# MODELING PLANT SPECIES DISTRIBUTIONS ACROSS IDAHO
# TO INFORM UNGULATE NUTRITION

A Thesis
Presented in Partial Fulfillment of the Requirements for the
Degree of Master of Science
with a
Major in Environmental Science
in the
College of Graduate Studies
University of Idaho
by
Tara M. Ball

Major Professor: Eva K. Strand, Ph.D.
Committee Members: Jocelyn L. Aycrigg, Ph.D.; Timothy R. Johnson, Ph.D.
Department Administrator: J. D. Wulfhorst, Ph.D.

May 2018

**Authorization to Submit Thesis**

This thesis of Tara M. Ball, submitted for the degree of Master of Science with a Major in Environmental Science and titled "MODELING PLANT SPECIES DISTRIBUTIONS ACROSS IDAHO TO INFORM UNGULATE NUTRITION," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor: ______________________________ Date____________________

Eva K. Stand, Ph.D.

Committee Members: ______________________________ Date:____________________

Jocelyn L. Aycrigg, Ph.D.

______________________________ Date:____________________

Timothy R. Johnson, Ph.D.

Department Administrator: ______________________________ Date____________________

J. D. Wulfhorst, Ph.D.

## Abstract

Mechanisms driving ungulate population declines are complex and poorly understood. Limitations in forage availability or quality may be contributing, but current habitat assessments lack fine-scale vegetation information needed to evaluate nutrition. To fill this gap, I developed predictive distribution models for ungulate forage species across Idaho using existing vegetation surveys, maps, and remotely-sensed data. Models predict plant species presence, and provide key insight to species-environment relationships that can aide habitat management strategies to improve nutritional quality. Additionally, I examined elk habitat selection on a summer range in north-central Idaho. Selection was influenced by the presence of herbaceous plant species and wildfire disturbance. Management strategies that re-open matured forest canopies that currently limit herbaceous understory vegetation will be useful for enhancing the nutritional quality of elk summer habitat. Considerations for non-native plant infestations in areas of highly recurrent and severe wildfires will also be important.

## Acknowledgements

Funding for this project was provided by the Idaho Department of Fish and Game and the University of Idaho. My committee (Eva K. Strand, Jocelyn L. Aycrigg, and Timothy R. Johnson) were instrumental in the overall design and review of this project. They provided generous support, guidance, and evocative questions to ensure scientific rigor. I thank members from the Idaho Department of Fish and Game (Leona Svancara, Mark Hurley, Jon Horne, and Shane Roberts) for providing valuable insight and criticisms throughout the process. I thank members from the University of Idaho (Ryan McCarley, Megan Lonneker, and Brian Stevens) for additional help with programming and statistical applications to the natural world. Most of all I thank my family, friends, fellow graduate students and coworkers who endured the many swings of my project, high and low, and for accepting my incredible hermit capabilities during the final three months.

**Dedication**

I dedicate this work to those who feel they are incapable.

If you don’t see the light, keep going.

‘Today is hard, tomorrow will be worse, but the day after tomorrow will be sunshine’

# Table of Contents

# List of Tables

## Chapter 1



## Chapter 2

## List of Figures

## Chapter 1 : Predicting plant species distributions to inform ungulate nutrition.

### Abstract

The continual decline of ungulate populations in the western U.S. suggests key mechanisms driving wildlife populations are complex and poorly understood. Nutrition affects individual fitness and population dynamics, but current vegetation maps are too coarse thematically and spatially to effectively characterize habitat nutritional quality. Additionally, temporal changes in vegetation structure and composition resulting from natural disturbance events or human management activities are often not considered. To fill these gaps, our study used existing vegetation surveys, maps, and remotely-sensed data to develop models that predict plant species distributions at finer scales, and across broad landscapes. We modeled 20 plant species in Idaho, that are accepted forage for mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*). Climatic, topographic, soil, vegetation, and disturbance variables were used to identify key environmental gradients. Lasso logistic regression was implemented to produce predictive models. We found that proximal environmental variables (e.g. 30-year normal minimum precipitation, 30-year normal minimum temperature, solar radiation) were more informative than distal environmental variables (e.g. elevation, aspect, slope) when predicting the probability of plant species presence. We also found that each plant species model selected different environmental variables suggesting individual species response to environmental gradients. All models provided high predictive accuracy (average AUC 0.82) and revealed key species-environment relationships that can be supported in ecological theory. Our approach is novel and can inform ungulate nutrition by predicting the occurrence of accepted forage species presence and aide habitat management strategies to improve nutritional quality across Idaho.

### Introduction

The continual decline of ungulate populations in the western U.S. suggests key mechanisms driving wildlife populations are complex and poorly understood (Tollefson et al. 2011, Cook et al. 2016, Proffitt et al. 2016). The recovery of large carnivores has resulted in increased predation on ungulates, directing management towards predator control, however, bottom up effects such as habitat nutrition and climate partially compensate the magnitude of predatory effects (Shallow et al. 2015, Proffitt et al. 2016). For example, prey populations are likely to experience greater adversity from predation in areas of less productive habitat or severe climates (Melis et al. 2009, Proffitt et al. 2016). Therefore, it is important to examine the bottom up effects, such as habitat nutritional quality, driving ungulate populations.

