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Scale of heterogeneity of forage production and winter foraging by elk and bison

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Abstract

The relationship between fine-scale spatial patterns of forage abundance and the feeding patterns of large ungulates is not well known. We compared these patterns for areas grazed in winter by elk and bison in a sagebrush-grassland landscape in northern Yellowstone National Park. At a fine scale, the spatial distribution of mapped feeding stations in 30 m x 30 m sites was found to be random where there were no large patches devoid of vegetation. In areas similar to the mapped sites, the underlying spatial distribution pattern of biomass was also determined to be random. At a broad scale, forage biomass differed among communities across the northern range but forage quality did not. These results suggest that ungulates are feeding randomly within forage patches (fine scale) but may select feeding sites based upon forage abundance at broader, landscape scales. Contrary to what has been suggested in other systems, ungulates were not 'overmatching' at finer scales.

1. Introduction

It is well known that spatial heterogeneity influences the dynamics and movements of animals in the landscape (*e.g.* Wiens 1976). Spatial variation in forage availability is of particular importance for mammalian herbivores who may make grazing choices at a variety of spatial and temporal scales (Senft *et al.* 1987). The spatial distribution of foraging activity can influence ecological processes at a variety of hierarchical levels (Senft *et al.* 1987). For example, herbivore foraging patches can be located near one another, thus concentrating areas of high forage intake with areas of high nutrient deposition. Such a juxtaposition can create microsites of high ecosystem 'metabolic activity' (Ruess and McNaughton 1987) and could result in these areas becoming preferred foraging sites on the landscape. The relationship between environmental heterogeneity and organismal function remains a high priority for ecological research (Lubchenco *et al.* 1991)

Several factors have been cited as proximal causes of ungulate foraging behavior. These include high forage biomass concentration that enables animals to maximize forage intake per bite (McNaughton 1984; Hudson and Frank 1987; Spalinger *et al.* 1988) and proximity to water and cover (Grover and Thompson 1986). The nutrient content of the forage is also critical and may be more important than forage quantity (Hobbs *et al.* 1980; Owen-Smith and Novellie 1982). Social interactions such as a dominance hierarchy will also play a role in the choice of foraging sites by individuals. Herd cohesion is rare and therefore is relatively unimportant (Shoesmith 1980) in both bison *(Bison bison)*

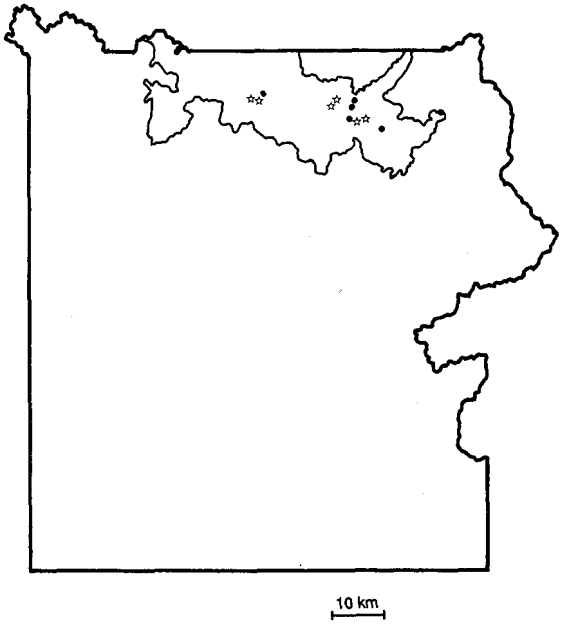

***Fig.** 1.* Locations of the sites where feeding stations were mapped in 1988–89 (closed circles) and the grid forage biomass sampling sites (open stars). The northern range is delineated within the boundaries of Yellowstone National Park.

and elk (*Cervus elaphus nelsoni),* the dominant ungulates in the system we studied. Many of these factors are important at several scales, from the individual feeding station (usually an area no greater than 0.5 m^2) to foraging patches on the landscape.

