

# Evaluating elk summer resource selection and applications to summer range habitat management



## Authors

Dustin Ranglack, Bob Garrott, and Jay Rotella - Department of Ecology, Montana State University

Kelly Proffitt and Justin Gude - Montana Fish, Wildlife, and Parks  
Jodie Canfield – Custer Gallatin National Forest

**February 2016**

## Background

In 2013, biologists from the United States Forest Service (USFS) and Montana Fish, Wildlife and Parks (MFWP) developed a set of recommendations for elk habitat management on the Custer, Gallatin, Helena, and Lewis and Clark National Forests and identified the need to better understand elk summer range resource selection (MFWP and USDA Forest Service 2013). Elk are a management indicator and/or a featured species in many Forest Land Management Plans, and for these National Forests in southwest and eastern Montana, Forest Plans were of late 80's vintage and had a variety of standards and guidelines relative to elk habitat management. Many of the Forest Plans are in the process of being revised, so there is an important opportunity to provide science-based recommendations for formulating standards and guidelines for elk habitat management into the future. Until recently, there was no real focus on summer range elk habitat management on public lands. However, the concept of habitat effectiveness is heavily referenced in the literature (Lyon 1979, Lyon 1983, Christensen et al. 1993). Habitat effectiveness for elk measures the actual elk use of an area in relation to the expected use of that area if no motorized routes were present. As such, roadless areas are designated as 100% effective for elk, while areas with motorized route densities of 1 mile/sq. mile are considered to

be 75% effective, 2 mile/sq. mile as 50% effective, etc., as actual elk use of those areas is estimated to be less than potential use (Lyon 1983). While elk preference for areas away from motorized routes is generally accepted (see McCorquodale 2013 for review), the traditional habitat effectiveness concept does not reflect many other potentially important factors, such as nutrition, that may affect elk summer resource selection.

The nutritional resources available to elk on summer range are of particular importance because females must meet the nutritional demands of lactation, while also accruing fat reserves for the winter (Cook et al. 1996, 2013, Monteith et al. 2014). During this critical summer period, nutritional resources slowly decrease as plants advance through phenological stages (Baker and Hobbs 1982, Monteith et al. 2011). Landscape processes, including wildfire and livestock grazing, may influence nutritional resources available to ungulates and create a mosaic of nutritional resources across the landscape. Depending on the intensity and timing of grazing or wildfire, these processes may increase or decrease ungulate nutritional resources (Fuhlendorf et al. 2009, Allred et al. 2011, Ranglack and du Toit 2015). This distribution of nutritional resources across the landscape is likely an important factor affecting elk summer habitat selection. The purpose of this project was to synthesize elk location data collected from elk in 9 southwestern and western Montana elk populations and evaluate the factors affecting elk summer resource selection. These results will be used to provide recommendations for elk summer habitat management.

## Study Areas

We captured adult female elk in 9 southwestern and western Montana winter ranges using helicopter net-gunning or chemical immobilization (Figure 1, Table 1). Elk were collared with GPS radio-collars. Collar functionality differed among populations and years, with most elk collared for a 1-year period and collecting 12–24 locations per day. Climate in these ranges is characterized by short, cool summers and long, cold winters. Our focus for this project was summer resource selection, which we defined as July 1 – August 31 of each year. We selected the July 1 seasonal start date to exclude any potential movements from calving to summer range (>95% of elk birthing events occur by the end of June, Cross et al. 2015) and the August 31 end date to correspond to just before the archery hunting season. Vegetation types across these summer ranges include a mix of montane forest (e.g. aspen [*Populus tremuloides*], Douglas fir [*Pseudotsuga menziesii*], lodgepole pine [*Pinus contorta*]), open sage-grassland (e.g. big sagebrush [*Artemesia tridentata*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], Idaho fescue [*Festuca idahoensis*]), and upland grasslands, meadows, and unvegetated areas, but the relative proportions of these habitat types vary among the populations. All areas contain a mix of public and private lands, with the majority of summer range occurring on Forest Service lands. Elevation and mean summer precipitation varied among the populations' ranges. Mule deer (*Odocoileus hemionus*), white tail deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) also occupy the elk summer ranges. Wolves (*Canis lupus*), mountain lions (*Puma concolor*), black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*) and coyotes (*Canis latrans*) are the elk predators in the system.

## Data Analysis

We developed third-order resource selection functions using a use-available framework (Johnson 1980, Manly et al. 2007). We treated summer locations collected from the GPS collars as the used sample. We randomly selected 4 locations per individual per day to ensure that

sample sizes were equal for all individuals regardless of collar scheduling and to reduce spatial autocorrelation in the data. We randomly generated available points at a 1:5 used:available ratio within the population-level summer range. We defined population summer range by randomly selecting 1 location per day per individual to reduce spatial autocorrelation among the locations, and then building 99% kernel density estimator (KDE) contours to represent the population-level summer range.

We evaluated 13 covariates describing elk resource selection based on a review of previous elk studies and current metrics used for elk habitat management. We divided the covariates into 3 covariate suites representing the potential effects of nutritional resources, motorized access, and general landscape attributes on elk resource selection (Table 2). The nutrition suite contained an elk nutritional resources model developed based on vegetation data collected in the southern Bitterroot Valley of Montana (Proffitt et al. *in revision*), as well as 2 remotely sensed metrics of greenness derived from the Normalized Difference Vegetation Index (NDVI): NDVI amplitude and time integrated NDVI. While the influence of forest canopy on NDVI values can limit the usefulness of unprocessed NDVI values in forested areas (Borowik et al. 2013), using NDVI amplitude or time integrated NDVI mediates the issue. NDVI amplitude values represent the increase in NDVI from the start of the growing season to the peak (Bradley and Mustard 2007), while time integrated NDVI represents the net primary production during the growing season (Jonsson and Eklundh 2002, White et al. 2009). The access routes suite included 3 metrics of disturbance: the density of all motorized routes, density of motorized routes, and a binary variable representing secure areas. Secure areas were defined as roadless areas of a given size ( $\geq 1$ , 2, or 4 sq. km) that were a given distance from the nearest motorized routes ( $\geq 805$ , 1,610, or 3,220 m). These definitions were based on current USFS management strategies. Lastly, the landscape suite contained 4 landscape attributes including landcover type, slope, elevation and solar radiation. We evaluated 3 landcover types: forest, grassland and shrubland and treated these as binary variables. Full details on covariate development are included in Appendix 1.

Although resource selection analyses are typically conducted at the resolution of the available covariate data, animals may perceive and select resource attributes at different spatial scales (Laforge et al. 2015), therefore we considered each continuous covariate over 6 different spatial scales (30, 100, 250, 500, 750, 1000 m). Additionally, because the relationship between selection and covariates may not always be linear, we evaluated multiple functional forms (linear, quadratic, pseudothreshold) for each continuous covariate. Binary covariates were only considered at the 30 m spatial scale, as that was the scale of the original data. We evaluated spatial scale and functional forms for each covariate in an exploratory analysis, unless the most appropriate functional form could be identified *a priori* from existing literature or the resolution of data did not allow for analysis at certain spatial scales (Table 2).

We standardized all continuous covariates and screened all covariate combinations for multi-collinearity. We used a multi-tiered approach to model selection (Franklin et al. 2000) to reduce the number of competing models. In tier 1, we examined all possible univariate models in an exploratory analysis to determine the most explanatory functional form(s) and spatial scale(s) for each covariate. We considered covariates from all the models within 5 AIC<sub>c</sub> units of the top model and advanced only these covariates to the next tier. We removed uninformative covariates, if any, from the models being moved forward to the next tier following Arnold (2010). In tier 2, we evaluated all combinations of informative covariates within the landscape suite and determined the best model using AIC<sub>c</sub>. For the tier 2 access and nutrition suites, we

evaluated all informative covariates and only advanced the single top covariate that best represented access and nutritional resources to the next tier. For tier 3, we combined the remaining informative covariates from the landscape suite in all possible combinations with the top covariate from the nutrition and access suites to determine the overall best model for summer elk resource selection.

We fit population-specific models using a conditional logistic regression model, conditioned on year using ‘cph’ in R v. 3.2.2. We choose this modeling framework to ensure that the available points for each year were evaluated against the used points for that year, as we had annually varying nutrition covariates and a different set of instrumented individuals for each year. Regional models of elk selection were constructed using two separate approaches: a consensus and a pooled approach. The consensus model was created following the same tiered-approach described above, though we forced all the populations to follow a consensus model structure for each tier in a meta-analysis framework. We determined the consensus model structure by ranking each model within a tier among populations and then summing the ranks. The model with the lowest summed rank was moved forward into the next tier, until the final model structure had been fit. We combined the results from all the populations for each covariate with equal weighting. The pooled model was created by pooling all the data across populations into a single dataset and following the same tiered-approach described for the population-specific models.

We validated population-specific models to determine both their internal accuracy and external applicability. Internal accuracy refers to how well the model is validated using the data for that population, while external applicability refers to how well the model predicts elk resource selection in areas outside the model development area. We assessed internal and external accuracy using Spearman’s rank correlations between population-specific models predicted relative use and actual used locations in 10 equal area bins (Boyce et al. 2002). Internal accuracy was assessed using k-folds with 5 random folds (Boyce et al. 2002), with 100 repetitions. To estimate external applicability, we assessed how well each population-specific model predicted relative use in the other 8 populations (Wiens et al. 2008). Given that the year of data collection did not always match among populations, we removed the stratification on year when testing the external applicability, but kept the remaining model structure intact. Lastly, we validated the consensus and pooled models by fitting the model with only data for 8 of the populations and predicting the use of the 9<sup>th</sup>. We repeated this process so that each population’s relative use was predicted using the model fitted with data from the other 8 populations.

Given that selection for areas with high nutritional value can overwhelm selection against areas near motorized routes (Gagnon et al. 2007, Dodd et al. 2007), we conducted a *post-hoc* exercise to examine these effects. For each of the top models, we included an interaction between the nutrition and access covariates. We compared the interaction model to the additive model using  $\Delta AIC_c$  to determine if the interaction term improved model fit.

## Results

We used a total of 83,946 elk locations collected from 339 individual elk in our analyses (Table 3). Of all the elk locations, 62.2% occurred in forested areas, 23.0% occurred in grasslands and 14.6% occurred in shrublands. Mean elevation of used points was 2,180 m ( $SD = 436$ ). Mean density of motorized routes and all routes (both open and closed to motorized use) of used points measured at the 1,000 m scale was 0.41 mi/mi<sup>2</sup> ( $SD = 1.00$ ) and 0.66 mi/mi<sup>2</sup> ( $SD = 1.24$ ) respectively (Figure 2). The mean slope of the used points was 13.2 degrees ( $SD = 8.5$ ).

Growing season conditions varied across summer ranges (Table 4). Mean NDVI amplitude and time integrated NDVI values of all used points were 50.0 (SD = 10.8) and 55.3 (SD = 11.2) respectively.

#### *Population-specific models*

The top population-specific models were consistent in that they each contained covariates from each of the nutrition, access, and landscape covariate suites (Table 5). The nutrition covariate was generally the most influential of all the covariates, as well as the only covariate that was consistent in the strength and direction of selection across all populations' top models, with all populations increasing selection for areas with increases in the nutrition covariate (Table 6, Figure 3). The two NDVI metrics, time integrated NDVI and NDVI amplitude were selected at roughly equal frequency and always in a pseudothreshold functional form, though the specific spatial scale used in each model was more variable. Holding all other covariates in the top population-specific model at their mean, the relative probability of selection (0-1) increased 0.39 (Bitterroot East Fork), 0.25 (Bitterroot West Fork), 0.63 (Paradise Valley), and 0.67 (Sage Creek) respectively as NDVI time integrated NDVI increased from 35 to 70 (within the range of observed values for all populations). For NDVI amplitude, relative resource selection increased 0.63 (Blacktail), 0.13 (Dome Mountain), 0.19 (Madison Valley), 0.45 (Pioneers), and 0.28 (Sapphires) respectively as NDVI amplitude increased from 35 to 70.

