
Proportion of total variance	0.412	0.371	0.217
	1992 grazing factors‡		
Variable	GRAZE1	GRAZE2	
Time period 1	0.21811	**0.82177**	
Time period 2	**0.69242**	0.42632	
Time period 3	−0.04642	**0.83586**	
Time period 4	**0.85293**	0.05022	
Time period 5	**0.89064**	−0.03389	
Time period 6	**0.84323**	0.13287	
Proportion of total variance	0.636	0.364	

* ENVFACT1 represents a gradient in grassland habitat type, elevation, and precipitation. ENVFACT2 represents variation in slope and aspect. ENVFACT3 represents burn status of map cells.

† For 1991, GRAZE1 represents grazing in late winter (time periods 4–6). GRAZE2 represents grazing in midwinter (time periods 2–3). GRAZE3 represents grazing in early winter (time period 1).

‡ For 1992, GRAZE1 primarily represents grazing in the late winter (time periods 2, 4–6). GRAZE2 represents grazing in early to midwinter (time periods 1, 3).

−0.47; all $P < 0.01$; $n = 4048$). Because the easting coordinate increases from west to east, this result indicates that grazing intensity shifted to the west during the middle to late winter. GRAZE3 (early winter) was positively correlated with easting ($r = 0.15$, $P = 0.001$). During 1992, however, this trend was reversed, and both the grazing factors GRAZE1 and GRAZE2 were positively correlated with UTM easting (Pearson correlation coefficients: GRAZE1, $r = 0.12$; GRAZE2, $r = 0.18$; all $P < 0.01$; $n = 3545$). Thus, during 1992, grazing intensity was consistently slightly higher in the east.

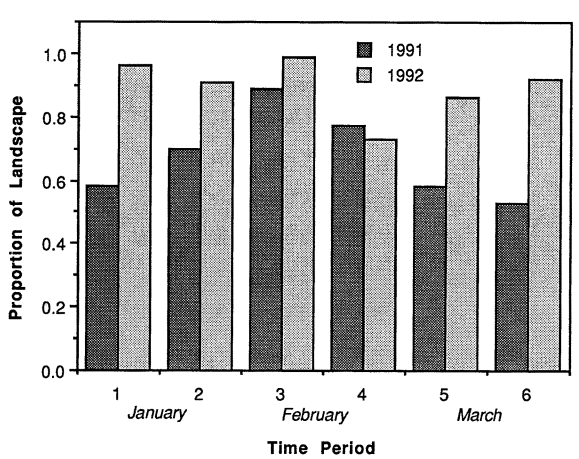

FIG. 2. The proportion of our 7518-ha study area that showed evidence of ungulate grazing during each time period for all viewing areas combined. See Table 3 for explanation of time periods.

The proportion of the landscape used by elk and bison changed through the winter during both years (Fig. 2). During 1991, the proportion of the landscape used increased during the winter, then declined. The greatest amount of area was used during time periods 3 and 4 and the least amount of area was used during time period 7. During 1992, the proportion of the landscape used was generally higher than during 1991 and declined during midwinter.

Effect of spatial pattern of burn.—Six viewing areas that were burned more extensively than the remaining study sites were used to examine the effect of the spatial arrangement of burning on grazing intensity. The proportion of the viewing area burned ranged from 35 to 83%, and the contagion index for these viewing areas ranged from 0.18 (fragmented) to 0.80 (clumped) (Fig.

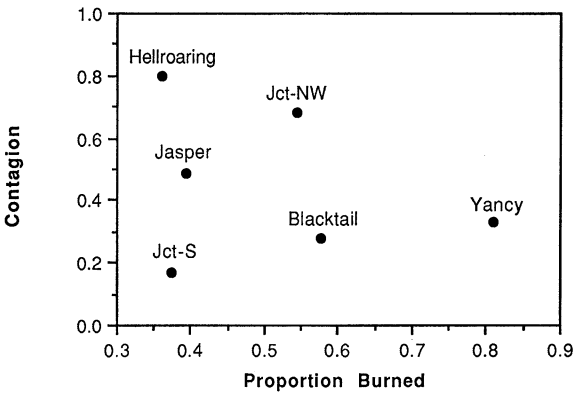

FIG. 3. Plot of the proportion of the area burned and the contagion index (O'Neill et al. 1988) for each of the six viewing areas used to address the effects of spatial pattern of burning on habitat use.

