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Landscape nutritional patterns and cattle distribution in rangeland pastures

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ABSTRACT

On rangelands, uneven or unmanaged livestock distribution can adversely affect plant community composition, riparian function, or displace wildlife. These issues have historic precedents and are still a challenge for those managing rangelands. A thorough understanding of the mechanisms governing livestock distribution can help land and livestock managers avoid or ameliorate many deleterious effects. To that end, this research tested hypotheses that grazing cattle seek nutritionally superior portions of rangeland pastures. Global positioning system (GPS) collars were used to track cattle movement and activity in three, 800+ ha pastures where the spatial distribution of standing crop, crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and forage digestibility (*in situ* dry matter disappearance (ISDMD)) were mapped in late spring. Four of five analyses implied grazing cattle spatially responded to forage quantity/quality attributes. Analyses indicated cattle favored higher than average CP ($P = 0.006$) and ISDMD ($P = 0.078$), and lower than average NDF ($P = 0.003$) and standing crop ($P = 0.069$) locales. No significant effect ($P = 0.954$) occurred with ADF analyses. Correlations among those variables imply cattle may simultaneously respond to more than one nutritional attribute as they select foraging locales. Stepwise regression, however, relating grazing distribution to geophysical and forage quantity/quality characteristics were extremely poor predictors of where cattle grazed. Listed in order of entry, the model implied elevation above or below stock water, horizontal distance to stock water, forage CP content, and degree of slope were the site specific attributes most associated with cattle distribution. We speculate that cattle interactions with landscape level nutritional dynamics may at least partially explain seasonal changes in distribution and forage use by cattle across the landscape. These findings should help land and livestock managers understand, explain, and manipulate livestock distribution on their holdings.

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1. Introduction

To the frustration of land and livestock managers, patterns of use and non-use by livestock in extensive pastures tend to persist across years (Willms et al., 1988; Ganskopp and Bohnert, 2006), and unmanaged livestock distribution can adversely affect rangeland plant community composition (Pinchak et al., 1991), riparian function (Smith et al., 1992), or displace wildlife (Coe et al., 2004). These issues have historic precedents and are still a challenge for rangeland managers today (Anonymous, 1936; Bailey et al., 2006). Understanding the mechanisms governing livestock distribution can help managers avoid or ameliorate many deleterious effects.

Several animal attributes affect distribution including: species or breed (Bailey et al., 2001a), need for escape or

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hiding cover (Stuth, 1991), prior experience with a landscape (Bailey et al., 1996), age (Wells, 2004), and reproductive status (Bailey et al., 2001b).

Environmental characteristics affecting distribution include: proximity and/or relative elevation of drinking water (Roath and Krueger, 1982); degree of slope (Ganskopp and Vavra, 1987); density of woody vegetation (Holechek et al., 1998); presence of trails (Ganskopp et al., 2000); location of mineral (Kruelen, 1985) or protein supplements (Bailey and Welling, 1999); grazing history of the landscape and its attending effects on herbage (Ganskopp and Bohnert, 2006); fertilizer and fire effects (Hooper et al., 1969; Bondini et al., 1999); plant community composition and its associated effects on forage quantity (Smith et al., 1992) and quality (Pinchak et al., 1991); diurnal temperature dynamics of the landscape (George et al., 2007); and even tides or prevailing winds (Lynch et al., 1992).

If physical features like extreme slope or distance from water are not limiting, managed or focused perturbations like mowing (Romo et al., 1997), prescribed fire (Hartnett et al., 1996), or high intensity grazing (Moisey et al., 2006) can be used to alter the nutritional status of the landscape and attract stock or native ungulates to historically ungrazed locales. Strategically placed supplements can also lure cattle to unused sites and are especially effective when pastures support low-quality herbage (Bailey and Welling, 1999).

Optimum foraging theory (MacArthur and Pianka, 1966) suggests foraging animals minimize energy expended and maximize energy returns. Livestock and wildlife often employ optimization strategies (Black and Kenney, 1984; Astrom et al., 1990), but ruminants do not always optimize nutrient intake during a meal or on a daily basis (Distel et al., 1995). While some have reported that crude protein and/or forage digestibility are perceived rewards for animals selecting patches of forage (Senft et al., 1985; Hirata et al., 2006), foraging decisions by large grazers at relevant temporal and spatial scales have not been studied (Laca et al., 1994).

The objective of this research was to test the hypothesis that grazing cattle seek nutritionally superior patches or locales within large pastures. Global positioning system (GPS) collars were used to track cattle movements and activities in three, 800+ ha pastures where the spatial distribution of standing crop, crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and forage digestibility as indexed by *in situ* dry matter disappearance (ISDMD) were mapped.

2. Materials and methods

2.1. Study site and forage sampling

Research was conducted in three pastures (829–864 ha, elevation 1400–1674 m) on the Northern Great Basin Experimental Range (43°29' N, 119°43' W (WGS-1984)) 52 km west of Burns, Oregon, USA (Fig. 1). Each pasture was serviced by a single water tank with *ad lib* trace mineral salt within 20 m of water. No other streams or surface water was available within the pastures. Mean ambient air temperature is 7.6 °C with extremes of −31 and 42 °C. Mean annual precipitation is 28.9 cm with about 60% occurring as snow (National Oceanic and Atmospheric Administration, 2005). During trials, temperatures ranged from 1.7 to 32.8 °C, with 10 mm of rainfall in a single event.

Plant communities include a sparse western juniper (*Juniperus occidentalis* ssp. *occidentalis* Hook.) over-story and a shrub layer dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young), mountain big sagebrush (*A. tridentata* ssp. *vaseyana* (Rydb.) Beetle), or low sagebrush (*A. arbuscula* Nutt.). Prominent cool-season grasses include bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Löve), Idaho fescue (*Festuca idahoensis* Elmer), or Sandberg's bluegrass (*Poa secunda* J. Presl) depending on locale.