All of the populations, with the exception of Paradise Valley, included one of the access density metrics, with the density of motorized routes being generally more common than the density of all routes. The pseudothreshold and linear forms were included at equal frequency and the largest spatial scale of the covariate was generally preferred. The direction of selection for the access covariates was variable and the strength of selection for or against routes was generally small relative to the strength of selection for nutrition (Figure 4, Table 6). Holding all other covariates in the top population-specific model at their mean, the relative probability of selection (0-1) changed 0.08 and 0.08 (Bitterroot East Fork), 0.08 and 0.00 (Bitterroot West Fork), and -0.12 and -0.01 (Sapphires) respectively when increasing the density of all routes from 0 to 2 km/km<sup>2</sup> and 2 to 4 km/km<sup>2</sup>. Following those same methods for the density of motorized routes, we saw changes in the relative probability of use of -0.15 and -0.01 (Blacktail), 0.15 and 0.01 (Dome Mountain), -0.03 and -0.04 (Madison Valley), -0.18 and -0.16 (Pioneers), and -0.14 and -0.14 (Sage Creek). For the Paradise Valley population, moving from secure to unsecure areas led to an increase in relative resource selection of 0.22.

Model selection results showed few generalities in the influence of landscape covariates on resource selection (Table 7, 8). Abiotic features such as slope and solar radiation were included in all the population-specific models, and elevation was included in all the population-specific models except for the Blacktail. These were included at both the large or small spatial scale, with little support for intermediate spatial scales. All of the continuous covariates in the landscape models were included in the quadratic functional form. Of the landcover covariates, grasslands were the most commonly included, followed closely by forests. Shrublands were only included in 4 of the 9 population-specific models. Despite these generalities, the direction and strength of selection for each landscape covariate was variable among the populations.

Model validation results indicated that each population-specific model was accurate in the area where it was created, though the transportability of the population-specific models to the other populations was variable (Table 9). Each of the population-specific models was unable to accurately predict at least one other population's resource selection.

In 7 of the 9 populations, a post hoc exploratory analysis found a significant interaction between nutrition and access covariates, resulting in improved model fit based on  $\Delta\text{AIC}_c$ . The top Madison Valley and Pioneers population-specific models showed support ( $\Delta\text{AIC}_c \leq 2$ ) for both the post hoc interaction and original additive model, while the other 7 top population-specific models were all improved by including the interaction ( $\Delta\text{AIC}_c \geq 22$ ). In areas of higher nutrition, elk responses to increased motorized route density were generally small. In areas of lower nutrition, elk responses to increased motorized route density were generally stronger. In addition, areas of higher nutrition had positive relative RSF values across the range of motorized route densities examined (0 – 2.5 mi/mi<sup>2</sup>), while areas of lower nutrition generally had negative relative resource selection values across all motorized route densities.

### *Regional models*

The top regional models of summer elk resource selection followed similar patterns to the population-specific models (Table 5). Both the top consensus and pooled models included covariates from each of the covariate suites, and nutrition had the strongest influence on resource selection (Table 6). The nutrition covariate at the 500 m spatial scale and a pseudothreshold functional form was included in both regional models, but they differed in which nutrition covariate was included. The consensus model included NDVI amplitude and the pooled model included time integrated NDVI. Holding the other covariates in the top model at their mean, increasing either NDVI amplitude (consensus) or time integrated NDVI (pooled) from 35 to 70 resulted in an increase in the relative probability of selection (0-1) of 0.39 and 0.36 respectively.

In both regional models, access was best represented by the density of motorized routes in a pseudothreshold functional form. The consensus model included this covariate at the 1,000 m spatial scale and the pooled model included this covariate at the 100 m spatial scale (Table 5). Both models predicted that motorized routes were negatively associated with resource selection (Table 6), though this association was stronger for the pooled model than the consensus model.

Similar to the population-specific models, the landscape covariates in the regional models included elevation, slope, and solar radiation in quadratic functional forms. Slope was included at the 100 m scale for both models, but elevation and solar radiation were selected at the 1,000 m and 100 m scales, respectively, for the consensus model and the 30 m scales for both covariates in the pooled model. The consensus model included grassland and shrubland, and the pooled model included grassland and forest. The direction of selection for the covariates that were included in both models was similar with the exception of slope and solar radiation (Tables 7, 8).

Model validation results indicated that each regional model predicted population-specific resource selection well. The consensus model accurately predicted elk resource selection in 7 of the 9 populations, and the pooled model accurately predicted elk resource selection in all of the individual populations (Table 9). On average, both regional models significantly and accurately predicted elk resource selection.

Given that the consensus model is built by averaging the coefficient estimates and standard errors of the population-specific models in a meta-analysis framework, it was not possible post hoc to assess if a nutrition and motorized route interaction improved model fit based on  $\Delta\text{AIC}_c$ . In the exploratory analysis, including a nutrition and motorized route interaction in the top pooled model improved model fit ( $\Delta\text{AIC}_c \geq 491$ ). Similar to the population-specific models, the pooled model showed that at high nutrition values, elk responses to increased motorized route density were generally small but at lower nutrition values, elk responses to increased motorized route density increased and were negative. Coefficient

estimates for the pooled regional model with an interaction between nutrition and access can be found in Table 10.

#### *Best overall model*

The model validation and model selection results showed that the pooled regional model was the best model representing elk summer resource selection, and we recommend using this regional model as the basis of forming habitat management recommendations. The model showed that nutrition, as indexed by time integrated NDVI, was the strongest predictor of elk summer resource selection (Figure 5). At a time integrated NDVI value of 55, the estimated relative probability of elk use of an area was 0.5 (assuming other covariates are at their mean values). Poor nutrition, resulting in a predicted relative probability of use  $\leq 0.4$ , was represented by time integrated NDVI values  $\leq 46$ . Optimal nutrition, resulting in a predicted relative probability of use  $\geq 0.6$ , was represented by time integrated NDVI values  $\geq 66$ . Based on these definitions of poor and optimal nutrition, as indexed by time integrated NDVI values, the Sage Creek and Blacktail summer ranges had the highest proportion of optimal nutrition and the Sapphire and West Fork Bitterroot summer ranges had the lowest proportion of optimal nutrition (Table 11). To explore the relationship between canopy cover and nutrition, we extracted the canopy cover and time integrated NDVI values from within the herd ranges and used a linear regression model to evaluate the relationship between canopy cover (in the quadratic form) and time integrated NDVI (Figure 6). We found that the highest nutrition values were generally associated with canopy cover of 20–30%, though the model has a very low  $R^2$  value ( $R^2 = 0.06$ ).

The effect of motorized routes on elk resource selection was best represented by the density of motorized routes in a pseudothreshold functional form. The pooled regional model predicted a negative relationship between motorized route density with selection that was stronger at low motorized route densities than high route densities (Figure 7). Increasing motorized route density from 0 to 1.25 mi/mi<sup>2</sup> and from 1.25 to 2.5 mi/mi<sup>2</sup> changed the relative probability of selection (0-1) by -0.010 and -0.000 for the consensus model, and -0.078 and -0.004 for the pooled model.

The effect of elevation on elk resource selection was best represented at the 30 m spatial scale and in a quadratic functional form. The pooled regional model predicted that elk show a negative response to mid-elevation areas (~2,000 m), with a positive response to low and high elevations (Figure 5). Increasing elevation from 1,000 m to 2,000 m and then from 2,000 m to 3,000 m changed the relative probability of selection (0-1) by -0.301 and 0.256 for the pooled model. This pattern of summer resource selection is partially an artifact of the available data values, as 3 of the 9 population summer ranges are found primarily below the least preferred mid-elevation, with the remaining population ranges being primarily above that elevation. We do, however, see bimodal patterns in the elevation of the used points for 6 of the populations, though the distance between the peaks and relative height of each peak is variable. This suggests that there may be different behavioral strategies within these herds, with some individuals selecting for relatively low elevation areas (e.g. irrigated agricultural fields), while others use higher elevation areas.

The effect of slope on elk resource selection was best represented at the 100 m scale in a quadratic functional form. The pooled regional model predicted a positive response to moderate slopes (~15°), with a negative response to relatively flat or steep slopes (Figure 5). Increasing slope from 0 to 15° and from 15 to 30° changed the relative probability of selection (0-1) by 0.017 and -0.203 for the pooled model. The effect of solar radiation on elk resource selection

was best represented at the 30 m scale in a quadratic functional form. The pooled regional model predicted a negative response to moderate levels of solar radiation (~265), with a positive response to areas of low or high solar radiation (Figure 5). This suggests that elk require both areas of high and low solar radiation (~ SW and NE aspects) during the summer season, with lower levels of use in other areas. Increasing solar radiation from 100 to 250 and from 250 to 400 changed the relative probability of selection (0-1) by -0.118 and 0.072 for the pooled model. The effect of landcover type on elk resource selection identified grassland as the most preferred landcover type during the summer season, followed by forests and all other landcover types (Figure 5). Moving from a grassland to a forest or to any other landcover type changed the relative probability of selection (0-1) by -0.059 and -0.111 respectively for the pooled model.

## Discussion

Our modeling of elk summer range resource selection across southwestern Montana suggests that nutritional resources are the primary factor affecting summer elk distribution. Indices of nutritional resources were consistently the strongest predictors of summer resource selection in each of the population-specific and regional models, highlighting the importance of nutrition in elk summer resource selection in this region and the need to incorporate nutritional resource considerations in elk summer habitat management. We recommend that the current elk summer habitat management paradigm based on managing motorized route density to maintain elk habitat effectiveness (MFWP and USDA Forest Service 2013) be expanded to also consider nutritional resources. The importance of summer nutritional resources on ungulate population dynamics is well documented (Cook et al. 2013, Monteith et al. 2014). In southwest Montana, most studies indicate that nutrition is not commonly limiting elk pregnancy rate or overwinter survival (Cook et al. 2004, Evans et al. 2006, White et al. 2011, MFWP *unpublished data*), however some populations do experience nutritional limitations (Proffitt et al. in revision). Managers should identify areas where elk are likely to be nutritionally limited, and be particularly thoughtful about incorporating nutrition into summer habitat management strategies in these areas.

Our results suggest that NDVI may be a useful index of ungulate nutritional resources, although additional field data is required to fully understand the relationship between NDVI and ungulate nutritional resources (Borowik et al. 2013). NDVI amplitude and time integrated NDVI may be indicators of ungulate nutritional resources, and we found that overall time integrated NDVI was the strongest predictor of nutritional resources. NDVI is a metric of greenness based on satellite imagery and has become one of the most widely used vegetation indices in ecology (Pettorelli et al. 2005). We found elk selected for areas that have the highest net primary production during summer growing season. Similar patterns have been documented in a wide variety of animal species, making NDVI an easily accessible and useful tool in wildlife ecology (Pettorelli et al. 2011).

In addition to the strong effect of nutritional resources on elk summer resource selection, motorized routes also affected elk summer resource selection, although the magnitude of the access effect was small relative to nutrition. While our results generally support that elk select for areas away from motorized routes, we found that the effects of access on summer resource selection was highly variable. Of the 9 top ranked population-specific resource selection models,

5 models included a covariate representing elk selection for areas away from motorized routes and 4 included a covariate representing elk selection for areas nearer motorized routes. The relative weakness of this preference for areas with less motorized access is contrary to expectations based on existing literature and current management strategies (Lyon 1979, Christensen et al. 1993, Forman and Alexander 1998, Montgomery et al. 2013, Monteith et al. 2014), and our results are likely due to the scale of selection that we evaluated.

Our models focused on elk resource selection within established home ranges, and we found that within their established home ranges, motorized access had a relatively small effect on selection, as compared to nutrition. However, we did not evaluate if elk positioned their summer home ranges in areas with lower motorized route density. If elk selected for areas with low motorized route density when they positioned their summer home ranges, then within their home ranges the effects of access may have been small. Additionally, the lack of a strong influence of access routes on elk resource selection in our study may indicate that the current management paradigm of limiting motorized route density has been effective and should continue. It is possible that current motorized route densities are low enough, or that traffic is light enough, that such routes during summer have only a minor influence on elk behavior (Johnson et al. 2000, Gagnon et al. 2007). Additionally, the best model explaining summer resource selection found that elk showed little response to route density in areas of high nutritional value, but showed stronger negative responses to route density in areas of low nutritional value. This result suggests that the effects of strong selection for areas of high nutritional value may mask or offset the potentially negative effects of motorized routes on elk selection within their home range.

