Rangeland Ecology & Management 69 (2016) 319–325

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Elk Foraging Site Selection on Foothill and Mountain Rangeland in Spring☆

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ARTICLE INFO

Article history:
Received 21 December 2015
Received in revised form 24 March 2016
Accepted 1 April 2016

Key words:
cattle
Cervus elaphus
forage conditioning
grazing facilitation
resource selection function
targeted livestock grazing

ABSTRACT

Previous research suggests facilitative grazing by cattle during the preceding summer-fall can enhance spring foraging habitat of Rocky Mountain elk *(Cervus elaphus nelsoni)*. However, previous studies were limited to 1 year or conducted within relatively small experimental pastures. We evaluated elk foraging site selection during spring across 4 years and 59 040 ha of foothill and mountain rangeland in northwestern Wyoming and west-central Montana. Elk in spring avoided foraging in nonforested portions of cattle-grazed pastures where cattle had not grazed during the previous summer − early fall. In contrast, elk selected foraging sites where cattle had grazed lightly (11 − 30% forage use) or moderately (31 − 60% forage use), and selection by elk was stronger for moderately grazed sites. Neither moderate nor light cattle grazing intensity were correlated with any other elk habitat attribute that we sampled, and both moderate and light cattle grazing intensity exerted more influence on elk foraging site selection than any other variables, including distance to security cover, distance to primitive roads, distance to improved roads, aspect, or slope. We developed and validated a resource selection model that correctly classified 80 − 89% of elk foraging observations across five study sites and 4 years. Resource managers can use our model to map predicted changes in elk grazing distribution when considering potential habitat adjustments in security cover, roads, or cattle grazing intensities and distribution. Our results indicate that resource managers can use targeted cattle grazing in summer − early fall to purposely modify elk forage conditions to 1) increase elk foraging efficiency in spring, 2) lure elk away from places needing rest or deferment from spring elk grazing, or 3) lure elk away from places where elk in spring are experiencing conflicts with humans, predators, or other wildlife.

Introduction

Habitat management for Rocky Mountain elk *(Cervus elaphus nelsoni)* presents varied challenges on foothill and mountain rangeland. In many areas, elk herd recruitment rates are declining due, at least in part, to nutritional limitations of their foraging habitat during spring (Cook et al., 2013). Poor foraging habitat quality in spring inhibits pregnant elk from 1) recovering body condition after winter losses, 2) satisfying nutritional requirements for accelerated fetal growth during the third trimester of gestation, and 3) preparing for the physiological demands of calving (Thorne et al., 1976; Cook et al., 2004; Cook et al., 2013). In contrast, Rocky Mountain elk populations in other areas are thriving, but excessive elk grazing is degrading vegetation and soil resources (Zeigenfuss et al., 2002; Gass and Binkley, 2011; Thrift et al., 2013). In these areas, elk grazing often occurs too frequently in the same locations, and habitat management is needed to provide periodic rest or deferment from spring elk grazing (Brewer et al., 2007; Thrift et al., 2013). In short, whether elk populations are thriving or declining, landscape-scale strategies are needed in many areas for managing Rocky Mountain elk spring foraging habitat (Brewer et al., 2007; Cook et al., 2013; Thrift et al., 2013).

Elk inhabiting foothill and mountain rangeland in the northern Rocky Mountains consume grass-dominated diets during spring (Stevens, 1966; Ngugi et al., 1992; Torstenson et al., 2006), and elk select foraging sites where the net rate of energy gain (i.e., foraging efficiency) is greatest (Fryxell, 1991; Gross et al., 1993; Wilmshurst et al., 1995). Foraging efficiency is maximized on graminoid-dominated sites with intermediate biomass and fiber content and without mature reproductive culms or excessive plant litter because tradeoffs are optimized among the amount, nutritional quality, and

☆ Funding was provided by the US Dept of Agriculture (USDA) National Research Initiative, the USDA Initiative for Future Agriculture and Food Systems, the USDA Joe Skeen Institute for Rangeland Restoration, the Montana Agricultural Experiment Station, Montana State University Extension, the Wyoming Agricultural Experiment Station, and University of Wyoming Extension.

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http://dx.doi.org/10.1016/j.rama.2016.04.001
1550-7424/

accessibility of the forage (Fryxell, 1991; Gross et al., 1993; Wilmshurst et al., 1995). Elk diets and foraging sites during spring in the northern Rocky Mountains often overlap greatly with those of cattle during the previous summer-fall (Stevens, 1966; Ngugi et al., 1992; Torstenson et al., 2006). This foraging niche overlap provides opportunities for facilitative grazing (Vesey-Fitzgerald, 1960; McNaughton, 1984), where cattle grazing during summer-fall can improve the accessibility or nutritional quality of forage available for elk to graze during the following spring.

