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# Seasonal Resource Selection and Distributional Response by Elk to Development of a Natural Gas Field

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## Abstract

Global energy demand is predicted to increase dramatically, suggesting the need to understand the role of disturbance from energy development better and to develop more efficient conservation strategies for affected wildlife populations. We evaluated elk (*Cervus elaphus*) response to disturbance associated with natural gas development in summer and winter, including shifts in resource selection and concomitant distribution. We collected elk locations prior to (1992–1995) and during (2008–2010) coal bed natural gas (CBNG) development in the ~498-km<sup>2</sup> Fortification Creek Area (FCA) of northeastern Wyoming, USA, where approximately 700 CBNG wells and 542 km of collector, local, and resource roads were developed from 2000 through 2010. We developed resource selection functions for summer and winter using coordinate data from VHF-collared female elk prior to CBNG development and similar location data from GPS-collared female elk during CBNG development to assess spatial selection shifts. By pooling across all locations we created population level models for each time period (e.g., pre- and during development) and incorporated individual variation through bootstrapping standard errors for parameter estimates. Comparison of elk resource selection prior to and during natural gas development demonstrated behavioral and distributional shifts whereby during development, elk demonstrated a higher propensity to use distance and escape cover to minimize exposure to roads. Specifically, during-development elk selected areas with greater Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) cover, increased terrain ruggedness, and farther from CBNG roads than prior to development. Elk distributional changes resulting from avoidance behavior led to a loss of high-use areas by 43.1% and 50.2% in summer and winter, respectively. We suggest reducing traffic, protecting woody escape cover, and maintaining refugia within the energy-development footprint to promote persistence of elk within energy fields.

**Key Words:** *Cervus elaphus*; coal bed natural gas; elk habitat; roads; resource selection functions; wildlife and energy development

## INTRODUCTION

Generally, the distribution of wildlife is the result of animals selecting for or against surrounding habitat characteristics (Boyce and McDonald 1999). Animals must often balance trade-offs between acquiring resources and reducing risk from predation or disturbance (Lima and Dill 1990; Schmitz et al. 1997; Frid and Dill 2002). Increasingly, animal resource selection is influenced by human disturbance, including energy-extraction activities, which is a rapidly expanding source of disturbance for a variety of species across the globe (e.g., Cameron et al. 2005; Bayne and Dale 2011; Smith et al. 2014). Large populations of ungulates overlap the distribution of extensive energy resources in forest and rangeland ecosystems across western North America (Sawyer et al. 2006; Hebblewhite 2008; Sorensen et al. 2008; Sawyer et al. 2009a, 2009b;), providing scientists and natural resource managers opportunities to evaluate the influences of energy development

on these populations and to identify factors that may provide options for mitigation.

Much of the Intermountain Region of western North America has low human population densities and thus wildlife experience relatively low disturbance from anthropogenic activities (Sanderson et al. 2002). However, the US Energy Information Administration has predicted a 44% increase in the world consumption of energy between 2006 and 2030 (Energy Information Administration [EIA] 2009). In contrast to land-use practices such as ranching, the development and extraction of energy resources includes substantial infrastructure and anthropogenic activity. For example, the Bureau of Land Management (BLM) has stated that one natural gas well is, on average, accompanied by 2 km of roads, which does not include the disturbance incurred by connecting pipelines, tanker truck transport of hydrocarbon products, or electrical power lines (Bureau of Land Management [BLM] 2003). Copeland et al. (2011) predicted the overall influence of energy development could directly or indirectly affect up to 21% or 96 million ha of the five major ecosystems in western North America, including grassland, boreal forest, shrubland, temperate forest, and wetland. A critical concern for wildlife conservation is the direct habitat loss resulting from energy extraction; however, the indirect impacts of energy development on ungulate species may be of greater concern than the direct loss of habitat (Van Dyke and Klein 1996; Sawyer et al. 2006; Hebblewhite 2008; Festa-Bianchet et al. 2011). Previous

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work demonstrated indirect influences of energy development on ungulates. For example, mule deer (*Odocoileus hemionus*) in western Wyoming avoided natural gas wells on winter range, thus shifting their distribution, resulting in population declines across the area of development (Sawyer et al. 2006; 2009a). Cumulative influences of energy development and forestry activities have been shown to result in changes in habitat use and population growth rate on boreal caribou (*Rangifer tarandus caribou*) in northern Alberta (Sorensen et al. 2008). Elk (*Cervus elaphus*) are known to avoid roads, thus reducing habitat availability (Rowland et al. 2000; Sawyer et al. 2007; Frair et al. 2008). Documented changes in levels of human activity were thought to drive shifts in elk avoidance behavior with respect to roads in south-central Colorado (Dzialak et al. 2011). Others have examined the influences of energy-extraction activities on elk populations (Hiatt and Baker 1981; Ward 1986; Van Dyke and Klein 1996); however, these studies typically lacked sufficient sample sizes or predevelopment data to provide a rigorous analysis of potential impacts of energy development on elk (Hebblewhite 2008).

The Fortification Creek Study Area (FCA), which encompassed Wyoming Game and Fish Department Elk Herd Unit 320 in northeastern Wyoming, provided us an opportunity to isolate the effects of energy development on elk. The FCA elk population experienced limited human-related impacts prior to the initiation of large-scale energy development in the early 2000s because of restricted access to the area and land use dominated by livestock grazing. Previous monitoring of elk in Elk Herd Unit 320 during the 1990s provided knowledge of elk resource selection prior to the initiation of coal-bed natural gas (CBNG) development (Wyoming Game and Fish Department [WGFD] 1996, 2007a). Our specific objectives were (1) to identify summer and winter elk resource selection within the study area prior to CBNG development, and (2) to compare two independent measures of population-level resource selection (e.g., pre- and during development) to assess elk distributional and resource selection shifts associated with energy development. We predicted elk would alter their distribution and resource selection in response to CBNG development.

## METHODS

### Study Area

We conducted our study in the 498-km<sup>2</sup> FCA, approximately 40 km west of Gillette, Wyoming. Elevation in the study area ranged from 1 130 m to 1 463 m. The northern portion of the study area included a 49-km<sup>2</sup> BLM wilderness study area (BLM 2008). The BLM (44%), State of Wyoming (6%), and private landowners administered the FCA, which encompassed portions of Campbell, Johnson, and Sheridan counties. Cattle grazing occurred across the FCA in pre- and during-development stages of CBNG development. Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) shrubland dominated land cover, with scattered patches of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.; hereafter, juniper) that comprised only 11% of the landscape. Grasses common to the northern mixed-grass prairie dominated our study area including bluebunch wheatgrass (*Pseudoroegneria*

*spicata* [Pursh] Á. Löve), cheatgrass (*Bromus tectorum* L.), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and western wheatgrass (*Pascopyrum smithii* [Rydb] Á. Löve). Northeast Wyoming is characterized by a semiarid climate with an average annual precipitation of about 22 cm (Western Regional Climate Center [WRCC] 2009). Annual precipitation during our study averaged 23 cm, of which >90% fell between April and October. During our study, the average temperature was 9.0 C° with an average daily maximum and minimum temperature of 15.4 and 3.4 C, respectively (WRCC 2009).