Finally, our results suggest that population-specific resource selection models may be poor predictors of resource selection outside the area in which they were generated. Broader scale, regional models built through meta-analysis of population specific models or by pooling data across populations are more reliable predictors of resource selection across multiple areas and are better suited to inform regional habitat management policies.

## Recommendations

- 1) We recommend that the current elk summer habitat management paradigm based on managing motorized route density to maintain elk habitat effectiveness (Lyon 1983) should be expanded to also consider nutritional resources.
- 2) We recommend managers use, as an assessment tool, time integrated NDVI to identify areas of optimal nutrition (i.e., values  $\geq 66$ , free access at [http://phenology.cr.usgs.gov/get\\_data\\_250w.php](http://phenology.cr.usgs.gov/get_data_250w.php)). This product is also available through the FWP mapper system.
- 3) We recommend that managers assess the relationships between time integrated NDVI and existing vegetation mapping products (e.g., R1VMAP) to determine the types of areas within their jurisdiction that contain optimal NDVI values (i.e., values  $\geq 66$ ). High values should be evaluated with respect to fire, grazing, weed treatments, etc. to help managers understand the relationships between management actions and summer range elk nutrition.
- 4) We recommend that managers continue to provide consideration for maintaining low open motorized route densities on elk summer range, especially in areas of poor nutritional resources (as indexed by time integrated NDVI values  $\leq 46$ ).

- 5) We recommend that habitat management recommendations be based on regional models constructed from multiple populations, and to use caution when extrapolating resource selection inferences based on a single study population to other populations.

### Acknowledgements

This project was developed with assistance from Montana Fish, Wildlife and Parks staff (Q. Kujala, A. Grove, N. DeCesare) and United States Forest Service staff (E. Tomasik), and funded by Montana Fish, Wildlife and Parks and the United States Forest Service. We thank the many field biologists and aircraft pilots that captured and radiocollared elk during 2005–2014 including J. Cunningham, M. Duffy, J. Grigg, K. Hamlin, B. Jimenez, C. Jourdonnais, M. Hebblewhite, M. Ross, J. Shamhart, M. Shelton, and R. Swisher. The data used in this project was collected by a variety of wildlife professionals, faculty and graduate students at Montana Fish, Wildlife and Parks, Montana State University, University of Montana, and MPG Ranch.

### Literature Cited

- Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution* 1:132–44.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Baker, D. L., and N. T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. *Journal of Wildlife Management* 46:694–703.
- Borowik, T., N. Pettorelli, L. Sönnichsen, and B. Jędrzejewska. 2013. Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. *European Journal of Wildlife Research* 59:675–682.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Bradley, B. A., and J. F. Mustard. 2007. Comparison of phenology trends by land cover class: a case study in the Great Basin, USA. *Global Change Biology* 14:334–346.
- Christensen, A. G., Lyon, L. J., and J. W. Unsworth. 1993. Elk management in the Northern Region: considerations for forest plan updates or revisions. Intermountain Research Station General Technical Report INT-303. 10 pp.
- Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, A. Robert, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. *The Journal of Wildlife Management* 60:528–541.
- Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of Northern Yellowstone elk. *Journal of Mammalogy* 85:714–722.
- Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. Mccorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. *Wildlife Monographs* 184:1–45.
- Dodd, N. L., J. W. Gagnon, S. Boe, and R. E. Schweinsburg. 2007. Assessment of elk highway permeability by using global positioning system telemetry. *Journal of Wildlife Management* 71:1107–1117.
- Evans, S. B., L. D. Mech, P. J. White, and G. a Sargeant. 2006. Survival of adult female elk in Yellowstone following wolf restoration. *Journal of Wildlife Management* 70:1372–1378.

- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207–231.
- Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- Fuhlendorf, S. D., D. M. Engle, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* 23:588–98.
- Gagnon, J. W., T. C. Theimer, N. L. Dodd, S. Boe, and R. E. Schweinsburg. 2007. Traffic volume alters elk distribution and highway crossings in Arizona. *The Journal of Wildlife Management* 71:2318–2323.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65.
- Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. *Journal of Wildlife Management* 64:685–697.
- Jonsson, P., and L. Eklundh. 2002. Seasonality extraction by function fitting to time-series of satellite sensor data. *IEEE Transactions on Geoscience and Remote Sensing* 40:1824–1832.
- Laforge, M. P., E. Vander Wal, R. K. Brook, E. M. Bayne, and P. D. McLoughlin. 2015. Process-focussed, multi-grain resource selection functions. *Ecological Modelling* 305:10–21.
- Lyon, L. J. 1979. Habitat Effectiveness for Elk As Influenced By Roads and Cover. *Journal of Forestry* 77:658–660.
- Lyon, L. J. 1983. Road Density Models Describing Habitat for Elk. *Journal of Forestry* 81:592–596.
- Manly, B. F., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2007. Resource selection by animals: statistical design and analysis for field studies. Second Edi. Springer Science & Business Media, New York, New York, USA.
- McCorquodale, S. M. 2013. A brief review of the scientific literature on elk, roads, and traffic. Washington Department of Fish and Wildlife. 26 pp.
- MFWP and USDA Forest Service. September 2013. U.S Forest Service and Montana Department of Fish Wildlife and Parks Collaborative Overview and Recommendations for Elk Habitat Management on the Custer, Gallatin, Helena, and Lewis and Clark National Forests. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Gallatin National Forest Supervisor's Office, Bozeman, MT, 36 pp.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere* 2:art47.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs* 186:1–62.
- Montgomery, R. A., G. J. Roloff, and J. J. Millspaugh. 2013. Variation in elk response to roads by season, sex, and road type. *Journal of Wildlife Management* 77:313–325.
- Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research* 46:15–27.
- Pettorelli, N., J. O. Vik, A. Mysterud, J.-M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005.

- Using the satellite-derived NDVI to assess ecological responses to environmental change.  
Trends in Ecology & Evolution 20:503–10.
- Ranglack, D. H., and J. T. du Toit. 2015. Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland. Ecological Indicators 56:145–151.
- Wiens, T. S., B. C. Dale, M. S. Boyce, and G. P. Kershaw. 2008. Three way k-fold cross-validation of resource selection functions. Ecological Modelling 212:244–255.
- White, P. J., R. A. Garrott, K. L. Hamlin, R. C. Cook, J. G. Cook, and J. A. Cunningham. 2011. Body condition and pregnancy in northern Yellowstone elk: evidence for predation risk effects? Ecological Applications 21:3–8.
- White, M. A., K. M. de Beurs, K. Didan, D. W. Inouye, A. D. Richardson, O. P. Jensen, J. O'Keefe, G. Zhang, R. R. Nemani, W. J. D. van Leeuwen, J. F. Brown, A. De Wit, M. Schaepman, X. Lin, M. Dettinger, A. S. Bailey, J. Kimball, M. D. Schwartz, D. D. Baldocchi, J. T. Lee, and W. K. Lauenroth. 2009. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. Global Change Biology 15:2335–2359.

**Table 1.** The mean and standard deviation (in parentheses) of elevation (Elev), density of motorized routes, density of all routes, time integrated NDVI (Time Int NDVI), NDVI amplitude (NDVI Amp), and the proportion of forest and grassland cover types for each elk summer range.

Population	Elev (m)	Density of Motorized Routes (mi/mi <sup>2</sup> )	Density of All Routes (mi/mi <sup>2</sup> )	Time Int NDVI	NDVI Amp	Prop Forest	Prop Grassland
<b>Bitterroot</b>	1,960	0.57	0.83	48.0	42.8	0.70	0.14
<b>East Fork</b>	(318)	(2.55)	(3.05)	(10.9)	(9.0)	(0.46)	(0.35)
<b>Bitterroot</b>	1,948	0.40	0.65	45.4	40.4	0.84	0.10
<b>West Fork</b>	(278)	(2.12)	(2.7)	(9.3)	(7.4)	(0.37)	(0.30)
<b>Blacktail</b>	2,280	0.40	0.57	58.2	53.7	0.37	0.24
	(266)	(2.17)	(0.57)	(8.4)	(8.9)	(0.48)	(0.43)
<b>Dome</b>	2,461	0.11	0.14	53.2	48.8	0.65	0.14
<b>Mountain</b>	(270)	(1.06)	(1.23)	(9.6)	(8.6)	(0.48)	(0.35)
<b>Madison</b>	2,359	0.30	0.50	54.1	49.0	0.57	0.18
<b>Valley</b>	(305)	(1.88)	(2.47)	(10.5)	(8.5)	(0.50)	(0.39)
<b>Paradise</b>	2,300	0.30	0.52	48.1	45.3	0.61	0.16
<b>Valley</b>	(398)	(1.89)	(2.46)	(10.4)	(9.1)	(0.49)	(0.37)
<b>Pioneers</b>	2,270	0.44	0.62	45.6	41.8	0.69	0.10
	(255)	(2.24)	(2.62)	(9.4)	(8.6)	(0.46)	(0.30)
<b>Sage Creek</b>	2,227	0.42	0.53	60.1	54.6	0.45	0.22
	(244)	(2.19)	(2.45)	(7.3)	(8.2)	(0.50)	(0.42)
<b>Sapphires</b>	1,516	1.03	1.11	40.6	36.1	0.55	0.26
	(358)	(3.47)	(3.62)	(11.7)	(7.5)	(0.50)	(0.44)

**Table 2.** The covariates evaluated as predictors of elk summer resource selection in southwest Montana, divided into 3 covariate suites (Nutrition, Access Routes, Landscape), where subscripts indicate the spatial scales that were evaluated (30, 100, 250, 500, 750, 1000 m, all) and superscripts indicate the functional forms (linear = L, quadratic = quad, pseudothreshold = ps, all = all) that were evaluated.

Nutrition	Access Routes	Landscape	
Bitterroot <sub>1000</sub> <sup>L,ps</sup>	Density of all routes <sub>all</sub> <sup>L,ps</sup>	Forest	Slope <sub>all</sub> <sup>all</sup>
NDVI – Amplitude <sub>≥250</sub> <sup>L,ps</sup>	Density of motorized routes <sub>all</sub> <sup>L,ps</sup>	Grassland	Solar radiation <sub>all</sub> <sup>all</sup>
NDVI – Time Integrated <sub>≥250</sub> <sup>L,ps</sup>	Security area	Shrubland	Elevation <sub>all</sub> <sup>all</sup>

**Table 3.** The years of GPS location data collection, the number of collared elk, and information regarding GPS radio-collar fix success and data censoring are presented for each of the 9 southwest Montana elk populations included in the analysis of elk summer resource selection.

Population	Year	# of collared individuals	Mean (range) of summer fix success	# of individuals included in the analysis	# of locations used in the analysis
<b>Bitterroot East Fork</b>	2011	30	80.0% (0-98.5%)	24	5,948
	2012	19	92.1% (0-100%)	18	4,463
	2013	16	98.0% (92.4-99.8%)	16	3,968
<b>Bitterroot West Fork</b>	2011	11	75.0% (0-96.9%)	9	2,232
	2012	17	91.8% (0-99.5%)	16	3,968
	2013	21	81.2% (0-99.1%)	18	4,464
<b>Blacktail</b>	2011	27	88.8% (0-97.9%)	25	6,200
	2012	7	84.2% (0-99.2%)	6	1,488
	2014	1	97.0%	1	248
<b>Dome Mountain</b>	2007	13	91.7% (1.3-100%)	12	2,976
	2008	27	94.4% (89.5-97.1%)	27	6,696
<b>Madison Valley</b>	2005	18	93.0% (0-99.8%)	17	4,216
	2006	27	94.5% (24.7-99.8%)	25	6,200
<b>Paradise Valley Pioneers</b>	2009	43	83.3% (0-98.6%)	38	9,424
	2013	30	88.5% (0-99.2%)	28	6,944
<b>Sage Creek</b>	2012	19	89.2% (0%-99.4%)	17	4,216
	2013	4	90.5% (80.5-95.8%)	3	744
<b>Sapphires</b>	2014	40	95.3% (0-100%)	39	9,551

**Table 4.** The mean and standard deviation (in parentheses) of growing season vegetation indices and weather for each elk summer range. Growing season vegetation indices are derived from remotely sensed NDVI data (<http://phenology.cr.usgs.gov/>). Time integrated NDVI (Time Int NDVI ) and NDVI amplitude (NDVI Amp) values are averaged across all years of the study. Weather data is from PRISM 2015.