The use of livestock grazing to enhance wildlife habitat was first advocated by Leopold (1933), and authors of several literature reviews, synthesis articles, and book chapters have reiterated that properly managed livestock grazing can be used to manage elk habitat (Mosley, 1994; Severson and Urness, 1994; Lyon and Christensen, 2002; Mosley and Brewer, 2006). In much the same way that prescribed burning prescriptions specify the timing and conditions for applying prescribed fire to achieve desired habitat modifications, facilitative or targeted livestock grazing prescriptions specify the livestock species and grazing conditions (e.g., timing, intensity, and frequency of livestock grazing) for using livestock grazing to enhance elk foraging habitat (Mosley and Brewer, 2006).

Facilitative cattle grazing can increase elk foraging efficiency by increasing elk forage digestibility and nutritive value, as well as by reducing excessive plant litter and standing dead plant material that impede plant growth and inhibit forage accessibility (Willms et al., 1979; Jourdonnais and Bedunah, 1990; Phillips et al., 1999; Short and Knight, 2003; Ganskopp et al., 2004). Consequently, elk during spring may favor foraging in areas that were grazed previously by cattle (Grover and Thompson, 1986; Jourdonnais and Bedunah, 1990; Frisina, 1992). Previous research results, however, are from 1-year studies or from within relatively small experimental pastures, or the studies did not adequately consider other habitat attributes that might have influenced elk foraging site selection (Vavra, 2005; Vavra and Riggs, 2010).

Our landscape-scale study investigated whether elk selected foraging sites in spring where cattle had grazed during the previous summer-fall. We also investigated whether cattle grazing intensity was positively related to elk foraging site selection independently of other habitat attributes, including distance to hiding cover, distance to security cover, distance to roads, slope, elevation, and aspect.

Methods

Study Area

We studied elk foraging site selection during spring on foothill and mountain rangeland of the Absaroka Mountains in northwestern Wyoming and the Big Belt Mountains in west-central Montana. The study area consisted of three study sites in Wyoming and two study sites in Montana. Study sites encompassed three large, private ranches and adjoining state and federal public lands, with nonforested rangeland totaling 30 180 ha in Wyoming and 28 860 ha in Montana. In Wyoming, the Rattlesnake study site was located 19 km northwest of Cody, Wyoming in the North Fork drainage of the Shoshone River. The Rock Creek study site and Diamond Bar study site were located in the South Fork drainage of the Shoshone River, 50 km and 60 km southwest, respectively, of Cody, Wyoming. In Montana, the Lingshire study site and Birch Creek study site were located 72 km northwest and 12 km west, respectively, of White Sulphur Springs, Montana.

Elk were abundant on the study area during winter and spring but not summer — early fall when elk occupied higher elevations outside the study area. Cattle had access to the entire 59 040-ha study area every year, and cattle grazing management was typical of many western ranches that incorporate foothill and mountain rangeland. Cattle grazed on native rangeland from approximately 1 June to 1 October each year (i.e., summer — early fall). Elk social avoidance of cattle (Mosley, 1999) did not influence elk foraging site selection on rangeland during spring (March to May) because cattle were confined to hayfields or seeded pastures until approximately 1 June. Cow/calf pairs grazed within rotational grazing systems in which cattle grazed every pasture every year, but cattle seldom remained in one pasture for more than 30–45 days at a time. Cattle stocking rate was moderate (2.8 ha/animal unit months [AUM] on the Wyoming study sites and 1.8 ha/AUM on the Montana study sites), and cattle grazing was distributed within fenced pastures via herding, placement of salt/mineral supplements, and the availability of drinking water.

Mean annual precipitation was 28 cm in the Wyoming study sites and 37 cm in the Montana study sites (Western Regional Climate Center, 2003). Elevations ranged from 1650 m to 3700 m on the Wyoming sites and 1280 to 2600 m on the Montana study sites. Topography varied from flat outwash plains and rolling foothills at lower elevations to steep mountains at higher elevations. Although forested plant communities were common at the higher elevations of our study area, nonforested habitats typically provide the majority of foraging opportunities for elk during spring (Stevens, 1966; Constan, 1972; Torstenson et al., 2006).