Using geographic information system (GIS) software Idrisi32 v.32.22 (Clark Labs., The Idrisi Project, Worcester, MA, USA), 453 coordinates were established on a georeferenced map of the three pastures (Fig. 1). Points were arranged in a grid such that each was equidistant (254 m) from its six closest neighbors (Fig. 1). Coordinates were downloaded to geographic positioning systems (GPS units), and on 9–11 June 2004, technicians visited each site to sample herbage.

At each locale, a 1-m^2 frame was dropped, standing herbage (grasses and forbs) rooted within the frame clipped to a 2.5-cm stubble, the material bagged, and the bag labeled with an identifying number. If harvested herbage was <30 g needed for sample processing, the frame was moved either left or right and additional herbage clipped to meet or exceed the 30-g minimum. The number of frames sampled was recorded for sites needing more than one frame to facilitate estimates of standing crop. There was no sorting of live/dead material or notation of species composition. At sampling and during the subsequent grazing trials, grasses were in the boot stage of phenology (seed stalks were forming but not yet visible above their enclosing leaves).

Herbage samples were oven dried (40 °C) to a constant mass over 5 d, weighed, ground to pass a 1-mm mesh (Wiley Mill, Model 4, Arthur H. Tomas Co., Philadelphia, PA, USA), and stored in labeled plastic bags for later analyses. Forage quality analyses included: crude protein (CP = nitrogen content × 6.25; Leco CN-2000, Leco Corp., St. Joseph, MI, USA), neutral detergent fiber and acid detergent fiber (Robertson and Van Soest, 1981) as modified for an Ankom-200 Fiber Analyzer (Ankom Technology, Macedon, NY, USA), and digestibility as indexed by *in situ* dry matter disappearance (Damiran et al., 2002) with samples incubated in a rumen canulated steer for 48 h, rinsed, dried and reweighed.

2.2. Forage quantity and quality maps

Our forage quantity and quality data and the accompanying coordinates for each sample's location were imported into Idrisi GIS software as point data. The point data maps depict values at sampled sites but have no values in the intervening space between sampled locations. To fill in the empty spaces of each map, the Idrisi "INTERPOL" or interpolate procedure rasterized a complete surface for each forage attribute using a distance-weighted-averaging algorithm with an exponent of 2 (Lam, 1983). The interpolated data were based upon the values of, and distance to the nearest four to eight original data points. Each pixel of the resulting rasterized image represented a 10 m × 10 m or 100-m^2 area. Because generated images exhibited a slight honeycomb appearance, the Idrisi "FILTER" function, with a 5 × 5 mean filter, smoothed the data. This procedure employs a 5 × 5-pixel window that traverses the original rasterized image, averages the window's contents at each 1-pixel shift in position, and assigns the mean value to the window's corresponding central pixel on a new smoothed image. Due to the interpolation and averaging in the filtering processes, ranges of data in the smoothed images were slightly truncated when compared with the original quantity/quality assays (Table 1).

Idrisi's "HISTO" (histogram) function was applied to the smoothed forage quantity/quality images for each pasture to compile the frequency of observations within 13 equal-width classes spanning the full range of data. As an example, CP data ranged from 5.4 to 16.9%, a span of 11.5 percentage points. Dividing 11.5 by 13 generated a class width of 0.88% CP. All forage quantity/quality frequency data were converted to percentages for subsequent analyses.

2.3. GPS collar schedule and cattle activity monitoring

On 12 June 2004, 60, 4-year-old cow/calf Hereford × Angus pairs (557 ± 5 kg S.E. and about 90 d post-calving), that had grazed neighboring pastures for the previous 2 months, were randomly separated into three groups of 20 pairs each. All cattle had been born on the experimental station and grazed study pastures as calves and adults. Four randomly selected cows from each group were fitted with Lotek GPS collars (Lotek Engineering Inc.,

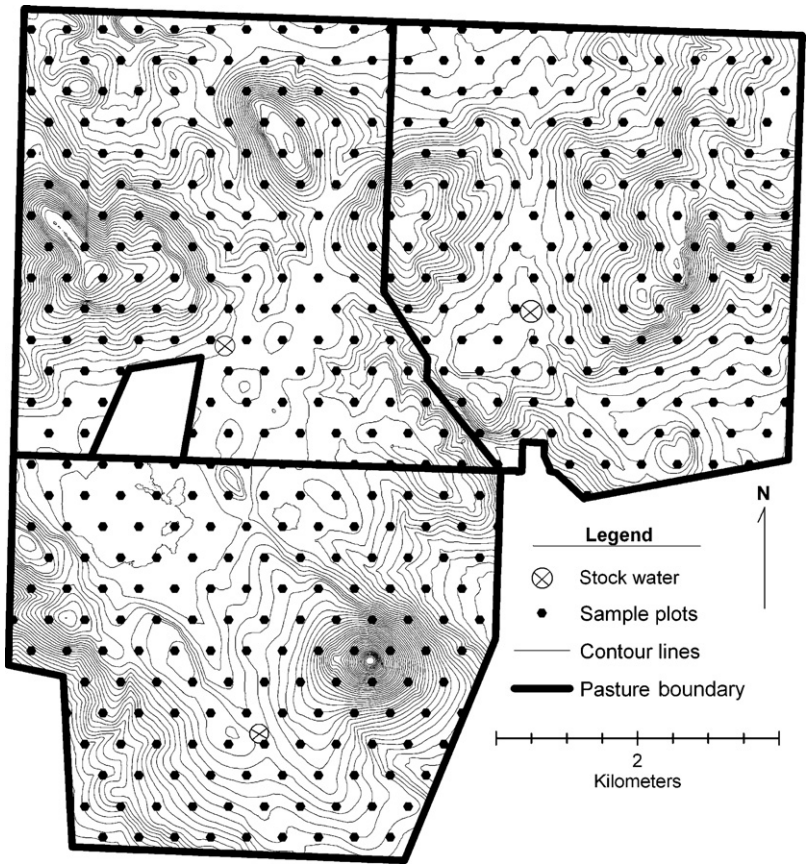

Fig. 1. Pasture boundaries, locations of forage sampling plots, 6-m contour intervals, and locations of stock water among three, 800+ ha pastures on the Northern Great Basin Experimental Range near Burns, Oregon, USA used to study the spatial dynamics of forage quantity/quality and the grazing distribution of GPS collared cattle in June 2004.

