Cattle grazing in semiarid forestlands: Habitat selection during periods of drought[1]

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ABSTRACT: Climate change models are predicting increased frequency and severity of droughts in arid and semiarid environments, and these areas are responsible for much of the world's livestock production. Because cattle (*Bos taurus*) grazing can impact the abundance, distribution, and ecological function of native plant and animal communities, it is important to understand how cattle might respond to increasingly arid conditions. Here, we evaluate changes in habitat selection by cattle across an 8-yr period as a function of rainfall and other environmental covariates. Using resource selection functions, we evaluated habitat selection based on 2 behaviors, stationary and mobile. Models revealed similarity in cattle habitat selection across years, with only modest changes in selection as a function of precipitation, despite marked seasonal and interannual differences in rainfall. Cattle preferred gentle slopes, forest edges, wet meadows, and areas near water as well as areas far from water on plateaus. Cattle avoided areas at intermediate distances from water, typically associated with steep slopes. As conditions became drier during the late season, cattle did not switch selection patterns but instead contracted their selection around water. Cattle also selected similar habitats whether they were mobile or stationary, possibly making microsite decisions therein. This consistent pattern of selection across years could be particularly problematic for riparian communities as climates become drier; however, it may also simplify cattle management, as range managers can focus vegetation monitoring efforts on riparian areas. Due to the uncertainty surrounding future climatic conditions, it is imperative that both range and wildlife managers develop long-term plans to continue managing these multiuse landscapes in an ecologically sustainable manner based on expected patterns of livestock grazing.

Key words: biodiversity, *Bos taurus*, cattle, climate change, impacts, public land

INTRODUCTION

Globally, livestock grazing is the most widespread land-use practice in arid and semiarid environments (Fuhlendorf and Engle, 2001; Gibson, 2012). In the western United States alone, as much as 70% of the land area is grazed by cattle, and public land constitutes approximately 108 million ha of this total (Fleischner, 1994). On publicly owned land, animals are released in relatively large pastures where they are free to make habitat selection decisions. Yet little is known about how cattle alter their selection in these large pastures during drought. Because droughts in the western United States are expected to become more frequent and more severe (Cook et al., 2004; Gutzler and Robbins, 2011), understanding this response will help inform cattle grazing practices and the management of plant and animal species impacted by cattle.
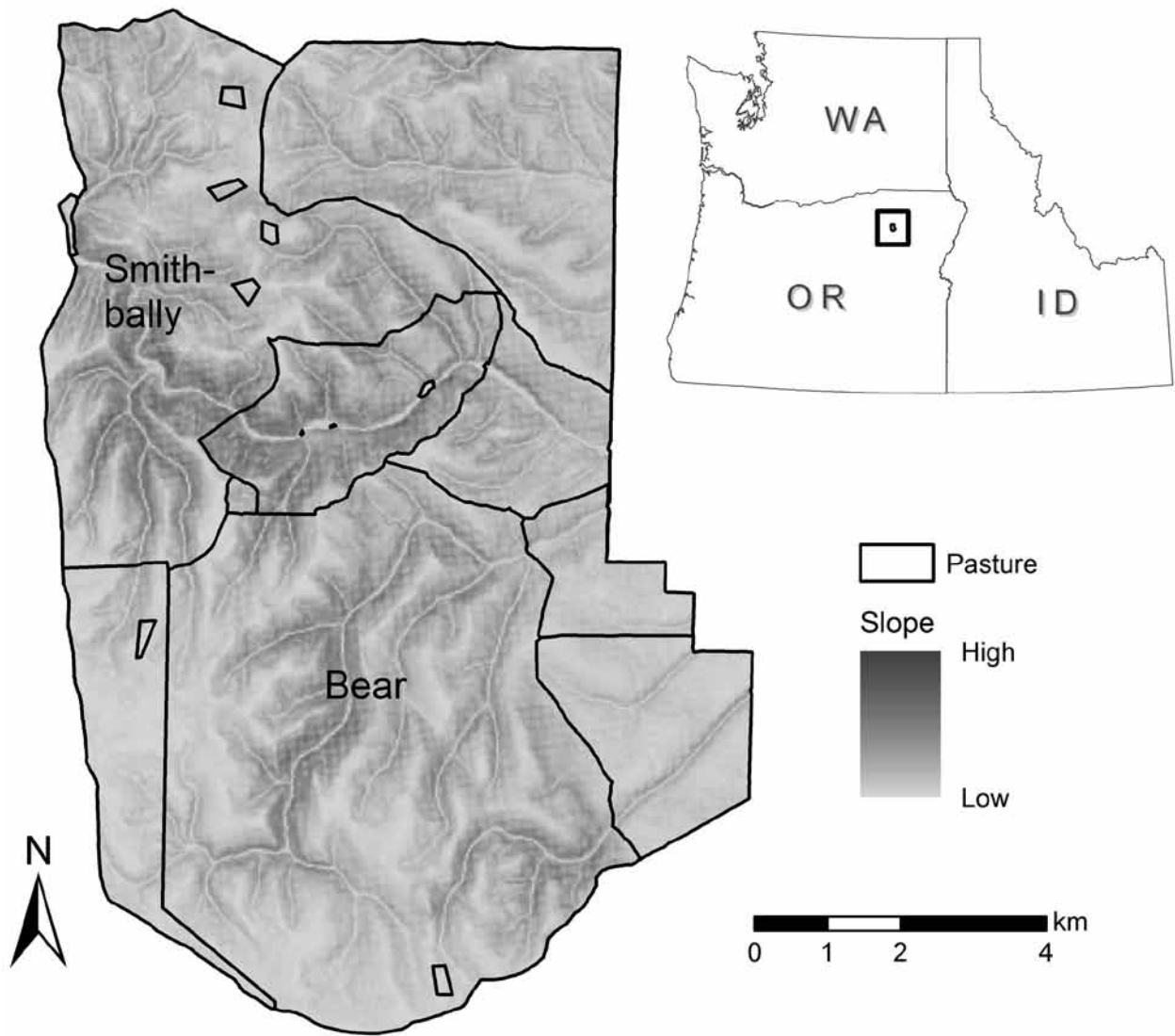
Figure 1. The Starkey Experimental Forest and Range located in eastern Oregon. Cattle habitat selection was analyzed in the Bear pasture and the Smith-bally pasture.

Here, we analyze the summer (June to October) habitat selection of cattle across 8 yr on 2 large pastures managed by the U.S. Forest Service. The arid landscapes of the western United States are subject to a predictable late summer drought (Peters et al., 2014), where slight increases or decreases in precipitation can dramatically alter the phenology of the forage base (Harris, 1954). We examine changes in selection by cattle as a function of 1) season, 2) yearly rainfall variability, 3) pasture characteristics, and 4) cattle behavior. Behavior was classified using the turn angle and step length characteristics of the sequential telemetry locations (Van Moorter et al., 2010). Our main purpose in classifying behavior was to ensure that the large quantity of resting locations did not mask the habitat selection preferences when the animals were active and more likely to be feeding. After comparing selection

models, we discuss the implications of our results for cattle management during periods of drought, particularly in a future with increased climate uncertainty.

