



## **Elk Shift Resource Selection Temporally in Response to Natural Gas Development★**

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Source: Rangeland Ecology and Management, 90(1) : 35-44

Published By: Society for Range Management

URL: <https://doi.org/10.1016/j.rama.2023.05.006>

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## Original Research

Elk Shift Resource Selection Temporally in Response to Natural Gas Development<sup>☆</sup>Clay B. Buchanan<sup>1, #</sup>, Shaun S. Wulff<sup>2</sup>, Shannon E. Albeke<sup>3</sup>, Jeffrey L. Beck<sup>1, \*</sup><sup>1</sup> Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA<sup>2</sup> Department of Mathematics and Statistics, University of Wyoming, Laramie, WY 82071, USA<sup>3</sup> Wyoming Geographic Information Science Center, University of Wyoming, Laramie, WY 82071, USA

## ARTICLE INFO

## Article history:

Received 25 May 2022

Revised 16 May 2023

Accepted 23 May 2023

## Key Words:

*Cervus canadensis*

Diel behavior

Disturbance risk response

Energy development

Mixed-effects models

Resource selection function

## ABSTRACT

Resource selection is a process in which animals maximize resource acquisition through unequal use of heterogeneous resources on the landscape. Thus, shifts in resource and disturbance gradients should cause animals to shift resource use and distribution. Although there is an increasing body of evidence about the impacts of disturbance risk on wildlife populations, relatively few studies have assessed fine-scale impacts of human disturbance on wildlife. Our objective was to identify differences in day and night resource selection. Elk (*Cervus canadensis*) may be able to reduce consequences of coal bed natural gas development through expansion of resource use at night, thus ameliorating population impacts. To collect fine-scale temporal data, we used locations from 55 female elk equipped with Global Positioning System collars, as well as habitat and human disturbance variables for a study system in northeastern Wyoming. We used a mixed-effects model framework integrating frequency of individual elk to quantify shifts between day and night elk resource selection within a coal bed natural gas field. Elk exhibited differences in day and night resource selection, whereby they used areas with decreased forested cover and closer to roads at night. However, there was greater variation in resource selection at night compared with daytime. Our results suggest across each day, elk shifted fine-scale resource selection to take advantage of local resource gradients and response to disturbance impacts.

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## Introduction

The study of space use by animals is of fundamental interest in wildlife ecology. Nonuniform distributions of animals are a common response to resource heterogeneity on landscapes. As availability of resources shifts, so do animal populations to maximize resource uptake and fitness. Recent research has documented the influence of risk of predation on animal distribution and resource selection (Luttbeg and Sih 2004; Creel et al. 2005). More specifi-

cally, predation risk has been shown to promote antipredatory behavior in prey species (Festa-Bianchet 1988; Lima and Dill 1990). Prey animals use mechanisms such as shifting feeding time budgets, aggregating in larger groups, or even changing phenotypes to address perceived or real predation risk (Schmitz et al. 1997; Lingle 2001; Relyea 2003; Harvey and Fortin 2013). Response to predation risk varies greatly across different predator-prey systems but can have great influence on wildlife populations and ecosystem function (Schmitz et al. 2004).

Disturbance risk response is considered to be analogous to predation risk response, focusing on the nonconsumptive effects of anthropogenic disturbance (Walther 1969; Frid and Dill 2002). As the human population continues to increase, there is an ongoing need to improve understanding of the impacts of anthropogenic disturbance on wildlife populations and develop appropriate conservation actions. Previous research has focused on disturbance events including aircraft flights (Krausman et al. 1998), hiking (Taylor and Knight 2003), skiing (Patthey et al. 2008), terrestrial vehicle traffic (on and off road), watercraft (Burger 1998), ecotourism (Weinrich and Corbelli 2009), and energy development (Sawyer et al. 2009a; Taylor et al. 2016). When coping with

<sup>☆</sup> This work was supported by the Bureau of Land Management (grant L08AC13039); University of Wyoming–Reclamation and Restoration Center (no grant number); and University of Wyoming–School of Energy Resources (grant UWCASHSER49255). The Bureau of Land Management also received funding for our study from Anadarko Petroleum Corporation, Marathon Oil, and Petro-Canada and (no grant numbers).

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<https://doi.org/10.1016/j.rama.2023.05.006>

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disturbance risk, animals may alter normal resource use and behavioral patterns. The cost of behavioral changes may manifest through population distribution shifts, decreased body condition, diminished reproductive output, and ultimately, population decline (Gill et al. 2001; Johnson et al. 2005).

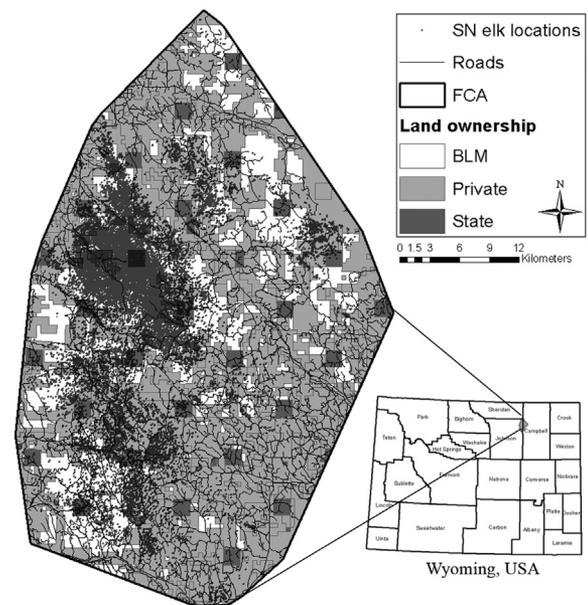
Similar to other taxa, ungulates must make trade-offs along gradients of resource availability and disturbance risk. In Nepal, a combination of habitat and disturbance variables best predicted the presence of barking deer (*Muntiacus muntjak*), Himalayan goral (*Naemorhedus goral*), and Himalayan serow (*Capricornis thar*) and abundance of all three species declined with proximity to human disturbance (Paudel and Kindlmann 2012). Resources available to animals often occur along multiple gradients. For instance, animal migration often capitalizes on increased forage occurring along temperature and water gradients. Many ungulates in mountainous regions take advantage of high-quality forage by tracking green-up patterns up-slope in the spring following a phenological wave (Sawyer and Kauffman 2011; Bischof et al. 2012). However, if human disturbance decouples ungulate movement pathways with timing of forage green-up, ungulates must make trade-off decisions between risk avoidance and forage intake, possibly affecting future fitness (Bischof et al. 2012). Ungulates also take advantage of resource gradients at smaller scales. Robinson et al. (2010) documented elk using habitat nearer human dwellings as refuge from wolf predation more at night than during the day. In comparison, Bonnot et al. (2013) recorded avoidance of human dwellings by roe deer (*Capreolus capreolus*), whereby they used distance or protective forest cover during the day to reduce perceived risk from human disturbance.