Newmarket, ON, Canada) and released in each of the three pastures. Collars were programmed to record data every 5 min starting at 00:00 h on 15 June 2004 and to stop 15 d later at 23:55 h on 29 June 2004. This schedule generated 12 records h^{-1}, 288 records d^{-1}, 4320 records over the 15-d trial for each collar, and a sum of 51,840 possible records across all 12 collars. Collar hardware and the type of data collected has previously been described by Ganskopp (2001) and Ungar et al. (2005). Specific data from collars used in this study included: time and date of each recorded position, motion sensor counts of left/right and forward/backward movements of the cow's head and temperature sampled within the collar's hardware box.

To accurately relate cattle activities with data acquired by the collar's motion sensors, each instrumented cow was continuously observed for 8–8.75 daylight hours with observations occurring between 06:00 and 17:00 h. Each collared cow was trailed by a single observer, with cattle tolerating observers within 10–15 m with no obvious effects on behaviour. Four observers worked each day, and a total of 3 d (15–17 June) were needed to complete the 8+ h of records needed for all 12 collared cattle.

Activities monitored included: foraging, walking, lying, standing, drinking, and grooming. While cattle can simultaneously walk and forage, such events were classified as foraging as long as the cow's head was down and it harvested herbage. Activity timing and duration were tallied on paper at a 1-min resolution. When a cow switched from one activity to another, observers mentally noted the precise transition time on a hand held GPS unit. If the new activity persisted for $\geq$30 s the transition time was recorded. If the cow resumed its prior activity in $<$30 s, the interlude was ignored. Most of the ignored interludes involved foraging cattle that paused to chew herbage or briefly look about. Data were compiled as the total number of min a cow participated in each activity during each 5-min interval. Time displays of the hand held GPS units assured 5-min observation intervals were accurately synchronized with the 5-min GPS collar sampling interval.

Table 1
Minimum and maximum values of forage quantity/quality samples harvested from 453 georeferenced coordinates among three, 800+ ha pastures and from rasterized images depicting forage quantity/quality of the same pastures in a study assessing the grazing distribution of cattle on the Northern Great Basin Experimental Range near Burns, Oregon, USA in June 2004. Crude protein, CP; *in situ* dry matter disappearance, ISDMD; neutral detergent fiber, NDF; acid detergent fiber, ADF.

Data source	Forage attribute									
	Yield (kg ha^{-1})		CP (%)		NDF (%)		ADF (%)		ISDMD (%)	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Forage samples	19	1909	5.3	17.4	36.4	75.8	14.7	50.8	49.0	87.1
Rasterized images	33	1792	5.4	16.9	38.3	75.4	16.0	49.1	50.3	86.2

2.4. GPS data processing and cattle grazing time estimates

All collars were retrieved on 30 June 2004. One collar failed completely, and a second unit stopped after 3932 records (13.7 d). Among the 12 GPS collars, 47,132 or 90.9% of a possible 51,840 records were acquired.

The coordinates were differentially corrected with N4 v.1.1895 software (Lotek Engineering Inc., Newmarket, ON, Canada) using base station files downloaded from a United States Forest Service/Bureau of Land Management station (http://www.fs.fed.us/database/gps/burns.htm) about 50 km east of our research area. Mean position error with uncorrected records is about 2.74 ± 0.25 m, while differential-correction reduces mean error to 2.09 ± 0.09 m (Ungar et al., 2005). Differential-correction of coordinates may fail if roving or base station units view slightly different satellite arrays (Hurn, 1993), and differential-correction failure averaged 4.9 ± 1.1 S.E. records per collar. Raw, uncorrected coordinates were available and substituted in all instances. Latitude and longitude measures were subsequently converted to Universal Transverse Mercator (UTM 11N, WGS-1984) coordinates with Idrisi32 v.32.22 software.

Forward, stepwise regression analyses was used to derive models to quantify the duration (min) of each cow's grazing activities (Ganskopp, 2001; Ungar et al., 2005) by relating timed grazing intervals (dependent variable) from our direct observations of the cattle with each cow's simultaneously acquired GPS collar data. Independent variables included: forward/backward and left/right motion sensor counts, distance-traveled between successive 5-min records, and GPS collar temperature. With eight collars or cattle, the left/right motion sensor counts and distances travelled between successive 5-min records were the first and second independent variables entering the regression models. In two of those eight instances the forward/backward motion sensor count entered the models as a third significant independent variable. With two other collars or cattle, the left/right motion sensor count was the first variable entering the model followed by the forward/backward motion sensors counts. With the last cow/collar combination, the forward/backward motion sensor counts entered the model first, and the left/right motion sensor count was the second and final significant variable gaining entry. The resulting models (mean $R^2 = 0.79 \pm 0.04$ S.E., $n = 11$) were applied to full collar data sets to predict the min cattle were foraging during each 5-min interval. After grazing times were derived for each cow/GPS collar combination, data were pooled among cattle within a pasture. Thereafter, data were sorted by increasing grazing time, and only coordinates where cattle had foraged for >2.5 min per 5-min interval were retained for further analyses ($n = 17{,}956$ across all three pastures). This step assured that only locations where grazing was the primary endeavor were included in the analyses, and that coordinates where a cow was resting or walking were excluded.