We studied elk foraging site selection exclusively on nonforested, foothill and mountain rangeland dominated by sagebrush grassland and mountain grassland plant communities. Prevalent perennial graminoids included bluebunch wheatgrass *(Pseudoroegnaria spicata)*, Idaho fescue *(Festuca idahoensis)*, prairie junegrass *(Koeleria macrantha)*, needle and thread *(Hesperostipa comata)*, and Sandberg bluegrass *(Poa secunda)*. Common forbs included western yarrow *(Achillea millefoilium)*, spiny phlox *(Phlox hoodii)*, rose pussytoes *(Antennaria rosea)*, milkvetch (*Astragalus* spp.), and lupine (*Lupinus* spp.). Mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) were the dominant shrubs on higher and lower elevation sagebrush grasslands, respectively.

Elk Observations

Elk foraging sites were identified with systematic aerial surveys from fixed-wing aircraft. We identified elk foraging sites in Wyoming during spring of 4 years (2000, 2001, 2002, 2003) and during spring of 2 years in Montana (2002, 2003). Aerial surveys were conducted once monthly March to May 2000 and 2001 and bimonthly March to May 2002 and 2003. Flight transects were 0.8-km wide and flown about 150 m above the ground. Flight crews included an experienced pilot and observer, both of whom assisted in recording elk foraging locations. Each flight provided a complete reconnaissance of nonforested habitat within the cattle pastures on each study site, and aerial surveys were initiated in different locations within the study sites to mitigate potential biases of sampling a specific area at similar times within a flight. Aerial surveys began at sunrise and averaged 3 hours in length because a majority of elk foraging occurs during this time of day (Collins et al., 1978; Wickstrom et al., 1984; Green and Bear, 1990). Elk group size and elk use of nonforested habitat also increases during this crepuscular period (Anderson et al., 1998), which improves elk sightability from aerial surveys (Unsworth et al., 1990; Anderson et al., 1998; Cogan and Diefenbach, 1998). Although the potential for undetected individuals existed, sightability was improved because we evaluated nonforested habitat only and our aerial surveys were conducted during spring when elk group sizes were relatively large. Aerial sampling under these conditions likely detected ≥ 90% of the elk in our study area (Samuel et al., 1987; Anderson et al., 1998; Eberhardt et al., 1998).

An instantaneous observation of a cohesive group of elk (≥2 adults) constituted a single, independent observation. We considered our elk group observations independent because the time interval separating our aerial surveys (i.e., 2–4 weeks) was large enough to allow elk ample opportunity to select any site within their home range. Also, our study sites were large enough (mean = 11 808 ha) to encompass seasonal elk home ranges (Van Dyke et al., 1998; Anderson et al., 2005) and thereby large enough to provide elk sufficient opportunity to select any part of their home range and remain within our survey area. Elk groups were the sample unit because each animal in a group did not independently select the foraging site. We excluded observations of solitary elk because their habitat selection is highly variable (Sheehy and Vavra, 1996). We used a global positioning system to record the centroid of each elk group, and we considered the centroid as the foraging site location. We also counted the number of elk in each group.

Habitat Sampling

We screened potential habitat variables to include in our study on the basis of their ease of measurement and interpretability, relevance to our study area and objectives, and merit as determined by previous studies of Rocky Mountain elk foraging site selection during spring. We excluded variables that did not meet one or more of these criteria. We selected eight habitat variables to sample: distance to hiding cover (i.e., nearest distance to forest edge), distance to security cover (i.e., nearest distance to ≥ 40% forest canopy cover in patch sizes ≥ 2.6 ha), nearest distance to improved roads (county, state, or federal highways), nearest distance to primitive roads (gravel or dirt), slope, aspect, elevation, and cattle grazing during the previous summer-fall (Grover and Thompson, 1986; Thomas et al., 1988; Johnson et al., 2000; Long et al., 2009; Coe et al., 2011). We generated 100 random points per year in 2000 and 2001 within each of the three Wyoming study sites ($n = 600$ random points). We restricted random points to be ≥ 60 m from each other to ensure that 2 or more random points did not sample the same available elk foraging site, and we restricted random points to nonforested habitat within the cattle-grazed pastures. For each random point and for each elk foraging site, we obtained slope, distance to nearest improved road, nearest distance to primitive road, nearest distance to hiding cover, nearest distance to security cover, elevation, and aspect from 30 × 30 m resolution digital elevation models (USGS, 1999, , 2002). Because elk readily use habitat < 1 200 m from forest cover (Sheehy and Vavra, 1996) and < 1 560 m from improved roads (Johnson et al., 2000), we extended our GIS mapping 1600 m beyond our cattle pasture boundaries when calculating nearest distances from observed and random points to roads, hiding cover, and security cover. We calculated slope and aspect from the elevations of surrounding cells. Percent slope was the maximum rate of elevation change from the surrounding 3 × 3 cell area, and aspect was the direction of the maximum downhill slope gradient. Aspect was measured in degrees clockwise from due north, transformed to radians, and then cosine transformed.