From 2008 to 2010, the FCA provided yearlong habitat for approximately 230 nonmigratory elk (WGFD 2007a). Elk population numbers have remained relatively stable since the initiation of consistent yearly harvest seasons in 2000, but ranged from 180 to 400 during the 1990s (WGFD 2007b). Over 700 CBNG wells and 542 km of roads were developed in the FCA since the early 2000s, and the BLM has projected potential field development of approximately 2 000 wells with 0.32-km<sup>2</sup> (80 ac) well spacing (BLM 2008).

### Elk Capture and Monitoring

Data used for our temporal control were collected from 1992 to 2000 by the Wyoming Game and Fish Department with the use of very-high-frequency (VHF) radio collars affixed to 17 female elk; however, we limited our analysis to data from 1992–1995 when bimonthly relocations were collected via fixed-wing aircraft flights (WGFD 1996). To obtain information on elk response to CBNG development, we used helicopter net-gunning (Leading Edge Aviation, Lewiston, Idaho) to capture 59 adult female elk in March and December 2008. Captured elk were fitted with global positioning system (GPS) collars (North Star Science and Technology, LLC, King George, Virginia) programmed to collect one location every 5 h over 3 yr (2008–2011). Across individuals we observed GPS fix rates ranging from 58% to 98%. Habitat characteristics that block satellite transmission or random collar failure can cause fix rates of less than 100%, which can result in erroneous conclusions (Moen et al. 1996; D'Eon et al. 2002; Nielson et al. 2009). We tested for differences in resource selection between animals with high ( $\geq 90\%$ ) and low ( $< 90\%$ ) GPS fix rates with the use of independent sample *t*-tests. Because we found no differences ( $P > 0.05$ ) in resource selection coefficients between high and low fix-rate groups we included all animals in resource selection modeling. We defined summer (1 April–31 October) and winter (1 November–31 March) seasons based on development timing stipulations and forage green-up (green-up based on field observations and Normalized Difference Vegetation Index [NDVI] measurements).

### Anthropogenic Predictor Variables

We digitized roads in a geographic information system (GIS) with the use of the National Agriculture Imagery Program (US Department of Agriculture–Farm Service Agency, Aerial Photography Field Office, Salt Lake City, Utah) and Landsat (US Geological Survey [USGS]–EROS Center, Sioux Falls, South Dakota) imagery at 1-m and 30-m resolutions, respectively. We then developed decay distance variables as a function of Euclidean distance to roads with the use of the form  $e^{-d/a}$ , where  $d$  was the distance from each pixel to roads in meters

and  $a$  were constant values of 100, 500, 1 000, 1 500, 2 000, 3 000, 4 000, and 5 000. The decay function scaled the distance variables between 1 and 0, with values increasing in proximity to roads. We had initially included well pads as a predictor variable, but a correlation ( $r$ )  $> 0.60$  with roads obligated removal of one of the variables. In the interest of interpretation simplicity, we kept roads and removed distance to well pads from further analysis.

### Environmental Predictor Variables

We developed a suite of environmental variables to assess elk resource selection. Previous work has suggested that elevation (Sawyer et al. 2007; Gregory et al. 2009; Beck et al. 2013), terrain ruggedness (Skovlin et al. 2002; Frair et al. 2005), cover type (Beck et al. 2006; Barbknecht et al. 2011; Beck et al. 2013), and distance to water (Beck et al. 2006) are important predictors of elk resource selection. Thus we included elevation, vector ruggedness measure (VRM; Sappington et al. 2007), percent juniper cover, and north- and south-oriented sagebrush cover in our analyses. In addition to being previously used by others, we determined these variables were important for the FCA elk herd. Because of the physical nature of the landscape, these variables provided the main sources of escape and thermoregulatory cover. We also included a viewshed metric, which measured the number of road segments from which any particular location on the FCA landscape could be observed. Landscape visibility has been demonstrated as an important variable for wildlife in response to disturbance (Ndaimani et al. 2013). The viewshed metric was driven by topography and line of sight, where locations on the landscape that could be observed from many road segments were assigned a high value and locations on the landscape that could be seen from few road segments were assigned a low value. We derived elevation from a 10-m resolution digital elevation map (National Elevation Dataset, USGS, Sioux Falls, SD). We identified and classified juniper and sagebrush cover with the use of 30-m land-cover data developed at the University of Wyoming (Landcover\_REGAP\_2007, Wyoming Geographic Information Science Center, University of Wyoming, Laramie, WY). We separated environmental variables into cover type and terrain groups, to simplify variable and model selection.

### Statistical Analyses

Our study used pre- and during-development data as two independent measures of elk resource selection and variation to assess change in selection through time. We modeled resource selection at the population level by pooling location data across all individuals. Similar to Nielson and Sawyer (2013) and Sawyer et al. (2006, 2007, 2009a), we used relative frequency of use as the response variable in a resource selection function (RSF; Manly et al. 2002) framework to model the probability of use for each elk as a function of anthropogenic and environmental predictor variables (Marzluff et al. 2004). RSF models using elk location data were developed for pre- and during development for summer (1 April–31 October) and winter (1 November–31 March) periods. We mapped probability of elk use across the FCA with the use of the best-fit population-level models and compared elk resource selection between pre- and during-development periods. Changes in the

distribution of elk selection probabilities across years provided a means to evaluate the influence of CBNG development on elk resource selection in summer and winter.

We used 3 000 randomly placed circular sampling units of 250-m radii to extract habitat variables and estimate intensity of use by elk (Sawyer et al. 2009a; Nielson and Sawyer 2013). Sampling unit size should reflect the scale of changes in animal concentrations and movement, but still include adequate locations to approximate a known error distribution (e.g., Poisson or negative binomial distributions; Millsaugh et al. 2006). Because a large number of sampling units contained no elk locations, we used a negative binomial distribution, which is more adapted for overdispersion than the Poisson distribution (White and Bennetts 1996; Millsaugh et al. 2006). Sampling units of a 250-m radius fit the scale of elk movement patterns (e.g., distance between consecutive GPS locations for an individual animal) in the FCA and sampling units of that size have been successfully used in another elk study with similar GPS fix rate schedules (Sawyer et al. 2007). We extracted both anthropogenic and environmental variable data, averaged across each sampling unit, and counted the number of elk locations within each sampling unit. With this method, sampling units may overlap; therefore they are not mutually exclusive and the unit-sum constraint does not apply (Aebischer et al. 1993). The size of the sampling unit also allows for a range of expected telemetry location error without affecting model results (Nielson and Sawyer 2013). The response variable within our analyses was a count of locations in each sampling unit allowing the treatment of elk locations as a random variable. Using location frequency within each sampling unit as the response variable removed any associated time stamp other than the period of interest (e.g., summer), while providing a measure of relative intensity of elk use with respect to predictor variables of interest. Thus, issues of sample size are less of a hindrance to analysis because we did not model resource selection based on a single point at a time (e.g., logistic regression), but rather two independent measures (e.g., pre- and during development) of relative intensity of resource use.