Because water was assumed to be a primary attractant for a roughly centralized focal point in each pasture, coordinates within 50 m of water troughs were also withdrawn from consideration (Fig. 2). This reduced our total grazing record count to 16,408 for a mean of 5469.3 ± 250.7 S.E. coordinates per pasture.

Grazing coordinates for each pasture were rasterized with Idrisi32 v.32.22 software. Rendered grazing distribution images displayed zeros in pixels that were not visited by cattle and the frequency of visits to pixels that were grazed. The number of pixels needed to render each pasture and a partial listing of how often grazed pixels were visited by cattle are shown in Table 2.

The next task was to determine the forage quality of areas visited by grazing cattle with Idrisi's "QUERY" function. This function layers a rasterized cattle distribution image on top of a corresponding forage quantity/quality image. The software uses the cattle distribution image as a mask, and looks only beneath the grazed, non-zero pixels of the mask for underlying data (Fig. 2). The underlying values are written to another file, which is simply a listing of forage quantity/quality for the pixels visited by grazing cattle.

Idrisi's "HISTO" (histogram) function was applied to each of the cattle-grazed forage quality listings. Again, the HISTO function compiled the frequency of observations occurring in each of 13 equal-width classes used to quantify the forage quality attributes of the pastures above. These frequencies were also converted to percentages.

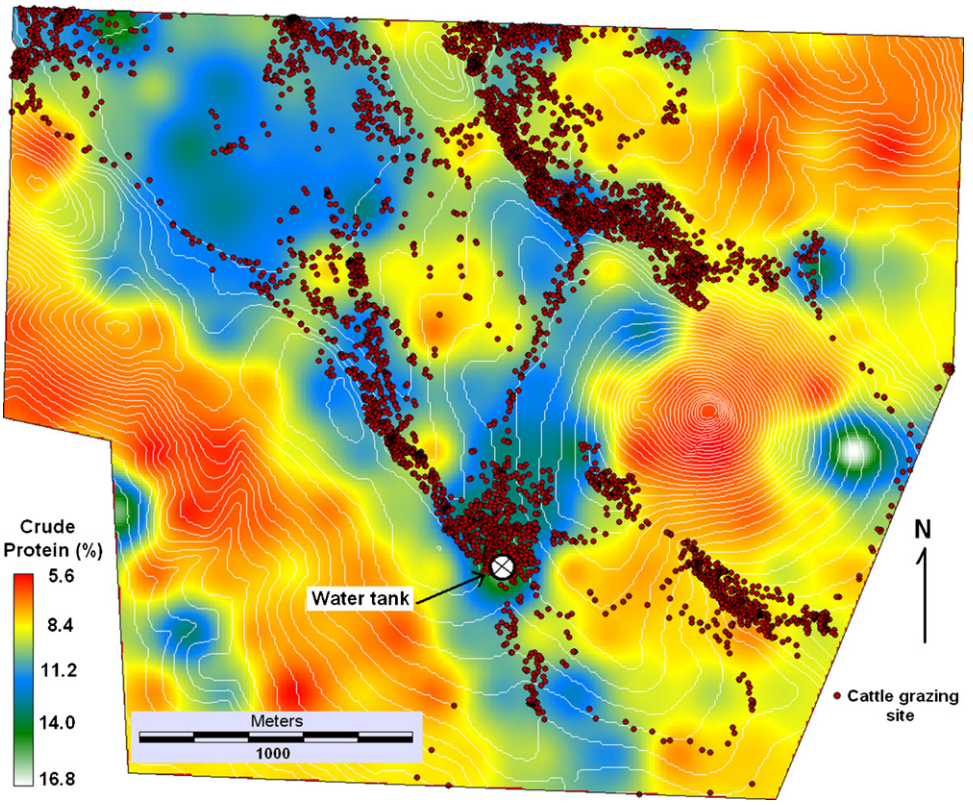

Fig. 2. A rasterized rendering of forage crude protein (CP) content, 6-m contour lines, and GPS collar coordinates ($n = 5287$) from four grazing cattle sampled over 15 d during June 2004 in a 849-ha pasture on the Northern Great Basin Experimental Range near Burns, Oregon, USA. GPS coordinates ($n = 946$) of grazing cattle within 50 m of stock water were not included in analyses.

Table 2
Pixel counts for three rasterized 800+ ha pasture maps on the Northern Great Basin Experimental near Burns, Oregon, USA and counts of pixels visited once, twice, three, or more than three times by GPS collared cattle. An individual pixel represented 100 m^2.

Pasture	Pixels				
	Per pasture	Visited once	Visited twice	Visited three times	Visited more than three times
Range 1	82,818	2815	733	242	172
Range 2	85,180	2609	599	160	136
Range 7	86,394	3209	553	105	74
Total	254,392	8633	1882	507	382

2.5. Experimental design and analyses

A relative preference (RP) value, proposed by Heady (1964), was used to quantify cattle preference for grazed locales in each pasture. RP is the ratio of the percent of cattle grazing records detected in a class and the percent of the pasture area contributing to that class (Heady, 1964). RP values <1 infer a class was avoided. A value of 1 implies cattle were indifferent and used areas in proportion to their presence, and values >1 suggest a class was favored. As an example, if 20% of cattle records occurred in a class constituting 5% of a pasture, an RP of four implies those areas were favored.

Each forage quantity/quality class ($n = 13$) was viewed as a treatment with pastures ($n = 3$) as blocks. After testing for skewness and kurtosis, with no transformations needed (Snedecor and Cochran, 1967), a randomized complete block analysis of variance tested the null hypothesis that relative preference indices were equal among classes. To avoid a potential bias of analyses by extremely inflated relative preference indices (a large number of visits to a small proportion of a pasture), only forage quantity/quality classes constituting >2% of the area within at least one of the three pastures were included. Under that constraint, CP, NDF, ADF, ISDMD, and standing crop effects were analyzed with seven, eight, seven, ten, and six classes, respectively. Among those five analyses, excluded data averaged 1.44 ± 0.39% S.E. of the pasture area and 1.68 ± 0.71% S.E. of our grazing cattle records (Table 3). To visually convey the relative contributions of excluded data, however, all 13 classes for each analysis are presented in our final figures (Fig. 3). Given the variability in plant community composition and geophysical characteristics among the three pastures, a P-value <0.10 was deemed significant in analyses of variance.