Declines in forage quality and nutritional conditions could be contributing to declining ungulate populations (Crete and Huot 1993, Enk et al. 2001, White et al. 2010, Tollefson et al. 2010, 2011, Monteith et al. 2015, Cook et al. 2004, 2016, Hurley et al. 2017). Yet, fine-scale vegetation assessments needed to examine habitat nutritional quality across broad landscapes are limited. National mapping efforts such as LANDFIRE (www.landfire.gov), the USGS Gap Analysis Project (http://gapanalysis.usgs.gov/), and the National Land Cover Database (www.mrlc.gov) have mapped vegetation across large spatial scales describing plant communities or ecological systems, but lack information regarding individual plant species distributions. Alternatively, species distribution models (SDMs) are used to study species-environment relationships and make predictions of species occurrence across their range. Approaches include data-driven statistical analyses (generalized linear models, Bayesian hierarchies, and occupancy models), principal component analyses (MaxEnt), and other algorithm-driven, machine learning analyses (Random Forests and regression trees) (Hegel et al. 2010). However, most SDMs are applied locally rather than across landscapes.

Plant species distributions vary with environmental gradients and disturbance events across landscapes (Harmon et. al. 1984, Austin 2002, Merow et al. 2014). In SDMs environmental variables are used to describe such influences based on their relationship to plant growth and adaptation. Proximal environmental variables exert direct physiological effects on plants (e.g. solar radiation, temperature, and disturbance) whereas distal environmental variables influence plant processes indirectly (e.g. elevation, slope, and aspect) (Austin 2002, Austin and Van Niel 2011, Merow et al. 2014). Distal variables are often used as surrogates for more proximal variables, but this may allude to inaccurate representations of species-environment relationships (Austin and Van Niel 2011, Merow et al. 2014). These relationships are relatively unknown across broad landscapes therefore we sought to understand why individual plant species occur where they do on the landscape to better inform ungulate nutrition.

As a part of a larger collaborative effort with the Idaho Department of Fish and Game (IDFG; Aycrigg et al. 2017), we used existing vegetation surveys, maps, and remotely-sensed data to develop models that predict plant species distributions at finer scales, and across broad landscapes. We focused on plant species in Idaho, that are accepted forage for mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*). Our objective was to build models that predict the probability of plant species presence and identify key environmental variables influencing forage species distributions to better inform ungulate nutrition. We hypothesized that lasso logistic regression would provide accurate predictions of plant species occurrence for multiple plant species across Idaho. To test this, we modeled plant species with different lifeforms, taxonomic groups, and environmental tolerances. We predicted all plant species models would provide better predictive accuracies than chance. In addition, we compared two models for each plant species (one containing proximal and distal environmental variables and a second containing only proximal environmental variables) to determine the relative effects of proximity on plant species distributions with regards to environmental gradients and disturbance events.

## Methods

### *Study area*

Idaho (216,440km$^2$) is ecologically diverse, comprising five Bailey's ecoregions, and fourteen ecological sub sections (Bailey et al. 1994, IDFG 2017). Key habitat types include: arable land, dry and mesic coniferous forests, subalpine forests, deciduous forests and shrublands, dry canyon grasslands, wetlands, riparian woodlands, xeric shrublands and steppe, Palouse prairie, non-native herbaceous lands, dunes, and rocklands (IDFG 2017). The state is naturally divided into two regions, North Idaho (i.e. the Panhandle) and southern Idaho, by east-west mountain ranges and a time change crossing the Salmon River near the town of Riggins. Indicators of statewide climate change between 1975 and 2010 show water availability, drought, and wildfire have departed from historic conditions (Klos et al. 2015). Documented changes include significant decreases in the volume of annual streamflow, increasing precipitation intensity, and extended wildfire seasons (Klos et al. 2015). Consequently, plant species compositions and wildlife habitat are being altered.

### *Unit of analysis*

To model plant species presence statewide, we created a spatial data layer of spectrally similar polygons to use as our sample unit of analysis. Polygons were developed by segmenting 2015 1m resolution NAIP imagery based on red, green, blue, and near infrared spectral values (http://www.insideidaho.org, Trimble 2015, Aycrigg et al. 2017). Our intent was to minimize variation in vegetation characteristics within polygons and capture variation between polygons.

*Vegetation surveys*

We compiled vegetation survey data collected by the Bureau of Land Management (BLM) and the IDFG between 2012 and 2016 to spatially join with our segmented polygons. Surveys consisted of 50-100m transects sampled every half meter or meter respectively (100 points) using line-point intercept (Herrick et al. 2005). At each point, a pin was dropped and all plant species intercepted were recorded, including interceptions with rock, litter, duff, bare ground, lichen, and moss. This method provides a less biased estimate of plant cover, because the only decision made is whether a plant species is intercepted at a given point (Elzinga et al. 2001). Canopy cover for each plant species was estimated for each polygon, by dividing the total number of point occurrences by the number of species interceptions.