MATERIALS AND METHODS

Study Area and Cattle Data

The study area was located in the Blue Mountains of northeast Oregon at the Starkey Experimental Forest and Range (**EFR**; Fig. 1; Rowland et al., 1997). Habitat consisted of mixed coniferous forest with Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) along with lodgepole (*Pinus contorta*) and ponderosa pine (*Pinus ponderosa*). Interspersed open grasslands with bunchgrass species (predominately Idaho fescue [*Festuca idahoensis*], Sandberg
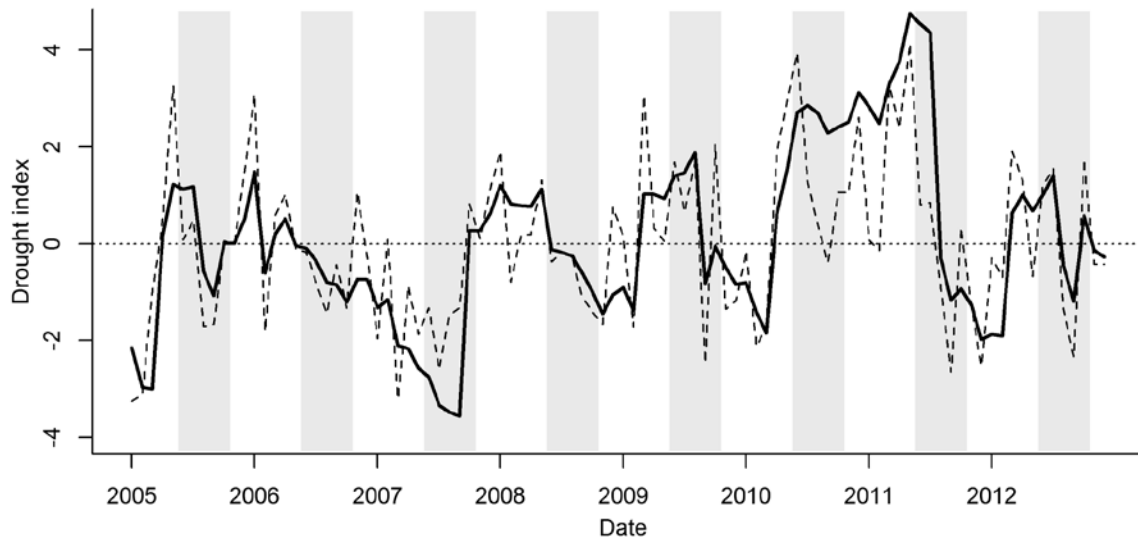
Figure 2. The Palmer drought severity index (solid line) and the z-index (dashed line) for northeastern Oregon measured on a monthly basis (NOAA National Climatic Data Center, 2014), with summer analysis periods highlighted (gray bar). The Palmer drought duration and intensity index indicates the severity of a wet or dry period, with values below –2 indicating a moderate drought. The z-index is a moisture anomaly index that measures departures from normal precipitation and is more sensitive to within-month rainfall events. Z-index values below –1.25 indicate moderate drought.

bluegrass [*Poa secunda*], and bluebunch wheatgrass [*Pseudoroegneria spicata*]) were located on higher elevation plateaus (Holechek et al., 1982a), and wet meadows were located at lower elevations. The region generally received higher, more consistent annual precipitation in early summer followed by a dry late-summer period with more sporadic showers. Drought was defined based on Palmer drought severity index (NOAA National Climatic Data Center, 2014), with values of less than –2.0 indicating moderate drought and values less than –3.0 indicating severe drought (Fig. 2; Palmer, 1965; Heddinghaus and Sabol, 1991). Based on this classification, a severe drought occurred in the summer of 2007. The Palmer drought severity index, however, is less sensitive to the short-term droughts that typify this region, so we also used the z-index, which is more indicative of within-month precipitation events (NOAA National Climatic Data Center, 2014). Values of less than –1.25 indicate moderate drought with the z-index, which occurred in the late summer of all years except 2010 (Fig. 2).

The Starkey EFR encompassed an area of 101 km^2, which was partitioned into 8 experimental pastures and 10 small exclosures (Rowland et al., 1997). Cattle were grazed in 5 of the 8 pastures; for this study, we focused on the 2 largest pastures, Bear (36.4 km^2) and Smith-bally (23.7 km^2; Fig. 1). Every year, cattle were rotated between the 2 pastures, spending between 4 and 8 wk in each. Cattle entered the first pasture in the early summer (mid June to mid July), were moved between pastures in early August or September, and exited the second pasture in late summer (late September to early

Table 1. Summary of cattle data and the grazing rotation schedule for each year. Rotation dates corresponded to the date animals were put onto the first pasture (enter), moved between pastures (switch), and removed from the second pasture (exit). The period when animals were in the first pasture (enter to switch) corresponded with the early summer, and time spent in the second pasture corresponded with late summer (switch to exit). Cumulative rainfall amounts for the early and late rotations are also presented

Year	No. of animals	No. of locations	Pasture rotation	Enter	Switch	Exit	Rainfall, mm	
							Early	Late
2005	29	62,289	Smith-bally to Bear	17 June	1 Aug.	25 Sept.	54.6	4.8
2006	29	48,053	Bear to Smith-bally	12 July	1 Sept.	10 Oct.	39.2	12.7
2007	23	41,891	Smith-bally to Bear	17 June	1 Aug.	10 Oct.	24.8	15.8
2008	19	23,681	Bear to Smith-bally	19 July	1 Sept.	11 Oct.	30.0	19.1
2009	23	48,772	Smith-bally to Bear	17 June	1 Aug.	2 Oct.	46.0	19.8
2010	25	33,927	Bear to Smith-bally	15 July	1 Sept.	9 Oct.	37.7	38.9
2011	20	30,072	Bear to Smith-bally	24 June	1 Aug.	13 Sept.	61.7	3.7
2012	15	17,970	Bear to Smith-bally	19 June	1 Aug.	13 Sept.	50.0	14.6

October; Table 1). The pastures were large enough that an animal never used the entire pasture in a season.