Prior to model development, we used multiple methods of variable screening. First, we evaluated collinearity between variables with the use of Pearson's pairwise correlation and excluded highly correlated variables ( $r > 0.60$ ) based on variable performance using Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002). We conducted this variable screening process for anthropogenic and environmental predictor variables. There were no highly correlated environmental predictor variables in our data set; however, we used  $AIC_c$  to select the top-performing or competitive environmental variables for cover type and terrain variable groups to reduce the number of variables in our candidate set. Many of the decay distance variables were highly correlated; thus we retained only one decay distance variable by selecting the top-performing variable using  $AIC_c$ . Second, we did not allow competing variables to remain in a model if the sign of either variable switched upon inclusion of the other variable. Lastly, we screened remaining variables to ensure they were informative by assessing whether 85% confidence intervals (CIs) around parameter estimates for

each variable included zeroes (Arnold 2010). Selected variables were carried forward to develop our list of candidate models.

We created population-level RSF models for summer and winter prior to and during CBNG development. The RSF models were developed following the form

$$\ln[E(t_i)] = \ln(T) + \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \dots + \beta_p x_{pi}, \quad [1]$$

where  $t_i$  is the total number of elk locations within sampling unit  $i$ ,  $\ln(T)$  is the offset term,  $\beta_0$  is the intercept term,  $\beta_1, \beta_2, \dots, \beta_p$  are the estimated coefficient terms,  $x_{1i}, \dots, x_{pi}$  are the measured values of  $p$  covariates on sampling unit  $i$ , and  $E[\cdot]$  represents the expected value (Sawyer et al. 2006, 2009a). The offset term rescales the response as a relative frequency of use rather than a count of locations. We bootstrapped (iterations=1 000) across individuals with the use of the final model to estimate standard errors for model coefficients for the during-development data set, which provided a means to account for individual variation (Nielson and Sawyer 2013). This approach addressed two major problems of resource selection functions: pooling across individuals and ignoring correlation among animal locations, by designating the individual animal as the experimental unit (Thomas and Taylor 2006). We bootstrapped (iterations=1 000) locations irrespective of individuals, to estimate standard errors for the predevelopment model coefficients. This was necessary because of the relatively small number of locations included in the predevelopment data set. Top-performing models were selected with the use of AIC<sub>c</sub> ( $\Delta AIC_c < 4$ ; Arnold 2010) from a multimodel candidate set for the predevelopment data set. We used model averaging to calculate mean coefficients, standard errors, and 95% confidence intervals when a single top model was not identified among candidate models (Burnham and Anderson 2002).

After identifying the top model for summer and winter predevelopment data sets, we applied these models to the during-development data sets for summer and winter, respectively. Application of the same models to both pre- and during-development data sets was necessary to make accurate comparisons of change in coefficient sign and magnitude, as inclusion of alternative or additional variables would have in itself influenced variable coefficients. Differences were identified by assessing overlap of 95% confidence intervals for each variable coefficient. We documented magnitude of change using a ratio of during-development ( $d$ ) coefficient estimates to predevelopment ( $b$ ) coefficient estimates with the use of

$$\text{ratio} = \frac{x_{i,d}}{x_{i,b}}, \quad [2]$$

and ratio standard errors were calculated using,

$$\text{SE}(\text{ratio}) = \frac{x_{i,d}}{x_{i,b}} \sqrt{\left(\frac{\text{SE}(x_{i,d})}{x_{i,d}}\right)^2 + \left(\frac{\text{SE}(x_{i,b})}{x_{i,b}}\right)^2 - \frac{2 \text{cov}(x_{i,d}, x_{i,b})}{x_{i,d} \times x_{i,b}}}, \quad [3]$$

where  $x_{i,d}$  was variable coefficient  $i$  during development and  $x_{i,b}$  was variable coefficient  $i$  predevelopment. Ratios less than 1 suggested a decrease in selection magnitude, and ratios greater than 1 suggested an increase in selection magnitude. We then mapped each model back on the FCA landscape as a relative probability of elk use. All map values were verified to

be between 0 and 1 so as not to fall outside of our range of inference. We then binned map pixel values into five quantiles: high use, 100–81%; medium-high use, 80–61%; medium use, 60–41%; medium-low use, 40–21%; and low use, 20–0%, to assist in interpretation of model probabilities.

We validated our predevelopment models by separating our probability of use maps during each season in 10 equal distribution bins. Predevelopment and validation locations were overlaid on probability distribution bin maps to assign each location with a distribution bin value. We used an independent data set of 290 elk locations recorded from 1993 to 2000 as a validation location data set. The validation data sets were opportunistic locations of uncollared elk taken during relocation flights with the use of a handheld GPS unit. We took an average distribution of five iterations of 100 randomly sampled locations across the 10 distribution bins to validate both summer and winter models. We used Spearman's rank correlations ( $r_s$ ) to compare location frequency distributions of predevelopment data with average frequency distributions of the validation data set. All statistical analyses were conducted in R language and environment (R Development Core Team 2011; Package MASS).

## RESULTS

We used 256 locations from 17 elk in our summer 1992–1995 predevelopment resource selection model and 69 307 GPS locations from 55 GPS-collared female elk to assess summer resource selection during CBNG development. Only 55 of 59 captured female elk were used in our during-development analysis because of collar failure. We used 149 locations from 17 female elk to model resource selection in winters 1992–1995 prior to CBNG development and 44 033 GPS locations from 55 GPS-collared female elk to assess winter resource selection during CBNG development.

### Elk Resource Selection

**Predevelopment.** The top model explaining elk resource selection in summer prior to CBNG development included three variables, and no other models were competitive with this top model (Table 1). In summer, prior to CBNG development, elk selected for areas with higher percent juniper cover, lower percent north-facing sagebrush cover, and away from roads (Table 2; Fig. 1a). High-use areas in summer predevelopment averaged 32% juniper cover, 21% north-facing sagebrush cover, and 1 136 m from roads. In winter prior to CBNG development, the top six models were competitive in explaining elk resource selection (Table 1). Prior to CBNG development in winter, elk selected for areas with increased juniper cover, increased terrain ruggedness, increased slope, decreased viewshed exposure, and away from roads (Table 2; Fig. 1b). Model-averaged 95% confidence limits bounding the parameter estimate of the variable coefficient for decay distance to roads overlapped 1; therefore, we considered decay distance to roads as uninformative for elk resource selection in winter predevelopment. However, we retained decay distance to roads for the application of our top predevelopment model to the

**Table 1.** Goodness-of-fit statistics for the top, second, null, and competitive models (if applicable), predicting elk resource selection at the population level within the Fortification Creek Area (FCA) of northeastern Wyoming, summer and winter, predevelopment (1992–1995). Number of parameters in each model ( $K$ ), Akaike's information criterion corrected for small sample sizes ( $AIC_c$ ), difference in  $AIC_c$  from the top model ( $\Delta AIC_c$ ), Akaike's weights ( $w_i$ ), and model rank are reported.