*Environmental variables*

We used remotely-sensed data and existing maps to generate environmental variables, which we attributed to our polygons using mean or mode values. We divided variables into five categories: climatic, topographic, soil, vegetation and disturbance. Climatic variables included 30-year normal temperature (°C) and precipitation (mm) values from PRISM climate data 1981-2010 (Gibson et al. 2002), downscaled to a 250 m resolution using cubic convolution (ArcGIS 10.3; ESRI, Redlands, California) for precipitation and an empirical algorithm for temperature (Holden et al. 2011). Topographic variables were generated from a 10 m digital elevation model (DEM; http://www.insideidaho.org) including elevation (m), slope (degrees), aspect (degrees), and indices for solar radiation (insolation), topographic wetness (determines hydrologic influence; Moore et al. 1993), slope position (classifies hilltops, valley bottoms, exposed ridges, and flat plains) and landscape curvature ( indicates if surface is convex or concave). Soil characteristic variables were generated by stitching the Natural Resource Conservation Service's (NRCS) soil surveys together, SSURGO and STATSGO 1902-2015, to generate a combined dataset across Idaho. Variables included soil available water supply (cm), percent clay, percent sand, percent silt, percent organic matter, percent calcium carbonate, pH, cation-exchange capacity (mEq/100g), and depth to restrictive layer (cm) (IDFG, unpublished data; SSURGO and STATSGO). Vegetation variables included percent canopy cover of trees (30 m; Homer et al. 2015) and percent canopy cover of shrubs (30 m; LANDFIRE 2011). Disturbance variables included wildfire characteristics generated from the Monitoring Trends in Burn Severity 30 m burn severity data between 1984 and 2014 (MTBS 2017). The two wildfire variables were time since most recent wildfire (years) and wildfire frequency (years). The centroid latitude and longitude of each polygon were also included to examine locational influences on plant species distributions. All environmental variables were included based on functional scale and data availability. Developed areas, agricultural areas, barren land, and perennial snow and ice were omitted for the purpose of modeling natural vegetation and ungulate habitat.

*Predictive distribution modeling*

We used lasso logistic regression (lasso hereafter; Tibshirani 1996) via the 'glmnet' package in R (Friedman et al. 2010) to predict the probability of plant species presence within polygons and to identify the most informative environmental variables influencing their distributions. The lasso applies a penalty term to the maximum likelihood function which forces coefficients towards zero if they do not improve model prediction (Tibshirani 1996, Hastie et al. 2017). This causes some coefficients to become zero, effectively eliminating their corresponding predictors (i.e. environmental variables) from the model, providing a pragmatic approach for variable selection (Tibshirani 1996, Hastie et al. 2017). We validated model predictive accuracy using cross validation (k=10) and the area under the curve (AUC) of the receiver-operating characteristic (ROC) curve (Hanley and McNeil 1982).

## Results

Approximately 44.3 million polygons were segmented across Idaho. Of these, 3,500 contained vegetation survey data which included 463,808 points (Table 1). We attributed 28 environmental variables across all polygons and modeled the probability of presence for 20 accepted forage species (Table 2 and 3). We identified 12 environmental variables as proximal, having direct physiological effects on plant growth. Thirty-year normal minimum temperature and depth to soil restrictive layer have direct effects on cellular and root growth respectively. Thirty-year normal minimum precipitation, total annual precipitation, and soil available water supply directly affect water uptake. Soil organic matter and calcium carbonate provide direct nutrient sources, and solar radiation directly regulates photosynthesis and soil moisture. Tree and shrub canopy cover directly influence space and competition, and lastly, time since last wildfire and wildfire frequency exhibit direct effects of disturbance.

For each plant species model, we generated a cross validation curve, which included the number of variables that were selected by the lasso and an average AUC at each penalty (See Figure 1 for an example). Further, we produced table outputs of the selected variables and their associated coefficients grouped by lifeform (grasses, forbs, shrubs, and trees; Appendix 1). Because models were fit using logistic regression, coefficients were placed on the logit scale therefore we exponentiated coefficients to be interpreted as odds ratios. Thus, the probability of plant species presence was interpreted based on a one unit change of the selected environmental variables. For example, in the model containing only proximal environmental variables for predicting the presence of sticky purple geranium (*Geranium viscosissimum*), soil available water supply was selected as an important variable with the exponentiated coefficient of 1.14. This meant for every one-unit increase in soil available water supply (1 cm), the odds of sticky purple geranium being present, increased by 14%.