Between 2005 and 2012, female Angus cattle were fitted with global positioning system telemetry collars (Lotek model 4400; Lotek Wireless Inc., Newmarket, ON, Canada), and their location was sampled every hour (Table 1). In 2007 and 2008, however, a combination of Angus and Salers cattle were collared. Collared cattle were part of a larger herd of 500 cow–calf pairs that are grazed each summer on the Starkey EFR under a standard U.S. Forest Service livestock permit using a rotational grazing system. Stocking rate was 1.7 animal unit month per hectare for all years, which is typical of management on adjacent public lands (Parsons et al., 2003). Cattle were actively moved between pastures by range riders; therefore, we discarded locations on the days of human handling. Occasionally, gates were left open or cattle escaped pastures, and these forays were retained in the data set. Between 2005 and 2007, hunters were present in the study area for much of the late summer period (25 August to 25 September and 30 September to 10 October). From 2008 to 2012, the hunting seasons were restricted to two 1-wk periods. To ensure that the higher concentration of human activity during these periods did not alter cattle habitat use, we excluded the 2008 to 2012 hunting period from the analysis. Individual cattle home ranges were then generated for each year and each pasture using 95% isopleths of a Gaussian kernel density (Beyer, 2012) and the smoothed cross-validation bandwidth estimators from the 'ks' library in R (Duong, 2012).

Because cattle are a herd-forming species, we wanted to ensure that the collared individuals were not highly associated. Resource selection function (**RSF**) models do not require complete statistical independence among animals but instead animals must be representative of the population of interest (Clark et al., 2014); however, highly associated individuals can bias the model results in the direction of those most heavily sampled. To assess animal association, we used the software program Assoc1 (Idaho State University, Pocatello, ID, http://giscenter.isu.edu/software/index.htm) to test for the level of association between individuals (Weber et al., 2001). We used 100 m as the criterion for identifying independence between animals, which was the mean distance traveled by cattle in 1 h. Given the 1-h telemetry sampling rate and the resolution of our landscape covariates (30 m; see below), this distance ensured that pairs were separated by 1 sampling iteration and a minimum of 2 landscape pixels, which we deemed adequate for the objective of this study (Clark et al., 2014). One pair of adult animals was associated 16.7% of the time and another pair was associated 11.4% of the time. All other col-

lared animals spent at least 90% of their time separated from other collared cows.

Movement Models

Following the methods of Van Moorter et al. (2010), we used the gap statistic to determine the number of possible behavioral subunits present within the data. The benefit of this method is that no a priori assumptions were made about the number of behaviors present (Van Moorter et al., 2010). We first calculated the turn angle and movement rate of sequential locations. Clusters were identified by plotting the turn angle against the movement rate and measuring the dispersion between points to identify clustering. We tested for the likelihood that the yearly data sets contained between $k = 1$ and $k = 10$ clusters. The dispersion between clusters was calculated and compared to a defined number ($\beta = 50$) of reference data sets created using Monte Carlo simulation and principle components to estimate a similar dispersion of the input data sets (Van Moorter et al., 2010). The dispersion of the reference data sets was used to create a decision rule to select the smallest number of clusters (i.e., behaviors) present within the data. Two levels of tolerance were evaluated ($T = 1$ and 2), with higher tolerance values equivalent to more rigorous standards of rejecting higher numbers of clusters (Van Moorter et al., 2010).

Once the number of behaviors was identified, we then used k-means clustering to classify locations into the k behaviors (MacQueen, 1967). K-means clustering is sensitive to changes in distribution and range of the predictor variables (Steinley, 2006; Van Moorter et al., 2010); therefore, we log transformed the movement rate to lessen the right skew of the data and took the absolute value of turn angle (in radians). Both unstandardized and standardized, $[x_i - \min(x)]/[\max(x) - \min(x)]$, movement rate and turn angle variables were analyzed. We then used a scatter plot to ensure that the identified behaviors were biologically plausible. We used the known crepuscular activity patterns of cattle to ensure that the identified behaviors from the cluster analysis were consistent with known cattle behavior (Howery et al., 1996; Gregorini et al., 2006). We conducted our analysis in R (R Core Team, 2012) using the package "clusterSim" (Walesiak and Dudek, 2014) and the gap statistic function developed by B. Van Moorter (http://ase-research.org/moorter/; accessed 24 September 2013).

Habitat Selection Models

We developed separate cattle habitat selection models for each year, behavior, and season (early and

late summer). The date separating early and late seasons was not a fixed calendar date but instead driven by the pasture rotation schedule, which varied by year (Table 1). We used a mixed-effect logistic regression model with a random intercept for individual animals. Beta coefficients from each logistic regression model were used to estimate the RSF using the equation

$$w(x_i) = \exp(\beta_1 x_{1i} + \ldots + \beta_n x_{ni}) / [1 + \exp(\beta_1 x_{1i} + \ldots + \beta_n x_{ni})], \qquad [1]$$

in which $w(x_i)$ is the RSF and β_n is the coefficient for the nth predictor variable x_n (Manly et al., 2002; Gillies et al., 2006).

Only animals with ≥600 locations per year were retained for analysis for a total of 95 animals over 8 yr and, on average, 23 animals per year (some animals were collared across multiple years). Cattle locations were compared with random locations generated within an animal's home range. To ensure an adequate number of random locations, we followed the methods of Northrup et al. (2013) and fit logistic regression models to incrementally increasing samples of random locations (100, 1,000, 5,000, 10,000, 20,000, and 30,000). We repeated this procedure 1,000 times and monitored the β coefficients of 3 representative covariates to identify the density at which coefficient values began to converge. Convergence occurred at a minimum of 5,000 random locations (Supplementary Appendix S1; Supplementary Fig. S1); therefore, we generated random locations at a density of 1 point per pixel (30 × 30 m) or 5,000 if home ranges contained fewer than 5,000 pixels. Because we calculated yearly home ranges, the sample of available locations for each year was specific to where the individual animal was located that year.

Habitat covariates for resource selection modeling fell within 4 broad categories or suites: 1) landscape, 2) anthropogenic, 3) soil, and 4) vegetation (Supplementary Table S1). Landscape covariates were derived from water and elevation layers. Surface water was identified using the National Hydrography Dataset (USGS, 2013), and distance to water was estimated separately for the early (all perennial water) and late (streams with late season standing water and man-made structures) summer periods. A 30-m digital elevation model (Landfire; U.S. Geological Survey, 2009) was used to estimate slope (degrees), north–south–facing slopes (the cosine of aspect), east–west–facing slopes (the sine of the aspect), and a midsummer (1 August 2008) solar radiation index. Anthropogenic covariates included distance to nearest fence, distance to nearest road of any type, distance to nearest road open to the public, and distance