There is abundant evidence for spatial patterning in natural vegetation (*e.g.* Hill 1973; Ripley 1978). The patterns result from the complex interplay of biotic competition (Levin 1987) and abiotic variability (Burrough 1983) and can be detected at a variety of spatial scales (O'Neill *et al.* 1991a). Significant spatial patterns have been demonstrated in forage vegetation at the 8–30 m scale (O'Neill *et al.* 1991b). It is clear that foragers can take advantage of spatial patterning (Bakker *et al.* 1983; Ring *et al.* 1985; O'Neill *et al.* 1988) to optimize their utilization of the resource. In addition, Senft *et al.* (1987) suggest that foraging behaviors ought to be predictable across spatial scales.

We examined the distribution of individual feeding stations within 30 m x 30 m sites of high feeding activity on the northern winter range of Yellowstone National Park (Fig. 1). We chose to look at winter feeding behavior because feeding stations are easily detected in snow. The questions addressed were: 1) are the location of ungulate feeding stations within a site predictable based upon an underlying fine-scale pattern in forage vegetation at that site, and 2) does the location of ungulate foraging sites across the landscape reflect broad-scale patterns of winter forage quantity and quality. We dealt with spatial patterning at two spatial scales identified by the following terms throughout this paper. Fine/community scale refers to the feeding site (30 m x 30 m), sampled by examination of the 0.5 m^2 feeding stations. The broad/landscape scale denotes the patterns noted across the 80,000 ha northern winter range sampled with 0.5 km^2 forage biomass plots within each community type (Table 1). In the snow, feeding stations are identified by 'craters' dug in the snow by ungulates using either their forefeet or head swings. Feeding sites are areas that contain feeding stations.

2. Methods

2.1. Study area

The northern range of Yellowstone National Park includes high elevation summer range and low elevation winter range locations. The landscape in the northern range is the most diverse in the Park, consisting of steep-sided ridges, high peaks and broad, open meadows. We conducted our work within the low-elevation winter range which covers approximately 80,000 ha and can support up to 750 bison and 10,000 elk (Houston 1982). Several grassland community types have been classified (Despain 1991) in this area. We describe our modification of this classification pattern below. This area of the Park contains heterogeneity of forage resources at many scales, from m^2 to km^2 as a result of gradients in elevation, substrate and fire history.

2.2. Spatial distribution of feeding stations within feeding sites

During the winter of 1988–1989, the distribution of elk *(Cerviselaphus nelsoni)* and bison *(Bison bison)* feeding stations was mapped at eight sites across the

Table 1. Scales at which sampling and analyses were conducted.

Scale	Extent	Sampling units
Fine/community	30 x 30 m feeding sites	0.5 m^2 feeding stations
Broad/landscape	80,000 ha northern winter range	0.5 km^2 forage biomass plots

Table 2. Elevations and community types (Despain 1991) of sites where feeding stations were mapped. Distribution of feeding stations within each site were analyzed using Chi-square.

Location	Elevation (m)	Community type	Chi-square	df	p	Distribution
Rainbow Lakes #1	1831	Dry grassland	12.3	6	.05	Nonrandom
Rainbow Lakes #2	1831	Dry grassland	53.2	4	.0001	Nonrandom
Phantom Lake	2144	Moist grassland	0.23	2	NS	Random
Crystal Bench	1958	Moist grassland	5.40	3	NS	Random
Slough Creek #1	1983	Wet grassland	28.1	4	.001	Nonrandom
Slough Creek #2	1983	Mesic grassland	15.3	5	.025	Nonrandom
Lamar Valley	2059	Wet grassland	3.0	3	NS	Random
Barronette	2212	Understory	5.0	3	NS	Random

northern range (Fig. 1). These sites were chosen as representative of the hundreds of possible feeding sites due to their temporal constancy on the landscape, *i.e.* ungulates tended to reuse these general areas each year. At each site, areas of heavy ungulate usage were found to average **30** m x **30** m in size. Measuring tapes were laid perpendicular to one another along two axes of the area. Each feeding station was identified as a 'crater' dug into the snow by either elk or bison. The different ungulate species do not share feeding areas. Stations were mapped by noting their locations on the x/y grid created by the two measuring tapes. Station distribution was compared with the Poisson distribution by determining the number of stations within **5** m x **5** m quadrats within the **30** m grid. Then using the Poisson distribution as the expected value, chi-square analyses were performed (Table 2). Values significantly different from expected were nonrandom.