Population	Time Int NDVI	NDVI Amp	Start of Growing Season	End of Growing Season	Growing Season Duration (days)	July- Aug Temp (°C)	July-Aug Precip (mm)
<b>Bitterroot East Fork</b>	48.0 (10.9)	42.8 (9.0)	May 2	Nov. 23	210	14.8 (1.39)	77.2 (17.8)
<b>Bitterroot West Fork</b>	45.4 (9.3)	40.4 (7.4)	May 8	Nov. 22	205	15.3 (1.05)	74.7 (9.7)
<b>Blacktail</b>	58.2 (8.4)	53.7 (8.9)	May 6	Nov. 18	196	14.3 (1.13)	84.1 (11.9)
<b>Dome Mountain</b>	53.2 (9.6)	48.8 (8.6)	May 18	Nov. 21	191	13.3 (1.26)	88.1 (15.2)
<b>Madison Valley</b>	54.1 (10.5)	49.0 (8.5)	May 14	Nov. 21	194	13.9 (1.41)	98.9 (20.0)
<b>Paradise Valley</b>	48.1 (10.4)	45.3 (9.1)	May 10	Nov. 20	198	14.1 (2.0)	99.5 (18.6)
<b>Pioneers</b>	45.6 (9.4)	41.8 (8.6)	May 11	Nov. 25	208	13.7 (0.8)	85.9 (20.9)
<b>Sage Creek</b>	60.1 (7.3)	54.6 (8.2)	May 7	Nov. 19	197	14.7 (0.9)	78.4 (13.7)
<b>Sapphires</b>	40.6 (11.7)	36.1 (7.5)	April 14	Nov. 18	221	16.7 (1.5)	70.5 (13.2)

**Table 5.** Model selection and validation results for the best population level and regional models explaining elk summer resource selection in southwest Montana. The number of parameters included in the best model (K) and AIC<sub>c</sub> score are presented. Model validation was based on the mean Spearman rank correlation ( $r_s$ ), which represented how well a model predicted the relative probability of selection to all populations within the study area. Covariate subscripts indicate the spatial scale in meters, superscripts indicate the functional form (none = linear, 2 = quadratic, ps = pseudothreshold).

Population	Top Model(s)	K	AIC <sub>c</sub>	Mean $r_s$
<b>Bitterroot</b>	Time Integrated NDVI <sub>500</sub> <sup>ps</sup> + Density of All Routes <sub>1000</sub> + Elevation <sub>1000</sub> <sup>2</sup> + Forest + Grassland + Shrubland + Slope <sub>30</sub> <sup>2</sup> + Solar Radiation <sub>1000</sub> <sup>2</sup> + strat(year)	11	287,433	0.99
<b>East Fork</b>				
<b>Bitterroot</b>	Time Integrated NDVI <sub>250</sub> <sup>ps</sup> + Density of All Routes <sub>1000</sub> <sup>ps</sup> + Elevation <sub>1000</sub> <sup>2</sup> + Forest + Shrubland + Slope <sub>30</sub> <sup>2</sup> + Solar Radiation <sub>100</sub> <sup>2</sup> + strat(year)	10	205,859	1.00
<b>West Fork</b>				
<b>Blacktail</b>	NDVI Amplitude <sub>1000</sub> <sup>ps</sup> + Density of Motorized Routes <sub>1000</sub> <sup>ps</sup> + Forest + Grassland + Slope <sub>1000</sub> <sup>2</sup> + Solar Radiation <sub>250</sub> <sup>2</sup> + strat(year)	8	152,214	0.99
<b>Dome Mountain</b>	NDVI Amplitude <sub>250</sub> <sup>ps</sup> + Density of Motorized Routes <sub>1000</sub> <sup>ps</sup> + Elevation <sub>30</sub> <sup>2</sup> + Forest + Grassland + Slope <sub>100</sub> <sup>2</sup> + Solar Radiation <sub>100</sub> <sup>2</sup> + strat(year)	10	194,129	1.00
<b>Madison Valley</b>	NDVI Amplitude <sub>250</sub> <sup>ps</sup> + Density of Motorized Routes <sub>1000</sub> + Elevation <sub>30</sub> <sup>2</sup> + Forest + Grassland + Slope <sub>100</sub> <sup>2</sup> + Solar Radiation <sub>100</sub> <sup>2</sup> + strat(year)	11	203,902	1.00
<b>Paradise Valley</b>	Time Integrated NDVI <sub>1000</sub> <sup>ps</sup> + Security Definition I + Elevation <sub>100</sub> <sup>2</sup> + Grassland + Slope <sub>1000</sub> <sup>2</sup> + Solar Radiation <sub>30</sub> <sup>2</sup>	9	197,127	1.00
<b>Pioneers</b>	NDVI Amplitude <sub>500</sub> <sup>ps</sup> + Density of Motorized Routes <sub>1000</sub> + Elevation <sub>1000</sub> <sup>2</sup> + Forest + Grassland + Shrubland + Slope <sub>100</sub> <sup>2</sup> + Solar Radiation <sub>1000</sub> <sup>2</sup>	11	138,601	1.00
<b>Sage Creek</b>	Time Integrated NDVI <sub>1000</sub> <sup>ps</sup> + Density of Motorized Routes <sub>1000</sub> + Elevation <sub>30</sub> <sup>2</sup> + Forest + Grassland + Slope <sub>250</sub> <sup>2</sup> + Solar Radiation <sub>1000</sub> <sup>2</sup> + strat(year)	10	94,242	1.00
<b>Sapphires</b>	NDVI Amplitude <sub>250</sub> <sup>ps</sup> + Density of All Routes <sub>750</sub> <sup>ps</sup> + Elevation <sub>1000</sub> <sup>2</sup> + Forest + Grassland + Shrubland + Slope <sub>250</sub> <sup>2</sup> + Solar Radiation <sub>1000</sub> <sup>2</sup>	11	203,681	1.00
<b>Consensus</b>	NDVI Amplitude <sub>500</sub> <sup>ps</sup> + Density of Motorized Routes <sub>1000</sub> <sup>ps</sup> + Elevation <sub>1000</sub> <sup>2</sup> + Grassland + Shrubland + Slope <sub>100</sub> <sup>2</sup> + Solar Radiation <sub>100</sub> <sup>2</sup>	10	NA	NA
<b>Pooled</b>	Time Integrated NDVI <sub>500</sub> <sup>ps</sup> + Density of Motorized Routes <sub>100</sub> <sup>ps</sup> + Elevation <sub>30</sub> <sup>2</sup> + Forest + Grassland + Slope <sub>100</sub> <sup>2</sup> + Solar Radiation <sub>30</sub> <sup>2</sup> + strat(herd_year)	10	1,708,407	1.00

**Table 6.** Coefficient estimates and 95% confidence intervals (in parentheses) representing the influence of nutrition and access routes on elk summer resource selection in southwest Montana, based on the top population-specific and regional models. All coefficient estimates are standardized with the exception of the consensus model, which is on the original scale to allow for the meta-analysis from the population-specific models. Covariate subscripts indicate the spatial scale in meters, superscripts indicate the functional form (none = linear, 2 = quadratic, ps = pseudothreshold).

Population	Nutrition Suite		Roads Suite	
	Covariate	$\hat{\beta}$ (CI)	Covariate	$\hat{\beta}$ (CI)
<b>Bitterroot East Fork</b>	Time Integrated NDVI <sub>500</sub> <sup>ps</sup>	1.20 (1.15, 1.25)	Density of All Routes <sub>1000</sub>	0.47 (0.44, 0.50)
<b>Bitterroot West Fork</b>	Time Integrated NDVI <sub>250</sub> <sup>ps</sup>	0.85 (0.80, 0.90)	Density of All Routes <sub>1000</sub> <sup>ps</sup>	0.32 (0.27, 0.37)
<b>Blacktail</b>	NDVI Amplitude <sub>1000</sub> <sup>ps</sup>	1.39 (1.32, 1.46)	Density of Motorized Routes <sub>1000</sub> <sup>ps</sup>	-0.57 (-0.62, -0.52)
<b>Dome Mountain</b>	NDVI Amplitude <sub>250</sub> <sup>ps</sup>	0.34 (0.29, 0.39)	Density of Motorized Routes <sub>1000</sub> <sup>ps</sup>	0.46 (0.42, 0.50)
<b>Madison Valley</b>	NDVI Amplitude <sub>250</sub> <sup>ps</sup>	0.60 (0.56, 0.65)	Density of Motorized Routes <sub>1000</sub>	-0.11 (-0.17, -0.05)
<b>Paradise Valley</b>	Time Integrated NDVI <sub>1000</sub> <sup>ps</sup>	1.85 (1.77, 1.93)	Security Area Definition I	-0.88 (-0.94, -0.82)
<b>Pioneers</b>	NDVI Amplitude <sub>500</sub> <sup>ps</sup>	0.92 (0.85, 0.98)	Density of Motorized Routes <sub>500</sub>	-0.63 (-0.69, -0.56)
<b>Sage Creek</b>	Time Integrated NDVI <sub>1000</sub> <sup>ps</sup>	1.04 (0.96, 1.12)	Density of Motorized Routes <sub>1000</sub>	-0.40 (-0.48, -0.32)
<b>Sapphires</b>	NDVI Amplitude <sub>250</sub> <sup>ps</sup>	1.05 (0.99, 1.10)	Density of All Routes <sub>750</sub> <sup>ps</sup>	-0.54 (-0.58, -0.50)
<b>Consensus</b>	NDVI Amplitude <sub>500</sub> <sup>ps</sup>	2.38 (2.32, 2.44)	Density of Motorized Routes <sub>1000</sub> <sup>ps</sup>	-2.68E-3 (-3.94E-3, -1.43E-3)
<b>Pooled</b>	Time Integrated NDVI <sub>500</sub> <sup>ps</sup>	1.08 (1.06, 1.11)	Density of Motorized Routes <sub>100</sub> <sup>ps</sup>	-0.22 (-0.23, -0.20)

**Table 7.** Coefficient estimates and 95% confidence intervals (in parentheses) representing the influence of the landcover covariates on elk summer resource selection in southwest Montana, based on the top population-specific and regional models. ‘NA’ is used where the covariate was not included in the top model for that population.

Population	Forest	Grassland	Shrubland
	$\hat{\beta}$ (CI)	$\hat{\beta}$ (CI)	$\hat{\beta}$ (CI)
<b>Bitterroot East Fork</b>	0.29 (0.22, 0.37)	0.23 (0.15, 0.32)	0.19 (0.12, 0.27)
<b>Bitterroot West Fork</b>	-0.31 (-0.36, -0.29)	NA	-0.35 (-0.43, -0.28)
<b>Blacktail</b>	0.55 (0.49, 0.62)	0.45 (0.39, 0.52)	NA
<b>Dome Mountain</b>	-0.43 (-0.48, -0.37)	0.52 (0.46, 0.58)	NA
<b>Madison Valley</b>	0.70 (0.62, 0.77)	0.80 (0.72, 0.88)	NA
<b>Paradise Valley</b>	NA (0.15, 0.27)	0.21	NA
<b>Pioneers</b>	1.03 (0.79, 1.27)	1.32 (1.09, 1.56)	0.73 (0.51, 0.96)
<b>Sage Creek</b>	0.71 (0.61, 0.81)	0.44 (0.33, 0.55)	NA
<b>Sapphires</b>	-0.10 (-0.17, -0.03)	-0.35 (-0.43, -0.27)	-0.20 (-0.27, -0.14)
<b>Consensus</b>	NA (7.38E-2, 1.14E-1)	9.37E-2 (-2.78E-1, -2.31E-1)	-2.55E-1
<b>Pooled</b>	0.21 (0.19, 0.23)	0.45 (0.43, 0.47)	NA

**Table 8.** Coefficient estimates and 95% confidence intervals (in parentheses) representing the influence of physical landscape covariates in the landscape suite on elk summer resource selection in southwest Montana, based on the top population-specific and regional models. The spatial scale (in meters) and functional form (Quad = quadratic) of elevation, slope and solar radiation index are displayed. For quadratics, the main effect is listed first. Bolded values indicate confidence intervals that do not overlap 0. ‘NA’ is used where the covariate was not included in the top model for that population.