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$	Rank
Summer predevelopment (16 candidate models)					
Percent juniper + percent north-facing sagebrush + decay distance to roads (500 m)	4	2 023.16	0.00	0.96	1
Percent sagebrush north + viewshed + dkrd3_500	4	2 029.37	6.22	0.04	2
Null	1	2 105.18	82.02	< 0.001	16
Winter predevelopment (32 candidate models)					
Percent juniper + slope + viewshed	4	1 426.26	0.00	0.28	1
Percent juniper + slope + viewshed + VRM	5	1 426.80	0.54	0.21	2
Percent juniper + viewshed + VRM	4	1 426.93	0.70	0.20	3
Percent juniper + slope + viewshed + decay distance to roads (500 m)	5	1 427.58	1.32	0.14	4
Percent juniper + slope + viewshed + VRM + decay distance to roads (500 m; global)	6	1 428.53	2.27	0.09	5
Percent juniper + viewshed + VRM + decay distance to roads	5	1 428.68	2.42	0.08	6
Percent juniper + viewshed	3	1 432.15	5.89	0.01	7
Null	1	1 462.24	35.98	< 0.001	32

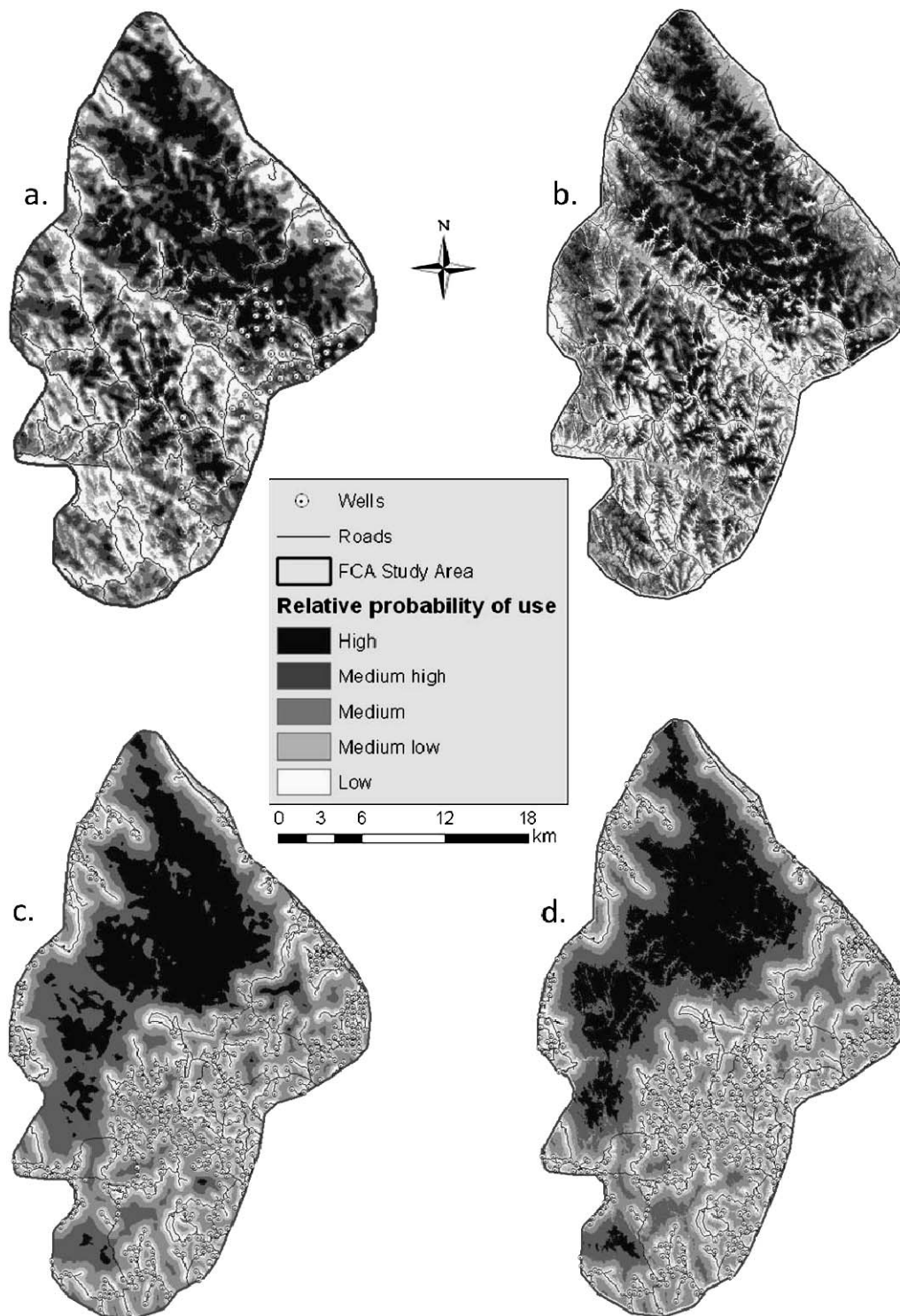
during-development data set to assess change in elk distribution as influenced by roads. Predevelopment, high-use areas in winter averaged 34% juniper cover, 0.05 VRM, 38% slope, 7.9 viewshed measurement, and 995 m from roads.

The Spearman's rank correlation coefficient ( $r_s$ ) for the summer season predevelopment model compared to validation data was 0.90 and was 0.86 for the top winter season predevelopment model compared to validation data. These

**Table 2.** Estimated variable coefficients ( $\beta$ ), bootstrapped SEs (iterations=1 000), and 95% confidence intervals for population-level resource selection models for elk in the Fortification Creek Area, northeastern Wyoming, summer and winter, pre- (1992–1995) and during (2008–2011) development. Coefficients for winter before development were model averaged because six competing models existed.

Variable	$\beta$	SE	95% LL	95% UL
Summer predevelopment				
Intercept	-7.05	< 0.01	-7.07	-7.03
Percent juniper	1.44	0.02	1.40	1.47
Percent north-facing sagebrush	-1.80	0.02	-1.84	-1.77
Decay distance to roads (500 m)	-1.05	0.01	-1.07	-1.03
Summer during development with the use of predevelopment top model				
Intercept	-7.36	< 0.01	-7.38	-7.34
Percent juniper	1.88	0.03	1.83	1.93
Percent north-facing sagebrush	-1.40	0.02	-1.44	-1.37
Decay distance to roads (500 m)	-5.90	0.10	-6.09	-5.72
Winter predevelopment				
Intercept	-8.23	0.06	-8.36	-8.11
Percent juniper	1.60	0.04	1.51	1.69
VRM <sup>1</sup>	4.11	1.79	0.60	7.61
Slope	< 0.01	< 0.01	< 0.01	0.01
Viewshed	< -0.01	< 0.001	-0.01	< -0.01
Decay distance to roads (500 m)	-0.07	0.05	-0.16	0.02
Winter during development with the use of predevelopment top model				
Intercept	-7.81	0.01	-7.84	-7.80
Percent juniper	0.35	0.03	0.29	0.42
VRM	7.44	0.15	7.15	7.72
Slope	< 0.01	< 0.001	< 0.01	< 0.01
Viewshed	< -0.01	< 0.001	< -0.01	< -0.01
Decay distance to roads (500 m)	-8.30	0.11	-8.52	-8.079

<sup>1</sup>VRM indicates vector ruggedness measure.