For each random point and for each elk foraging site, we also recorded the cattle grazing intensity received during the previous summer — early fall. Cattle grazing intensity was inventoried in October after the cattle grazing season ended each year (Anderson and Currier, 1973). We mapped cattle grazing intensity in Wyoming during October 1999, 2000, 2001, and 2002 and in Montana during October 2001 and 2002. Landscape appearance guidelines (USDA-USDI, 1996) were used to categorize cattle grazing intensity into four strata: 1) heavy (>60% use), 2) moderate (31 — 60% use), 3) light (11 — 30% use), or 4) no cattle grazing (≤10% use). Cattle grazing intensity was inventoried and mapped via horseback and all-terrain vehicles, and polygon boundaries of cattle grazing intensity were later digitized. To calibrate our ocular estimates of cattle use, we used the Paired-Plot Method (USDA-USDI, 1996) and clipped vegetation inside and outside 1.2-m high, 6-m^2 grazing exclosures. Immediately before ocular inventories began each year, we sampled inside and out 9 or 10 exclosures per vegetation type (sagebrush grassland, mountain grassland) for a total of 18 exclosures per year during 1999 and 2000 (9 exclosures/vegetation type × 2 vegetation types = 18 exclosures) and a total of 40 exclosures per year in 2001 and 2002 [10 exclosures/vegetation type × 2 vegetation types × 2 states (Wyoming, Montana) = 40 exclosures]. We calculated percentage forage use by comparing the oven-dried weights of herbage that we clipped from paired 50 × 50 cm quadrats inside and outside each exclosure (USDA-USDI, 1996). Grazing exclosures and paired plots were reestablished in new locations each year after clipping in October.

Data Analyses

We used a use-availability study design to investigate elk foraging site selection (Boyce et al., 2002; Manly et al., 2002; Johnson et al., 2006). Our study design was observational (Cochran, 1983; Eberhardt and Thomas, 1991) because we did not control the slope, aspect, elevation, cattle grazing intensity, distance to cover, or distance to roads of our research units (i.e., the 30 × 30 m parcels of land that characterized our elk foraging sites and random sites within our five predefined study site populations). However, our study was replicated in time (4 years) and space (three Wyoming study sites and two Montana study sites). Statistical inferences from our observational study cannot be extended beyond our 59 040-ha study area (Wester, 1992).

We used elk observations from the three Wyoming study sites during 2000 and 2001 to 1) compare habitat attributes of used and available foraging sites; 2) determine whether elk avoided foraging where cattle had not grazed during the previous summer — early fall; and 3) develop a resource selection model. Elk observations recorded from all three Wyoming study sites during 2000 and 2001 were combined to incorporate potential variability in foraging site selection among sites and years (Hanley, 1984; Jenkins and Wright, 1988). Elk observations recorded during 2002 and 2003 at both the Wyoming and Montana study sites were reserved for use later when we evaluated our resource selection model for robustness across years and study sites.

We tested random points and elk foraging locations for outliers (PROC UNIVARIATE, SAS Institute, Inc., Cary, NC), as recommended by Barnett and Lewis (1994). Suspected outliers were analyzed with Grubbs' test (Grubbs, 1969) and eliminated if the critical Z value was significant ($P \le 0.05$).

We used the Shapiro-Wilk test (PROC UNIVARIATE, SAS Institute, Inc., Cary, NC) to examine residuals for deviations from normality ($P \le 0.05$). Subsequently we used the Mann–Whitney U test (PROC NPAR1WAY, SAS Institute, Inc., Cary, NC) to compare habitat attributes of used and available foraging sites ($P \le 0.05$). These tests were for descriptive purposes only (Beck et al., 2013). Per Anderson and Burnham (2002), we did not use these tests to screen potential variables for inclusion later in our resource selection model.

We used binary logistic regression (PROC LOGISTIC, SAS Institute, Inc., Cary, NC) to determine whether elk avoided foraging during spring where cattle had not grazed during the previous summer — early fall (Hosmer and Lemeshow, 2000). We contrasted elk foraging sites with random sites (Manly et al., 2002). For the parameter estimate of "no cattle grazing," we calculated an odds ratio (Hosmer and Lemeshow, 2000) and 85% confidence intervals (CIs) as recommended by Arnold (2010). Negative coefficients implied avoidance, whereas positive coefficients suggested attraction (Manly et al., 2002).