3). Analysis of variance showed no effect of proportion of the viewing area burned or contagion on habitat use in either 1991 or 1992 as measured by the mean MCGI for these sites (all $F_{1,2} \leq 1.05$, all $P > 0.41$). Therefore, the null hypothesis was not rejected for either year. Spatial pattern of burning as measured by contagion was not important within the spatial extent of individual viewing areas.

Spatial scale of ungulate foraging choices

Broad-scale measurements of environmental variables were more useful for statistically predicting MCGI on a per-grid-cell basis than fine-scale measurements (Table 7). Burn status (ENVFACT3) and slope and aspect (ENVFACT2) were important at the broadest scale (225 ha) for both years during mid- and late winter. Burn status at the scale of 1 ha met the selection criteria for the 1991 model and for mid- and late winter, but its explanatory power was low. However, ENVFACT1, which represents elevation, precipitation, and grassland habitat type, was significant at the finer scales (1–9 ha) in both years. Distance to cover was statistically significant in the midwinter model for 1991; 1991 was the more severe of the two winters. Environmental factors and distance to cover at the 1-ha scale had low explanatory power (r^2) relative to broader scale measurements (Table 7). Furthermore, comparison of the model between time periods indicates that the environmental characteristics were not useful for predicting ungulate foraging during early winter (Table 7). These results suggest that ungulate grazing is less predictable using the environmental characteristics we measured during early winter. However, in mid- to late winter, ungulates appear to respond strongly to broad-scale environmental variation (225 ha) in topography and the presence of burning and to fine-scale variation (1 ha) in grassland habitat type.

TABLE 7. Results from stepwise regression of minimum cumulative grazing intensity (MCGI). Independent variables included distance to cover and the factor scores for the environmental parameters at four spatial scales: 1, 9, 81, and 225 ha. The analyses were conducted for three observation periods in 1991 (time period 1, time periods 2–3, time periods 4–6; see Table 6) and two periods in 1992 (time periods 1–3 and time periods 4–6). Only the factors that were significant in the model are listed.

Variable*	Partial r^2	P	Coefficient	N
	1991			
Early winter				
ENVFACT2-1 ha	0.020	0.055	2.50	174
Model total	0.020			
Midwinter				
ENVFACT3-225 ha	0.191	0.0001	3.51	140
ENVFACT2-225 ha	0.109	0.001	4.35	
Distance to cover	0.028	0.018	−15.50	
ENVFACT1-9 ha	0.016	0.071	4.10	
Model total	0.344			
Late winter				
ENVFACT3-225 ha	0.135	0.0001	5.08	135
ENVFACT1-1 ha	0.038	0.016	−2.07	
ENVFACT2-225 ha	0.050	0.004	1.99	
ENVFACT3-1 ha	0.020	0.069	−1.24	
Model total	0.243			
	1992			
Early winter				
ENVFACT3-225 ha	0.050	0.038	5.23	86
Model total	0.050			
Late winter				
ENVFACT3-225 ha	0.153	0.0001	10.97	101
ENVFACT2-225 ha	0.027	0.074	5.07	
ENVFACT1-1 ha	0.034	0.042	−4.62	
Model total	0.214			

* See Table 6 for explanation of the ENVFACT variables.

DISCUSSION

Topography had a strong influence on winter ungulate grazing in northern YNP. In general, sites at lower elevations on steeper, south-facing slopes, where snow accumulations are generally lowest, received more grazing. Although forage availability certainly reflects site fertility gradients, the effect of parameters such as elevation, slope, and aspect on winter ungulate foraging is most likely manifested in the spatial variability of snow conditions. Houston (1982) reported preferential use of ridgetops having less snow under relatively severe winter conditions, even when elk numbers were low. In a boreal forest habitat, Cairns and Telfer (1980) observed strong selection by elk and bison for upland grassland habitat, which was the least available of the habitats they studied. In a study of radio-collared elk in Idaho, Irwin and Peek (1983) found that elk preferentially used southwest-facing areas during the middle of the winter but moved to other areas as snow melted in late winter.

The 1988 fires also influenced winter grazing intensity, with burned sites being used more than expected based on their availability and receiving greater cu-

mulative grazing. However, the frequency of use of burned sites changed over the course of the winter during both years (Tables 4 and 7), with use of burned areas being greatest in mid- to late winter. Within the spatial extent of individual viewing areas, the spatial pattern of burning as measured by contagion did not influence ungulate foraging. However, this result does not preclude the potential for the effects of burn pattern to be manifest at broader spatial or temporal scales (e.g., across the entire landscape between fire events). Variation in burning at the scale of 225 ha influenced grazing intensity in 1991 and 1992 (Table 7), with grazing intensity at the 1-ha scale increasing with the amount of the surrounding landscape that was burned. Results from a detailed spatial simulation model also suggest that both fire size and fire pattern influence ungulate survival at the scale of the entire northern range (Turner et al. 1994), at least for some ungulate densities. This model also demonstrated strong interactions between burn pattern and winter severity. Therefore, the effect of spatial patterning may be manifest at scales exceeding the spatial extent of a single viewing area.