Population	Elevation		Slope		Solar Radiation	
	Scale and Form	$\hat{\beta}$ (CI)	Scale and Form	$\hat{\beta}$ (CI)	Scale and Form	$\hat{\beta}$ (CI)
<i>Bitterroot</i> <i>East Fork</i>	1,000	<b>-0.08</b>	30 m, Quad.	<b>-0.45</b>	1,000	<b>-0.58</b>
	m, Quad.	(-0.13, -0.03);  <b>0.48</b>  (0.41, 0.54)		(-0.49, -0.40);  <b>-0.84</b>  (-0.93, -0.76)	m, Quad.	(-0.64, -0.52);  <b>-0.37</b>  (-0.44, -0.31)
<i>Bitterroot</i> <i>West Fork</i>	1,000	<b>-0.57</b>	30 m, Quad.	<b>-0.81</b>	100	<b>-0.11</b>
	m, Quad.	(-0.63, -0.51);  0.07  (-0.00, 0.15)		(-0.87, -0.76);  -0.07  (-0.14, 0.00)	m, Quad.	(-0.16, -0.05);  <b>-0.18</b>  (-0.26, -0.10)
<i>Blacktail</i>	NA	NA	1,000	<b>1.45</b>	250	<b>0.37</b>
			m, Quad.	(1.36, 1.53);  <b>-1.36</b>  (-1.48, -1.24)	m, Quad.	(0.32, 0.42);  <b>-0.06</b>  (-0.12, -0.01)
<i>Dome</i> <i>Mountain</i>	30 m, Quad.	<b>0.52</b>	100	<b>-0.33</b>	100	<b>0.23</b>
		(0.46, 0.58);  <b>-0.14</b>  (-0.20, -0.08)	m, Quad.	(-0.40, -0.27);  <b>-1.28</b>  (-1.39, -1.17)	m, Quad.	(0.16, 0.30);  <b>0.16</b>  (0.10, 0.22)
<i>Madison</i> <i>Valley</i>	30 m, Quad.	<b>1.81</b>	100	<b>0.45</b>	100	<b>0.61</b>
		(1.72, 1.90);  <b>-1.67</b>  (-1.79, -1.54)	m, Quad.	(0.39, 0.51);  <b>-1.42</b>  (-1.53, -1.32)	m, Quad.	(0.56, 0.67);  <b>-0.09</b>  (-0.17, -0.01)
<i>Paradise</i> <i>Valley</i>	100	<b>0.11</b>	1,000	<b>1.44</b>	30 m, Quad.	<b>0.65</b>
	m, Quad.	(0.04, 0.18);  <b>1.19</b>	m, Quad.	(1.37, 1.52);  <b>-1.35</b>		(0.59, 0.70);  <b>-0.13</b>

		<b>(1.07, 1.32)</b>		<b>(-1.48, -1.22)</b>		<b>(-0.20, -0.05)</b>
<i>Pioneers</i>	1,000 m, Quad.	<b>0.66</b>  <b>(0.57, 0.75);</b>  <b>-1.00</b>  <b>(-1.12, -0.88)</b>	100 m, Quad.	<b>-1.11</b>  <b>(-1.19, -1.04);</b>  <b>-0.19</b>  <b>(-0.31, -0.07)</b>	1,000 m, Quad.	<b>0.62</b>  <b>(0.56, 0.68);</b>  <b>0.84</b>  <b>(0.78, 0.91)</b>
<i>Sage Creek</i>	30 m, Quad.	<b>0.48</b>  <b>(0.34, 0.61);</b>  <b>-0.54</b>  <b>(-0.71, -0.37)</b>	250 m, Quad.	<b>0.32</b>  <b>(0.19, 0.45);</b>  <b>-1.13</b>  <b>(-1.29, -0.97)</b>	1,000 m, Quad.	<b>-0.17</b>  <b>(-0.25, -0.09);</b>  0.04  (-0.01, 0.09)
<i>Sapphires</i>	1,000 m, Quad.	<b>-0.46</b>  <b>(-0.54, -0.38);</b>  <b>-0.62</b>  <b>(-0.72, -0.53)</b>	250 m, Quad.	<b>-0.62</b>  <b>(-0.70, -0.54);</b>  <b>-1.97</b>  <b>(-2.09, -1.86)</b>	1,000 m, Quad.	<b>-0.21</b>  <b>(-0.27, -0.14);</b>  <b>-0.41</b>  <b>(-0.48, -0.34)</b>
<i>Consensus</i>	1,000 m, Quad.	<b>9.55E-3</b>  <b>(8.92E-3, 1.02E-2);</b>  <b>-2.07</b>  <b>(-2.20E-6, -1.93E-6)</b>	100 m, Quad.	<b>8.78E-5</b>  <b>(8.36E-5, 9.19E-5);</b>  <b>-3.63E-9</b>  <b>(-3.77E-9, -3.48E-9)</b>	100 m, Quad.	<b>-9.12E-3</b>  <b>(-1.80E-2, -3.26E-3);</b>  <b>1.58E-5</b>  <b>(7.90E-6, .36E-5)</b>
<i>Pooled</i>	30 m, Quad.	<b>0.18</b>  <b>(0.15, 0.20);</b>  <b>0.86</b>  <b>(0.83, 0.88)</b>	100 m, Quad.	<b>-0.06</b>  <b>(-0.08, -0.04);</b>  <b>-1.20</b>  <b>(-1.23, -1.16)</b>	30 m, Quad.	<b>0.26</b>  <b>(0.24, 0.28);</b>  0.09  <b>(0.07, 0.11)</b>

**Table 9.** The generalizability of each population-specific and regional top model of summer elk resource selection in southwest Montana was estimated by predicting resource selection for the other populations (subsequent columns) and assessing accuracy of predictions using the Spearman rank correlation coefficient. Values on the diagonal represent the results of the k-fold cross validation with 5 random folds and 10 equal area bins, averaged over 100 repetitions. Model generalizability is the mean Spearman rank correlation coefficients for the top model for each population (rows). Population generalizability is the mean Spearman rank correlation coefficient for each population (columns). Bolded values are significant ( $\alpha = 0.05$ ) and negative values (italics) indicate that the model predicted resource selection worse than random.

Top Model	Spearman rank correlation coefficient									Mean
	EF	WF	BT	DM	MV	PV	PI	SC	SA	
<i>Bitterroot East Fork (EF)</i>	<b>0.99</b>	<b>0.99</b>	<b>0.77</b>	<b>0.71</b>	0.56	<b>1.0</b>	-0.26	<b>0.78</b>	0.49	<b>0.67</b>
<i>Bitterroot West Fork (WF)</i>	<b>0.95</b>	<b>1.00</b>	<b>-0.78</b>	<b>0.81</b>	-0.30	<b>0.82</b>	0.61	<b>-0.40</b>	0.61	0.37
<i>Blacktail (BT)</i>	<b>0.66</b>	<b>-0.73</b>	<b>0.99</b>	0.59	<b>1.00</b>	0.59	<b>0.94</b>	<b>1.00</b>	<b>0.92</b>	<b>0.66</b>
<i>Dome Mountain (DM)</i>	0.59	<b>0.92</b>	<b>0.76</b>	<b>1.00</b>	<b>0.94</b>	<b>0.99</b>	<b>0.96</b>	-0.35	<b>0.82</b>	<b>0.74</b>
<i>Madison Valley (MV)</i>	-0.14	<b>-0.86</b>	<b>1.00</b>	<b>0.96</b>	<b>1.00</b>	0.56	<b>0.90</b>	<b>0.83</b>	<b>0.66</b>	0.55
<i>Paradise Valley (PV)</i>	<b>0.84</b>	<b>0.95</b>	<b>1.00</b>	0.16	<b>1.00</b>	<b>1.00</b>	0.01	<b>0.76</b>	0.36	<b>0.68</b>
<i>Pioneers (PI)</i>	-0.08	-0.25	<b>1.00</b>	<b>0.99</b>	<b>1.00</b>	0.27	<b>1.00</b>	<b>0.989</b>	<b>0.70</b>	0.62
<i>Sage Creek (SC)</i>	<b>0.73</b>	-0.15	<b>1.00</b>	0.07	<b>0.99</b>	<b>0.95</b>	<b>0.99</b>	<b>1.00</b>	<b>0.75</b>	<b>0.70</b>
<i>Sapphires (SA)</i>	<b>0.99</b>	0.58	-0.50	<b>-0.85</b>	<b>-0.92</b>	0.60	<b>-0.93</b>	<b>0.98</b>	<b>1.00</b>	0.11
<i>Consensus</i>	0.20	<b>-0.71</b>	<b>0.95</b>	<b>0.99</b>	<b>0.96</b>	<b>0.93</b>	<b>0.99</b>	<b>0.99</b>	<b>0.75</b>	<b>0.67</b>
<i>Pooled</i>	<b>0.96</b>	<b>0.99</b>	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>	<b>0.92</b>	<b>0.92</b>	<b>0.96</b>	<b>0.70</b>	<b>1.00</b>
<i>Mean</i>	0.57	0.17	0.62	0.54	0.62	<b>0.77</b>	0.52	<b>0.66</b>	<b>0.70</b>	<b>0.94</b>

**Table 10.** Coefficient estimates and 95% confidence intervals representing the influence of nutrition and access routes on elk summer resource selection in southwest Montana, based on the pooled regional model with an interaction between time integrated NDVI and motorized route density. All coefficient estimates are standardized.

Covariate	Coefficient Estimate	Lower Confidence Interval	Upper Confidence Interval
<b>Time Integrated NDVI – 500 m</b>	1.11	1.09	1.13
<b>Motorized Route Density – 100 m</b>	-0.27	-0.29	-0.26
<b>Elevation – 30 m</b>	0.16	0.13	0.18
<b>Elevation<sup>2</sup></b>	0.88	0.86	0.91
<b>Forest</b>	0.22	0.20	0.24
<b>Grassland</b>	0.45	0.42	0.47
<b>Slope – 100 m</b>	-0.06	-0.08	-0.04
<b>Slope<sup>2</sup></b>	-1.21	-1.24	-1.17
<b>Solar Radiation - 30</b>	0.26	0.24	0.28
<b>Solar Radiation<sup>2</sup></b>	0.09	0.07	0.12
<b>Time Integrated NDVI * Motorized Route Density</b>	0.41	0.38	0.45

**Table 11.** The proportion of each population summer range comprised of poor, average, and optimal time integrated NDVI values based on estimates from the pooled regional model. Time integrated NDVI values were used as an index of nutrition. Poor nutrition values were associated with the probability of elk use  $\leq 0.4$ , average values with the probability of elk use 0.4–0.6, and optimal values with the probability of elk use  $\geq 0.6$ .

Population	Poor Time Integrated NDVI	Average Time Integrated NDVI	Optimal Time Integrated NDVI
<b>Bitterroot East Fork</b>	0.438	0.522	0.040
<b>Bitterroot West Fork</b>	0.570	0.413	0.017
<b>Blacktail</b>	0.071	0.766	0.163
<b>Dome Mountain</b>	0.189	0.761	0.050
<b>Madison Valley</b>	0.176	0.746	0.078
<b>Paradise Valley</b>	0.359	0.632	0.009
<b>Pioneers</b>	0.596	0.386	0.018
<b>Sage Creek</b>	0.026	0.787	0.187
<b>Sapphires</b>	0.710	0.283	0.006

Figure 1. The study area included 9 elk population summer ranges in southwest Montana.