Before developing our resource selection model, we tested all habitat variables (i.e., distance to hiding cover, distance to security cover, distance to roads, slope, elevation, aspect, and cattle grazing intensity) for collinearity using Spearman's Rank Correlation (PROC CORR, SAS Institute, Inc., Cary, NC). If significant correlation ($P \le 0.05$ and $|r| > 0.70$) was detected between a pair of variables (Green, 1979; Fielding and Haworth, 1995), the variable that contributed most to interpretation of elk foraging site selection or the one correlated with fewer variables was retained and the other variable in the pair was eliminated from the analyses (Hosmer and Lemeshow, 2000). We detected significant correlation between two pairs of habitat variables. Distance to hiding cover and distance to security cover were highly correlated ($P < 0.01$, $r = 0.91$), as were elevation and distance to improved roads ($P < 0.01$, $r = 0.86$). We eliminated distance to hiding cover and elevation. Collinearity among all other pairs of habitat variables was nonsignificant ($P > 0.05$ and $r \le 0.70$).

We included eight habitat variables in our global resource selection model: distance to security cover, distance to improved roads, distance to primitive roads, aspect, slope, heavy cattle grazing intensity, moderate cattle grazing intensity, and light cattle grazing intensity. Heavy, moderate, and light cattle grazing were indicator variables of the categorical variable "cattle grazing intensity." "No cattle grazing" was the reference category. We used binary logistic regression (PROC LOGISTIC, SAS Institute, Inc., Cary, NC) to develop a set of candidate resource selection models (Hosmer and Lemeshow, 2000). We contrasted elk foraging sites with random sites, and we examined the global model and all possible subsets of our prescreened predictor variables (Beck et al., 2013, McNew et al., 2013).

We assessed the strength of evidence for each candidate model with Akaike's Information Criterion (AIC), and we ranked all models by calculating Δ AIC (Δ_i), the difference in AIC between the lowest-AIC model and AIC for each candidate model. Per Burnham and Anderson (2003), we included models with $\Delta_i \leq 2$ in our subset of high-ranked models. We used the natural average method to develop a composite model using exponentiated AIC values and Akaike weights to calculate weighted averages of the parameter estimates that were common among our high-ranked models (Anderson and Burnham, 2002; Burnham and Anderson, 2003; Grueber et al., 2011). For each parameter estimate in our composite model, we calculated odds ratios (Hosmer and Lemeshow, 2000) and 85% CI (Arnold, 2010).

Resource selection models should be validated (Guthery et al., 2005; Johnson et al., 2006), and the reliability of prediction is the most important measure when evaluating resource selection models (Boyce et al., 2002). Accordingly, we assessed the performance of our composite model by tallying the proportion of elk foraging sites that were correctly classified in the three Wyoming study sites during 2000 and 2001, in the three Wyoming study sites during 2002 and 2003, and in the two Montana study sites during 2002 and 2003. We used the unstandardized coefficients in our composite model, and we used the exponential form because our resource selection model contrasted elk foraging sites versus random (i.e., available) sites, rather than elk foraging sites versus nonforaging sites (Manly et al., 2002).

Our validation procedure accommodated concerns that probabilities and model sensitivities computed from presence-absence logistic regression functions (Hosmer and Lemeshow, 2000) are inappropriate for use-availability studies (Boyce et al., 2002; Keating and Cherry, 2004). Rather than using probabilities from the logistic regression functions to assess performance of our resource selection model, we used the raw (i.e., unscaled) values from the exponential form (i.e., without intercept and without denominator) of our composite model. We calculated the optimal cutpoint (Youden, 1950; Hosmer and Lemeshow, 2000) for our composite model similarly to Olivier and Wotherspoon (2005) and Slauson et al. (2007), except that we substituted the raw resource selection values calculated from the exponential form of our composite model in place of probabilities from the nonexponential form of presence-absence logistic regression functions.

We also assessed the performance of our resource selection model by ranking from lowest to highest the raw resource selection values calculated from the exponential form of our composite model. Next, we categorized the raw values into five quantile bins representing habitat classes that were progressively more strongly selected (Johnson et al., 2006). Finally, we linearly regressed (PROC REG, SAS Institute, Inc., Cary, NC) the proportion of elk observations categorized in each quantile bin of the Wyoming 2000–2001 data set against the proportion of elk observations categorized in each quantile bin of the Wyoming 2002–2003 data set and against the proportion of elk observations in each quantile bin of the Montana 2002–2003 data set (McNew et al., 2013).