All models provided higher predictive accuracy than chance, with a mean AUC of 0.82. Models containing both distal and proximal variables had AUC values that ranged from 0.69-0.97 with a mean value of 0.83, selecting on average 11 variables (Table 4, Appendix 1). Whereas models containing only proximal variables had AUC values ranging from 0.67-0.96 with a mean value of 0.81, selecting on average 5 variables (Table 4, Appendix 1). The most common selected environmental variables across all plant species models were: 30-year normal minimum precipitation, 30-year normal minimum temperature, soil available water supply, percent tree canopy cover, percent shrub canopy cover, soil percent organic matter, and soil percent calcium carbonate. Species models that selected wildfire as key indicators of presence were: Sandberg bluegrass (*Poa secunda*), Idaho fescue *(Festuca idahoensis*), arrowleaf balsamroot (*Balsamorhiza sagittata),* lupine (*Lupinus ssp.*), yarrow (*Achillea millefolium*), mountain big sagebrush (*Artemisia tridentata ssp. vaseyana*), antelope bitterbrush (*Purshia tridentata*), and mallow ninebark (*Physocarpus malvaceus*). Remaining variables were either less common or specific to certain lifeforms—e.g. soil percent clay was commonly selected for grass species.

Pinegrass (*Calamagrostis rubescens*), sticky purple geranium, mallow ninebark, and lodgepole pine (*Pinus contorta*) had models with the highest predictive accuracies for each plant lifeform (Appendix 1). Pinegrass presence was positively correlated with 30-year normal minimum precipitation, soil available water supply, and percent tree canopy cover and negatively correlated with 30-year normal minimum temperature, soil depth to restrictive layer, and percent shrub canopy cover (Appendix 1). Sticky purple geranium presence was positively correlated with 30-year normal minimum precipitation and soil available water supply and negatively correlated with 30-year normal minimum temperature and soil percent calcium carbonate (Appendix 1). Mallow ninebark presence was positively correlated with soil percent calcium carbonate and percent tree canopy cover, and negatively correlated with time since last wildfire (Appendix 1). Lodgepole pine presence was positively correlated with 30-year normal minimum precipitation and soil percent organic matter, and negatively correlated with percent shrub canopy cover and 30-year normal minimum temperature (Appendix 1).

**Discussion**

Using lasso logistic regression we predicted the probabilities of plant species presence for 20 accepted forage species for mule deer and Rocky Mountain elk across Idaho. We identified key environmental gradients using climatic, topographic, soil, vegetation, and disturbance variables that were included based on functional scale and data availability. A growing consensus in the ecological literature suggests the incorporation of variables based on their operative (i.e. functional) scale will yield more robust models, provide stronger predictions, and provide more reliable inferences of ecological relationships (Store and Jokimaki 2003, Weaver et al. 2012, Miller et al. 2015, McGargial et al. 2016). Similarly, we found the inclusion of environmental variables at their functional scale provided accurate predictions of plant species presence statewide, and provided insight for underlying mechanisms driving their distributions.

We predicted all models would provide higher predictive accuracy than chance, which was observed, with an average AUC of 0.82. Predictive accuracies between models containing both distal and proximal variables versus models containing only proximal variables were similar. Yet, models containing only proximal variables were reduced by the lasso considerably in terms of the number of selected variables, suggesting a more practical approach for future modeling efforts. In addition, the most commonly selected environmental variables across all models were proximal (Appendix 1). Therefore, we suggest proximal environmental variables are the most informative to include in plant species distribution models.

Our use of the lasso to achieve model optimization, variable selection, and coefficient estimation in regression for plant species distribution modeling has rarely been implemented in ecological research (Elith et al. 2006, Phillips and Dudik 2008, Breiner et al. 2015). One of the greatest challenges in species distribution modeling is selecting appropriate candidate variables (Araujo and Guisan 2006, Elith and Leathwick 2009), and the lasso provides a reasonable solution. It restrains the effects of the coefficients to identify variables that contribute little to the explanation of the response and removes those variables from the model. Consequently, the lasso treats issues with multi-collinearity and reduces model complexity (Tibshirani 1996, Dormann et al. 2013, Hastie et al. 2017). This approach is useful in situations like ours, where the information about numerous environmental variables and their relative influence on multiple plant species distributions is limited.

Alternatively, other techniques have been implemented to model plant species distributions. Growing applications of MaxEnt have emerged in the ecological literature and resource management with over 1000 published applications since 2006 (Merow et al. 2013). However, the use of MaxEnt requires a considerable number of decisions regarding appropriate data inputs and software settings, and the basis for these decisions has been unclear in many studies, or resorted to default selections (Merow et al. 2013). Phillips and Dudik (2008) found with specific parameter tuning, MaxEnt was effective in modeling plant species distributions of 226 plant species from 6 regions, but this kind of detailed parameter tuning requires good statistical knowledge, and their findings suggest more regularization may be needed if the number of environmental variables exceeds the number they analyzed which was 11-13. Further, MaxEnt outputs (i.e. raw values) are not intuitive, and would not have met our study expectations for the following reasons: 1) MaxEnt raw values give important insight about features (variables) by estimating their relative suitability compared to one another, but do not produce estimates of variable effects on the response, 2) raw values must sum to 1 resulting in very small values for each data point making interpretation difficult, and 3) projections of raw values are not necessarily proportional to the probability of occurrence (Phillips and Dudik 2008, Baldwin 2009, Elith et al. 2011).