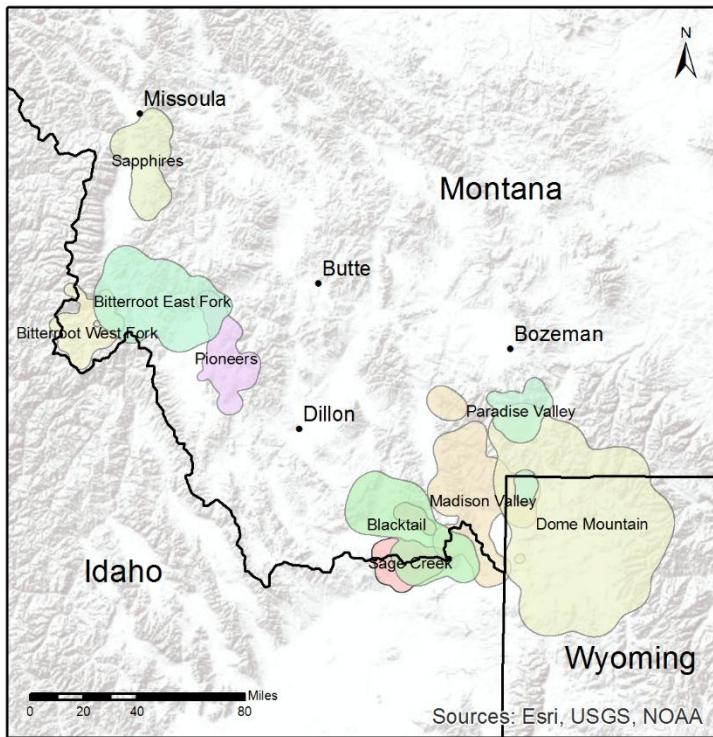


Figure 2. The density of motorized routes (in miles) in each of the 9 elk summer ranges in the southwest Montana study area. Population-level summer ranges were defined as the 99% kernel density estimator and represented as black polygons.

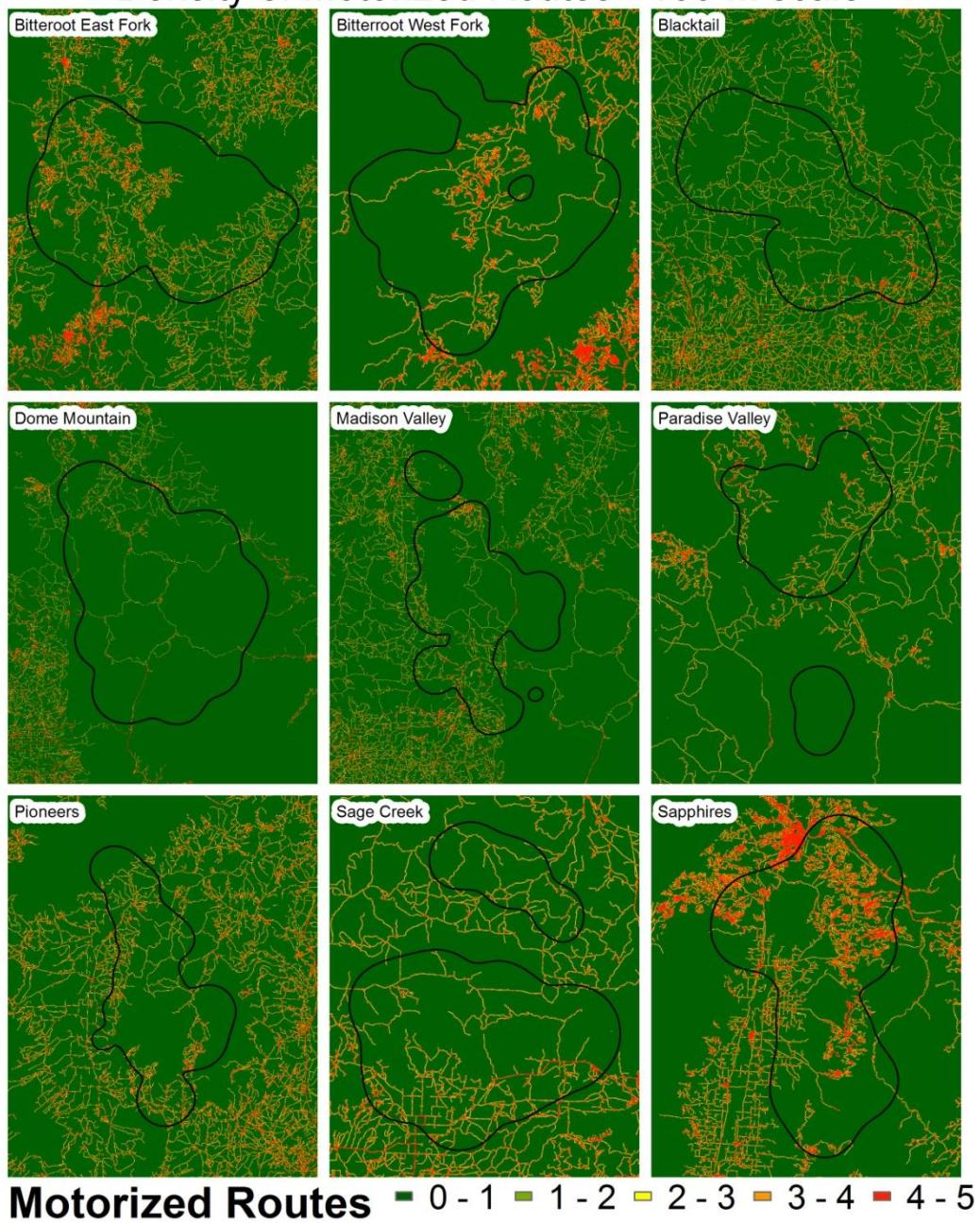


Figure 3. The predicted relative resource selection function (RSF) as a function of the nutrition covariate included in the top-ranked population-specific model. Estimates were created holding other covariates at their mean values. NDVI Amp. refers to NDVI amplitude and Time Int. NDVI refers to time integrated NDVI.

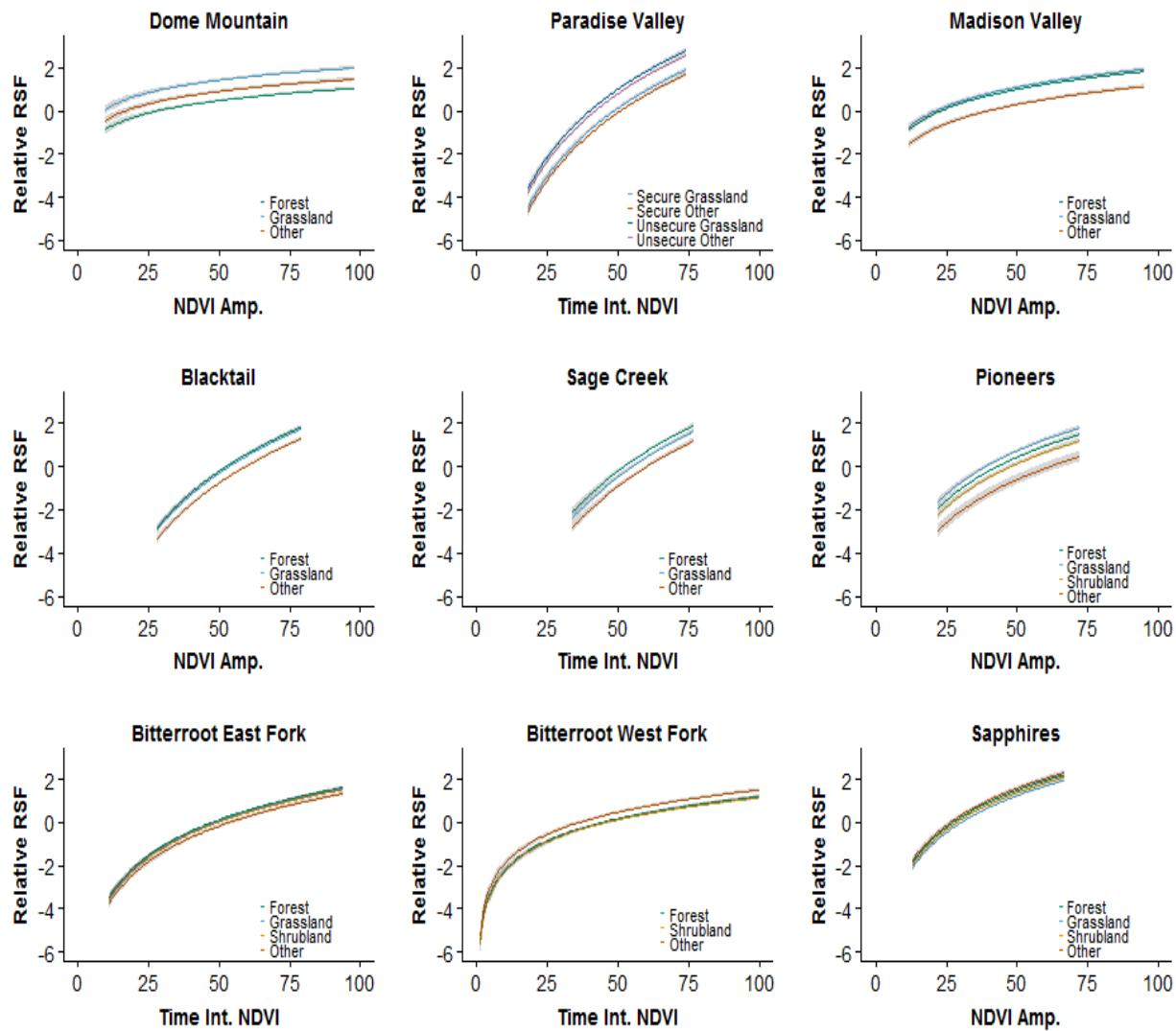


Figure 4. The predicted relative resource selection function (RSF) as a function of the access routes covariate included in the top-ranked population-specific model. Estimates were created holding other covariates at their mean values. Motorized routes (in miles/miles<sup>2</sup>) are roads and trails open during summer to motorized use, all routes (in miles/miles<sup>2</sup>) includes motorized and nonmotorized routes, and security areas definition 1 was an area >1,000 acres and least 2 miles from the nearest motorized route.

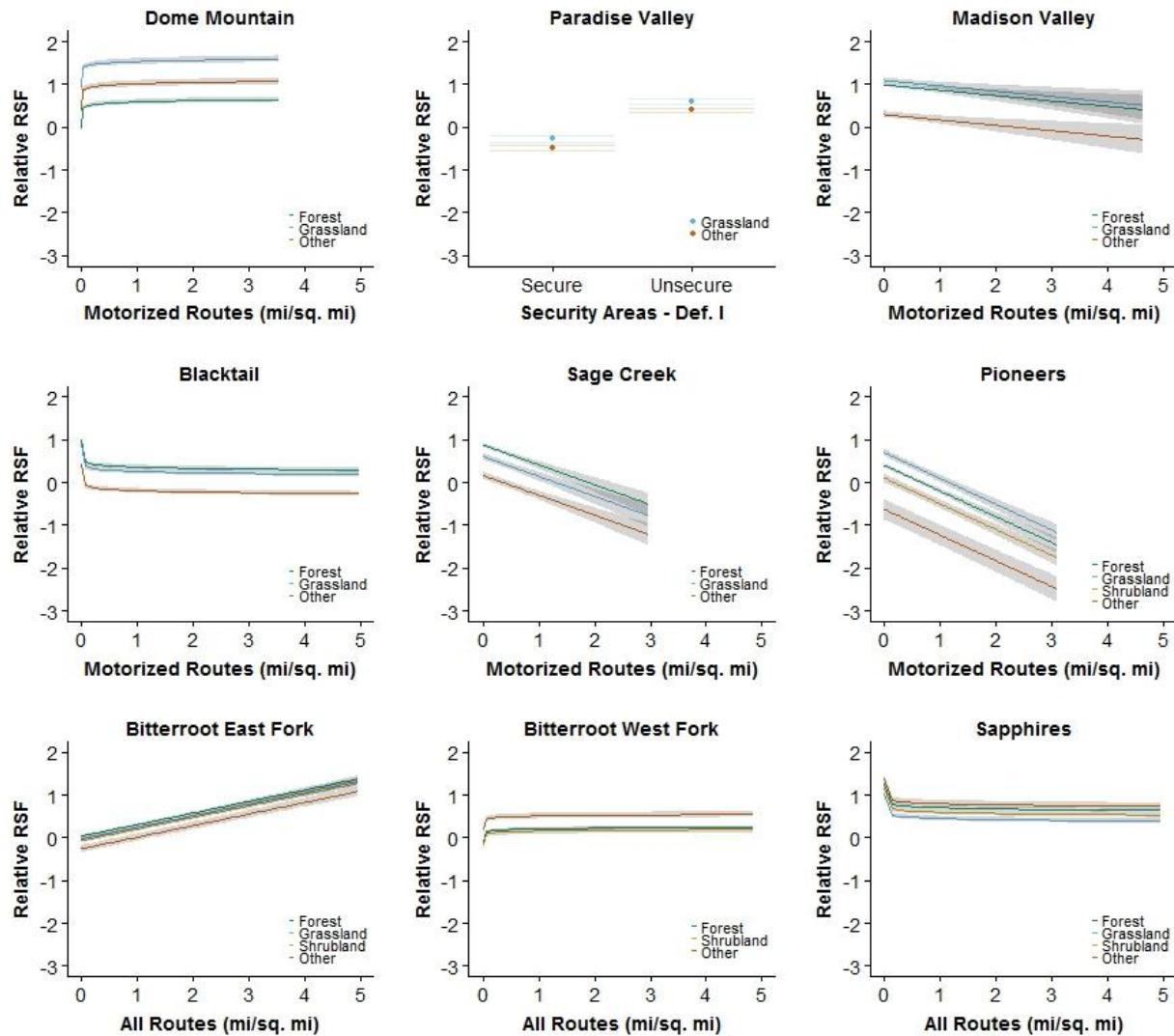


Figure 5. The predicted relative resource selection function (RSF) across the available range for each covariate based on estimates from the pooled regional model and holding other covariates at their mean value.