Grazing in burned habitats may result in enhanced forage procurement for ungulates in YNP. In the Front Range of Colorado, Hobbs and Spowart (1984) observed small changes in the quality of individual forages after fire but dramatic enhancements in the nutritional quality of winter diets of mule deer and mountain sheep. The improvement resulted from higher levels of crude protein in diets chosen on burned sites. Mule deer and mountain sheep obtained more green grass on burned plots than controls during winter. We observed no differences in crude protein between burned and unburned habitats in YNP but noted substantial increases in forage quantity in burned habitats (Wallace et al., *in press*). Fire also reduces standing dead and litter, which may obscure available green forage (Hobbs and Spowart 1984). The nutritional advantage of feeding in burned areas is lost by spring because of the greenup of high-quality forage (Hobbs and Spowart 1984), and our data from 1991 support the lack of selection for burned sites during greenup (Table 4).

Snow, which varies spatially and temporally on the northern range (Houston 1982), is an important influence on the spatial extent and geographic location of habitat use. We observed a shift in habitat use from east to west during 1991 but not during 1992. Our data also suggested differences in the spatial extent of the landscape used for grazing between years. The proportion of the landscape used by ungulates for foraging increased during 1991 as winter proceeded. During 1992, however, ungulates used a greater proportion of the landscape compared to 1991, and the proportion declined in late winter rather than increasing (Fig. 2). During normal to severe winters, high-elevation sites are the first to become inaccessible, and then deep snows cover successively lower elevations as winter progresses. Houston (1982) reported that the area occupied by ungulates generally decreased between early winter (December–January) and mid- to late winter (February–mid-April) during an 11-yr period (1968–1979). However, 1991 and 1992 were both relatively mild winters, during which only a small portion of the total winter range became unavailable to ungulates because of snow conditions. Houston (1982) observed that the area used by ungulates increased during the latter part of the extremely mild winter of 1976–1977, similar to our observation during 1991. The differences in our data between 1991 and 1992 are likely to reflect the temporal dynamics of the individual winters. The winter of 1991 was uniformly mild, whereas the winter of 1992 began with severe winter storms followed by mild conditions. The early snows of 1992 forced animals to lower elevations (some out of the park), and they returned gradually to their typical feeding areas as the winter progressed, resulting in spatially dispersed foraging.

During early winter, the location and intensity of ungulate foraging could not be predicted by using the environmental characteristics measured in this study. This lack of explanatory power could result from the wide dispersion of ungulates over the northern range typical in early winter (Houston 1982), the lack of deep snow, and greater availability of forage. Forage availability may not be limiting under these conditions, and ungulate foraging choices might occur at finer spatial scales than those measured here. However, as winter conditions became more severe and forage availability diminishes, ungulates may be more sensitive to the environmental characteristics at the scales that we considered.

Ungulates appeared to respond to environmental heterogeneity at several spatial scales during mid- to late winter. Our ability to explain variation in MCGI with environmental variables was dependent on the scale at which the environmental parameters were measured (Table 7). Environmental factors representing burn status and topography had their strongest influences on grazing intensity at broad scales (225 ha), and grassland habitat type was important at the finest scale (1 ha). The broad-scale measurements of environmental variables also accounted for most of the variation in grazing intensity in both years. These results suggest that ungulates respond strongly to environmental variation at broad scales, although variation in the environment at finer scales is not unimportant.

The influence of hierarchical environmental patterns on habitat use has been recognized in other taxa, especially birds (Bergin 1992, Russell et al. 1992, Pearson 1993). Searching for suitable foraging areas is a multiscale process (Johnson 1980, Senft et al. 1987, Russell et al. 1992). Highly mobile animals are capable of first choosing a large area that is unlikely to contain suitable foraging conditions and then making additional decisions at finer and finer scales to eventually po-

sition individual foraging efforts. The scale of these choices is bounded at the broadest scale by the movement capability of the organism and at the finest scale by the spatial and temporal extent of an individual foraging bout (feeding crater). The resulting pattern of foraging depends on the spatial heterogeneity of forage (Morse and Fritz 1982) and the organism's foraging choices. Elk and bison are highly mobile; they are capable of moving across the northern range in a period of a few days. Therefore, the observed patterns of grazing should reflect their habitat preferences and provide some insight into their selection of foraging sites. Our results suggest that these ungulates were most sensitive to broad-scale patterns.