Classification and regression trees (CART) have also been used to model plant species distributions. These applications however do not provide continuous response curves to illustrate species-environment relationships, nor do they provide generalized probabilistic estimates of species occurrence (Vayssieres et al. 2000). MaxEnt and CART applications may be better suited for analyses looking to capture a broader overview of plant community dynamics. Our use of generalized linear models (GLMs) was best suited to provide more robust, species-specific models (Guisan et al. 1999). Additionally our implementation of lasso logistic regression provided the following advantages: 1) it allowed for consideration of a greater number of environmental variables, 2) did not require refinements of software settings or statistical parameter tuning, 3) provided accurate predictions of the probability of presence for multiple plant species, and 4) provided direct estimates of environmental variable effects (coefficients), that can be used to extrapolate and project forage species distributions statewide.

*Limitations*

Ideally, expert knowledge regarding the underlying mechanisms, interactions, and complex relationships between plant species and environmental variables, and between variables themselves should be incorporated in SDMs (Austin 2002, Evans et al. 2011). However, this fine-scale information is limited across Idaho. We were unable to predict response curves for the numerous plant species and environmental variables involved therefore we assumed a linear combination between the two. This was the simplification of the ecological process that dictates where a plant species occurs. Alternatively, we could have examined the use of non-parametric algorithmic approaches like MaxEnt to explore non-intuitive relationships (Evans et al. 2011). But parametric tests provide structure on otherwise unstructured problems, which is helpful for providing a starting point for data analysis in situations like ours, where the number of possible outcomes is markedly high. Also, our expectations were to estimate the relative effects of environmental variables on plant species occurrence, and extrapolate this information to predict distributions statewide, which is not as straight forward with nonparametric methods (Whitley and Ball 2002, Phillips and Dudik 2008).

Plant species detectability was also limited in our models because vegetation surveys (line-point intercept) did not provide identification of true absences. For example, if a plant species was not recorded at a given point, we presumed it absent, however, this may be inaccurate if the plant species was misidentified, or was intercepted but not seen by the observer. For future analyses, we suggest our polygons be thoroughly sampled including a greater number of vegetation points recorded by different observers to assess detectability.

We also encountered a few limitations with our environmental variables. Percent shrub canopy cover and wildfire variables were generated using LANDFIRE (2011) data, which is not recommended for use in analyses with resolutions < 30 m (Vogelmann et al. 2006). Also, LANDFIRE generates wildfire layers using entire fire perimeters meaning unburned or low severity areas within perimeters are not accounted for separately. Regardless, LANDFIRE products represent an integration of the best available data in remote sensing, landscape fire and succession modeling, and predictive landscape mapping (Vogelmann et al. 2006). Additional variables were questionable providing either the same affect across all plant species models (solar radiation and total annual precipitation) or no affect at all (landscape curvature and topographic slope position). We recommend these variables be further evaluated prior to their inclusion in additional plant species distribution models.

*Ecological inference*

Our models demonstrated good predictive properties, and revealed key species-environment relationships that can be supported in ecological theory. For example, pinegrass is predominately a forest species and exhibits increased growth response to disturbance in years with higher precipitation and/or cooler temperatures (Parish et al. 1996, FEIS 2017). Respectively, our model exhibited positive correlations with percent tree canopy cover and 30-year normal minimum precipitation, and negative correlations with percent shrub canopy cover and 30-year normal minimum temperature. Pinegrass also has high soil water usage during its rapid early-season growth and acts as an aggressor for soil moisture which may explain the positive correlation observed with soil available water supply (FEIS 2017). Our model also designated a negative correlation with depth to soil restrictive layer which may be explained by pinegrass' sod-forming root system and occupancy of shallower sites (Agee 1996, FEIS 2017). Furthermore, pinegrass presence is indicative of wildfire disturbance and highly severe wildfire events (Johnson 1998, FEIS 2017). Therefore, high presence of this species may indicate areas of high nutritional quality for ungulates following a recent wildfire disturbance. Such inferences are needed to better examine plant species distributions, habitat nutritional quality, and related effects influencing ungulate populations statewide.