to nearest service (i.e., administrative) road. In 2011, 2 roads were decommissioned, so a revised distance to road grid was created to reflect this change in the 2011 and 2012 models. Soil covariates were obtained from the Soil Survey Geographic database (Soil Survey Staff, 2013) and included vector classifications of the percent clay, sand, silt, and organic material present in the soil. Soil pH, available water capacity (cm of water/cm of soil), and soil depth (cm) were also obtained in vector form (Soil Survey Staff, 2013). Finally, vegetation covariates were used to estimate the type, density, and diversity of existing habitats in the study area. We used Landfire data sets at a 30-m resolution to estimate percent tree canopy cover, canopy height (m × 10), and canopy bulk density (mass of canopy per unit canopy; U.S. Geological Survey, 2010a). Distance to forest edge was then calculated, with forest being defined at intervals of 20, 30, and 40% canopy cover (Supplementary Table S1). Existing vegetation types from Landfire (U.S. Geological Survey, 2010b) were generalized into 5 habitat categories (grand/Douglas-fir, lodgepole/ponderosa pine, pine/fir mix, grassland, and wet meadow). Using these 5 vegetation categories, we also calculated a habitat heterogeneity covariate, which identified the number of habitat types within a 90- by 90-m square surrounding each pixel. Low values indicated larger, contiguous patches of habitat and high values indicated smaller, heterogeneous patches of habitat.

A portion of the Smith-bally pasture (4.3 of 23.7 km^2) was incorrectly identified as "wet meadow" in the Landfire land cover classification (U.S. Geological Survey, 2010b), which further compromised any classification that used existing vegetation type within its algorithm (e.g., canopy cover and height). Instead of attempting to correct this misclassification through additional field validation or by substituting a mosaic from other data sources, we simply excluded this area from all analyses and projections. This ensured that the habitat selection models were estimated using publicly available, free data sources. The availability of input data was important because larger project objectives were to ensure that our models could be extrapolated to and validated in areas beyond the Starkey EFR, if necessary, where field-validated spatial information may be less well available.

Within each suite of habitat covariates, we tested for correlations between covariates using Pearson's correlation coefficient (Supplementary Table S2). If covariates were correlated ($|r| \geq 0.60$), univariate models were compared in both the linear and quadratic form, and the covariate that explained the greatest variability in the data set was retained. After correlated covariates were removed within each suite, we repeated the procedure between suites of covariates,

examining all remaining covariates in a correlation matrix. The resulting covariates were considered for inclusion in model selection procedures. Nine candidate models were ranked using Bayesian information criterion (Supplementary Table S3), which is less sensitive than Akaike information criterion to biases toward fuller models when sample size is large (Grueber et al., 2011).

For the top-ranked habitat selection models, k-fold cross-validation ($k = 5$) was used to evaluate model fit using the Spearman rank correlation coefficient (r_s; Boyce et al., 2002). To assess model robustness across behaviors and seasons, models created for one behavior for each year were further tested for robustness using the other location data from that same year (e.g., the fit of the early season model for behavior A was evaluated using the late season locations for behavior A, both early and late season locations for behavior B, and all locations combined). This out-of-sample model fit was also assessed using the Spearman rank correlation coefficient. Finally, RSF probability surfaces were created in ArcGIS 10.1 (ESRI, Redlands, CA) using Eq. [1]. Continuous probability values were classified into 10 equal-area (i.e., quantile) bins for ease of comparison. Finally, models created using the mobile location data were averaged and the variance was calculated. Habitat selection analysis was conducted in R (R Core Team, 2012) using the lme4 package (Bates et al., 2014).

RESULTS

The gap statistic identified 2 distinct behaviors for each of the 8 yr of location data (Supplementary Fig. S2). In classifying the telemetry locations into these behaviors, the k-means clustering classification was sensitive to the distribution of movement rate and turn angle, as the standardized and unstandardized values provided distinctly different classifications (Supplementary Fig. S3). Standardized values placed stronger emphasis on the turn angles, splitting the data into forward-moving and reverse-turning categories. Conversely, unstandardized values emphasized movement rate, which was more consistent with the resting and foraging/searching behavior of cattle. We therefore retained the unstandardized classification, resulting in 2 behaviors: 1) fast movement rates (>0.028 km/h) with a slight emphasis on forward-oriented turn angles (mobile) and 2) slow movement rates (<0.058 km/h) with a slight emphasis on backward-oriented turn angles (often an artifact of telemetry collar error; stationary; Fig. 3). The 2 behaviors were consistent with cattle activity patterns, as animals were more mobile during the crepuscular hours and stationary during the heat of the day and at night.

With the 2 behaviors identified, we then developed separate cattle habitat selection models for each behavior, season, and year for a total of 32 models. The full model (with 15 covariates) was best supported by the data in 12 of the 32 instances (Supplementary Table S4). However, model selection did not always support the full model. The simplest model (model 1 with 8 covariates) was the top-ranked model in one instance, the late summer of 2008. That year was also the year in which Salers cattle were collared. Model 8, which excluded habitat heterogeneity, and model 7, which excluded east–west aspects, also had support in 7 and 5 instances, respectively. Soil covariates were excluded from models 5 and 6, and these models were ranked highest in 6 instances.

Model fit was excellent for all top-ranked habitat selection models using k-fold cross-validation (r_s > 0.987, $P < 0.001$). Out-of-sample model fit was also significant for all early season models, with the exception of 2011 (Supplementary Table S5), which had an exceptionally wet early summer and moderately dry late summer (Fig. 2). Whereas early season models provided good fit to all data irrespective of behavior and season, late season models performed less well at predicting early season selection patterns, with only half of the models having significant Spearman rank correlation coefficients for the 2 behaviors (Supplementary Table S5). Consequently, areas used by cattle in the early summer were still used in the late summer but at differing intensities; however, areas used in the fall do not fully describe use in the early summer.

Despite the seasonal (i.e., precipitation) and topographic variability present within the study area, consistent patterns of selection were apparent across years, seasons, and behaviors. Cattle always selected gentle slopes, areas close to forest edges (when forest was defined as >20% canopy cover), and habitats classified as wet meadows (Table 2). Nearly all (31 of 32) models also showed a preference by cattle for habitats classified as lodgepole and ponderosa pine, which generally occurred on south-facing slopes. Cattle also displayed a curvilinear, U-shaped selection for water (27 of 32 models), preferring areas near water and areas far from water on the plateaus (Fig. 4). Cattle avoided areas at intermediate distances from water, which were generally associated with steep slopes. Although selection for roads was not consistent, cattle generally avoided roads open to the public (25 of 32 models). Cattle also selected areas of moderate canopy cover (26 of 32 models) and areas with higher habitat heterogeneity (20 of 32 models).