The development of energy resources such as oil and gas, wind energy, and coal form a major source of disturbance that creates gradients of risk for many wildlife species. In the western United States, impacts of energy development have been noted for ungulate species including elk (*Cervus canadensis*; Buchanan et al. 2014), mule deer (*Odocoileus hemionus*; Sawyer et al. 2017), and pronghorn (*Antilocapra americana*; Beckmann et al. 2012; Reinking et al. 2019). Our study focused on an elk population (2008–2011) in the Fortification Creek Area (FCA) of the Powder River Basin in northeastern Wyoming, a region that was experiencing rapid expansion of coal bed natural gas (CBNG) extraction (BLM 2010). In our previous work on elk resource selection within the FCA, we identified long-term, landscape-scale shifts in resource use and distribution on the basis of avoidance of road traffic associated with CBNG development activity (Buchanan et al. 2014), suggesting that elk were making behavioral tradeoffs at a large scale. On the basis of earlier findings, we hypothesized that animals may make fine-scale tradeoffs in response to effects of energy development (Hebblewhite and Merrill 2009). We expected elk would use less risky areas farther from roads during the day when energy development activity was higher and use riskier areas closer to roads at night when development activity decreased. We used a novel combination of sampling units to collect frequency of use and predictor variable values (Sawyer et al. 2009a; Clapp and Beck 2016) with a mixed-effects modeling framework to assess shifts in elk resource selection between day and night in a CBNG development field (Gilles et al. 2006). Through this approach, we demonstrate temporal resource selection shifts used by elk to exploit resource availability in the FCA in the face of expanding energy development.

## Methods

### Study area

The FCA is a 498 km<sup>2</sup> area approximately 40 km west of Gillette, Wyoming, United States (*sensu* Buchanan et al. 2014). Our



**Figure 1.** The Fortification Creek Area (FCA) and study area boundary, depicting the original (498 km<sup>2</sup>) and expanded study area (1 432 km<sup>2</sup>), combined. For simplicity, we term the entire 1 432 km<sup>2</sup> area as the FCA. The FCA, located in northeastern Wyoming and occupied year-round by a resident elk (*Cervus canadensis*) herd, served as a site for natural gas development, from 2008–2011. Summer night (SN) elk locations are plotted on this figure.

study area included the FCA, but approximately 10% of elk locations occurred outside of the defined FCA boundary. To include all locations, our study boundary extended outside of the FCA, which encompassed 1 432 km<sup>2</sup> (Fig. 1). For the sake of simplicity, we continue to use FCA when referring to our study area. Our expanded FCA study area encompassed portions of Campbell, Johnson, and Sheridan counties, Wyoming and was administered by the US Department of Interior Bureau of Land Management (34%), State of Wyoming (6%), and private landowners (60%). Cattle grazing has been a consistent land use in the FCA before and during CBNG development. Our study area included 2 441 km of roads and 3 293 oil and gas wells. Elevation in the study area ranged from 1 095 to 1 550 m. Land cover was dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) shrubland with scattered patches of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.; hereafter, juniper) that comprised only 6% of the landscape. Grasses common to the northern mixed-grass prairie 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) dominated our study area. The FCA and surrounding area was characterized by a semiarid climate with an average annual precipitation of about 22 cm (Western Regional Climate Center 2009). Annual precipitation during our study averaged 23 cm, of which > 90% fell between April and October. The average temperature was 9.0°C with an average daily maximum and minimum temperature of 15.4°C and 3.4°C, respectively (Western Regional Climate Center 2009).

### Location data

We used helicopter net-gunning (Leading Edge Aviation, Lewis-ton, ID) to capture  $n = 59$  adult female elk in separate capture operations in March ( $n = 39$ ) and December ( $n = 20$ ) 2008. We were approved to conduct our field research including capture, handling,

and marking female elk according to the Wyoming Game and Fish Department Chapter 33–396 permit and the University of Wyoming Institutional Animal Care and Use Committee protocol 04172008. Each elk was fitted with a real-time Global Positioning System (GPS) collar (North Star Science and Technology, LLC, King George, VA) programmed to collect 1 location every 5 h over 3 yr (2008–2011). We observed GPS collar fix rates of < 100%, which can be a result of interference of local habitat characteristics (Moen et al. 1996; Nielson and Sawyer 2013). We tested for differences in resource selection between animals with high ( $\geq 90\%$ ) and low (< 90%) GPS fix rates using independent sample *t*-tests. We found no differences ( $P > 0.05$ ) in resource selection coefficients between high and low fix rate groups (Buchanan et al. 2014), although four animals were removed due to full collar failure. We did not differentially correct GPS locations due to a high percentage (99%) of three-dimensional locations. We separated elk locations into four periods: summer (1 Apr–31 Oct) day (SD; 0700–1900 h), summer night (SN; 0000–0700 h and 1900–0000 h), winter (1 Nov–31 Mar) day (WD; 0700–1900 h), and winter night (WN; 0000–0700 h and 1900–0000 h). These periods coincided with development timing stipulations (BLM 2010) and traffic patterns directly associated with energy development activities.

#### Forage collections and analyses

We collected forage samples to assess forage quality across the FCA, as we expected elk to select areas of greater forage quality. We collected 10 forage samples for perennial forb and perennial grass forage classes from 10 randomly selected sites within three dominant cover types in the FCA including north-facing sagebrush, south-facing sagebrush, and juniper in early (1 June–15 June) and late summer (15 July–1 August) 2009 and 2010. Samples were clipped to ground level in 10 quadrats placed every 10 m along two 50-m transects randomly located within the three cover types. We also estimated forb and grass production in 10 quadrats every 10 m alternating with clipped quadrats along the 2 transects. We estimated forage mass for perennial forb and grass classes using a double sampling method within 0.1-m<sup>2</sup> quadrats (Bonham 2013). We dried all forage samples at 60°C for 48 h and reweighed to obtain dry mass measurements. We ground-dried samples to 1-mm particle size (Svejcar and Vavra 1985) and stored them before further analyses. Due to small sample size, we combined all forb, and separately all grass, subsamples from each sample site before nutritional analyses.

Percent nitrogen of each forage sample was evaluated using McGeehan and Naylor's (1988) combustion technique, and crude protein (CP) was approximated as  $6.25 \times [\%N]$  [40]. We followed techniques described by Tilley and Terry (1963) to estimate apparent in vitro dry-matter digestibility (IVDMD) for all forage samples. Rumen inoculum was collected from fistulated beef cows provisioned with forage available during similar phenological periods as forage collections in the FCA (Beck and Peek 2005). We used 25-micron pore ANKOM filter bags (Ankom Technology, Macedon, NY) during digestion trials. Samples were digested in triplicate following Tilley and Terry (1963) to obtain average IVDMD, with additional replicates as needed to achieve a  $\leq 5\%$  coefficient of variation computed from the average of at least 2 replicates. We used bomb calorimetry on duplicate forage samples to evaluate gross energy (GE). We approximated digestible energy (DE) as the product of mean apparent IVDMD and mean GE for each sample (Robbins 1993). We calculated standing CP and DE per forage class through multiplication of forage production values with the respective protein or energy values per forage class at sampling sites. We assessed differences in forage quality using analysis of variance tests.