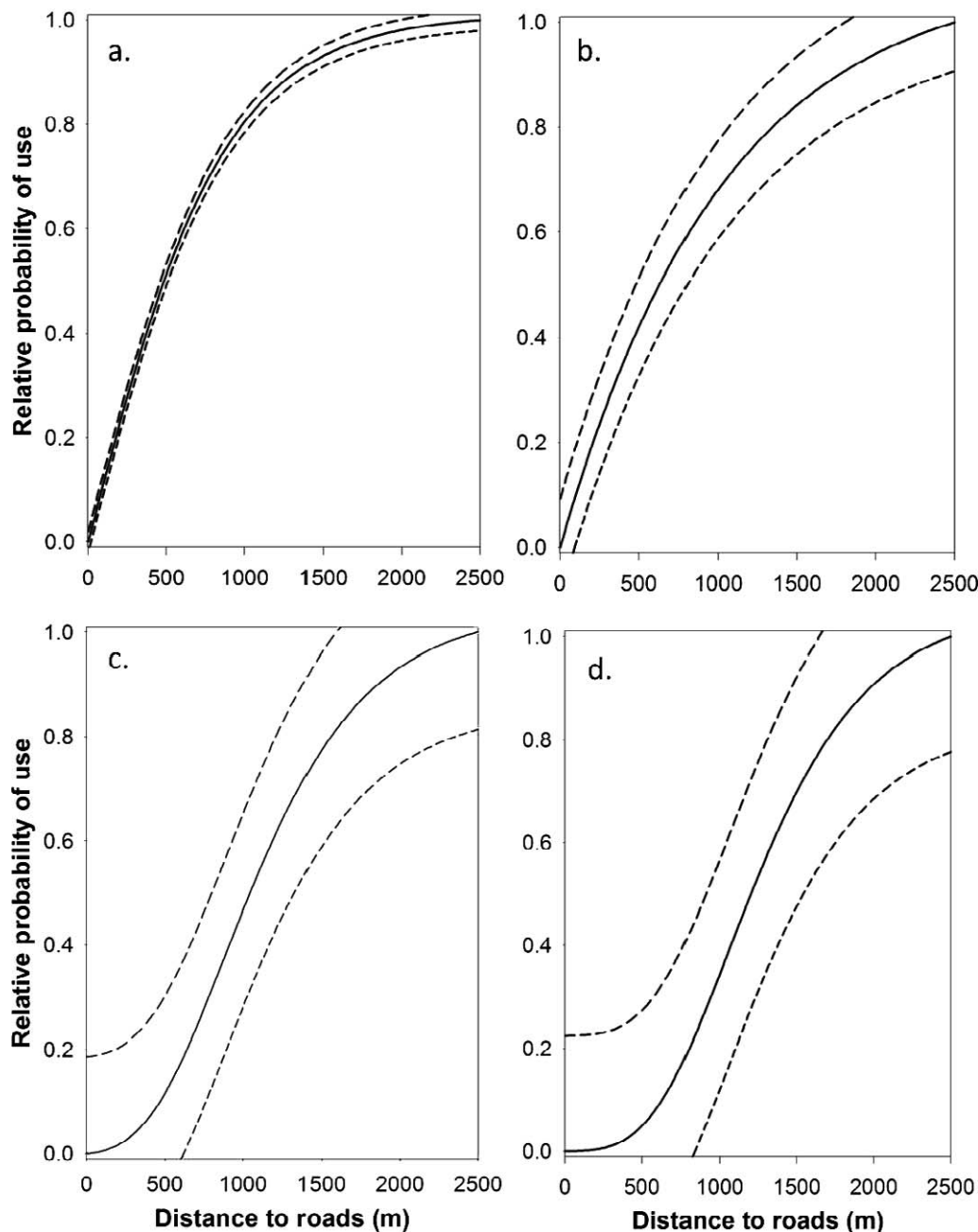
**Figure 1.** Population-level probability of use based on five quartiles of elk use in **a**, summer, and **b**, winter pre- (1992–1995) coal bed natural gas development, and in **c**, summer, and **d**, winter, during development (2008–2010) within the Fortification Creek Area of northeastern Wyoming.

correlation coefficients indicated our top models in summer and winter predevelopment were strong, positive predictors of elk resource selection.

#### Comparison of Pre- and During-Development Resource Selection.

By applying the top-performing predevelopment model to the during-development data set we compared pre- and during-development RSF results in summer and winter (Fig. 1). In

summer, pre- and during-development coefficients differed across all variables (Table 2). The coefficient for decay distance to roads (calculated with a constant value of 500 m) demonstrated the greatest change, resulting in an increased avoidance behavior of elk from roads of more than five times (Fig. 2a and 2c). When we applied the top-performing predevelopment model to the during-development GIS and



**Figure 2.** Probability (solid line) and 95% confidence limits (dashed lines) of elk use in summer as a function of distance to roads during different time periods; **a**, summer predevelopment, **b**, winter predevelopment, **c**, summer during development, and **d**, winter during development in the Fortification Creek Area of northeastern Wyoming. Predevelopment data were collected from 1992 to 1995 and during-development data collected 2008–2010. Probability curves were developed from the top predictive model for elk resource selection predevelopment. Variables of interest were allowed to vary, whereas others within the model were held at their mean values.

location data, high-use areas averaged 26% juniper cover, 27% north-facing sagebrush cover, and 2 459 m from roads in summer. Comparisons of predicted high-use areas indicated a change of –6% juniper cover, +6% north-facing sagebrush cover, and +1 323 m from roads in summer. In winter, pre- and during-development coefficients differed across percent juniper, viewshed, and decay distance to roads (Table 2). Again, the coefficient for decay distance to roads (calculated with a constant value of 500 m) demonstrated the greatest change, resulting in an increased avoidance of 118-fold

(Table 2, Fig. 2b and 2d). Ratios for VRM and distance to roads were not expressed graphically as 95% confidence limits overlapped 1 (Table 3). When we applied the top-performing predevelopment model to the during-development GIS and location data, high-use areas averaged 21% juniper cover, 0.04 VRM, 33% slope, 2.3 viewshed measurement, and 2 594 m from roads in winter. Comparisons of predicted high-use areas indicated a change of –13% juniper cover, –0.1 VRM, –5% slope, –7.6 viewshed measurement, and +1 599 m from roads in winter



**Table 3.** Response ratios and 95% confidence limits comparing the magnitude of coefficients during development to predevelopment for each predictive variable during the summer and winter seasons within the Fortification Creek Area of northeastern Wyoming. A value greater than 1 suggests increased elk use, a value less than 1 suggests decreased use, and a value of 1 represents no change in coefficient magnitude during development in comparison to before development.<sup>1</sup>

Variable	Response ratio	95% LL	95% UL
Summer			
Juniper (%)	1.31	1.26	1.35
North-facing sagebrush (%)	0.78	0.76	0.81
Distance to road	5.73	5.52	5.95
Winter			
Juniper (%)	0.22	0.18	0.26
VRM	1.81	0.27	3.35
Slope	0.59	0.24	0.93
Viewshed	0.80	0.17	1.43
Distance to road	118.71	-39.43	276.82

<sup>1</sup>LL indicates lower confidence limit; UL, upper confidence limit; and VRM, vector ruggedness measure.