When the mobile habitat selection results were summarized by season and pasture, other patterns be-
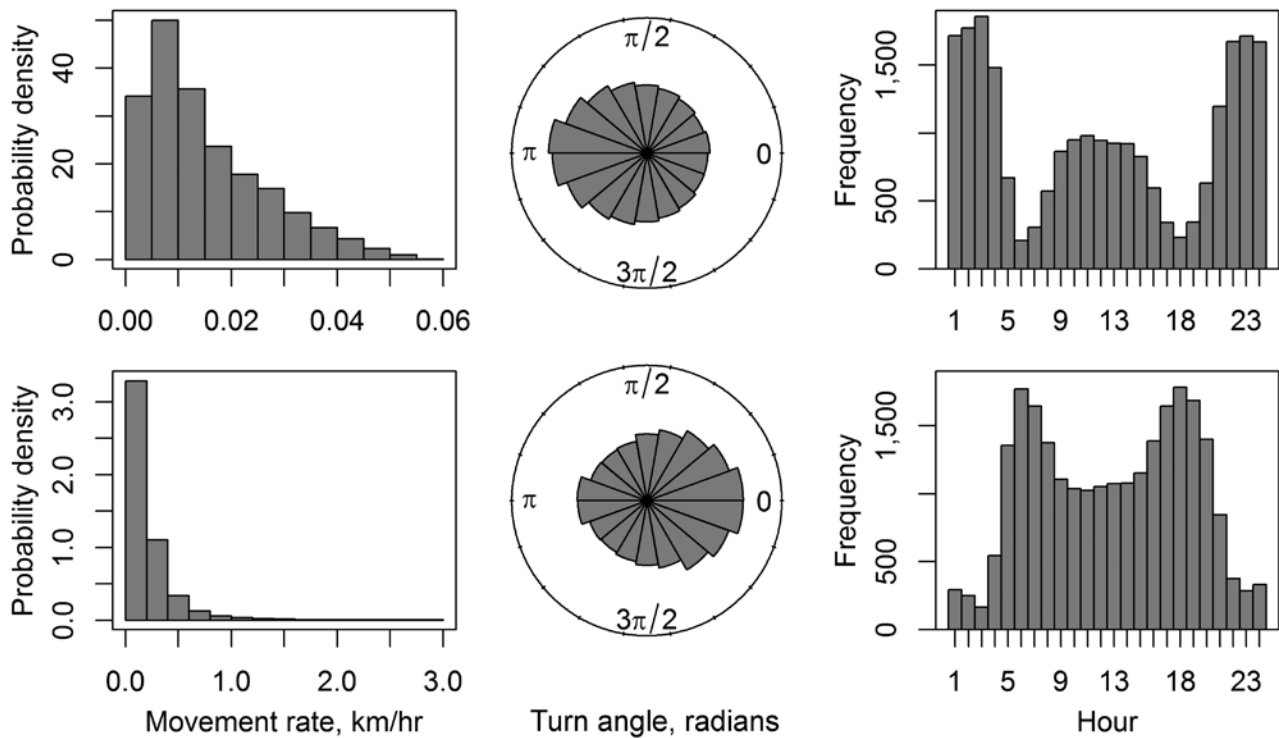
Figure 3. *K*-means classification of cattle location data based on movement rate and turn angle. Stationary locations (top row) had slower movement rates (note scale of the *x*-axis) and backward-directed turn angles. Mobile locations (bottom row) had longer step lengths and forward-oriented turn angles. These classifications were then compared against time of day (hour) to ensure they conformed to the known crepuscular activity patterns of cattle (Howery et al., 1996; Gregorini et al., 2006).

came apparent (Table 2). Cattle in the Bear pasture selected south- and west-facing slopes and generally had stronger selection (steepest slopes of β coefficients) for south-facing slopes in the early season (Table 2). Conversely, in Smith-bally, cattle often selected north-facing slopes (5 of 8 models), and they selected east-facing slopes in the early season and west-facing slopes in the late season. Selection for service roads was variable by pasture, with most (5 of 8) models showing selection for areas near these roads in the Smith-bally pasture and most (5 of 8) models showing avoidance in the Bear pasture. In the late season of 2008, cattle in the Smith-bally pasture avoided all roads, irrespective of road class. Cattle consistently selected for sandy soils in the Smith-bally pasture, whereas selection was variable in the Bear pasture (4 negative, 3 positive). This stronger association in the Smith-bally pasture could be a result of the steeper terrain in the pasture, as sandy soils were generally associated with the gentle terrain of the valleys and plateaus. Although cattle consistently selected wet meadows, this tendency was stronger during the late season (i.e., coefficient values generally increased across seasons within a year). Cattle also tended to select open grasslands in the late season (7 of 8 models), and they avoided open grasslands in the early season in Smith-bally (3 of 3). Selection for

grasslands in the Bear pasture in the early season was variable (3 selected and 2 avoided).

Rainfall patterns also influenced selection patterns of mobile cattle in both pastures and seasons. The covariate for distance to water had a curvilinear, U-shaped relationship, as most cattle selected areas near and far from water as animals moved between drinking sources and food patches on plateaus. However, the curvilinear relationship with water was not consistent across years, as cattle had a stronger preference for areas close to water during dry years (i.e., early summer of 2007) and for areas far from water during more mesic years (i.e., early 2010–2011; Fig. 4). In the late summer of 2010, which was particularly wet (Fig. 2), cattle had a slight preference for areas close to water in the late summer; however, the relationship was relatively weak (Fig. 4). This weak relationship to water continued into the late summer of 2011, which experienced a moderate drought (Fig. 2), possibly because adequate ground water remained within the system. During wetter periods, irrespective of pasture and season, cattle consistently selected shallow soils, and during dry periods, they selected deeper soils. Rainfall also influenced cattle's propensity to avoid open roads. In the Smith-bally pasture, cattle avoided open roads during wetter periods and selected areas near open roads when rainfall was low.

Table 2. Covariate coefficient values for the top-ranked habitat selection models by pasture, season, and year for mobile cattle location data. Water and canopy cover had quadratic terms to create a curvilinear relationship. Blank values indicate that the coefficient was not included in the model.