**Table 1**

Resource variables measured within sampling units across the Fortification Creek Area of northeastern Wyoming, 2008–2011.

| Variable             | Description  |
|----------------------|--|
| <b>Environmental</b> |  |
| AFDE                 | Average forb digestible energy (kcal·m <sup>-2</sup> ·h <sup>-1</sup> )  |
| AGDE                 | Average grass digestible energy (kcal·m <sup>-2</sup> ·h <sup>-1</sup> ) |
| AFP                  | Average forb protein (g·m <sup>-2</sup> ·h <sup>-1</sup> )               |
| AGP                  | Average grass protein (g·m <sup>-2</sup> ·h <sup>-1</sup> )              |
| ELEV                 | Elevation (m)  |
| DWAT                 | Distance to water (m)  |
| DJUN                 | Distance to juniper patch (m)  |
| PERJUN               | Percent juniper cover  |
| PNS                  | Percent north-facing aspect  |
| PSS                  | Percent south-facing aspect  |
| SLOPE                | Slope  |
| VRM                  | Vector ruggedness metric (Sappington et al. 2007)                        |
| <b>Anthropogenic</b> |  |
| DKRD                 | Decay distance to road (m; $\alpha = 100$ –5 000 m)                      |
| DKWL                 | Decay distance to well (m; $\alpha = 100$ –5 000 m)                      |
| KRD                  | Kernel road density (km·km <sup>-2</sup> ·h <sup>-1</sup> )              |
| KWD                  | Kernel well density (number·km <sup>-2</sup> ·h <sup>-1</sup> )          |
| VROAD                | Road viewshed  |
| VWELL                | Well viewshed  |

#### RSF predictor variables

##### Anthropogenic predictors

We considered multiple anthropogenic variables related to CBNG development to predict elk resource use (Table 1) including roads, which were identified in previous work as influential on elk habitat use (Buchanan et al. 2014). The primary purpose of the road network developed in the FCA was to service CBNG development and extraction (Buchanan et al. 2014; Buchanan 2015). To quantify the impact of roads, we digitized roads in the FCA using 2009 and 2012 National Agriculture Imagery Program (USDA-FSA, Aerial Photography Field Office, Salt Lake City, UT) and Landsat (USGS-EROS Center, Sioux Falls, SD) imagery at 1 m and 30 m resolution, respectively. We developed decay distance variables as a function of Euclidean distance from all roads using the form  $e^{-d/\alpha}$  where  $d$  was the distance from each pixel to roads in meters and  $\alpha$  represented constant values of 100, 500, 1 000, 1 500, 2 000, 3 000, 4 000, and 5 000. The decay transformation scaled road distance variables between 1 and 0, where values increased in proximity to roads. As distance variables are naturally autocorrelated, we used AIC to identify the more predictive distance to road variable and retained it for further analyses. We also considered density of roads (km·km<sup>-2</sup>·h<sup>-1</sup>) as a predictor variable.

We included metrics in our analysis that represented the influences of well pads. We obtained well location data from the Wyoming Oil and Gas Conservation Commission (WOGCC). Wells were included in the analyses if they had been initiated (i.e., spudded) before or during our study period. As CBNG development is often quick paced, WOGCC data may not reflect on the ground activity; thus, we assessed existence of wells through on-the-ground observations and satellite imagery including National Agriculture Imagery Program and Landsat. We developed decay distance variables following the methods used in developing road variables as explained earlier. A well density (number·km<sup>-2</sup>·h<sup>-1</sup>) variable and well viewshed variable were also developed. The viewshed variable defined the number of wells from which a point on the landscape could be observed and was developed for every point (30 × 30 m GIS raster pixel) on the landscape. Variable names and descriptions are listed in Table 1.

##### Environmental predictors

Previous work has suggested that elevation (Sawyer et al. 2007; Gregory et al. 2009), terrain ruggedness (Skovlin et al. 2002;

Frair et al. 2005), and cover type (Beck et al. 2006; Barbknecht et al. 2011) are important predictors of elk resource selection, thus, we developed a suite of environmental variables (see Table 1). In addition, due to the physical nature of the landscape, the aforementioned variables provided the main sources of escape and thermoregulatory cover. We derived ELEV and SLOPE from a 10-m resolution digital elevation map (National Elevation Dataset, USGS, Sioux Falls, SD). We identified and classified juniper and sagebrush-grassland cover using 30-m landcover data developed at the University of Wyoming (Landcover\_REGAP\_2007, Wyoming Geographic Information Science Center, University of Wyoming, Laramie). We developed landscape level forage quality data layers by combining average standing crop CP ( $g \cdot m^{-2}$ ) and DE ( $kcal \cdot m^{-2}$ ) for both forb and grass vegetation classes. We then applied the forage quality values relative to the distribution of each cover type across the landscape. We then used these landscape-level forage quality layers in modeling elk resource selection. We list variable names and descriptions in Table 1.

### Statistical analyses

We used a negative binomial (NB2; Cameron and Trividi 1998) mixed-effects resource selection function (RSF; Thomas and Taylor 2006; Hilbe 2011) to assess day and night elk resource selection seasonally (e.g., summer day [SD]). A mixed-modeling approach is advantageous for, minimally, two reasons. First, it allows for unbalanced data, where one individual may have more relocations than another. Second, random intercepts and coefficients can be used to account for variation between individual elk in their resource selection and functional response (Gilles et al. 2006). We applied this RSF model in a relative frequency of use design at the individual home-range level (Thomas and Taylor 2006; Nielson and Sawyer 2013) while assessing population-level response to CBNG development.

We considered resources available to an elk if they were within the animal's home range. We developed individual animal home ranges using a 90% fixed kernel estimator. We used a 90% kernel estimator rather than 95% because kernel estimators often overestimate home range sizes (Ryan et al. 2006; Boyle et al. 2009). We used random 250-m radii sampling units to extract predictive variable values from the landscape, as well as the number of elk locations or frequency of use (Sawyer et al. 2007, 2009a). The size of our sampling units was larger than the expected GPS location error (< 20 m), thereby removing concern of error influencing model results. We based the quantity of sampling units on the absolute value of sampling unit area that approximated 60% coverage of the target home range. We used sampling unit area of 60% coverage because it best characterized the variation in resource use without oversampling elk locations. We extracted values for each predictive variable and the number of elk locations from each sampling unit. This method removed temporal relationships between locations beyond the seasonal or time of day classifications (e.g., summer, night; Nielson and Sawyer 2013).