High-use areas made up 20% of the landscape; however, these areas encompassed approximately 60.5% and 59.2% of during-development elk locations in summer and winter, respectively. Spatial comparisons between relative probabilities of elk use pre- and during development across the FCA identified losses of areas categorized as high use prior to CBNG development. In summer, the loss of previously identified high use areas was 43.1% (Fig. 3a). During winter, the loss of high-use habitat was 50.2% (Fig. 3b).

## DISCUSSION

Our results indicate that elk responded to CBNG development by avoiding roads during both summer and winter. The avoidance response was especially evident in winter, where the model coefficient for distance to roads was two orders of magnitude greater during than prior to development. Predictive environmental variables differed somewhat between winter and summer selection and with the exception of VRM and slope in winter, variables demonstrated some change from the pre- to during-development data sets. In summer during development, elk selected for areas with greater juniper cover while avoiding north-facing sagebrush in comparison to predevelopment selection. In winter during development, elk selected for areas of decreased juniper cover and visibility than they did prior to development.

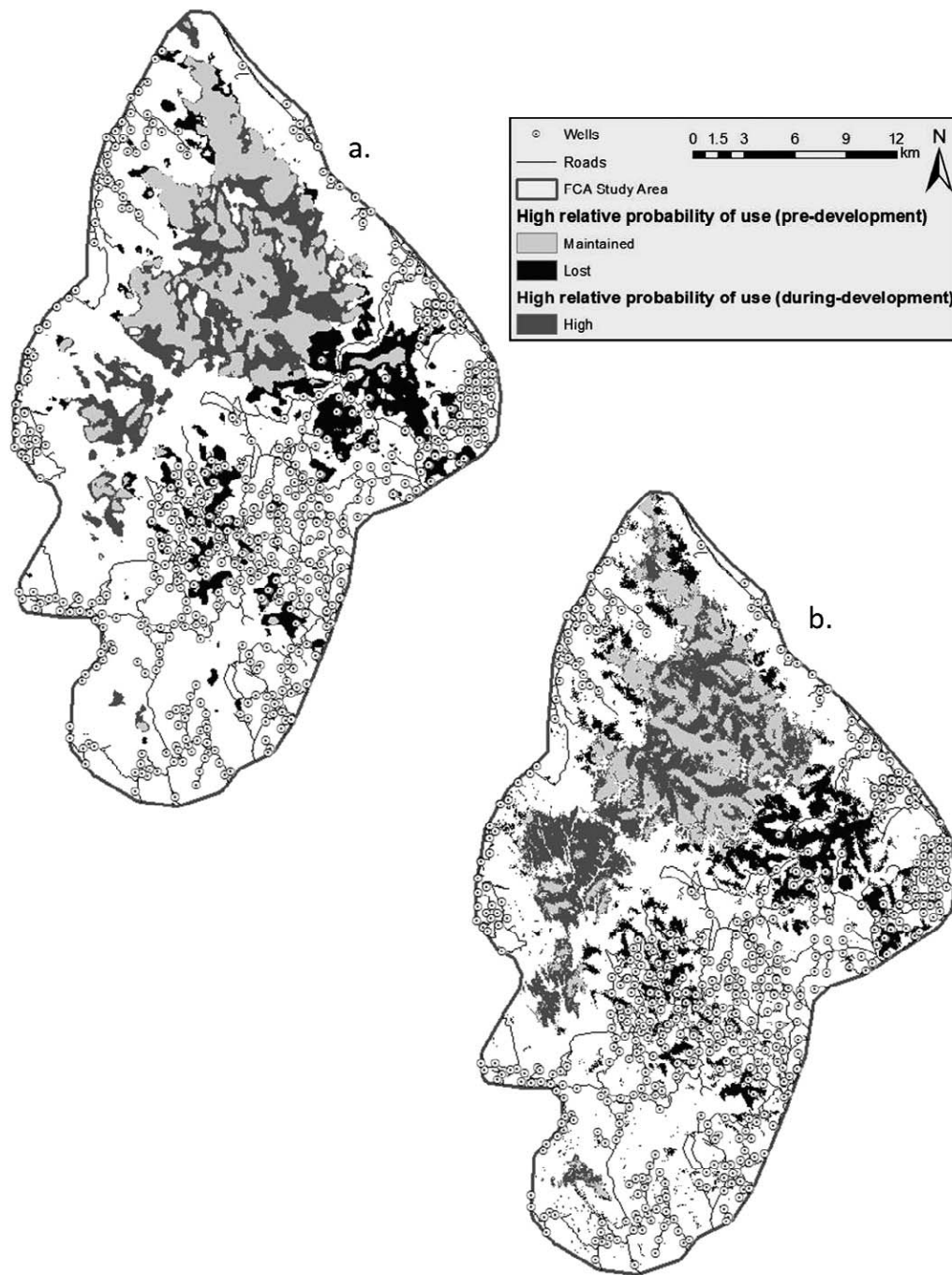
As observed in other ungulate populations (Cameron et al. 2005; Sawyer et al. 2009a), elk avoidance behavior resulted in a distribution that mirrored the distribution of development through time. In the FCA, elk distribution shifts resulted in approximately 43% and 50% loss of habitat classified as high use predevelopment in summer and winter seasons, respectively. Our results suggest the observed shifts were likely driven by elk avoidance of human activity associated with CBNG development. Others have made similar observations of a direct relationship between the level of human activity and the

level of observed response in wildlife species (Nellemann et al. 2001; Vistnes et al. 2001; Gavin and Komers 2006). Human activities with varying levels of intensity (e.g., recreation or energy development) are important to consider because of their spatial and temporal unpredictability (Haskell and Ballard 2008; Neumann et al. 2010). Reducing the footprint of CBNG development and extraction should be a priority to mitigate impacts from energy development (Sorensen et al. 2008); however, it may be equally beneficial for stakeholders to focus efforts toward reducing traffic levels (Fahrig and Rytwinski 2009; Sawyer et al. 2009a; but see Vistnes and Nellemann 2001).