*Management implications*

Large carnivore recovery in the western U.S. has led managers to place greater efforts towards controlling top-down effects on ungulate populations, such as predation (Proffitt et al. 2016). However, the magnitude of predatory effects is partially compensated by bottom-up drivers like habitat nutrition (Shallow et al. 2015, Proffitt et al. 2016). Nutrition drives individual fitness and various aspects of ungulate population dynamics (Crete and Huot 1993, Enk et al. 2001, White et al. 2010, Tollefson et al. 2010, 2011, Monteith et al. 2015, Cook et al. 2004, 2016, Hurley et al. 2017). However, current vegetation maps are too coarse thematically and spatially to effectively characterize nutrition. Our predictive plant species distribution models provide resource managers a tool to evaluate nutritional quality across broad landscapes. Estimated probabilities of plant species presence can be extrapolated and mapped statewide to exhibit areas of high or low forage occurrence. Further, model parameters can be used to investigate key relationships between plant species distributions, environmental gradients, and disturbance events. To strengthen our models, we suggest field validation and greater sampling efforts be executed statewide to build upon existing vegetation surveys. We also suggest variables be considered relative to their proximate effects on plant growth and adaptation. Additional variables that might be considered include: seasonal effects of temperature and precipitation (e.g. growing season precipitation), shrub and tree canopy cover at finer resolutions, influences of other plant species and interactions, and wildfire severity. Our study provides a novel approach for predicting fine-scale vegetation across broad landscapes to inform ungulate nutrition and better understand why plant species occur where they do on the landscape.

## References

Agee, J.K., 1996. Fire ecology of Pacific Northwest forests. Island Press. Washington, D.C. 493 pp.

Araujo, M. B. and A. Guisan, 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography (33): 1677-1688.

Austin, M. P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecological Modeling (157): 101-118.

Austin, M. P. and K. P. Van Niel, 2011. Improving species distribution models for climate change studies: variable selection and scale. Journal of Biogeography 38: 1-8.

Aycrigg, J. A., T. R. McCarley, E. K. Strand, T. R. Johnson, R. Long, and M. Lonneker, 2017. Development of a vegetation map for predicting nutritional condition of ungulate habitat in Idaho. Final Project Report, Submitted to the Idaho Department of Fish and Game, Boise, USA.

Bailey, R. G., P. E. Avers, T. King, and W. H. McNab, 1994. Ecoregions and subregions of the United States (map) (supplementary table of map unit descriptions compiles and edited by McNab, W.H. and Bailey, R.G.): Washington, D.C., USFS, scale: 1: 7,500,000.

Baldwin, R. A. 2009. Use of Maximum Entropy Modeling in Wildlife Research. Entropy 11(4): 854-866.

Breiner, F. T., A. Guisan, A. Bergamini, and M. P. Nobis, 2015. Overcoming limitations of modeling rare species by using ensembles of small models. Methods in Ecology and Evolution 6(10): 1210-1218.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. I. M. Delcurto, L. D. Bryant, and L. L. Irwin, 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 1551:1-61.

Cook, J. G., R. C. Cook, R. W. Davis, and L. L. Irwin, 2016. Nutritional Ecology of Elk During Summer and Autumn in the Pacific Northwest. Wildlife Monographs 195:1-81.

Crête, M. and J. Huot, 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 7111:2291-2296.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carre, J. R. Garcia Marquez, B. Gruber, B. Lafourcade, P. J. Leitao, T. Munkemuller, D. Zurell, and S. Lautenbach, 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography (36): 027-046.

Elith. J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, A., R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. M. Overton, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón,, S. Williams, M. S. Wisz, and N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2): 129-151.

Elith, J. and J. R. Leathwick, 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. The Annual Review of Ecology, Evolution, and Systematics 40: 677-97.

Elith, J., S. J. Phillips, T. Hastie, M. Dudik, Y. E. Chee, and C. J. Yates, 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17(1): 43-57.

Elzinga, C. L., D. W. Salzer, J. W. Willoughby, and J. P. Gibbs, 2001. Monitoring plant and animal populations. Blackwell Science, Massachusetts. 368 p.

Enk, T. A., H. D. Picton, and J. S. Williams, 2001. Factors Limiting a Bighorn Sheep Population in Montana Following a Dieoff. Northwest Science 75(3): 280-291.

Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman, 2011. Modeling Species Distribution and Change Using Random Forest. In: Drew C., Wiersma Y., Huettmann F. (eds) Predictive Species and Habitat Modeling in Landscape Ecology. Springer, New York, NY, USA.

Fire Effects Information System (FEIS), 2017. Syntheses about fire ecology and fire regimes in the United States. United States Department of Agriculture. https://www.feis-crs.org/feis/. Accessed 4 November 2017.

Friedman, J., T. Hastie, and R. Tibshirani, 2010. Regularization Paths for Generalized Linear Models via Coordinate Descent. Journal of Statistical Software 33(1): 1-22.

Gibson, W.P., C. Daly, T. Kittel, D. Nychka, C. Johns, N. Rosenbloom, A. McNab, and G. Taylor. 2002. Development of a 103-year high-resolution climate data set for the conterminous United States. In: Proc., 13th AMS Conf. on Applied Climatology, Amer. Meteorological Soc., Portland, OR, May 13-16, 181-183.

Guisan, A., S. B. Weiss, and A. D. Weiss, 1999. GLM versus CCA Spatial Modeling of Plant Species Distributions. Plant Ecology 143: 107-122.