Our null hypothesis assumed forage quantity/quality classes would be used by grazing cattle roughly in proportion to their presence in the pastures. Under that circumstance, the RP value for each forage quantity/quality class would be ≈1. If the null hypothesis was rejected, a 90% confidence interval about an expected RP value of 1 was derived to determine whether individual classes were avoided, used indifferently, or preferred by cattle. RP values >1 were scored as preferred and given a "+" mark ($P \leq 0.10$). Values <1 were deemed avoided ($P \leq 0.10$) and labeled with a "−" designation. RP values within the ±90% confidence interval were given a "0" designation with the assumption they were used indifferently or in proportion to their presence ($P > 0.10$).

To examine the potential that cattle may simultaneously respond to combinations of CP, fiber, ISDMD, and standing crop when foraging, correlation matrices were derived among our forage sample assays within each pasture and among the rasterized images of each pasture. In both instances, mean correlation coefficients were developed among pastures, and a paired t-test (2 d.f.) was used to evaluate the hypothesis that corresponding coefficients were similar between the harvested forage samples and the rasterized images of pastures.

Last, a forward stepwise regression analysis was used to relate the frequency of visits by cattle to each grazed pixel (dependent variable) with the nutritional and geophysical attributes of visited pixels (independent variables). Pixels visited by cattle totaled 11,404 across the three pastures. Independent variables for each pixel included our forage quantity/quality attributes (standing crop, CP, ISDMD, and NDF) and the geophysical characteristics of distance from stock water, elevation above or below stock water, and degree of slope. ADF data were not included in this portion of the study, because our initial analyses suggested cattle were insensitive to its spatial dynamics across the pastures. Slope and elevations relative to stock water were derived or extracted from U.S. Geological Survey digital elevation models (DEMs) available from http://jollyroger.science.oregonstate.edu/dem/.

3. Results

Four of the five analyses of variance suggested grazing cattle spatially responded to forage quantity/quality dynamics. Relative preferences indices and the percentage of the landscape and grazing cattle records occurring in each forage quality class for our five assays are found in Fig. 3. The four statistically significant attributes included CP ($P = 0.006$), NDF ($P = 0.003$), standing crop ($P = 0.069$), and ISDMD ($P = 0.078$). Cattle used ADF classes roughly in proportion ($P = 0.954$) to their presence (Fig. 3E and Table 3).

Table 3
The percent of study area and cattle records excluded from analyses of variance and the percent of study area and grazing cattle records occurring in areas classified as being avoided, used indifferently, or preferred by cattle among five forage quantity/quality attributes during research evaluating landscape nutritional patterns and livestock distribution on the Northern Great Basin Experimental Range near Burns, Oregon, USA in June 2004. Crude protein, CP; *in situ* dry matter disappearance, ISDMD; neutral detergent fiber, NDF; acid detergent fiber, ADF.

Forage attribute	Data source	Data excluded from analyses	Relative preference classifications		
			Avoided by cattle	Used indifferently	Preferred by cattle
CP	Pasture area	2.2	29.1	34.6	34.1
CP	Cattle records	3.5	14.6	31.1	50.8
ISDMD	Pasture area	0.9	28.5	40.7	29.9
ISDMD	Cattle records	0.3	16.0	40.3	43.4
NDF	Pasture area	1.2	16.9	43.2	38.7
NDF	Cattle records	0.5	7.5	39.5	53.4
Standing crop	Pasture area	0.3	22.3	38.5	38.9
Standing crop	Cattle records	0.8	9.5	33.6	56.1
ADF	Pasture area	2.4	–	97.6	–
ADF	Cattle records	3.3	–	96.7	–