Although ranch access and utility roads have existed in the FCA for decades, there was little change in elk distribution associated with these roads prior to CBNG development (WGFD 1996, 2007a). Consistent elk distribution across the FCA suggests conditions dictating elk resource selection were also relatively consistent prior to CBNG development. However, during development we observed increases in the magnitude of elk avoidance behavior in relation to roads. Model comparisons between pre- and during-development data sets revealed differences between selection coefficients, suggesting changes in behavior through time. Seasonal avoidance distances from roads increased 1.3–1.5 km during development based on the average distance to roads in high-use areas. In the time between our pre- and during-development data sets there was little change in land-use practices or land cover aside from the impacts caused by CBNG development. As there were no other landscape-level changes in the FCA during this time period, we are confident that we isolated the impacts of development and therefore the driving factors behind elk distributional shifts. In addition, high correlation coefficients from our validation exercise with an independent sample of elk locations suggest strong support for the ability of our models to predict elk distribution predevelopment in summer and winter. Our models thus provided a useful tool to measure elk resource use across the FCA in response to CBNG activity.

In an ideal setting, our predevelopment data set would have equaled our during-development data set; however, that was not the case. The predevelopment data set was, however, consistent with VHF sample sizes from data collected that were subsequently used to model home range and resource selection (Kochanny et al. 2009; Beck et al. 2013). There are two reasons we feel confident in making comparisons between our VHF and GPS data sets. First, by comparing the outputs of the same RSF model applied to both data sets we are assessing differences between two independent measures of the same phenomenon, thus creating sound basis for comparison. Second, our modeling is based on intensity of use; thus the response variable in both the pre- and during-development models becomes a relative frequency of use rather than sets of spatial points (e.g., use vs. nonuse), thus decreasing the issue of sample size. It was also anticipated that the location error for the two data sets was different. However, we were able to ignore the difference in error because our sampling unit size was likely larger than the expected error for both VHF and GPS collars.

Elk population numbers in the FCA remained relatively constant ( $\bar{X}$ =256, SE=16.5, range: 220–400) from 1990 to 2010 with average calf:cow ratios of 40:100 in 1992–1995 and



**Figure 3.** Population-level model and categories of elk use in **a**, summer, and **b**, winter, during coal bed natural gas development (2008–2010) overlain with areas identified as high relative probability of use predevelopment (1992–1995) within the Fortification Creek Area of northeastern Wyoming. Predevelopment high use areas that were maintained during development are in orange, whereas areas lost during development are in red. Loss of habitat previously identified as high use equaled 43.1% and 50.2% in **a**, summer, and **b**, winter, respectively.

47:100 in 2008–2010 (WGFD 2007a, 2007b, 2010), which suggests no detectable population response to disturbance associated with CBNG field development during our study. However, the intensity of behavioral response by elk may change as refugia become less available and density dependence begins to play a larger role in population dynamics (Vistnes et al. 2001; Nellemann et al. 2003). Longer time scales are likely needed to parse the influence of energy development on demography for the FCA elk population.

## IMPLICATIONS

Our results indicate that human access facilitated by road development indirectly resulted in a 43–50% loss of high-use elk habitat during CBNG development of the FCA in northeastern Wyoming. Eliminating the impacts of CBNG development on elk is unlikely; however, decreasing impacts on elk should be considered. For example, reducing daily traffic levels on high-use collector and local roads from levels ranging from 70–319 vehicles per day to less than 10 could reduce

indirect habitat loss for elk in the FCA (C. B. Buchanan, unpublished data). Decreasing impacts may also be possible by reducing human presence through new technologies such as directional drilling, telemetered well monitoring, and piping, rather than trucking liquid by-products off site (Sawyer et al. 2009a); however, some human presence is necessary to monitor equipment and perform maintenance to energy field infrastructure. Our results suggest management plans that consider multiple mitigation factors including reducing traffic, maintaining visual obstruction (e.g., patches of woody vegetation and ridgelines), and retaining undeveloped refugia should be implemented to conserve elk populations within developing energy fields. An added benefit of reducing traffic volumes would likely be a reduction of the influx of exotic species into areas disturbed by energy development (Trombulak and Frissell 2000). Within the FCA, there remains a wilderness study area that is off limits to development, thus possibly providing refuge for elk during development. Although the wilderness study comprised only 10% of the FCA, it included 26% to 40% of the elk locations during CBNG development years. These same implications should also be considered in light of conserving other wildlife species impacted by energy development.

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## LITERATURE CITED

- AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175–1178.
- BARBKNECHT, A. E., W. S. FAIRBANKS, J. D. ROGERSON, E. J. MAICHAK, B. M. SCURLOCK, AND L. L. MEADOWS. 2011. Elk parturition site selection at local and landscape scales. *Journal of Wildlife Management* 75:646–654.
- BAYNE, E. M., AND B. C. DALE. 2011. Effects of energy development on songbirds. In: D. E. Naugle [ed.]. *Energy development and wildlife conservation in western North America*. Washington, DC, USA: Island Press. p. 95–114.
- BECK, J. L., J. M. PEEK, AND E. K. STRAND. 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. *Journal of Wildlife Management* 70:283–294.
- BECK, J. L., K. T. SMITH, J. T. FLINDERS, AND C. L. CLYDE. 2013. Seasonal habitat selection by elk in north central Utah. *Western North American Naturalist* 73:442–456.
- BOYCE, M. S., AND L. L. McDONALD. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14:268–272.
- [BLM] BUREAU OF LAND MANAGEMENT. 2003. Final environmental impact statement and proposed plan amendment for the Powder River Basin oil and gas project. Buffalo, WY, USA: BLM.
- [BLM] BUREAU OF LAND MANAGEMENT. 2008. Fortification Creek planning area resource management plan amendment/environmental assessment. Buffalo, WY, USA: BLM. 247 p.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York, NY, USA: Springer-Verlag. 488 p.
- CAMERON, R. D., W. T. SMITH, R. G. WHITE, AND B. GRIFFITH. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. *Arctic* 58:1–9.
- COPELAND, H. E., A. POCEWICZ, AND J. M. KIESECKER. 2011. Geography of energy development in western North America: potential impacts on terrestrial ecosystems. In: D. E. Naugle [ed.]. *Energy development and wildlife conservation in western North America*. Washington, DC, USA: Island Press. p. 7–22.
- D'EON, R. G., R. SERROUYA, G. SMITH, AND C. O. KOCHANNY. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430–439.
- DZIALAK, M. R., S. M. HARJU, R. G. OSBORN, J. J. WONDZELL, L. D. HAYDEN-WING, J. B. WINSTEAD, AND S. L. WEBB. 2011. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. *PLoS One* 6:e14597.
- [EIA] ENERGY INFORMATION ADMINISTRATION. 2009. Annual energy outlook 2009. Available at: [http://www.eia.doe.gov/oil\\_gas/natural\\_gas/info\\_glance/natural\\_gas.html](http://www.eia.doe.gov/oil_gas/natural_gas/info_glance/natural_gas.html). Accessed 22 January 2010.
- FAHRIG, L., AND T. RYTWINSKI. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14:21.
- FESTA-BIANCHET, M., J. C. RAY, S. BOUTIN, S. COTE, AND A. GUNN. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.
- FRAIR, J. L., E. H. MERRILL, H. L. BEYER, AND J. M. MORALES. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology* 45:1504–1513.
- FRAIR, J. L., E. H. MERRILL, D. R. VISSCHER, D. FORTIN, H. L. BEYER, AND J. M. MORALES. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20:273–287.
- FRID, A., AND L. DILL. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11–26.
- GAVIN, S. D., AND P. E. KOMERS. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology* 84:1775–1780.
- GREGORY, A. J., M. A. LUNG, T. M. GEHRING, AND B. J. SWANSON. 2009. The importance of sex and spatial scale when evaluating sexual segregation by elk in Yellowstone. *Journal of Mammalogy* 90:971–979.
- HASKELL, S. P., AND W. B. BALLARD. 2008. Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. *Canadian Journal of Zoology* 86:627–637.
- HEBBLEWHITE, M. 2008. A literature review of the effects of energy development on ungulates: implications for central and eastern Montana. Report. Miles City, MT, USA: Montana Fish, Wildlife, and Parks. 121 p.
- HIATT, G., AND D. BAKER. 1981. Effects of oil/gas drilling on elk and mule deer winter distributions on Crooks Mountain, Wyoming. Cheyenne, WY, USA Wyoming Game and Fish Department.
- KOCHANNY, C. O., G. D. DELGIUDICE, AND J. FIEBERG. 2009. Comparing global positioning system and very high frequency telemetry home ranges of white-tailed deer. *Journal of Wildlife Management* 73:779–787.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- MANLY, B. F. J., L. L. McDONALD, D. L. THOMAS, AND T. L. McDONALD. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Boston, MA, USA: Kluwer Academic. 221 p.
- MARZLUFF, J. M., J. J. MILLSPAUGH, P. HURVITZ, AND M. S. HANDCOCK. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- MILLSPAUGH, J. J., R. M. NIELSON, L. McDONALD, J. M. MARZLUFF, R. A. GITZEN, C. D. RITTENHOUSE, M. W. HUBBARD, AND S. L. SHERIFF. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70:384–395.
- MOEN, R., J. PASTOR, Y. COHEN, AND C. C. SCHWARTZ. 1996. Effects of moose movement and habitat use on GPS collar performance. *Journal of Wildlife Management* 60:659–668.