Hanley, J. A. and B. J. McNeil, 1982. The Meaning and Use of the Area under the Receiver Operating Characteristic (ROC) Curve. Radiology (143):29-36.

Harmon, M. E., S. P. Bratton, and P. S. White, 1984. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. Plant Ecology 55(3): 129-139.

Hastie, T., R. Tibshirani, and J. Friedman, 2017. The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Second Edition. Springer, Stanford, California. 745p.

Hegel, T. M., S. A. Cushman, J. Evans, and F. Huettmann, 2010. Current State of the Art for Statistical Modelling of Species Distributions. In: Cushman S. A., Huettmann F. (eds) Spatial Complexity, Informatics, and Wildlife Conservation. Springer, Tokyo.

Herrick, J. E., J. W. Van Zee, K. M. Havstad, L. M. Burkett, and W. G. Whitford, 2005. Monitoring manual for grassland, shrubland, and savanna ecosystems. Volume I: Quick Start. USDA-Ars Jornada Experimental Range, New Mexico. 15p.

Holden, Z. A., J. T. Abatzoglou, C. H. Luce, and L. S. Baggett, 2011. Empirical downscaling of daily minimum air temperature at very fine resolutions in complex terrain. Agricultural and Forest Meteorology 151: 1066-1073.

Homer, C.G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N.D., Wickham, J.D., and Megown, K., 2015, Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing, v. 81, no. 5, p. 345-354

Hurley, M. A., M. Hebblewhite, P. M. Lukacs, J. J. Nowak, J-M. Gaillard, and C. Bonenfant, 2017. Regional-scale models for predicting overwinter survival of juvenile ungulates. The Journal of Wildlife Management 81(3):364-378.

Idaho Department of Fish and Game (IDFG), 2017. Idaho State Wildlife Action Plan, 2015. Boise (ID): Idaho Department of Fish and Game. Grant No.: F14AF01068 Amendment #1. Available from: http://fishandgame.idaho.gov/. Sponsored by the US Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program.

Johnson, C. G. Jr., 1998. Vegetation response after wildfires in national forests of northeastern Oregon. R6-NR-ECOL-TP-06-98. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 128 p.

Klos, P. Z., J. T. Abatzoglou, A. Bean, J. Blades, M. A. Clark, M. Dodd, T. E. Hall, A. Haruch, P. E. Higuera, J. D. Holbrook, V. S. Jansen, K. Kemp, A. Lankford, T. E. Link, T. Magney, A. J. H. Meddens, L. Mitchell, B. Moore, P. Morgan, B. A. Newingham, R. J. Niemeyer, B. Soderquist, A. A. Suazo, K. T. Vierling, V. Walden, and C. Walsh, 2015. Indicators of Climate Change in Idaho: An Assessment Framework for Coupling Biophysical Change and Social Perception. Weather, Climate, and Society 7: 238-254.

LANDFIRE, 2011. Existing Vegetation Cover Layer, LANDFIRE 1.1.0, U.S. Department of the Interior, Geological Survey. Accessed 9 December 2017.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman, 2016. Multi-scale habitat selections modeling: a review and outlook. Landscape Ecology 31(6): 1161-1175.

Melis, C., B. Jędrzejewska, M. Apollonio, K. A. Bartoń, W. Jędrzejewski, J. D.C. Linnell, I. Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykyy, K. Krapinec, L. Mattioli, A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvyrya, V. E. Sidorovich, B. Zawadzka, and S. Zhyla, 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global Ecology and Biogeography 19: 724-734.

Merow, C., M. J. Smith, and J. A. Silander Jr., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36(10): 1058-1069.

Merow, C., M. J. Smith, T. C. Edwards, A. Guisan, S. M. McMahon, S. Normand, W. Thuiller, R. O. Wüest, N. E. Zimmermann, and J. Elith, 2014. What do we gain from simplicity versus complexity in species distribution models. Ecography 37: 1267-1281.

Miller, B. A., S. Koszinski, M. Wehrhan, and M. Sommer, 2015. Impact of multi-scale predictor selection for modeling soil properties. Geoderma 239-240: 97-106.

Monteith, K. L., R. W. Klaver, K. R. Hersey, A. A. Holland, T. P. Thomas, and M. J. Kauffman. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. Oecologia 178:1137-1148.

Moore, I. D., P. E. Gessler, G. A. Nielsen, and G. A. Petersen, 1993. Terrain attributes: estimation methods and scale effects. In Jakeman, A.J.; Beck, M.B.; McAleer, M. Modelling Change in Environmental Systems. London: Wiley. p. 189 – 214.

MTBS Data Access: Thematic Burn Severity (2017, July - last revised). MTBS Project (USDA Forest Service/U.S. Geological Survey). http://mtbs.gov/data/direct-download. Accessed 9 December 2017.

Parish, R., R. Coupe, and D. Lloyd, 1996. Plants of the Southern Interior British Columbia and the Inland Northwest. B.C. Ministry of Forests and Lone Pine Publishing, Alberta. 463p.