Before model selection, we tested for collinearity among variables using a Pearson correlation matrix. We omitted one variable from analyses from all correlated variable pairs where correlation coefficients ( $r$ ) were  $\geq |0.6|$ . We examined collinearity further using a collinearity-tolerance statistic, which provided a measure of interdependence that may not be detected by the correlation matrix (Allison 2009; Kiroi et al. 2012). Variables were subject to removal based on low tolerance scores ( $t \leq 0.40$ ). We based removal of variables in response of both correlation and tolerance statistics on individual variable importance in accordance with published literature and biological relevance in reference to elk natural history.

The negative binomial distribution was used to model the counts,  $t_{ij}$ , representing the total number of locations within sampling unit  $i$  for individual  $j$ . The use of negative binomial distribution allows the variance to be greater than the mean, which is common for count data (Cameron and Trividi 1998; Hilbe 2011). Using the log link, the linear predictor conditional on the random effects is given by:

$$\ln[E(t_{ij})] = \ln(T) + \beta_0 + \gamma_{0j} + \gamma_{1j}x_{1ij} + \beta_1x_{1ij} + \dots + \beta_nx_{nij} \quad (1)$$

where  $t_{ij}$  was the total number of locations within sampling unit  $i$  for individual  $j$ , as a function of  $x_{1...n}$  covariates measured in sampling unit  $i$ ,  $\beta_{1...n}$  and  $\gamma_{ij}$  were the fixed and random selection coefficients, and  $\beta_0$  and  $\gamma_{0i}$  were the fixed and random intercepts from the mixed-effects regression, respectively. The term  $\ln(T)$  is the offset where  $T$  was the total number of locations during the time period of interest, which scaled the response to model relative frequency of use rather than integer counts (Nielson and Sawyer 2013) and was constant across  $i$  and  $j$ . Frequency of use per sampling unit can be regressed against predictor variables (Nielson and Sawyer 2013) in contrast to a traditional binary approach (1 = used; 0 = available) where the actual state of available locations is unknown (Keating and Cherry 2004). We carried out sequential model selection using AIC ( $\Delta AIC < 4$ ; Arnold 2010) to select the top performing model in two tiers. The first tier of selection identified predictive environmental models. The second tier added anthropogenic models and assessed improvement of model fit to test the hypothesis that anthropogenic variables had greater impact on elk resource selection.

We then mapped each model back onto the FCA landscape as a relative probability of use to assist in interpretation and visualization of model probabilities. We verified all map values to be within our range of inference of 0 and 1. We compared mapped, raw RSF value distributions between day and night to assess changes in use, where elk may have shifted daily use patterns to offset the impacts of CBNG development. We compared day and night probability of use distributions during summer and winter using Kolmogorov-Smirnov tests (Massey 1951). We developed separate generalized linear mixed models for day and night RSFs with respect to environmental and anthropogenic variables to identify possible drivers of diel variation in selection. In addition to including road metrics in resource selection modeling, we also measured the distance from each elk location to the nearest road and found the average distance to road by individual elk. We used a paired  $t$ -test to compare day and night distance to roads by individual elk.

An independent sample of 35 adult female elk was captured in March 2011 to continue monitoring the FCA elk herd. Because 9 individuals were recaptured from our first sample of collared elk, we used location data from 26 of these elk to form an independent sample for model validation. Locations from these animals in summer 2011 (validation summer day, 5 630; validation summer night, 6 099) and winter 2011–2012 (validation winter day, 2 807; validation winter night, 2 591) were used to validate our models. We separated locations during each season and time of day (e.g., summer, night) into 10 equal distribution bins. We then applied the respective models from the development data (2008–2010) to the 2011 summer and 2011–2012 winter landscapes and overlaid probability maps from these models with 2011 summer or 2011–2012 winter elk locations, which we binned as previously described. We used Spearman's rank correlations ( $r_s$ ) to evaluate location frequency distributions during 2008–2010 with location frequency distributions of the validation data set (e.g., binned summer elk distribution compared to the summer 2011 binned elk distribution) to test the ability of each model to measure elk resource selection for each season. We conducted all statistical analyses in the R language and environment (packages MASS and glmLambdab).

**Table 2**

Mean ( $\pm$  95% confidence interval) standing crude protein (CP [ $\text{g m}^{-2}$ ]) and digestible energy (DE [ $\text{kcal m}^{-2}$ ]) for north-facing sagebrush, south-facing sagebrush, and juniper cover types, Fortification Creek, northeastern Wyoming. These estimates were averaged over early and late summer 2009 and 2010.

|       | CP ( $\text{g m}^{-2}$ ) |                        |                | DE ( $\text{kcal m}^{-2}$ ) |                        |                 |
|-------|--------------------------|------------------------|----------------|-----------------------------|------------------------|-----------------|
|       | North-facing sagebrush   | South-facing sagebrush | Juniper        | North-facing sagebrush      | South-facing sagebrush | Juniper         |
| Forb  | 13.3 $\pm$ 2.2           | 7.6 $\pm$ 1.4          | 10.4 $\pm$ 1.7 | 210.3 $\pm$ 7.2             | 124.1 $\pm$ 4.9        | 159.7 $\pm$ 5.3 |
| Grass | 8.3 $\pm$ 1.3            | 16.3 $\pm$ 2.4         | 7.1 $\pm$ 0.8  | 259.2 $\pm$ 3.5             | 534.4 $\pm$ 2.3        | 220.5 $\pm$ 2.8 |

**Table 3**

Top-ranked environmental models with random intercept and environmental plus anthropogenic models with random term coefficients demonstrating elk resource selection in the Fortification Creek Area, northeastern Wyoming, 2008–2010. No models were competitive with the top model during any time period, so we do not report Akaike weights.

| Model   | AIC      | $\Delta$ AIC | Intercept | Coefficient |
|---|----------|--------------|-----------|-------------|
| Summer day  |          |              |           |             |
| <i>Environmental + Anthropogenic model</i>  |          |              |           |             |
| AGDE + PERJUN + VRM + DKRD (100 m) + VWELL + random coefficient for DKRD (100 m) by animal          | 34 977.8 |              | 1.3       | 0.8         |
| <i>Environmental model</i>  |          |              |           |             |
| AGDE + PERJUN + VRM + random intercept by animal  | 35 207.2 | 229.4        | 1.2       |             |
| Summer night  |          |              |           |             |
| <i>Environmental + Anthropogenic model</i>  |          |              |           |             |
| PERJUN + ELEV + DJUN + DKRD (500 m) + VWELL + random coefficient for DKRD (500 m) by animal         | 39 754.8 |              | 1.1       | 0.9         |
| <i>Environmental model</i>  |          |              |           |             |
| PERJUN + ELEV + DJUN + random intercept by animal   | 39 997.0 | 242.2        | 1.0       |             |
| Winter day  |          |              |           |             |
| <i>Environmental + Anthropogenic model</i>  |          |              |           |             |
| AGDE + PERJUN + VRM + ELEV + DKRD (500 m) + VWELL + random coefficient for DKRD (500 m) by animal   | 23 664.2 |              | 3.2       | 1.0         |
| <i>Environmental model</i>  |          |              |           |             |
| AGDE + PERJUN + VRM + ELEV + random intercept by animal   | 23 895.4 | 231.2        | 3.2       |             |
| Winter night  |          |              |           |             |
| <i>Environmental + Anthropogenic model</i>  |          |              |           |             |
| AGDE + VRM + ELEV + DJUN + DKRD (1 000 m) + VWELL + random coefficient for DKRD (1 000 m) by animal | 24 492.0 |              | 2.2       | 2.0         |
| <i>Environmental model</i>  |          |              |           |             |
| AGDE + VRM + ELEV + DJUN + random intercept by animal   | 24 652.0 | 160.0        | 3.1       |             |

## Results

We used 37 092 and 38 502 GPS elk locations from 55 elk to model resource selection during SD and SN, respectively. We used 22 587 and 21 766 GPS elk locations from 55 elk to model resource selection during WD and WN, respectively.