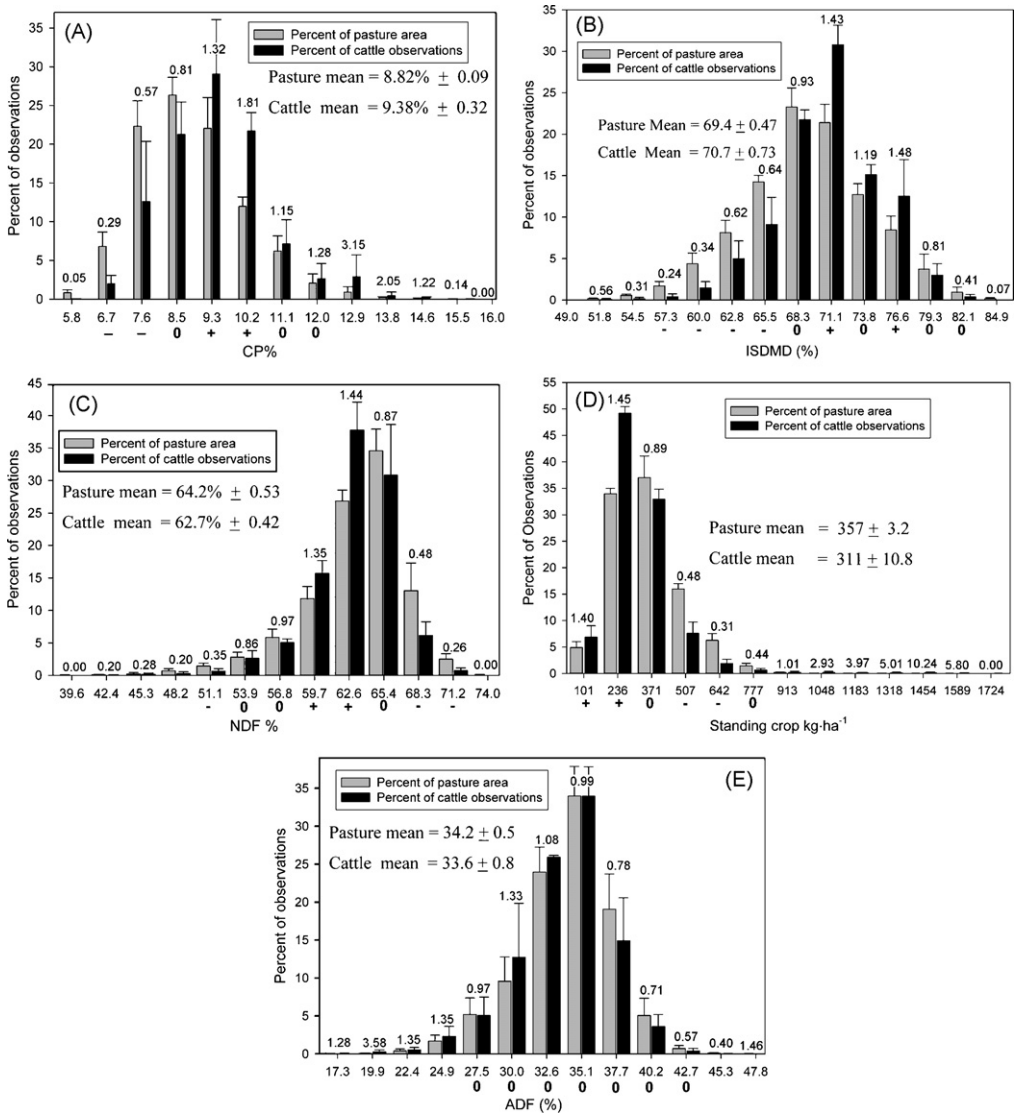

Fig. 3. Mean percentages (±S.E.) of the landscape and mean percentages of GPS collar records from grazing cattle occurring among 13 forage quantity/quality classes from analyses of crude protein (CP), *in situ* dry matter disappearance (ISDMD), neutral detergent fiber (NDF), standing crop, and acid detergent fiber (ADF) sampled in June 2004 among three pastures on the Northern Great Basin Experimental Range near Burns, Oregon, USA. Values above paired pasture/cattle bars are relative preference indices and are the ratio of the percent of grazing cattle records detected in each class divided by the percent of pasture area occurring in the same class. The +, 0, and − symbols beneath the *x*-axes are indicative of classes that were preferred, used indifferently, or avoided ($P < 0.10$) by cattle, respectively. Forage quantity/quality classes not having a +, 0, or − symbol were not included in statistical analyses because they constituted <2% of the landscape.

The spatial dynamics of forage CP content and cattle grazing locations for one of our pastures are shown in Fig. 2. Fig. 2 also illustrates that cattle visited only about half of the available pasture, and that steep topography often limited their travels. Cattle were indifferent to or avoided portions of pastures supporting lower than average CP, preferred the 9.3 and 10.2% CP classes, and were again indifferent to CP classes >11.1% (Fig. 3A). The two preferred classes constituted 34% of the landscape and supported 51% of grazing cattle coordinates (Table 3).

A similar pattern occurred with ISDMD. Four of five ISDMD classes supporting less than the pasture mean ($\bar{X} = 69.4 \pm 0.47\%$) were avoided (Fig. 3B). Avoided classes constituted 28.5% of the landscape and contained 16% of cattle grazing records (Table 3). The remaining classes with greater than, or equal to 68.3% ISDMD received either indifferent or preferred rankings (Fig. 3B). The two preferred classes, 71.1 and 76.6%, constituted 30% of the pasture area and supported 43% of grazing observations (Table 3).

Neutral detergent fiber analyses (Fig. 3C) indicated cattle favored two classes immediately beneath the pasture average ($\bar{X} = 69.4 \pm 0.47\%$). When pooled, they constituted 39% of the study area and supported 55% of grazing records. Cattle avoided the lowest (51.1% NDF) and two highest (68.3 and 71.2% NDF) classes. ADF analyses implied cattle were oblivious to this forage component, and a rendering of data also suggested grazing cattle

Table 4
Mean correlation coefficients (±S.E.) among forage quantity/quality measures (above the diagonal) for samples harvested from 453 georeferenced coordinates among three, 800+ ha pastures and from rasterized images (beneath the diagonal) depicting forage quantity/quality characteristics across the same three pastures in a study of landscape nutritional patterns and cattle distribution on the Northern Great Basin Experimental Range near Burns, Oregon, USA in June 2004. Corresponding forage sample/rasterized image values rendered in **bold font** are significantly different ($P < 0.03$). Crude protein, CP; *in situ* dry matter disappearance, ISDMD; neutral detergent fiber, NDF; acid detergent fiber, ADF.

Pasture attribute	Forage sample attributes				
	CP	ISDMD	NDF	ADF	Yield
CP	–	**0.54 ± 0.03**	−0.50 ± 0.07	**−0.53 ± 0.04**	−0.11 ± 0.05
ISDMD	**0.63 ± 0.04**	–	**−0.48 ± 0.08**	−0.43 ± 0.04	−0.14 ± 0.04
NDF	−0.62 ± 0.06	**−0.51 ± 0.08**	–	0.52 ± 0.13	−0.15 ± 0.08
ADF	**−0.58 ± 0.04**	−0.50 ± 0.04	0.53 ± 0.12	–	0.12 ± 0.07
Yield	−0.19 ± 0.07	−0.22 ± 0.06	−0.10 ± 0.13	0.20 ± 0.13	–

occupied classes roughly in proportion to their presence (Fig. 3E).