2.3. Forage patterns within feeding sites

The spatial distribution of forage biomass at the feeding site scale was determined in October, 1990. Forage biomass was sampled by establishing two **30** m by **30** m grids of sampling points in three areas that were visually similar to the feeding station areas mapped in 1988–1989. The two grids were located near one another, but one was placed in grassland which was burned in 1988 and one was placed in grassland which was not burned during that fire season. Biomass was clipped to ground level at points located every 2 meters yielding a total of 225 sampling points per grid. Material was clipped within a 0.04 m^2 quadrat, oven dried at **60°C** to constant mass and weighed. Grid locations are shown on Fig. 1 and descriptions are given on Table 3. Burned locations were included in the analysis to see if fire would impose a pattern on biomass distribution in potential feeding sites.

The reason for making these measurements was to discern if these montane grasslands tended to have discrete patterns in biomass distribution. These presence of these patterns could be used to explain partially the existence of (but not predict) any patterns in ungulate foraging behavior. Although an analysis of forage biomass patterns *prior* to ungulate grazing would be optimal, it is not possible due to our inability to predict exactly where ungulates would graze the following winter. Similarly, it might have be better to look at forage biomass the fall following the time of crater measurement. However, since the winter of 1988–1989 was much wetter than the winter preceding it,

Table 3. Elevations and community types of the sampling grids. Each location had two grids, burned and unburned. Average biomass values at the different sampling sites (n = 225/grid) followed by the same letter are not significantly different from one another, $p \leq 0.05$, Duncan's Multiple Range Test.

Location		Elevation (m)	Community type	Biomass (g m^{-2})
Blacktail	Burned	2128	Mesic grassland	90.8[c]
	Unburned	2147		53.0[d]
Hellroaring	Burned	2097	Moist grassland	129.5[b]
	Unburned	1926		103.0[c]
Lamar	Burned	2071	Wet grassland	118.8[b]
	Unburned	2059		203.0[a]

forage biomass patterns the following summer and fall would be expected to be different than those seen in the fall of 1988 (Merrill *et al.* 1988), since winter range forage biomass correlates closely with precipitation levels the previous winter. Thus, since precipitation during the winter of 1989–1990 was similar to that experienced in the winter of 1987–1988, forage biomass patterns in the fall of 1990 would be expected to be similar to those in the fall of 1988. This temporal offset in measurements follows the principle of 'ecological necessity' as described by Hargrove and Pickering (1992), Peters (1992) and Pickett (1989). Given this temporal gap, it was not possible (due to National Park policy) to permanently mark the sites measured in 1988 for two years. We therefore chose to use sites which were visually similar to those measured in 1988 to look for the existence of biomass patterns.

Biomass distribution within these grid-sampled sites was analyzed for autocorrelation using semivariance analysis. Isotropic and anisotropic analyses were done with GS + Version 1.1 (Gamma Design, Inc.). Significant autocorrelation was considered to exist if slope values in either isotropic or anisotropic analyses were significantly different from zero.

In addition, the amount of biomass that could have been procured by an ungulate feeding within each sampling grid was determined by sampling the biomass grid data using different simulated foraging patterns. A random foraging pattern was developed using a random number distribution of x/y coordinates. One additional pattern was obtained by sampling the 30 highest biomass points within each grid. This was called the 'smart' feeding pattern since an ungulate with perfect knowledge of biomass distribution presumably would use this pattern. Thirty sampling locations were used since this was average number of feeding stations found in the feeding sites mapped in 1988–1989. The distribution of these high biomass points within each grid was also compared with the Poisson distribution as described above.