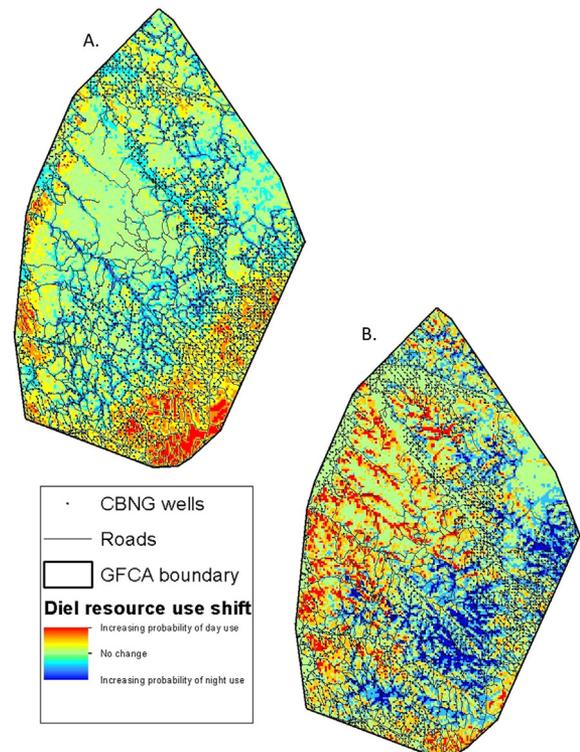
### Forage analyses

We collected 2 400 forb and grass subsamples from three cover types in the FCA and an equal number of forage estimates from double sampling efforts. After pooling samples by site, we used 240 samples in forage quality analyses. There were greater differences in standing DE ( $\text{g m}^{-2}$ ;  $F=595.2$ ,  $P < 0.01$ ) than standing CP ( $\text{kcal m}^{-2}$ ;  $F=27.6$ ,  $P < 0.01$ ; Table 2) between cover types. Post-hoc Tukey tests suggested that all groups differed ( $P < 0.05$ ) in DE except grasses and forbs in juniper and north-facing sagebrush communities. All significant differences in standing CP occurred between functional groups (i.e., forbs and grasses) across cover types with no differences in CP across cover types within the same functional group according to post-hoc Tukey tests.

### Resource selection

#### Summer

There were differences between SD and SN elk resource selection (Fig. 2A). The top environmental model predicting elk selection during SD included three variables, and no other models were competitive (Table 3). During SD, elk selected for areas with greater grass DE, percent juniper, and terrain ruggedness (Table 4). Addition of the top disturbance model, decay distance to road ( $\alpha = 100$  m), and well viewshed improved model fit by 229.4 AIC points (see Table 3). High-use (highest probability of use as binned during analysis) areas in SD averaged  $371.9 \text{ kcal m}^{-2}$  grass



**Figure 2.** Difference in day and night elk resource selection across the Fortification Creek Area in northeastern Wyoming during summer (A) and winter (B), 2008–2010. Cooler colors (light blue to dark blue) represent areas of higher probability of use during the night, and warmer colors (yellow to red) represent areas of higher probability of use during the day.

**Table 4**

Top model variables for each time period with variable coefficients ( $\beta$ ), standard errors (SE), and  $P$  values, Fortification Creek Area (FCA), northeastern Wyoming, 2008–2010. Summer and winter models were developed using data from 13 418 and 9 907 sampling units, respectively, from elk within the FCA.

| Variable                 | $\beta$  | SE      | $P$     |
|--------------------------|----------|---------|---------|
| <b>Summer day</b>        |          |         |         |
| Intercept                | -12.200  | 0.223   | < 0.001 |
| Grass DE                 | 0.001    | 0.0004  | < 0.001 |
| Percent juniper          | 0.042    | 0.001   | < 0.001 |
| VRM                      | 25.600   | 2.110   | < 0.001 |
| Distance to road (100 m) | -0.870   | 0.170   | < 0.001 |
| Well viewshed            | -0.006   | 0.0008  | < 0.001 |
| <b>Summer night</b>      |          |         |         |
| Intercept                | -11.200  | 0.524   | < 0.001 |
| Percent juniper          | 0.014    | 0.0014  | < 0.001 |
| Elevation                | 0.0006   | 0.0004  | 0.137   |
| Distance to juniper      | -0.00009 | 0.00002 | < 0.001 |
| Distance to road (500 m) | -0.067   | 0.148   | 0.646   |
| Well viewshed            | -0.003   | 0.0007  | 0.001   |
| <b>Winter day</b>        |          |         |         |
| Intercept                | -16.200  | 0.759   | < 0.001 |
| Grass DE                 | 0.003    | 0.0004  | < 0.001 |
| Percent juniper          | 0.024    | 0.002   | < 0.001 |
| VRM                      | 36.700   | 2.330   | < 0.001 |
| Elevation                | 0.003    | 0.0005  | < 0.001 |
| Distance to road (500 m) | -1.010   | 0.191   | < 0.001 |
| Well viewshed            | -0.005   | 0.0010  | < 0.001 |
| <b>Winter night</b>      |          |         |         |
| Intercept                | -22.700  | 0.768   | < 0.001 |
| Grass DE                 | 0.007    | 0.0004  | < 0.001 |
| VRM                      | 17.400   | 2.430   | < 0.001 |
| Elevation                | 0.008    | 0.0005  | < 0.001 |
| Distance to juniper      | -0.00010 | 0.00002 | < 0.001 |
| Distance to road (500 m) | -1.130   | 0.267   | < 0.001 |
| Well viewshed            | -0.003   | 0.001   | < 0.001 |

DE, 23.1% juniper, 0.03 terrain ruggedness, and 561.4 m from roads and were visible from 18.2 wells. The top environmental model predicting elk selection during SN included three variables, and no other models were competitive (see Table 3). During SN, elk selected for areas with greater percent juniper and elevation and distance to juniper (see Table 4). Addition of the top disturbance model, decay distance to roads ( $\alpha = 500$  m) and well viewshed, improved AIC model fit by 242.2 AIC units. High-use areas in SN averaged 25.2% juniper cover, 1 330.7 m in elevation, 57.6 m from juniper, and 536.7 m from roads and were visible from 17.3 wells. The Spearman's rank correlation coefficient ( $r_s$ ) for the summer models evaluated against our validation data were 0.94 for both SD and SN, where our RSF models predicted location distribution of an independent dataset. These correlation coefficients indicated our top SD and SN models were strong, positive predictors of elk resource selection.