Mean standing crop among pastures was 357 ± 3.2 kg ha^{-1} (Fig. 3D). Cattle preferred the two classes with less than average yield and were indifferent to or avoided classes with greater than average standing crop (Fig. 3D). The two preferred classes constituted 39% of the landscape and contained 56% of cattle grazing records (Table 3).

Pearson correlation coefficients (r) quantifying relationships among our forage quantity/quality variables are listed in Table 4. With the exceptions of standing crop/NDF and ADF/NDF pairings among our forage samples, correlations were generally stronger among variables in our rasterized pasture images than among our herbage samples. Correlations were significantly stronger with the CP/ISDMD, CP/ADF and ISDMD/NDF pairings among our rasterized pasture images ($P \leq 0.03$) than among the same pairings in our herbage samples. Briefly, CP and ISDMD were positively related, and both CP and ISDMD were negatively correlated with NDF and ADF. Fiber assays (NDF and ADF) were positively related, and standing crop exhibited negative correlations with CP, ISDMD and NDF, but not ADF (Table 4).

Results of forward stepwise regressions modeling frequency of cattle visits to pixels from underlying forage quantity/quality and geophysical characteristics are listed in Table 5. Order of variables entering the model was: elevation above or below stock water, horizontal distance to stock water, forage CP content, and degree of slope. This suggested the elevation of stock water and horizontal distance to stock water had a greater effect on the distribution of grazing cattle than forage CP content. The first non-significant variable entering the model was standing crop ($P = 0.118$). Overall, the model was woefully inadequate at predicting the frequency of cattle visits to pixels and accounted for <1.0% of the variation in visiting frequency. Given that a preponderance of grazed pixels were visited only once (76%), twice (17%) or three times (4%) by cattle (Table 2), there was little chance of a strong predictive model being derived due to the narrow range of values for our dependent variable. Although P-values of all significant independent coefficients were ≤0.031, this analysis illustrates that high residual degrees of freedom in the error term (d.f. = 11, 399) can easily convey statistical significance in regression analyses, that actually offer little explanatory power (Table 5).

Table 5
Results of forward stepwise regression relating frequency of visits (dependent variable) by GPS collared cattle to grazed pixels with independent variables of percent forage crude protein content (CP), percent *in situ* dry matter disappearance (ISDMD), percent neutral detergent fiber (NDF), standing crop, and geophysical attributes including degree of slope, distance from stock water, and the elevation of grazed sites above or below stock water among three, 800+ ha pastures on the Northern Great Basin Experimental Range near Burns, Oregon, USA in June 2004. n = 11,404.

Independent variables	Regression coefficient	S.E.	P-value
Stock water elevation$_1$	−0.00257	0.00064	0.00006
Distance to stock water$_2$	−0.00008	0.00002	0.00194
Forage crude protein$_3$	0.020790	0.00969	0.03199
Degree of slope$_4$	−0.00809	0.00357	0.02350
	Intercept = 1.342	R^2 = 0.0035	

Subscripts denote order of variable entry into the model with all listed coefficients significant at $P \leq 0.032$.

4. Discussion

Free-ranging cattle preferred locations in pastures with higher than average CP and ISDMD, and lower than average NDF and standing crop. ADF content did not affect where cattle grazed. Of the four forage quality attributes studied, CP is the only constituent with an approximate threshold for adequate rumen function. With admitted variation among sources regarding CP requirements, a 9.3% CP content typically equals or exceeds maintenance for a 544 kg lactating beef cow (National Research Council, 2000). While approximately 36 ± 3% of the study area supported forage having ≥9.3% CP, 51% of the cattle grazing records occurred within the two preferred classes ranging from 8.9 to 10.7% CP (Fig. 3A). The higher quality 11.1 and 12.0 classes received indifferent rankings.

Intuitively, we expected greater concentrations of grazing cattle in locales supporting the highest levels of CP. With 36% of the study area, however, meeting or exceeding cattle CP needs, there was little physiologic need for stock to seek areas with exceptionally high CP concentrations. On our study area, CP classes with ≥12.9% (Fig. 3A) made up only 3.5% of the landscape. One could argue that returns might not justify expenditures for cattle to find and exploit scattered and limited supplies (Logue, 1986). A *post hoc* visit to the two higher than average CP sites (>14% CP) in Fig. 2 (left-center and right-center) revealed both locales were historic stock

watering locales supporting near pure stands of high quality, but relatively unpalatable tumble mustard (*Sisymbrium altissimum* L.). Cattle in the sagebrush biome focus on grasses for 85–95% of their diet during summer months (McInnis and Vavra, 1987), and their preference for grasses may partially explain the less than expected use of those forb dominated sites.

Other studies have shown that cattle will occasionally focus their attentions on relatively small portions of their available range. A nearby season-long grazing study on sagebrush/forest transition rangeland, about 68 km north of our study site, found cattle acquired 81% of their forage needs from riparian areas making up 3.5% of a pasture (Roath and Krueger, 1982). That study, however, extended well past the end of the growing season when upland herbage in the region has turned brown and is typically nutrient deficient (Ganskopp and Bohnert, 2001). With water and succulent high-quality herbage in close proximity, cattle probably fulfilled both their nutritional and water needs by focusing on a limited portion of their pasture (Roath and Krueger, 1982).

ISDMD is an index of forage degradation or digestibility by ruminants, and measures are usually positively correlated with intake and passage rate. Passage rate among ruminants, however, is also affected by a myriad of forage characteristics like the physical nature of herbage, particle size, specific gravity, and amount of forage eaten (Church, 1976). About 62% of our grazing cattle records occurred within ISDMD classes exceeding the pasture mean (Fig. 3B). Again, we anticipated the highest preference by cattle for locations exhibiting extremely elevated digestibility values, but that was not the case. The greatest relative preference value ($\bar{X} = 1.47 \pm 0.08$) occurred in the 71.1% ISDMD class that just exceeded our mean digestibility (Fig. 3B). That class supported 31% of our grazing records and occupied 21% of the study area.