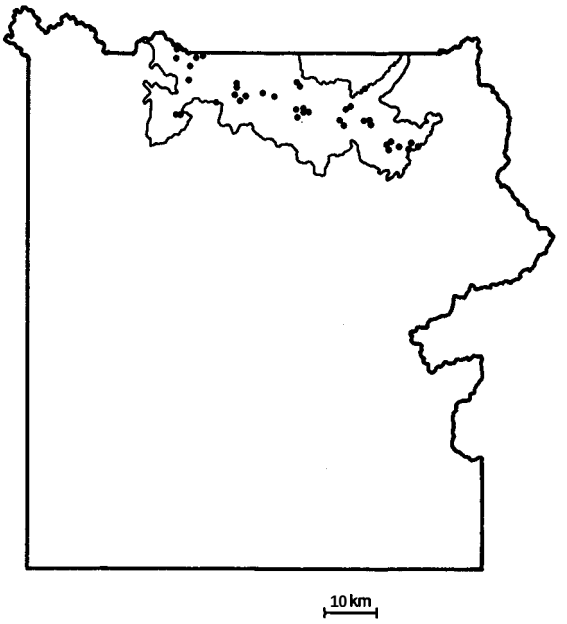

Fig. 2. Locations of the landscape-scale biomass sampling sites.

2.4. Landscape-level analyses

At the landscape scale, average biomass abundance was determined at **38** locations within nine general

community types that we had identified across the northern range of the Park (Fig. 2). These grassland community types were characterized by average moisture regimes and whether or not that area had burned during the fires of 1988. Canopy communities were in the understory of *Psuedotsuga menziesii* stands. Dry grasslands were dominated primarily by *Agropyron cristatum;* mesic grasslands were dominated by *Festuca idahoensis;* moist grasslands were dominated by *Artemisia tridentata* and wet grasslands were dominated by *Phleum pratense* and *Agropyron caninum.* Nomenclature follows that of Cronquist *et al.* (1977). Each community type was sampled in October, 1990, along two 100 m transects which were perpendicular to one another, crossing at the 50 m point. Biomass was sampled within 0.04 m^2 quadrats every 10 m along both transects. If **a** shrub fell within the quadrat, only the current year's growth was sampled. Biomass samples were dried, weighed, ground to pass a **2** mm sieve and then analyzed for forage quality (crude protein, acid detergent fiber, neutral detergent fiber) using a LECO Nitrogen Determinator Model 601-700-400 for protein and the van Soest method for fiber at the Agronomic Services Lab, Oklahoma State University. Biomass quantity and quality were compared among community types using a two-way ANOVA with moisture and burn status as main effects. Quality data were normalized using an arcsine square root transformation.

3. Results

3.1. Feeding station distribution

The distribution of winter feeding stations within feeding sites across the northern range was not significantly different from the Poisson distribution (Table **2)** in four of the eight sites. We observed large areas of bare ground in the four sites where there was a significant difference from the Poisson distribution. Where vegetation appeared to be more homogeneously distributed, a random distribution of feeding stations was found.

Table4. Average biomass that could be procured by an ungulate using a random search pattern, or a pattern sampling the 30 highest biomass points in a site (smart). Means followed by the same letter are not significantly different ($p \leq .05$, Duncan's multiple range test) from one another within each site – burn status combination. Burn status: b = burned, u = unburned.

Site	Burn status	Sampling type	Biomass (g m^{-2})
Blacktail	b	Random	81.3b
(dry grassland)		Smart	154.8a
	u	Random	38.3b
		Smart	83.0a
Hellroaring	b	Random	104.3b
(moist grassland)		Smart	201.5a
	u	Random	85.0b
		Smart	149.5a
Lamar	b	Random	90.0b
(wet grassland)		Smart	204.8a
	u	Random	145.3b
		Smart	315.0a

3.2. Feeding site analyses

No significant autocorrelation was found in the spatial distribution of biomass in any of the sampling grids. However, at both Blacktail and Hellroaring, significantly more biomass was available in the burned areas. At Lamar, significantly more biomass was found in the unburned area. The average biomass also differed significantly among sites, with the greatest amount in the Lamar site, followed by Hellroaring and Blacktail, respectively.

The ability of an ungulate to obtain forage in the six grids was compared by simulating alternative foraging patterns. Significantly more biomass could be procured if an ungulate had perfect knowledge of the site with the 'smart' sampling protocol yielding over twice the biomass of the random pattern (Table 4).