Probability of use distributions between day and night RSFs during summer differed (Kolmogorov-Smirnov  $D = 0.027$ ,  $P < 0.001$ ) where night probabilities were more broadly distributed (Fig. 3). In summer, differences in day and night selection were best predicted by distance to juniper cover and roads. At night, elk used areas farther from juniper cover and closer to roads than during the day. Within the original 498-km<sup>2</sup> FCA before development (1992–1995), average distance ( $\pm$  SE) to roads was 734.0  $\pm$  0.2 m and elk locations averaged 836.4  $\pm$  132.7 m from roads [22]. Average distance to roads available within FCA elk home range during development was 284.3  $\pm$  0.2 m. We detected a difference in the average distance to roads for elk between SD (623.1  $\pm$  64.3 m) and SN (552.0  $\pm$  77.9 m;  $t_{75591} = 20.43$ ,  $P < 0.01$ ; Fig. 4). The shift in habitat use between SD and SN due to behavioral avoidance of roads resulted in a 17 355-ha shift in available habitat for FCA elk in summer.

## Winter

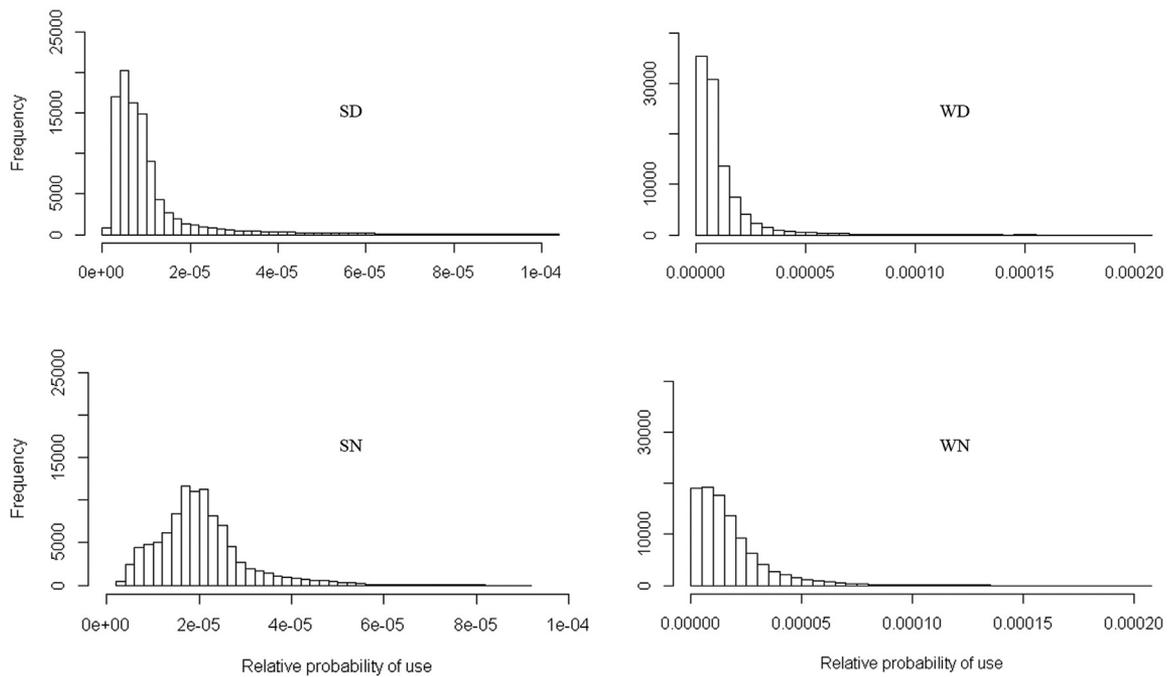
There were differences between WD and WN elk resource selection (see Fig. 2B). The top model predicting elk selection during WD included four variables, and no other models were competitive (see Table 3). During WD, elk selected for areas with greater grass DE, percent juniper, terrain ruggedness, and elevation (Table 4). Addition of the top disturbance model, decay distance to roads ( $\alpha = 500$  m) and well viewshed, improved model fit by 231.2 AIC points. High use areas in WD averaged 375.0 kcal·m<sup>-2-1</sup> grass DE, 20.3% juniper, 0.03 terrain ruggedness, 1322.7 m elevation, 641.4 m from roads, and visible from 16.6 wells. The top model predicting elk selection during WN included 6 variables and no other models were competitive (see Table 3). During WN, elk selected for areas with greater grass DE, terrain ruggedness, elevation, and distance to juniper cover (see Table 4). Addition of the top disturbance model, decay distance to roads ( $\alpha = 1000$  m) and well viewshed, improved model fit by 160.0 AIC points. High-use areas in WN averaged 397.7 kcal·m<sup>-2-1</sup> grass DE, 0.02 terrain ruggedness, 1 352.3 m elevation, 749.4 m from juniper cover, and 555.6 m from roads and were visible from 31.3 wells. The Spearman's rank correlation coefficient ( $r_s$ ) for the winter models against our validation data were 0.99 and 1.00 for WD and WN, respectively, where our RSF models predicted location distribution of an independent dataset. These correlation coefficients indicated our top WD and WN models were strong, positive predictors of elk resource selection.

Probability of use distributions between day and night RSFs during winter differed (Kolmogorov-Smirnov  $D = 0.018$ ,  $P < 0.001$ ) where night probabilities were more broadly distributed (see Fig. 3). In winter, differences in day and night selection were best predicted by distance to juniper cover and roads, where, at night, elk were using areas farther from juniper cover and closer to roads than during the day. Within the original 498-km<sup>2</sup> study area, before development average distance ( $\pm$  SE) to roads for elk locations in winter was 874.6  $\pm$  156.2 m. We detected a marginal difference in the average distance to roads for elk between WD (656.2  $\pm$  21.1 m) and WN (626.2  $\pm$  38.7 m;  $t_{44079} = 6.67$ ,  $P < 0.01$ ; see Fig. 4). The shift in habitat use between WD and WN due to behavioral avoidance of roads resulted in a 7 323-ha increase in available habitat for FCA elk in winter during the night.