Season	Year	Slope	North aspect	East aspect	Water	Water* water	Open roads	Service roads	Sand²	Soil depth²	Canopy cover²	Canopy cover²	Forest edge	Hetero-geneity	Pine	Pine/fir mix	Grass	Meadow
Bear pasture																		
Early	2006	-0.08	-0.18		-2.91	2.47	0.24	0.47	0.29	0.38	1.45	-0.03	-6.46	0.02	0.20	0.13	-0.04	0.37
Early	2008	-0.06	-0.08	-0.06	-2.42	2.17	0.22	0.29	0.47	0.30	1.45	-0.04	-4.04		0.27	0.13	-0.04	0.51
Early	2010	-0.08	-0.21		-3.42	3.50	0.14	0.34			1.72	-0.03	-7.75	-0.02	0.28	0.28	0.12	0.59
Early	2011	-0.07	-0.20	-0.14	-0.01	0.80	0.33	-1.25	-1.90	-0.36	1.64	-0.02	-7.83		0.36	-0.05	0.16	0.61
Early	2012	-0.06	-0.14	-0.09	-0.96	1.11	0.45	-0.55	-1.48	-0.30	2.18	-0.05	-7.13		0.29	-0.08	0.05	0.39
Late	2005	-0.08	-0.15	-0.05	-3.25	2.52	0.32	-0.22	0.11	0.56	0.76	-0.03	-2.45	0.03	0.13	0.26	0.01	0.50
Late	2007	-0.06	-0.14		-2.60	2.04	0.18	0.23	0.88	-0.20	1.91	-0.06	-4.94		0.20	0.03	0.19	0.50
Late	2009	-0.07	-0.09	-0.09	-2.28	1.81	0.20	0.44	-1.46	-0.10	1.58	-0.06	-3.81	0.06	0.28	0.27	0.29	0.55
Smith-bally pasture																		
Early	2005	-0.06	-0.05	0.14	-2.09	1.90	0.11	-1.07			0.91	-0.02	-8.15	0.13	0.06	-0.31	-0.27	0.26
Early	2007	-0.05	0.03		-1.86	1.14	-0.05	-1.17	1.43	0.49	0.07	-0.02	-5.05	0.09	0.16	-0.17	-0.26	0.62
Early	2009	-0.05	0.07	0.09	-2.30	1.81	0.25	-0.40	1.35	-0.07	0.44	-0.02	-3.29	0.13	0.07	-0.06	-0.26	0.39
Late	2006	-0.04	0.15	-0.17	-0.67	0.09	-0.24	0.13	1.98	0.24	1.62	-0.07	-7.31	0.10	0.18	-0.01	0.30	0.55
Late	2008	-0.06			-2.43	2.18	-1.43[1]				1.79	-0.08			0.31	0.24	0.74	0.89
Late	2010	-0.08	0.17	-0.18	-1.21	0.07	0.17	-0.55			-0.18	-0.04	-3.99	0.22	0.14	-0.09	0.25	0.52
Late	2011	-0.06	0.03	-0.09	-0.99	-0.06	-0.12	-0.51	4.02	1.12	2.95	-0.09	-2.77	0.11	-0.01	0.34	-0.05	0.54
Late	2012	-0.07	-0.04	-0.24	-2.08	1.60	0.02	0.44	3.43	0.32	0.57	-0.02	-1.54	0.19	0.12	0.15	0.17	0.74

[1]Road covariate included in the top model was distance to all roads.
²Coefficient was multiplied by 100.

Although cattle generally selected areas of intermediate canopy cover, during the wettest late summer observed during the study period (2010), they selected areas of low canopy cover. During wetter periods, irrespective of season and pasture, cattle also avoided habitats with pine/fir mix forests.

Overall, behavior had less influence on cattle selection than anticipated, with cattle selecting similar areas whether they were mobile or stationary; however, some notable differences were apparent. Cattle mostly (12 of 16 models) avoided open grasslands when they were stationary (Supplementary Table S6). Whereas the covariate for habitat heterogeneity was mostly absent from the top model in the Bear pasture during the early season (3 of 5 models), cattle at rest during that same period tended to select areas of low heterogeneity (3 of 5 models). Although they always selected wet meadows, selection was stronger in the early season when cattle were stationary, but it was strongest in the late season when cattle were mobile. In years observed here with higher relative early summer rainfall (2011 and 2012), stationary cattle selected areas of intermediate distance from water, which they always avoided when they were mobile.

DISCUSSION

Previous research into cattle habitat selection has shown that cattle distribution patterns were predominately driven by water, topography, and vegetation composition (listed in order of importance; Brock and Owensby, 2000; Ager et al., 2005; Holechek et al., 2011; Kaufmann et al., 2013), and we found a similar response. Cattle in the Starkey EFR consistently selected areas with gentle slopes and areas both near and far from water, as animals were using both riparian corridors and upland plateaus but spent less time on the intervening hillsides. This curvilinear relationship to water has been observed elsewhere with cattle, as animals deplete resources near water and then travel farther afield in search of available forage (Pinchak et al., 1991). As precipitation increased, cattle moved far-
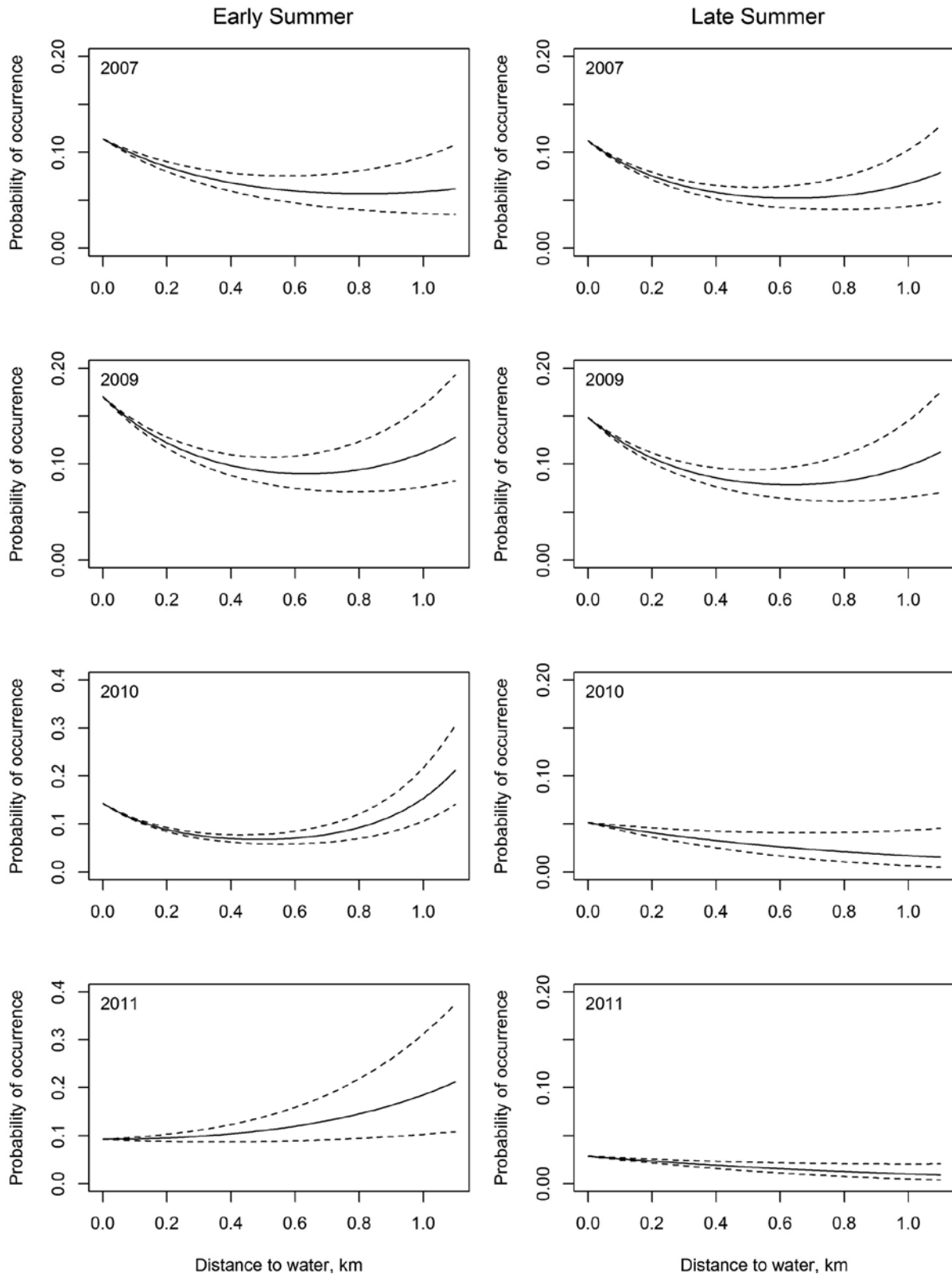
Figure 4. Relative probability of selection for water across the early summer and late summer periods during a subsample of years with 95% confidence intervals (dashed line). A severe drought occurred in 2007, rainfall was more typical with a wet early summer and dry late summer in 2009, and precipitation was high in 2010 and early 2011.