Results

Aerial surveys provided 764 independent observations of elk groups foraging during March to May 2000–2003. Mean group size per observation was 28 adult elk in Wyoming during 2000–2001, 21 adult elk in Wyoming during 2002–2003, and 37 adult elk in Montana during 2002–2003. Altogether we recorded 20 738 foraging elk during our 4-year study (8 344 elk recorded in Wyoming during 2000–2001; 6 363 elk recorded in Wyoming during 2002–2003; and 6 031 elk recorded in Montana during 2002–2003). Elk foraging sites were closer to security cover ($P < 0.001$), farther from improved roads ($P < 0.001$), and on gentler slopes than available sites ($P = 0.013$; Table 1).

Elk in spring avoided foraging in areas where cattle had not grazed during the previous summer — early fall (parameter estimate of "no cattle grazing" $= -0.7816$, $P < 0.001$, 85% CI [−0.9895, −0.5737], $n = 298$ elk foraging sites). The odds ratio of 0.4580 (85% CI [0.3718, 0.5634]) indicated that elk were 54% less likely to forage during spring in nonforested portions of cattle-grazed pastures where cattle had not grazed during the previous summer — early fall. Forty-six percent of elk foraging sites occurred where cattle had not grazed during the previous summer — early fall, but 66% of the nonforested habitat available within the cattle-grazed pastures was not grazed by cattle during the previous summer — early fall.

We found support for three of our candidate resource selection models (Table 2). These top models included six, seven, or eight predictor variables. The Δ_i for the intercept-only model (AIC = 1143.32) was 79.21.

Our composite model included all eight predictor variables, but the 85% CI for coefficients of two predictor variable s (i.e., heavy cattle grazing intensity and aspect) overlapped zero (Table 3), indicating that these variables were uninformative and did not have any substantive ecological effect (Arnold, 2010). In addition, the odds ratios for four of the six remaining variables (i.e., distance to security cover, distance to primitive roads, slope, and distance to improved roads) were nearly zero, indicating that these variables had very limited predictive power (Hosmer and Lemeshow, 2000; see Table 3). In contrast, the odds ratio for moderate cattle grazing (i.e., 2.0436) indicated that elk were twice as likely to forage in spring where cattle had grazed moderately during the previous summer — early fall than where cattle had not grazed. Thirty-four percent of elk foraging sites in spring were grazed moderately by cattle during the previous summer — early fall, but sites moderately grazed by cattle comprised only 17% of the nonforested habitat available within the cattle-grazed pastures. The odds ratio for light cattle grazing intensity (i.e., 1.3066) indicated that elk were 31% more likely to forage in spring where cattle had grazed lightly during the previous summer — early fall than where cattle had not grazed. Seventeen percent of elk foraging sites in spring were grazed lightly by cattle during the previous summer — early fall, but sites lightly grazed by cattle comprised only 15% of the nonforested habitat available within the cattle-grazed pastures. Distance to improved roads was positively related to elk foraging site use, but distance to security cover, distance to primitive roads, and slope were negatively related to elk foraging site selection.

Our composite model correctly classified 85% of the 298 elk group foraging observations in Wyoming during 2000 and 2001, 80% of the 303 elk group foraging observations in Wyoming during 2002 and 2003, and 89% of the 163 elk group foraging observations in Montana during 2002 and 2003. The optimal cut point for our composite model was 0.36. Linear regression validations also indicated that our composite model was a strong predictor of elk foraging site selection during

Table 1
Mean (SE) habitat attributes of elk-used ($n = 298$) and available ($n = 600$ random points) foraging sites during spring 2000 and 2001 on foothill and mountain rangeland in northwestern Wyoming, United States.

Habitat variable	Elk-used	Available	P
Security cover distance (m)	584 (35)	920 (34)	<0.0001
Improved road distance (m)	4 422 (147)	3 942 (125)	0.0004
Primitive road distance (m)	1 748 (85)	2 008 (95)	0.6506
Slope (%)	25 (1)	29 (1)	0.0130
Cosine of aspect (northness)	−0.0630 (0.04)	−0.0645 (0.03)	0.8359

Table 2
Fit statistics for top models of elk foraging site selection during spring 2000 and 2001 on foothill and mountain rangeland in northwestern Wyoming, United States ($n = 298$ elk foraging sites). Models are ranked by Akaike's Information Criterion (AIC), K is the number of parameters, ΔAIC is the difference of each model's AIC value from that of the highest ranked model, and w_i is the Akaike weight (sum of all Akaike weights = 1.00).