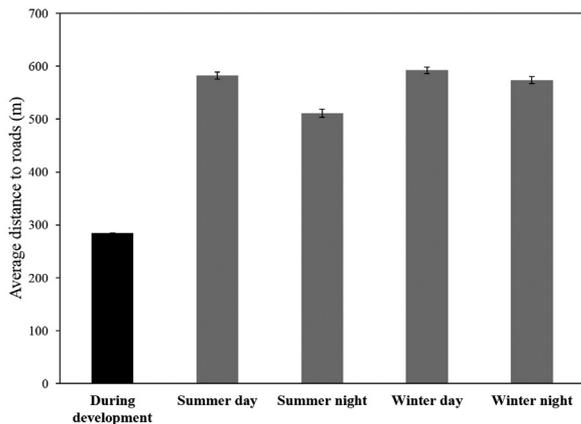
## Discussion

Animals should select and forage in areas that provide the greatest energy gain (MacArthur and Pianka 1966); however, perceived risk (e.g., predation or disturbance) should compel animals to make trade-offs between maximizing fitness and minimizing risk (Lima and Dill 1990). The pattern of resource selection exhibited by FCA elk exemplified a trade-off of risk avoidance during the day for expanded resource availability at night. Our results indicate that during the day elk used escape cover and distance from development to avoid the large proportion of daily human activity and then moved from escape cover to take advantage of resources (grass DE in three of four RSF models) closer to roads at night. Similarly, Guertin et al. (2012) found North American river otters (*Lontra canadensis*) were able to mitigate the effects of chronic contaminants in their environment by altering habitat use.

It is well documented that the daily pattern of foraging and resting changes for elk between seasons. For instance, Green and Bear (1990) reported elk in Rocky Mountain National Park, Colorado alternated between feeding and resting during the day in summer and rested during the day in winter but fed and rested during the night in winter. Elk in that study reduced diurnal feeding by 70% from summer to winter (Green and Bear 1990). The pattern and magnitude of the responses we saw differ from this Colorado study due to differences in habitat availability and dis-



**Figure 3.** Distributions of relative probability of use during summer day (SD), summer night (SN), winter day (WD), and winter night (WN) across the Fortification Creek Area in northeastern Wyoming, 2008–2010. Kolmogorov-Smirnov tests confirmed differences ( $P < 0.07$ ) in distribution between day and night during summer and winter, where distribution of relative probability of use was broader at night.

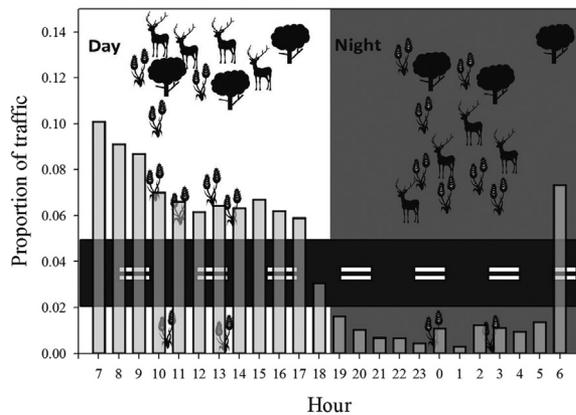


**Figure 4.** Average distance (m) to roads ( $\pm$  SE) for elk locations [grey bars] in the Fortification Creek Area for elk locations during day and night in summer and winter during development, 2008–2010. During development, [solid black bar] data were the Euclidean distance from roads for each  $30 \times 30$  m raster pixel across the FCA.

turbance from energy development, which elk perceived as a risk. In addition, the elk in the FCA were hunted, while elk in Rocky Mountain National Park were not, adding actual risk for elk using areas near roads in our study. Also, many of the main roads constructed for coal bed natural gas in the FCA were at the highest elevations with subsidiary roads extending into lower elevations. Thus, diurnal patterns of habitat selection by FCA elk are expected to differ from elk that occur in landscapes less influenced by anthropogenic disturbance. Our findings suggest a behavioral response where elk were reducing CBNG impacts by using areas closer to infrastructure at night when development activity was reduced. Previous work in the FCA documented impacts of CBNG development on elk, resulting in changes in elk resource selection and distribution compared with patterns observed before develop-

ment (Buchanan et al. 2014). In our initial study, we documented avoidance behavior by elk during development, leading to a loss of 43.1% of summer and 50.2% of winter high-use habitat before development (Buchanan et al. 2014). In summer during development, elk selected areas farther from roads, with more cover from Rocky Mountain juniper and less from north-facing sagebrush than they did before development. In winter, elk selected areas with less juniper cover, farther from roads, and in more rugged terrain than they did before energy development (Buchanan et al. 2014). In our current study (this paper), we documented shifts in resource selection as a behavioral response to the effects of CBNG development, where elk appeared to alter resource selection between day and night in response to activity associated with energy development. Specifically, elk were moving out of steep or forested areas at lower elevations during the day to access nutritious forage closer to CBNG development and roads at higher elevations during crepuscular and night hours, when there was less human activity. By comparison, to avoid hunters during fall, elk in north-central Utah selected steeper habitats at higher elevations in areas with greater aspen (*Populus tremuloides*) and mountain brush cover than was randomly available (Beck et al. 2013), indicating a behavioral response by these elk to avoid the risk of hunting. This response in habitat selection to the risk of human hunters is comparable with elk response to the disturbance risk associated with energy development in the FCA.

It is common to observe differences in animal resource selection across time and space (Hopcraft et al. 2012). Many species often take advantage of variability in the availability of resources and risk to obtain forage, thereby reducing exposure to disturbance or predation (Gill et al. 1996; Sawyer et al. 2009b; Middleton et al. 2013). Annual migration is a prime example of animals exploiting resource gradients (Sawyer and Kauffman 2011). However, our study evaluated a nonmigratory elk population, so animal movement and use of resources or riskier habitats were more subtle in comparison to many other resource-use studies (but see Neumann et al. 2013). Resource and perceived risk gradients operated on a



**Figure 5.** Proportion of traffic events during each hour period of a 24-h day in Fortification Creek, northeastern Wyoming. The graph begins at 07:00 h, so all day and night hours are grouped together for visualization. The distribution of traffic in this figure summarizes > 64 000 individual traffic events collected by infrared monitors. In the background of the figure, Fortification Creek Area elk were moving closer to roads at night and away from juniper cover when traffic levels were relatively lower than levels during daytime hours.

smaller time scale in our study system, where elk use shifted on a diel cycle in response to levels of CBNG development activity (also see [Burkepile et al. 2013](#)); however, because disturbance occurred throughout the year, elk avoidance response also occurred throughout the year. Our results suggest distance metrics from cover and roads were the important variables driving differences in diel resource selection in summer and winter. We argue that the difference in selection represented a release of CBNG development impacts on elk at night, although there was greater variation in resource selection at night compared with during the day. This selection pattern corresponded with the broader selection distributions observed at night and greater average distance to roads during day than at night in summer and winter. In summer, approximately 82% of vehicle traffic in the FCA occurred during the day; thus, our results suggest elk were moving from escape cover to areas closer to roads where human activity was reduced during nighttime hours ([Fig. 5](#); [Buchanan 2015](#)). Similar to our findings that elk used areas at night when disturbance risk was lower, plains zebra (*Equus quagga*) used burns with greater visibility when the risk of predation was higher ([Burkepile et al. 2013](#)). Brown bears (*Ursus arctos*) were documented increasing movement at night after day-time encounters with humans ([Ordiz et al. 2013](#)), resulting in a long-term response similar to FCA elk. These daily resource selection shifts likely allowed access to resources at night that were deemed unavailable or risky during the day.