We analyzed the distribution patterns of the 30 highest biomass points at all of the sites and found that in all except one site, their distribution was not significantly different from the Poisson distribution (Table ***5)***. The exception was the burned area in Lamar, where the high biomass points were significantly clumped in distribution (Fig. **3).**

Table 5. Distribution of the highest biomass points at each sampling grid. df = 29 for each site, b = burned, u = unburned.

Site	Burn status	Chi-square	p	Distribution
Blacktail	b	13.69	NS	Random
	u	16.00	NS	Random
Hellroaring	b	***5.58***	NS	Random
	u	4.10	NS	Random
Lamar	b	24.81	.05	Nonrandom
	u	2.42	NS	Random

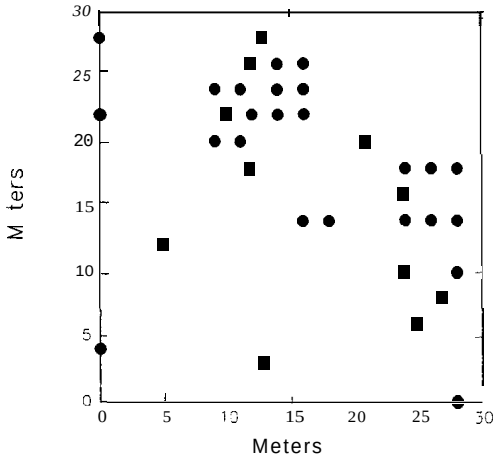

Fig. 3. Mapped distribution of the highest biomass points in the Lamar burned grid. Grid dimensions were 30 m x 30 m; biomass was sampled every two meters. This was the one grid in which the distribution of the high biomass points was found to be nonrandom.

3.3. Landscape-level analyses

At the landscape scale, biomass quantities followed a moisture gradient from the wet grassland type to the canopy understory vegetation (Table ***6)***. There were no significant differences in biomass quantities between the dry grasslands and the canopy understories. However, there was significantly more biomass in the wet grassland type with intermediate quantities found in the mesic and moist grasslands. Although biomass quantity was consistently higher in burned areas, differences were not always significant. Forage quality (crude protein, acid detergent fiber and neutral detergent fiber) did not differ between community types.

4. Discussion

4.1. Feeding station distribution

Within feeding sites, ungulates appear to select feeding stations at random unless they encounter large areas with no biomass. At the four sites in which feeding stations distribution was nonrandom, bare areas could be detected and avoided. The two Rainbow Lakes sites were located in xeric grasslands with large interstitial spaces between plants. The Slough Creek #1 location had a dried pond in the center of the feeding site while Slough Creek #2 was dotted with a series of large boulders. Since ungulates somehow avoided these large areas devoid of forage, grazing within the **30** m plots was nonrandom (*e.g.* in Slough Creek #1, there were not even footprints in the area where the dried pond was located). However, ungulates apparently did not differentiate between areas of low and high biomass (as opposed to no biomass) at the individual feeding station scale and thus maximize intake. In areas without large patches of bare ground, the location of individual feeding stations within a feeding site was random.

4.2. Feeding site forage distribution

In areas similar to the feeding sites without large bare areas, the distribution of the underlying biomass was found to be random in five of the six areas sampled (Table 5, Fig. **3).** The consistency in the randomness of the pattern is particularly interesting because the six sites spanned a range of community types and biomass abundance. This suggests that the pattern may indeed be general. The one location where the high biomass points were found to be significantly clumped had been burned two years prior to sampling. It is possible that the biomass distribution was influenced by a heterogeneous burning pattern.

The present study failed to detect any nonrandom spatial pattern in the forage biomass at a fine scale (30 m x 30 m) in sites without large patches of bare ground. Nevertheless, foraging choices occurred at broader scales since ungulates recog-

Table 6. Biomass quantity and quality (crude protein, acid digestible fiber and neutral digestible fiber) at the landscape scale grassland sampling sites across the northern range. Means followed by the same letter within columns are not significantly different from one another, Duncan's Multiple Range Test.