Neutral detergent fiber components include cellulose, hemicellulose, lignin, and ash (Van Soest and Robertson, 1980). Because NDF is negatively correlated with forage digestibility and intake (Robinson, 1999), we anticipated cattle would prefer areas with NDF values lower than the pasture mean and conversely avoid higher than average locales. This proved correct for the most part (Fig. 3C), but cattle again avoided or were indifferent to the three classes exhibiting the lowest NDF levels. The two favored classes (59.7 and 62.6% NDF) supported 53% of the foraging activities and constituted 38% of our pasture area.

Acid detergent fiber contains cellulose and lignin from cell walls (Van Soest and Robertson, 1980). ADF is negatively correlated with forage digestibility in ruminants, and we anticipated preference for locales with low ADF and avoidance of sectors with high values. Analyses rejected that hypothesis, however, as cattle grazed ADF classes roughly in proportion to their presence (Fig. 3E).

Cattle favored areas where standing crop was the lowest and were indifferent to, or avoided all classes exceeding the pasture mean (Fig. 3D). In controlled experiments with monocultures and manipulations of standing crop via stem density or herbage height, livestock favor patches where they can maximize intake rate (Black and Kenney, 1984; Laca et al., 1994). Loehle and Rittenhouse (1982) analyzed forage preference indices and reported herbage mass was of little interest to grazers in mixed composition pastures. They suggest interacting attributes like herbage cover, leaf size, plant frequency and moisture, sugar, and protein content may be more relevant to a grazer's perception (Loehle and Rittenhouse, 1982) than physical features.

A confounding factor associated with high herbage mass among bunch grasses is a tendency toward accumulations of dense standing dead material (Arnold, 1963) that can make green forage inaccessible or undesirable (Moisey et al., 2006). In this study, increasing standing crop was associated with declines in CP, ISDMD, and NDF (Table 4). Among caespitose grasses, cattle are cognizant of a single cured stem within a green tussock (Ganskopp et al., 1993) and they select quality over quantity by initially grazing plants (Moisey et al., 2006) or portions of pastures not contaminated with dead standing herbage (Ganskopp and Bohnert, 2006). When forced to graze among a mix of green and dead herbage, cattle can, with selective foraging, exceed expectations and harvest a high quality diet (Ganskopp and Bohnert, 2006). Intake rate or foraging efficiency, however, is maximized when old reproductive tillers are absent, and cattle can graze without sorting (Flores et al., 1993; Wallis de Vries and Daleboudt, 1994). In hindsight, we should have sorted live and dead herbage to re-examine those hypotheses in a spatial context.

On conservatively stocked rangeland, much of the landscape may be ungrazed in a given year (Fig. 2) leaving an overburden of cured, low-quality herbage (Moisey et al., 2006). With a preponderance of plant nutrients held in standing herbage on ungrazed sites, and accelerated nitrogen cycling and urease activities in grazed locales (Frank and Evans, 1997; McNaughton et al., 1997), a flush of growth and nutrient availability in a subsequent growing season can make the previously grazed areas even more attractive to herbivores than ungrazed sites (Westoby, 1986; Milchunas et al., 1995).

Correlations among the forage quantity/quality attributes (Table 4) illustrate that cattle may simultaneously respond to several nutritional characteristics when grazing. Selection for elevated CP for instance may be accompanied by elevated digestibility and lower fiber levels. While negative feedback relationships are easily linked with food preference or avoidance by ruminants, the effects of interacting positive feedback mechanisms are more difficult to quantify (Provenza, 1995). Physical and nutritional characteristics of grasses cannot consistently be used to predict the relative preference of cattle for individual species across seasons (Cruz and Ganskopp, 1998), so it is unlikely one can persistently link the grazing distribution of cattle with a single forage attribute.

Our efforts to model frequency of visits by cattle with independent forage quantity/quality and landscape variables were woefully poor, accounting for <1.0 percent of variability (Table 5). With 97% of our grazed pixels visited ≤ 3 times by cattle (Table 2), the narrow range of values across our dependent variable may have offered little chance of statistical success. Also, a mean standing crop of

357 ± 3.2 kg ha^{-1} reduces to 3.57 kg 100 m^2, the dimension of a single pixel among our analyzed images. That amount of herbage could be quickly depleted by an avidly foraging cow and leave little reward for subsequent grazers. Another analysis option might be to decrease the resolution of our rasterized images which would increase the frequency of cattle visits per pixel. Whether or not that approach would strengthen our regression analyses will be left for subsequent study. Senft et al. (1985), in a more confined environment, found cattle focused on specific plant communities with elevated site quality characteristics. A detailed map of our study area's plant communities might also strengthen our findings and require a less intensive forage sampling regime.

5. Conclusions

Many landscape and animal attributes interact to affect livestock foraging patterns in extensive pastures. This study suggested grazing cattle spatially respond to pasture level nutritional dynamics with more frequent than expected use of higher than average CP and ISDMD locales, and more frequent than expected visits to lower than average NDF and standing crop sites. The specific reasons why cattle did not seek out rare but exceptionally high-quality locales is unknown, but may be related to energy balance relationships between the animal and the demands of functioning in its environment. Correlations among our forage quantity variables suggest cattle could simultaneously be responding to more than one nutritional characteristic as they select areas to graze. Regression analyses, however, implied that models relying solely on forage quality characteristics were poor and inconsistent predictors of grazing cattle distribution. Our model suggested that elevation of stock watering sites, horizontal distance to stock water, forage CP content, and degree of slope (listed in order of forward stepwise entry) were all significant predictors of grazing livestock distribution.

While further research is needed to determine how standing crop quantity and quality affect free ranging animal distribution, we speculate that management programs affecting locale-specific nutritional characteristics can be used to manipulate grazing distribution in some instances. In rugged terrain, however, landscape geophysical characteristics are likely to be the primary determinant of cattle distribution patterns.

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