ther afield (Fig. 4). Cattle dependence on water is well documented in both arid (Smith et al., 1992; DelCurto and Johnson, 2000; Clark et al., 2014) and mesic (Zuo and Miller-Goodman, 2004) environments. Cattle also

selected wet meadows and lodgepole and ponderosa pine forests, similar to selection observed by other studies in the Blue Mountains (Roath and Krueger, 1982), and they selected vegetation structure that had

intermediate canopy cover, high heterogeneity, and areas near forest edges.

Although consistent patterns were observed across years, pastures, and behaviors, habitat selection patterns by cattle indicated that animals were responding to differences in landscape and environmental factors across the study area. In the Smith-bally pasture, which had more extreme topography and streams running in an east–west trajectory, cattle selected south-facing slopes and had a stronger avoidance of steep terrain. In the Bear pasture, streams had a north–south trajectory, and cattle responded by selecting east-facing slopes early in the summer and west-facing slopes late. Rainfall, in particular, appears to be a driving factor in the variation in habitat selection. Cattle used areas with deeper soils during periods of low rainfall, as these soils also have higher plant-available water (Soil Survey Staff, 2013). Animals also generally avoided open roads except during periods of low rainfall when they used man-made watering points located near roads. This association with roads during times of water scarcity is not unique to cattle, as selection for roads in western conifer forests has also been seen by wildlife and roads in mountainous regions are often associated with gentle terrain and food resources (Roever et al., 2008a,b).

An unexpected result, however, was that cattle did not respond to low rainfall by switching selection patterns, but instead they had stronger selection for areas with easy access to water (Fig. 4). We postulate that this is why the early season model accurately predicted late season use, but late season models did less well at predicting early season use, as cattle habitat selection contracted around water sources. Other large-bodied herbivores, such as elephants, have a bimodal use pattern during the dry season, alternating between drinking water sources and traveling far afield to find sufficient forage (Roever et al., 2012). Cattle had a similar pattern of selection when water was readily available, but as conditions became more arid, cattle use of areas far from water sources declined (Fig. 4). Areas with the greatest variability in cattle use across seasons were generally upland areas, far from water (Fig. 5B). This dependence on water means that cattle did not compensate spatially as conditions became drier but likely compensated via their diet by switching from grass to forbs and shrubs as preferred forage became less available (Holechek et al., 1982a,b; Walburger et al., 2007). Over prolonged periods of drought, this selection pattern could put increased pressure on riparian vegetation (Parsons et al., 2003; DelCurto et al., 2005).

The positioning of water sources has been suggested as a means to alter cattle selection patterns (Ganskopp, 2001; Porath et al., 2002; Bailey, 2005),

and our results support this, as upland areas near man-made water sources were still used by cattle during drier periods (Fig. 5). However, our results also suggest that it is unlikely to completely alleviate pressure on riparian zones. The availability of water points did not reduce use of riparian areas during periods of low rainfall. In modeling habitat selection by cattle, we tested 2 levels of water availability: early season water, which included all streams, and late season water, which included only streams that were known to retain water into the late season. Surprisingly, the early season water covariate outperformed the late season water covariate even in the late season, when these streams were unlikely to contain standing water. Howery et al. (1996) found cattle had a similar fidelity to known water sources even after they were dry; however, in our study area, the motivation for continued use of riparian areas after they were dry was likely complicated by spatial correlations among landscape covariates. Cattle could continue to use riparian corridors because vegetation remained relatively green, a result of increased soil depth and moisture even after surface water has disappeared (Castelli et al., 2000). In areas with steep terrain, these large-bodied animals could also be using the riparian corridor as easy conduits for travel (see Noss et al., 1996).

Cattle appear to respond more to the short-term, monthly drought indices predicted by the z-index than to the long-term droughts as predicted by the Palmer drought severity index (NOAA National Climatic Data Center, 2014). For example, in 2007, precipitation began to increase in the late summer, which resulted in an increase in the z-index by August of that year but was only later reflected by the Palmer drought severity index in October (Fig. 2). Cattle were removed from the study area on October 10 (Table 1), but before they were removed, they were responding to the short-term precipitation indicated by the z-index by selecting areas far from water at a higher frequency than in the early summer (Fig. 4). Similarly, in 2010, when the study area experienced moderately moist conditions throughout the summer based on the Palmer drought severity index, cattle still altered selection in the late summer, using areas close to water (Fig. 4). Although this response was not as strong as in more arid years, it nonetheless indicates that cattle responded to the sharp decline in short-term precipitation in September of 2010 as observed in the z-index (Fig. 2).