The importance of broad-scale environmental heterogeneity in predicting ungulate grazing intensity could result from several reasons. First, ungulates may actually be making foraging choices based on landscape cues that are apparent at broad spatial scales. Although foraging ungulates are known to respond to very fine-scale (1–10 m^2) variation in forage (Hobbs et al. 1981, Hanley 1982, Wydeven and Dahlgren 1983), differences in forage quality may diminish during winter (Wallace et al., *in press*), and snow may obscure fine-scale cues used to select the most profitable foraging sites. Thus, ungulates may become more sensitive to coarse-scale (1–100 ha) features of the landscape, such as topography and snow, to find the most suitable foraging areas. Second, ungulates may increase the duration of time and number of foraging bouts in patches that are more profitable, e.g., burned areas containing greater forage abundance than unburned areas. Third, the temporal scale of this study differs substantially from some other studies of ungulate foraging. Whereas other studies (e.g., Hobbs et al. 1981, Wydeven and Dahlgren 1983) have measured foraging choices at fine temporal (minutes to hours) and spatial (centimetres to decimetres) scales, this study sampled ungulate foraging and habitat use at a relatively coarse temporal scale (2 wk) and broad spatial scale (kilometres). With highly mobile animals, broader scale environmental patterns could become more influential as temporal scale of observation increases.

Our study addressed foraging activities only, but other habitats are also important to ungulates in winter. Elk often use forested habitats for resting (Constan 1972, Cairns and Telfer 1980, Wydeven and Dahlgren 1983, Green and Bear 1990) and, although we found foraging to be associated with south-facing slopes, elk in Rocky Mountain National Park frequently use cooler north-facing slopes for resting (Green and Bear 1990). We also did not study foraging dynamics in burned forested habitats of the northern range. In Glacier National Park, Singer (1979) found that elk selected fire-induced lodgepole pine savanna as well as spruce forest more than expected. In addition, elk used grasslands during the mild winter of 1972–1973 but were more confined to spruce forests during the more normal snow depths of the winter of 1973–1974 (Singer 1979). Singer attributed the importance of spruce habitats during more severe winters to reduced snow depths, excellent cover, and profuse browse.

Our results suggest the following insights relevant to management of native ungulates in natural areas. First, the effects of fire on ungulate winter range are likely to be manifest at broad scales, and the amount of variation area in the surrounding landscape had the greatest explanatory power in predicting grazing intensity per hectare. Second, the effects of burning on winter ungulate grazing were still manifest 4 yr after the fires, although effects appeared to be diminishing. Third, interpreting or predicting the grazing of ungulates at any given location requires an understanding of the environmental heterogeneity of the surrounding landscape, not simply a description of the local site attributes. Thus, managers must consider their lands at these broader scales. For example, one cannot simply preserve a small productive meadow and ignore the surrounding landscape matrix. Undesirable changes in the surrounding landscape may reduce the utility of the desirable habitat patch for ungulate foraging. While wildlife managers generally are not naive to these types of concerns, quantifying the relative importance of environmental heterogeneity at multiple scales may help managers estimate the actual size of the area that must be considered. Finally, managers often have some control over fire occurrence, fire size, and burn pattern, but no control over winter weather and topographic variability. Because these factors are of critical importance for ungulate population dynamics (e.g., Hobbs 1989, Turner et al. 1994), managers must recognize that some of the factors affecting ungulates are beyond their control. Fire effects on northern Yellowstone ungulates are likely to be relatively short-lived, and in the long term, may have minimal impact on population dynamics compared to winter conditions.

In summary, measurements of environmental heterogeneity at broad scales seem to be most important for winter ungulate grazing. Areas that were burned in 1988 received more grazing, presumably because burning had enhanced the abundance of forage. Our results suggest that the effect of fire on ungulate winter grazing in northern Yellowstone may be manifest primarily at coarse scales. Topography was also an important influence on grazing. Sites with lower elevations, steep slopes, and southerly aspects had less snow throughout the winter and therefore received more grazing. Temporal and spatial changes in grazing intensity were related to the temporal patterns of snowfall during the two winters of study and the migratory movements of ungulates in response to snow accumulation. Finally, grazing intensity in this study was best predicted by environmental heterogeneity, especially burn status, slope, and aspect, at broad scales rather than on a per-hectare basis, suggesting that wintering ungulates in

YNP respond most strongly to coarse-grained variation in this landscape.

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