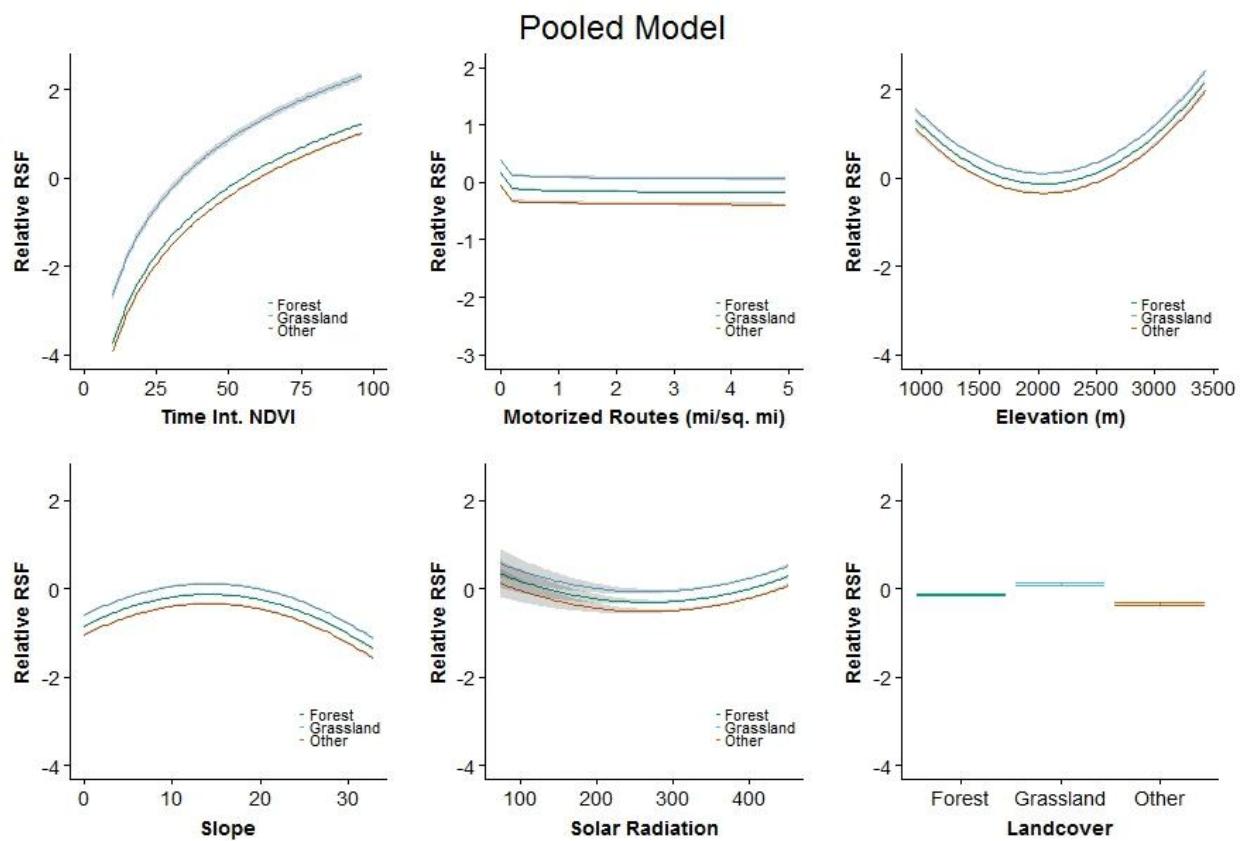
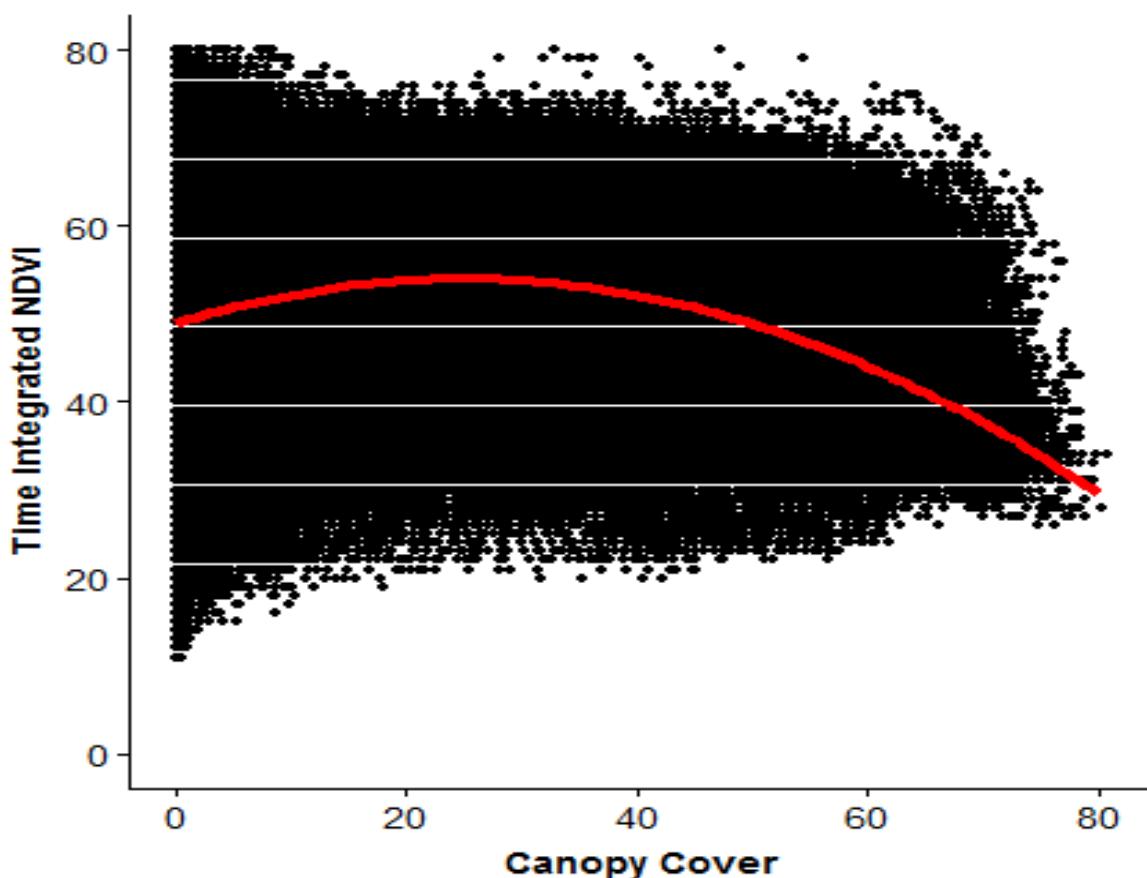
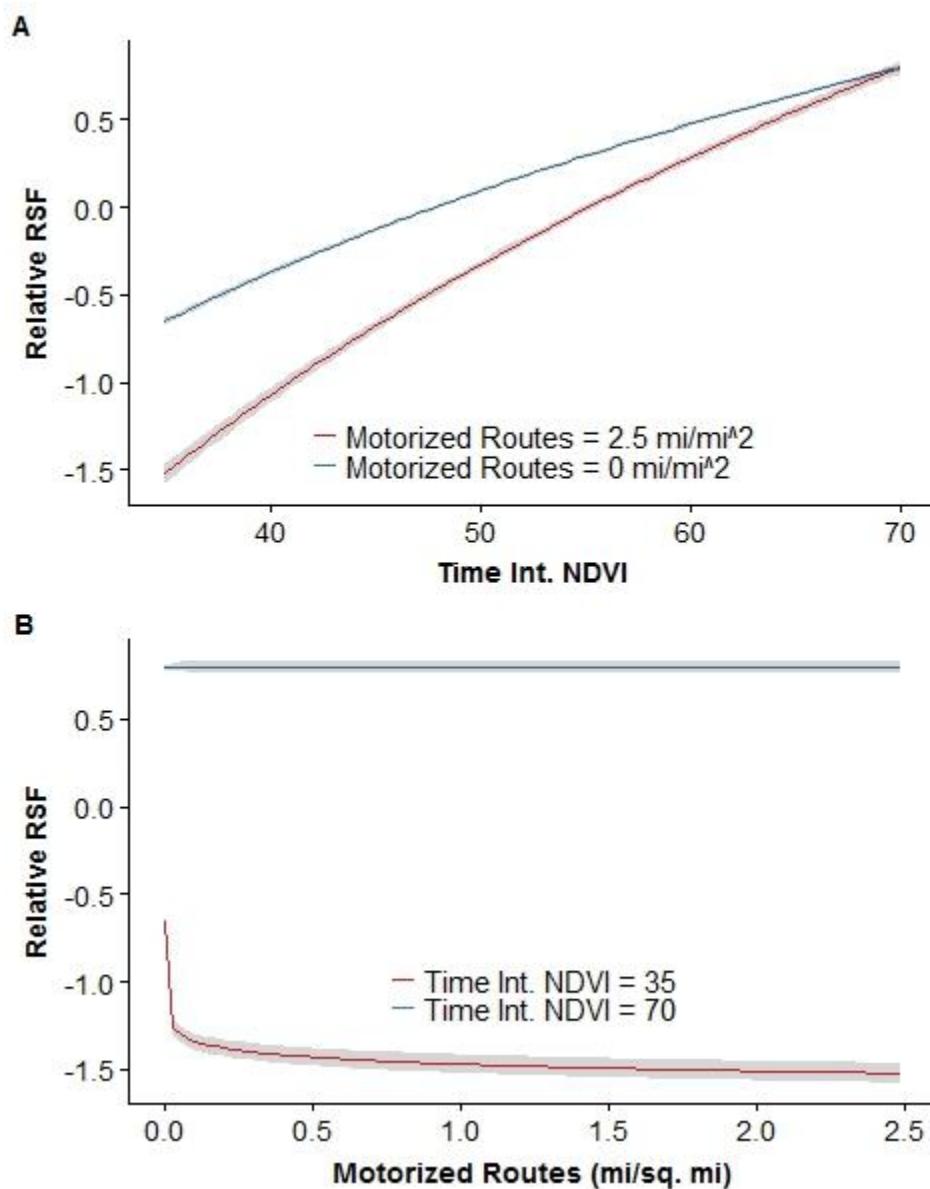


Figure 6. The relationship between canopy cover and time integrated NDVI values. Black dots represent extracted values from within the herd ranges along a 250 m grid and the red line represents the predictions of the linear regression model.



**Figure 7.** The interactive effect of motorized routes and nutrition, as represented by time integrated NDVI, based on the pooled regional model that included a motorized route  $\times$  nutrition interaction. Panel A shows the change in relative resource selection function (RSF) across the observed range of time integrated NDVI values at low motorized route density (blue, 0 miles/miles<sup>2</sup>) and high motorized route density (red, 2.5 miles/miles<sup>2</sup>). Panel B shows the change in relative RSF across the observed range of motorized route density in low nutrition areas (red, time integrated NDVI = 35) and high nutrition areas (blue, time integrated NDVI = 70). The grey shaded area is the 95% confidence interval. Predictions were generated by varying motorized route density or nutrition, and holding all other covariates in the model at their mean value.