Available population data suggest few impacts of CBNG development on elk population dynamics. Elk population numbers in the FCA remained relatively constant ( $\bar{X} = 256$ ,  $SE = 16.5$ , range: 220–400) from 1990–2010 with average calf:cow ratios of 40:100 in 1992–1995 and 47:100 in 2008–2010 ([WGFD 2010](#); [Buchanan 2015](#)). We assessed pregnancy rates of 91.6% ( $n = 36$ ), 86.3% ( $n = 36$ ), and 97.1% ( $n = 35$ ) in 2008, 2011, and 2014, respectively, from three separate capture events ([Buchanan 2015](#)). Although we observed some variability in pregnancy rates, they were still in the expected range for Rocky Mountain elk ([Raithe et al. 2007](#)). While we did not collect these data annually in connection with resource selection, they do provide some support for maintenance of herd fitness and mitigation of disturbance impacts. Furthermore, heart fat content was also lower for elk in the FCA compared with an elk population that served as an offsite reference population with similar habitat conditions, predator communities, and population densities, but no energy development ([Buchanan](#)

[2015](#)). However, fat deposition was highly variable within both populations, and we did not estimate forage nutritional levels in the reference population, so we could not compare forage quality between the two areas. Despite possible decreased body condition, population numbers and calf:cow ratios remained consistent and above Wyoming Game and Fish Department ([Wyoming Game and Fish Department 2010](#)) herd objectives of 150 elk throughout the period of CBNG development. These mixed signals in population health may provide evidence for a possible disturbance threshold where continued development may increase the impacts of development on elk fitness in the FCA.

Other factors may have reduced the impact of development on population dynamics. First, elk are rather long-lived animals, so our study timeframe may have been too short to measure population declines. However, population numbers and calf:cow ratios were collected over a time period representative of an elk life span and showed no consistent declines ([Wyoming Game and Fish Department 2010](#)). Second, there was a decrease in CBNG development as our study progressed. While the development footprint was not reduced, the amount of human activity likely declined post construction, thus possibly reducing the perceived risk. If decreased development were the driver allowing continued population success, we would expect probability of use to return to patterns more similar to predevelopment; however, that did not occur ([Buchanan et al. 2014](#)).

Although we argue in support of possible self-mitigation as a beneficial adaptation of FCA elk in response to activity associated with CBNG development, we caution possible downplaying of the impacts of CBNG development on elk. Changes in resource use and distribution have been demonstrated for the FCA elk herd in response to development ([Buchanan et al. 2014](#)), and while severe population fitness consequences have not been documented, we have yet to fully understand disturbance effects on population dynamics. External to possible mitigation, elk, in general, are rather robust, mobile animals, so development in the FCA may not have reached a point where population dynamics were greatly influenced. Continued development may increase density dependent effects as areas available as refugia will likely decline. Areas of high use may become depleted of resources, or at least reduced in quality, possibly leading to reduced resistance to stochastic climate events ([Owen-Smith et al. 2011](#)). To compensate, individual elk may have used areas of higher risk to obtain necessary resources or moved to other habitat patches if available similar to behavior observed in moose (*Alces alces*) ([Eldegard et al. 2012](#)). Indeed, we note that two elk emigrated from our study area with one leaving and then returning 4 mo later. To maintain elk populations in the FCA, it should be a priority to retain escape cover. Retention of conifer patches within rugged terrain may be especially critical in areas like the FCA, where the landscape was dominated by sagebrush steppe with little available concealment. Development protocols often avoid rugged terrain due to erosion issues; thus, creating greater buffers around these areas may provide greater concealment opportunities for elk and offer greater refugia to avoid development activity during the day. Some combination of these processes could provide some relief of development impacts. Continued monitoring and study of the FCA elk population may provide crucial information on density-dependent effects and thresholds of energy development impacts on elk and other ungulate populations experiencing expansion of energy resource extraction.

Finally, our methodology successfully combined the benefits of using frequency of use as the response variable and a mixed-effects model framework. Our statistical method did require a large dataset and greater computing power than traditional resource selection methods; however, these restrictions were outweighed by the ability to meet or remove assumptions limiting other methods.

Increased availability of large datasets through the use of GPS and other innovative technologies extends the need for sampling and statistical methods such as those used in our study. These methods offered the capacity to accurately assess small-scale shifts in elk resource selection and elk ability to respond to the impacts of CBNG development.

## Implications

Rangeland ungulates such as elk may avoid the risk of disturbance associated with increasing exposure to development similar to avoiding lethal risk from predation. Elk management in disturbed rangelands can be challenging, given the inherent lack of roadless areas, cover, or escape terrain in open landscapes. Elk within our study system in northeastern Wyoming behaviorally acclimated to a rapidly changing landscape by temporally avoiding disturbance from natural gas development. Our study system provided elk opportunity to coexist with CBNG disturbance in three ways. First, a wilderness study area, off limits to development, in the northern portion of the study area comprised only 10% (49 km<sup>2</sup>) of the FCA, yet 26–40% of elk locations occurred there during years of CBNG development (Buchanan 2015). Second, juniper cover and steep terrain offered elk escape from roads and other development during the day. Third, elk left tree cover using the cover of darkness, when most activity had ceased, to access nutritious grasses closer to roads during nights. Instead of leaving the study area, elk used these options to persist despite development. Consequently, rangeland wildlife managers and energy developers should consider maintaining refuge options in energy fields, such as roadless areas, patches of dense cover, and rough terrain free from development, to encourage persistent use by ungulates during development, as well as to encourage use following development.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

We thank the Hayden, Powder River, and Maycock ranches for property access. H. O'Brien, J. Verplanke, L. Jahnke, J. Hobbs, T. Achterhof, L. Driessen, M. Pike-Bieganski, and J. Ongstad provided logistical and field assistance. We particularly thank T. Bills from the Buffalo Wyoming Field Office of the Bureau of Land Management for his insights and leadership throughout our study. C. Molle (Ruminant Nutrition Laboratory, University of Wyoming) provided technical assistance with forage quality analysis. M. Kauffman provided assistance with study design and statistical support. J. Pope and M. Atchison (Leading Edge Aviation, LLC.) provided assistance in capture operations. We thank anonymous reviewers and A. Beckerman and M. Boyce for improving earlier drafts and A. Gregory and an anonymous reviewer for providing further suggestions for improvement of our manuscript.

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