Top models	K	AIC	ΔAIC	w_i
HCG,[1] MCG,[2] LCG,[3] SC,[4] IR,[5] PR,[6] S[7]	8	1 064.11	0	0.41
HCG, MCG, LCG, SC, PR, S	7	1 065.23	1.12	0.23
HCG, MCG, LCG, SC, IR, PR, S, A[8]	9	1 065.70	1.59	0.19

[1] HCG indicates heavy cattle grazing intensity.
[2] MCG, moderate cattle grazing intensity.
[3] LCG, light cattle grazing intensity.
[4] SC, distance to security cover.
[5] IR, distance to improved roads.
[6] PR, distance to primitive roads.
[7] S. slope.
[8] A, aspect.

spring, with the classification of Wyoming observations from 2000 and 2001 correlating well with classification of the Wyoming observations from 2002 and 2003 ($r^2 = 0.74$, $P = 0.062$, $n = 5$) and Montana observations from 2002 and 2003 ($r^2 = 0.82$, $P = 0.034$, $n = 5$).

Discussion

Elk in spring avoided foraging in areas not grazed by cattle during the previous summer — early fall. In addition, elk selected foraging sites where cattle had grazed moderately or lightly during the previous summer — early fall. Elk selection was stronger for sites grazed moderately by cattle than sites grazed lightly by cattle.

Neither moderate nor light cattle grazing intensity was correlated with any other elk habitat attribute that we sampled, and both moderate and light cattle grazing intensity exerted more influence on elk foraging site selection than any other variables, including distance to security cover, distance to primitive roads, distance to improved roads, aspect, or slope. Per Burnham and Anderson (2003), our composite model should be considered an excellent model if it correctly classified ≥ 75% of elk foraging observations. Our composite model exceeded this standard across five study sites and 4 years, correctly classifying 80 — 89% of elk foraging observations.

The nonforested foothill and mountain rangeland in our study area provided excellent foraging habitat for elk in spring due to the infrequent occurrence of persistent snow cover. Elk use of grassland habitats is not constrained by snow depths < 30–41 cm (Sweeney and Steinhoff, 1976; Peck and Peek, 1991), and elk observations during our study never coincided with snow depths > 30 cm. Elk in spring typically exhibit a highly mobile and discriminating foraging strategy that enables them to select among sites with varied forage conditions (McCorquodale, 1993), and the absence of deep snow in our study area offered elk the opportunity to select foraging sites on the basis of the amount, nutritive quality, and accessibility of the available forage.

Elk in spring prefer foraging sites with intermediate amounts of graminoid biomass and few seed-heads because such sites maximize elk foraging efficiency (Fryxell, 1991; Gross et al., 1993; Wilmshurst et al., 1995). Moderate- and light-intensity cattle grazing causes residual forage plants to have intermediate amounts of biomass and few, if any, seed-heads (Anderson and Currier, 1973). Therefore, in our study it is likely that elk foraging site selection during spring responded to the forage conditions mediated by moderate- and light-intensity cattle grazing during the previous summer — early fall. However, our study was observational, making cause-effect conclusions inappropriate. We acknowledge the possibility that elk may have preferred their foraging sites for reasons unrelated to cattle grazing intensity during the previous summer — early fall and for reasons unaccounted for by slope, aspect, distance to security cover, or distance to roads.

Our correlative evidence suggests that elk did not prefer to forage during spring in the same areas preferred by cattle during summer — early fall. During spring, elk preferred to forage where cattle grazing intensity during the previous summer — early fall was light or moderate, not where previous summer — early fall cattle grazing intensity was heavy. Forage use by cattle varied across our study sites due to habitat features including slope, aspect, forage abundance, and distances to water, shade, and fences (Brewer, 2004). We are confident that the varied forage conditions we mapped at the end of the summer — early fall cattle grazing seasons resulted from cattle grazing and not summer — early fall grazing by elk or mule deer because most elk and mule deer had migrated to higher elevations during summer — early fall. However, grazing by elk or mule deer during late fall or winter may have further modified the spring forage conditions created by cattle grazing during the previous summer — early fall.

At least three other smaller-scale studies reported results similar to ours and concluded that elk in spring were attracted to cattle-grazed areas because cattle grazing during the previous summer-fall had reduced the standing dead plant biomass within and around elk forage plants (Grover and Thompson, 1986; Jourdonnais and Bedunah, 1990; Frisina, 1992). All three of these previous studies also concluded that targeted cattle grazing during summer-fall could be applied to purposely improve forage conditions for elk during spring. Frisina (1992) further advocated that cattle grazing during the previous summer-fall could be used purposely to create improved forage conditions and lure elk away from places where elk grazing pressure might be excessive. These previous studies were limited to 1-year duration or were conducted within relatively small experimental pastures. Our study results support these relationships across five large landscapes and 4 years.