By separating out the 2 coarse-scale behaviors, we demonstrated that the consistency in habitat selection by cattle was not a result of resting-site selection masking the habitat selection patterns while the animal is mobile and more likely to be foraging (Roever et al., 2014). The habitat selection patterns when cattle were
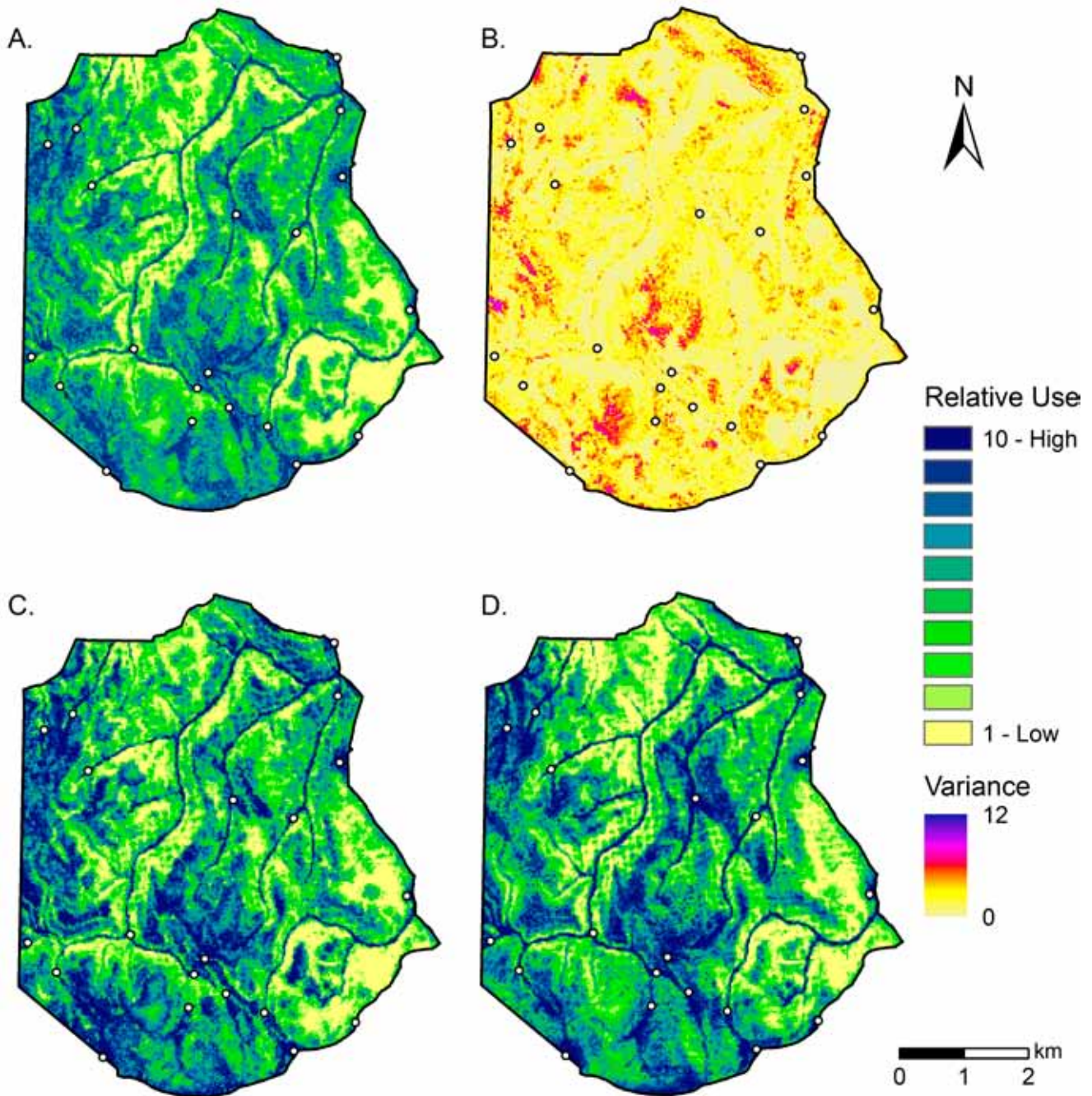
Figure 5. Mean habitat selection across years (A) and the variance in selection (B) for mobile cattle in the Bear pasture. Habitat selection during the wettest (61.7 mm of precipitation) early summer (C) and the driest (4.8 mm) late summer (D) for the Bear pasture illustrate that during dry periods, selection increased in areas near man-made water (white points) and selection in the uplands became more focused around smaller patches of habitat.

stationary and mobile were consistent; consequently, cattle appear to rest where they forage, possibly making microsite decisions at that location, which would not be evident at the scale examined here. This consistency of use is unlike that shown for other large herbivores, which alter resting site location to decrease predation risk (Creel et al., 2005; Poole et al., 2007). Although we cannot say whether our mobile and stationary classifications directly equated to foraging and resting behaviors of cattle without direct observation data (Ungar et al., 2005), we did find a correlation be-

tween the classifications and the known crepuscular behavior of cattle (Howery et al., 1996; Gregorini et al., 2006). Based on these results, we conclude that it may not be necessary to differentiate behavior when studying cattle habitat selection at the landscape scale as suggested by Roever et al. (2014), unless there is strong evidence for behavioral segregation in a given area.

The consistency in habitat selection by cattle should be considered when managing livestock on large pastures and public lands. Cattle did not switch

use spatially, but instead they contracted their use in response to late season water stress. Cattle also prefer to forage on vegetation that has been previously grazed (Ganskopp and Bohnert, 2006), further reinforcing repeated use of previously selected habitats. This could be deleterious if cattle are being used as a vegetation management tool, as some areas will be used repeatedly whereas others may not be grazed at all, particularly in areas where terrain is variable. This repeated use pattern has been proposed as a means to increase spatial landscape heterogeneity in grassland ecosystems, increasing grass structural heterogeneity as well as the niche space for other fauna (Fuhlendorf and Engle, 2001; Bailey et al., 2006). Whether similar patterns of cattle use will increase heterogeneity in arid and semiarid environments, however, is less apparent and could even be deleterious (Fuls, 1992). In arid environments, native bunchgrass communities are vulnerable to repeated defoliation particularly during a drought (Loeser et al., 2007), and long lag times of potentially decades are necessary for plant recovery (Valone et al., 2002). As the frequency and intensity of droughts are likely to increase in arid environments (Cook et al., 2004; Gutzler and Robbins, 2011), such compounding environmental stressors are only likely to increase plant vulnerability, and therefore, vegetation must therefore be closely monitored for signs of stress and degradation.

The main benefit of the predictability and consistency of habitat selection patterns by cattle across years and seasons is that cattle management then becomes more straightforward. In times of decreased rainfall, managers should focus their efforts on monitoring vegetation structure and species composition in those areas most preferred by cattle. The consistency of selection also indicates that cattle may be less sensitive in their functional responses to resource availability (Aarts et al., 2008; Matthiopoulos et al., 2011), as we found consistent selection patterns across our 2 pastures where availability differed. This supposition requires testing across a larger spatial scale, but if selection patterns hold, then the habitat selection models identified here could be applied across a much larger region, and this information will further assist with cattle management across a large spatiotemporal scale. As grazing of livestock on large tracts of publicly managed land is likely to continue as a dominate land use practice in the western United States, additional effort must be devoted to ensure that the practice remains ecologically sustainable in a future with increasing climate uncertainty.

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