- NDAIMANI, H., A. MURWIRA, AND S. KATIVU. 2013. Comparing terrain and vegetation-based visibility for explaining sable flight behavior in a Southern African savanna. *Geocarto International* 28:130–143.
- NELLEMANN, C. I., I. VISTNES, P. JORDHOY, AND O. STRAND. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. *Biological Conservation* 101:351–360.
- NELLEMANN, C. I., I. VISTNES, P. JORDHOY, O. STRAND, AND A. NEWTON. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological Conservation* 113:307–317.
- NEUMANN, W., G. ERICSSON, AND H. DETTKI. 2010. Does off-trail backcountry skiing disturb moose? *European Journal of Wildlife Research* 56:513–518.
- NIELSON, R. M., B. F. MANLY, L. L. McDONALD, H. SAWYER, AND T. L. McDONALD. 2009. Estimating habitat selection when GPS fix success is less than 100%. *Ecology* 90:2956–2962.
- NIELSON, R. M., AND H. SAWYER. 2013. Estimating resource selection with count data. *Ecology and Evolution* 3:2233–2240.
- R DEVELOPMENT CORE TEAM [environment and language for statistical computing]. 2011. Version 3.0.0. Vienna, Austria: R Foundation for Statistical Computing.
- ROWLAND, M. M., M. J. WISDOM, B. K. JOHNSON, AND J. G. KIE. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64:672–684.
- SANDERSON, E. W., M. JAITEH, M. A. LEVY, K. H. REDFORD, A. V. WANNENO, AND G. WOOLMER. 2002. The human footprint and the last of the wild. *BioScience* 52:891–904.
- SAPPINGTON, J. M., K. M. LONGSHORE, AND D. B. THOMPSON. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management* 71:1419–1426.
- SAWYER, H., M. J. KAUFFMAN, AND R. M. NIELSON. 2009a. Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management* 73:1052–1061.
- SAWYER, H., M. J. KAUFFMAN, R. M. NIELSON, AND J. S. HORNE. 2009b. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications* 19:2016–2025.
- SAWYER, H., R. M. NIELSON, F. G. LINDZEY, L. KEITH, J. H. POWELL, AND A. A. ABRAHAM. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. *Journal of Wildlife Management* 71:868–874.
- SAWYER, H., R. M. NIELSON, F. LINDZEY, AND L. L. McDONALD. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396–403.
- SCHMITZ, O. J., A. P. BECKERMAN, AND K. M. OBRIEN. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- SKOVLIN, J. M., P. ZAGER, AND B. K. JOHNSON. 2002. Elk habitat selection and evaluation. In: D. E. Towell and J. W. Thomas [eds.]. North American elk: ecology and management. Washington, DC, USA: Smithsonian Institution Press. p. 531–556.
- SMITH, K. T., C. P. KIROL, J. L. BECK, AND F. C. BLOMQUIST. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. *Ecosphere* (in press).
- SORENSEN, T., P. D. McLOUGHLIN, D. HERVIEUX, E. DZUS, J. NOLAN, B. WYNES, AND S. BOUTIN. 2008. Determining sustainable levels of cumulative effects for boreal caribou. *Journal of Wildlife Management* 72:900–905.
- THOMAS, D. L., AND E. J. TAYLOR. 2006. Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management* 49:397–405.
- TROMBULAK, S. C., AND C. A. FRISSELL. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- VAN DYKE, F., AND W. KLEIN. 1996. Response of elk to installation of oil wells. *Journal of Mammalogy* 77:1028–1041.
- VISTNES, I. C., AND C. NELLEMAN. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. *Journal of Wildlife Management* 65:915–925.
- VISTNES, I., C. NELLEMAN, P. JORDHOY, AND O. STRAND. 2001. Wild reindeer: impacts of progressive infrastructure development on distribution and range use. *Polar Biology* 24:531–537.
- WARD, L. 1986. Displacement of elk related to seismograph activity in south-central Wyoming. [ANONYMOUS]. Proceedings II: Issues and technology in the management of impacted western wildlife. Glenwood Springs, CO, USA: Thorne Ecological Institute. p. 246–254.
- [WRCC] WESTERN REGIONAL CLIMATE CENTER. 2009. Remote Automatic Weather Station, Echeta, WY, USA. Available at: <http://www.wrcc.dri.edu/>. Accessed October 2009.
- WHITE, G. C., AND R. E. BENNETTS. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549–2557.
- [WGFD] WYOMING GAME AND FISH DEPARTMENT. 1996. Fortification elk completion report, Appendix A: Fortification elk study final report. Gillette, WY, USA: WGFD. 77 p.
- [WGFD] WYOMING GAME AND FISH DEPARTMENT. 2007a. Fortification elk study progress report. Gillette, WY, USA: WGFD. 19 p.
- [WGFD] WYOMING GAME AND FISH DEPARTMENT. 2007b. Job Completion Report: EL320—Fortification. Gillette, WY, USA: WGFD. 19 p.
- [WGFD] WYOMING GAME AND FISH DEPARTMENT. 2010. Job Completion Report: EL320—Fortification. Gillette, WY, USA: WGFD. 19 p.