Elk in our study avoided improved roads. Johnson et al. (2000) and Coe et al. (2011) similarly reported that during spring elk avoided roads with moderate or heavy vehicular traffic, while other studies did not detect any influence from improved roads during spring (Long et al., 2009; Beck et al., 2013). Foraging site selection was stronger near primitive roads in our study, in contrast with results reported by other studies that found low-traffic roads did not affect elk habitat selection during spring (Johnson et al., 2000; Long et al., 2009; Coe et al., 2011; Beck et al., 2013). During summer, however, Beck et al. (2013)

Table 3
Unstandardized resource selection function coefficients, weighted unconditional standard errors (SE), odds ratios, and 85% confidence intervals (CIs) for the composite model of elk foraging site selection during spring 2000 and 2001 on foothill and mountain rangeland in northwestern Wyoming, United States ($n = 298$ elk foraging sites). Optimal cutpoint was 0.36.

Predictor variable	β	Weighted unconditional SE	85% CI (β)		Odds ratio	85% CI (Odds ratio)	
			Lower	Upper		Lower	Upper
Heavy cattle grazing intensity	0.3704	0.4041	−0.2115	0.9523	1.4472	0.5628	2.5917
Moderate cattle grazing intensity	0.7147	0.1488	0.5004	0.9290	2.0436	1.6495	3.9176
Light cattle grazing intensity	0.2674	0.1732	0.0180	0.5168	1.3066	1.0186	1.6766
Distance to security cover	−0.0007	0.0001	−0.0008	−0.0006	0.9993	0.9992	0.9994
Distance to primitive roads	−0.0002	0.0001	−0.0003	−0.0001	0.9998	0.9997	0.9987
Slope	−0.0162	0.0043	−0.0224	−0.0100	0.9839	0.9778	0.9900
Distance to improved roads	0.0001	0.00004	0.00004	0.0002	1.0001	1.0000	1.0002
Cosine of aspect (northness)	0.0740	0.1156	−0.0925	0.2405	1.0768	0.9116	1.2796

documented that distance to minor roads was positively related to elk use, but these authors believed that the influence of minor roads was merely an artifact of elk using the flatter terrain where minor roads often exist. In our study, distance to primitive roads was not correlated with slope. We speculate that the negative relationship between distance to primitive roads and elk foraging sites in our study area was an artifact of elk accessing drinking water and palatable forage in riparian areas where primitive roads tended to be.

Distance to security cover was negatively related to elk foraging site selection during spring in our study, but not in northeastern Oregon (Coe et al., 2011). Elk in our study avoided steeper slopes during spring, as similarly reported by Johnson et al. (2000); Long et al. (2009), and Coe et al. (2011), although elk use was unrelated to slope in north-central Utah (Beck et al., 2013). Finally, elk use in our study and in Beck et al. (2013) was not strongly related to aspect, but elk in other areas selected southerly (Coe et al., 2011) or westerly aspects (Johnson et al., 2000; Long et al., 2009) during spring.

Implications

Resource managers can use our foraging site selection model to map predicted changes in elk grazing distribution when considering potential habitat adjustments in security cover, roads, or cattle grazing intensities and distribution. Our results also suggest that resource managers can use targeted cattle grazing in summer — early fall to purposely modify elk forage conditions to 1) increase elk foraging efficiency in spring, 2) lure elk away from places needing rest or deferment from spring elk grazing, or 3) lure elk away from places where elk in spring are experiencing conflicts with humans, predators, or other wildlife. Finally, research scientists studying cattle-grazed habitats should strongly consider including previous cattle grazing intensity as a predictor variable in future global models of elk foraging site selection.

Acknowledgments

Authors thank Curt Bales, Bill Galt, Bob Model, and Dick Geving for access to study sites; Joe Hicks and John Julien for logistical support; Craig Lotspiech, Craig Geving, Reese McClain, Kelly Idema, Beth Hoobler, Mike Henn, Lisa Landenburger, Josh Bilbao, and Debbie Hohler for assistance with data collection and analysis. This paper benefited from comments and suggestions provided by Steve Cherry, Fred Lindzey, Lance McNew, Rich Olson, Dan Rodgers, two anonymous reviewers, and the associate editor.

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