## **Appendix A. Description of covariates evaluated in the elk summer resource selection models and the GIS data used to estimate covariates.**

### **Access Suite**

This suite was set up to encompass the various impacts that humans have imposed on elk habitat, primarily through the use of access routes (i.e., roads and trails, Forman and Alexander 1998, McCorquodale 2013, Montgomery et al. 2013). All of these covariates represent various impacts access routes can present through their density and arrangement.

**Density of all routes – denar** – We included all roads, as hunters and recreationists will often use closed roads for non-motorized travel (or illegal motorized travel), thus elk may still respond to closed roads (Hayes et al. 2002, Rowland et al. 2005) as well as all other routes open to motorized use during any portion of the year. This covariate was developed at 30 x 30 m resolution based on road data from the Montana Department of Transportation, the Montana Spatial Data Inventory, and the United State Forest Service. All roads (open, closed, public, and private) were used for this analysis. We used the Line Density tool in ArcGIS 10.2 to estimate road density in km/km<sup>2</sup>. The larger spatial scales were calculated using a moving window where the radius of the circle within which density was being calculated was equal to the spatial scale. The resulting density estimates contained extremely small values, thus they were multiplied by 1000 to allow for easy extraction in integer form. This covariate was evaluated for the linear and pseudothreshold functional forms.

**Density of motorized routes – denor** – We included only routes open for motorized use during the summer because impacts of motorized routes is likely to be stronger than impacts of non-motorized use routes. This covariate was developed using the same methods as the density of all routes, but included routes that were designated as open for motorized use during the summer, or routes with unknown open/closed status. The resulting density estimates contained extremely small values, thus they were multiplied by 1000 to allow for easy extraction in integer form. This covariate was evaluated for the linear and pseudothreshold functional forms.

**Percent secure area – sec\_(a-i)** – The Hillis paradigm (Hillis et al. 1991) is often used for defining security areas for elk, and is a combination of canopy cover, distance to roads, and size of the security block. Here, we used 9 different definitions of “security area” by varying two of the three security area factors. We varied distance to road (0.5, 1, and 2 mi) and size of the block (250, 500, 1,000 acres) varied. The secure area definitions are as follows (distance to road, size of block): A: >0.5, >250; B: >1, >250; C: >2, >250; D: >0.5, >500; E: >1, >500; F: >2, >500; G: >0.5, >1,000; H: >1, >1,000; and I: >1, >1,000. The influence of canopy cover was ignored as hiding cover may or may not be important to elk during the

non-hunting seasons. All rasters were generated at 30 x 30 m resolution as a binary secure/unsecure (1/0). Functional forms were not considered as this was a binary covariate.

## Landscape Suite

The landscape suite was designed to represent the landscape features that elk experience separate from the impacts of roads and nutrition. In this case, it represents various characteristics of both the biotic (vegetation types, predators), as well as the abiotic (topography) environment.

**Elevation – elev** – Elevation is a key component of the physical landscape that has dramatic influences on water availability and vegetation and is often used in resource selection modeling. This layer was obtained at 30 x 30 m resolution. Larger spatial scales represent the moving window average elevation with a search radius equal to that of the designated spatial scale. This covariate was evaluated for all three functional forms to provide full flexibility in fitting the model.

**Forest – paf** – Forests represent potential hiding cover for elk, but may also provide foraging opportunities in the understory if the canopy is not closed. This covariate was developed using data from the Montana Spatial Data Inventory ReGAP landcover layer, reclassified to represent forested areas (1) and non-forested areas (0). Forests included coniferous and deciduous forests and woodlands, as well as recently burned/harvested forests. The raster was generated at 30 x 30 m resolution.

**Grassland – pag** – As grazers, elk may seek out grassland areas for the foraging opportunities that they provide. This covariate was developed similarly to forest, only using grassland instead of forest. Grasslands included both high and low elevation grasslands, prairies, meadows, and wetland/riparian areas where grasses and forbs were the dominant vegetation type. The raster was generated at 30 x 30 m resolution as a binary grassland/non-grassland (1/0).

**Shrubland – pas** – Shrublands, similar to grasslands, may provide elk with a variety of foraging opportunities. This covariate was developed similarly to forest, only using shrubland instead of forest. Shrublands included sagebrush-steppe areas as well as deciduous shrublands. The raster was generated at 30 x 30 m resolution as a binary shrubland/non-shrubland (1/0).

**Slope – slp** – Slope has various impacts on the landscape that can influence elk responses to different areas. Steep slopes may present barriers to travel and foraging, and may also be drier, impacting the vegetation types that are found there. There may also be differing risks of predation with slope, as mountain lions often hunt on steeper slopes that allow them to ambush their prey more easily (Logan and Irwin 1985, Husseman et al. 2003), but steep slopes may offer protection from wolf

predation (Laporte et al. 2010). Slope was generated at 30 x 30 m resolution based on the digital elevation model for the area using the Slope tool in ArcGIS 10.2. The larger spatial scales were calculated using a moving window average with a search radius equal to that of the spatial scale. The resulting rasters contained extremely small values, thus they were multiplied by 1000 to allow for easy extraction in integer form. This covariate was evaluated for all three functional forms to provide full flexibility in fitting the model.

**Solar radiation – sr** – Solar radiation in this study is used as a surrogate for aspect. The amount of solar radiation received by an area can impact the water balance and thus the vegetation types that are found in the area (Fu and Rich 2002). This was generated at 30 x 30 m using the Area Solar Radiation tool in ArGIS 10.2. Inputs were the elevation DEM and the time frame of July 1 – August 31, 2009, as that represented the desired months of the year and roughly the mid-point of the study. All other options were set to their defaults. The larger spatial scales were calculated using a moving window average with a search radius equal to that of the spatial scale. The resulting rasters contained extremely large values, thus they were divided by 1000 to allow for extraction. This covariate was evaluated for all three functional forms to provide full flexibility in fitting the model.

## Nutrition Suite

The nutrition suite of covariates was designed to provide a detailed representation of the quality of forage available to elk. Two different models of nutrition were used, one created in the Bitterroot Mountains of western Montana, and the other in the Blue Mountains of Oregon and Washington. We also included several remotely sensed metrics of vegetation greenness as a proxy for forage. All covariates in this suite varied annually, thus allowing us to capture the impacts of differing precipitation and disturbance (fire, harvest, etc) on forage quality.

**Bitterroot – *bitt\_gs\_YY*** – This nutrition model estimated the herbaceous forage quality (measured as grams of digestible biomass per  $m^2$ ) available during late summer based on forage biomass, forage phenology and forage digestibility data collected in the Bitterroot Mountains of western Montana during 2012-2013 (Proffitt et al. in review). As it was only available at 1,000 m resolution, no further spatial scales were evaluated. This covariate was only evaluated for the linear and pseudothreshold functional forms, as there is no reason to expect selection for/against an intermediate value.

**NDVI – Amplitude – *amp\_gs\_YY*** – NDVI amplitude is a measure of the maximum increase in canopy photosynthetic activity (maximum NDVI) above the baseline (start of season NDVI) for each pixel. As such, it represents the slope of the NDVI curve, differentiating areas that have large changes in NDVI values over the course of the growing season (highly productive grasslands) to areas with less change (shrubland and coniferous forests that maintain some greenness year-

round) and is therefore often used in landcover classification (Bradley and Mustard 2007). As such, the influence of forest canopy on forage available to ungulates (Borowik et al. 2013) is mediated, as the value is simply the total increase in NDVI from the start of the growing season to the max NDVI. This was downloaded for each year in a pre-processed format from [http://phenology.cr.usgs.gov/get\\_data\\_250w.php](http://phenology.cr.usgs.gov/get_data_250w.php) at 250 m resolution, with the larger spatial scales calculated using a moving window average with a search radius equal to that of the spatial scale. This covariate was only evaluated for the linear and pseudothreshold functional forms. Data for 2014 was not available at the time of analysis, so the average value from 2004-2013 was used for the 2014 values.

**NDVI – Time Integrated – tin\_gs\_YY** – Time integrated NDVI is the daily (interpolated) integration of NDVI values above the start of season NDVI baseline for the entirety of the growing season. It therefore represents the net primarily production during the growing season for each pixel (Jonsson and Eklundh 2002, White et al. 2009). As such, the influence of forest canopy on forage available to ungulates (Borowik et al. 2013) is mediated, as the value is simply the entire area under the NDVI curve from the start of the growing season to the end. This was downloaded for each year in a pre-processed format from [http://phenology.cr.usgs.gov/get\\_data\\_250w.php](http://phenology.cr.usgs.gov/get_data_250w.php) at 250 m resolution, with the larger spatial scales calculated using a moving window average with a search radius equal to that of the spatial scale. This covariate was only evaluated for the linear and pseudothreshold functional forms. Data for 2014 was not available at the time of analysis, so the average value from 2004-2013 was used for the 2014 values.

## References

- Borowik, T., N. Pettorelli, L. Sönnichsen, and B. Jędrzejewska. 2013. Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. *European Journal of Wildlife Research* 59:675–682.
- Bradley, B. A., and J. F. Mustard. 2007. Comparison of phenology trends by land cover class: a case study in the Great Basin, USA. *Global Change Biology* 14:334–346.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207–231.
- Fu, P., and P. M. Rich. 2002. A geometric solar radiation model with applications in agriculture and forestry. *Computers and Electronics in Agriculture* 37:25–35.
- Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2008. Prey Risk Allocation In A Grazing Ecosystem. *Ecological Applications* 16:285–298.
- Hayes, S. G., D. J. Leptich, and P. Zager. 2002. Proximate factors affecting male elk hunting mortality in northern Idaho. *Journal of Wildlife Management* 66:491–499.
- Hillis, J., M. Thompson, J. Canfield, L. Lyon, C. Marcum, P. Dolan, and D. McCleerey. 1991. Defining elk security: the Hillis paradigm. Pages 38–43 Proceedings of a Symposium on Elk Vulnerability, Bozeman, Montana.
- Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* 101:591–601.
- Jonsson, P., and L. Eklundh. 2002. Seasonality extraction by function fitting to time-series of satellite sensor data. *IEEE Transactions on Geoscience and Remote Sensing* 40:1824–1832.
- Laporte, I., T. B. Muhly, J. A. Pitt, M. Alexander, and M. Musiani. 2010. Effects of wolves on elk and cattle behaviors: implications for livestock production and wolf conservation. *PloS one* 5:e11954.
- Logan, K. A., and L. L. Irwin. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. *Wildlife Society Bulletin* 13:257–262.
- Lyon, L. J. 1979. Habitat Effectiveness for Elk As Influenced By Roads and Cover. *Journal of Forestry* 77:658–660.
- Lyon, L. J. 1983. Road Density Models Describing Habitat for Elk. *Journal of Forestry* 81:592–596.

McCorquodale, S. M. 2013. A Brief Review of the Scientific Literature on Elk , Roads , & Traffic.

Montgomery, R. A., G. J. Roloff, and J. J. Millspaugh. 2013. Variation in elk response to roads by season, sex, and road type. *The Journal of Wildlife Management* 77:313–325.

Robinson, H. S., T. Ruth, J. A. Gude, D. Choate, R. DeSimone, M. Hebblewhite, K. Kunkel, M. R. Matchett, M. S. Mitchell, K. Murphy, and J. Williams. 2015. Linking resource selection and mortality modeling for population estimation of mountain lions in Montana. *Ecological Modelling* 312:11–25.

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and M. A. Penninger. 2005. Effects of roads on elk: implications for management in forested ecosystems. Pages 42–52 2004 Transactions of the North American Wildlife and Natural Resources Conference. Alliance Communications Group, Lawrence, Kansas.

White, M. A., K. M. de Beurs, K. Didan, D. W. Inouye, A. D. Richardson, O. P. Jensen, J. O'keefe, G. Zhang, R. R. Nemani, W. J. D. van Leeuwen, J. F. Brown, A. De Wit, M. Schaepman, X. Lin, M. Dettinger, A. S. Bailey, J. Kimball, M. D. Schwartz, D. D. Baldocchi, J. T. Lee, and W. K. Lauenroth. 2009. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. *Global Change Biology* 15:2335–2359.