Community	Quantity (g m^{-2})	Protein (%)	ADF (%)	NDF (%)
Wet, Burned	232.0[a]	5.42[a]	59.43[a]	37.43[a]
Wet, Unburned	225.8[a]	5.02[a]	63.23[a]	37.50[a]
Moist, Burned	150.3[b]	5.06[a]	61.45[a]	38.85[a]
Moist, Unburned	122.3[b]	6.99[a]	60.57[a]	39.03[a]
Mesic, Burned	170.5[b]	5.46[a]	60.99[a]	38.85[a]
Mesic, Unburned	63.3[c]	6.04[a]	51.00[a]	33.60[a]
Dry, Unburned	34.0[d]	5.45[a]	63.55[a]	37.90[a]
Canopy, Burned	76.5[cd]	5.54[a]	50.67[a]	38.87[a]
Canopy, Unburned	32.3[d]	6.43[a]	58.00[a]	40.20[a]

nized and avoided large areas without forage. Thus animals may be taking advantage of a broader-scaled spatial pattern. Theoretical calculations (O'Neill *et al.* 1988) suggest that foragers may travel across the landscape in large spatial increments, moving through areas devoid of forage into areas where foraging could occur. In this study, it appears that once a foraging ungulate is inside of a patch of forage vegetation, no finer-scaled pattern exists and feeding is random. This random pattern would reduce overall amounts of movement needed by the animals, thus keeping energy expenditure low. This type of movement is typically expected when forage quality is as low as seen here (Wickstrom *et al.* 1984; Klein and Bay 1990).

4.3. Landscape-level patterning

At the landscape scale, we did identify significant patterning to which ungulates might respond. There was significantly more biomass in the wettest areas of the system (Table *6).* However, biomass quantities were not significantly different between our designations of moist and mesic grassland types. There probably is a fairly continuous distribution of biomass quantity along a moisture gradient on the northern range with large differences found at either moisture extreme. What was especially interesting was the lack of difference in biomass quality. With the exception of forage nitrogen content, burned areas are noted for their high quality live forages immediately following fire (Ojima *et al.* 1990). However, plants sampled were two years post-fire and dormant. Thus, most nutrients were probably already translocated belowground (Adams and Wallace 1985; Seip and Bunnell 1985) and fire effects may be reduced in winter forage.

Since there were no differences in forage quality found in this study, we suggest that ungulate feeding site selection may be based primarily on forage quantity at these broad landscape scales. Ungulate use of different landscape types will be modified by other factors such as snow depth and density as well, of course. However, within the limits of an ungulate's searching distance, their choice in that landscape region would be based on forage quantity since this is variable and quality was not. This is supported by observations that ungulate feeding was found to be concentrated more in wet grassland types across the entire northern range (Pearson *et al.* in press). The lack of response to forage quality is contrary to what McNaughton (1988) found in tropical grasslands. Since elk are intermediate feeders, focusing both on quantity and quality, and bison are bulk feeders, focusing on forage quantity (Hofmann 1989), a foraging strategy based upon biomass quantity would be reasonable. If an ungulate were a concentrate feeder, focusing primarily on quality of the available food, then such a selection procedure for foraging sites would not be feasible.

The randomly distributed foraging within a feeding site that we documented on the Yellowstone winter range is also counter to the hypotheses presented by Senft *et al.* (1987). They stated that

there should be an overmatching aggregate response pattern at the feeding station level with a maximization of nutrient intake. Within the winter range landscape we studied here, nutrient maximization was apparently not the goal of ungulate foragers, nor was there an overmatching pattern. However, in a summer range where forage is not hidden by snow, and where there are large differences in forage nutrient quality, then the expected responses may be similar to the predictions of Senft *et al.* (1987) and to the findings of McNaughton (1988).

In the winter situation we measured, the answer to both questions one an two would appear to be negative, since feeding station locations are not predictable based upon an underlying fine-scale pattern in forage biomass. Also it does not appear that there were broad-scale patterns of forage quality during the winter. Ungulates may be responding primarily to forage biomass since broad-scale patterns of forage quantity were found.

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