Phillips, S. J. and M. Dudik, 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2): 161-175.

Shallow, J. R. T., M. A. Hurley, K. L. Monteith and R. T. Bowyer, 2015. Cascading effects of habitat on maternal condition and life-history characteristics of neonatal mule deer. Journal of Mammology 96:194-205.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database for Idaho. Accessed 9 December 2017.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. U.S. General Soil Map (STATSGO2). Accessed 9 December 2017.

Store, R. and J. Jokimaki, 2003. A GIS-based multi-scale approach to habitat suitability modeling. Ecological Modelling 169(1): 1-15.

Tibshirani, R., 1996. Regression Shrinkage and Selection via the Lasso. Journal of the Royal Statistical Society. Series B (Methodological), Volume 58, Issue 1: 267-288.

Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler, and N. Dasgupta, 2010. Influence of Summer and Autumn Nutrition on Body Condition and Reproduction in Lactating Mule Deer. Journal of Wildlife Management 74(5): 974-986.

Tollefson, T. N., L. A. Shipley, W. L. Myers, and N. Dasgupta, 2011. Forage Quality's Influence on Mule Deer Fawns. The Journal of Wildlife Management 75(4): 919-928.

Trimble, 2015. Trimble eCognition Suite. www.eCognition.com. Accessed 9 December 2017.

Vayssieres, M. P., R. E. Plant, and B. H. Allen-Diaz, 2000. Classification trees: An alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11(5): 679-694.

Vogelmann, J., Z. Zhu, J. Kost, B. Tolk, and D. Ohlen, 2006. Perspectives on LANDFIRE Prototype Project Accuracy Assessment. USDA Forest Service Gen. Tech. Rep. RMRS-GTR-175: 397-411.

Weaver, J. E., T. M. Conway, and M. J. Fortin, 2012. An invasive species' relationship with environmental variables changes across multiple spatial scales. Landscape Ecology 27: 1351-1362.

White, C. G., P. Zager, and M. W. Gratson, 2010. Influence of Predator Harvest, Biological Factors, and Landscape on Elk Calf Survival in Idaho. Journal of Wildlife Management 74(3): 355-369.

Whitley, E. and J. Ball, 2002. Statistics review 6: Nonparametric methods. Critical Care 6(6): 509-513.

Table 1—1 Summary of vegetation survey data compiled from line-point intercept transects across Idaho to use in predictive ungulate forage species distribution models. Data source, description and location, total number of vegetation transects, total number of point interceptions, and years collected are included. BLM: Bureau of Land Management, IDFG: Idaho Department of Fish and Game, DIMA: Database for Inventorying and Monitoring.

| Source | Description/ Location | # transects | # points | Years |
|---|---|---|---|---|
| BLM | Sand Creek vegetation data | 118 | 35,400 | 2015 |
| BLM | DIMA data for Lemhi | 398 | 170,750 | 2014-2016 |
| IDFG | DIMA data for Craig Mountain | 107 | 26,750 | 2012 |
| IDFG | Mule deer composition data | 323 | 88,503 | 2012-2014 |
| IDFG | DIMA data for Antelope pocket, Cecil D Andrus, CJ Strike, Fish Creek, Fort Boise, Mountain Home, Payette River, Roswell Marsh, Sand Creek, Ted Trueblood, Tilden flats, Thousand Springs Creek—Whiskey Springs, and Weiser River Ranches | 611 | 151,790 | 2011-2015 |

Table 1—2 Environmental variables used to model plant species distributions across Idaho. Plant species are accepted forage for mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*). Variable category, variable, data description, and data source are included. DEM: digital elevation model. Centroid latitude and longitude of polygons were also included to assess locational influence.

| Category | Variable | Description | Source |
|---|---|---|---|
| Climatic | Minimum precipitation | 30-year normal | Prism.oregonstate.edu |
| | Maximum precipitation | 30-year normal | Prism.oregonstate.edu |
| | Total annual precipitation | 30-year normal | Prism.oregonstate.edu |
| | Minimum temperature | 30-year normal | Prism.oregonstate.edu |
| | Maximum temperature | 30-year normal | Prism.oregonstate.edu |
| Topographic | Elevation | DEM | InsideIdaho.org |
| | Slope | Degree of slope | Calculated from DEM |
| | Aspect (sine & cosine) | North-south, east-west | Calculated from DEM |
| | Topographic wetness | Steady-state wetness | Calculated from DEM |
| | Landscape curvature | Convex, concave, flat | Calculated from DEM |
| | Solar radiation | Incident insolation | ESRI tool |
| | Topographic position | Valleys, ridges | Jennessent.com |
| Soil | Available water supply | Water storage capacity | Nrcs.usda.gov |
| | Percent clay | Soil structure | Nrcs.usda.gov |
| | Percent sand | Soil structure | Nrcs.usda.gov |
| | Percent silt | Soil structure | Nrcs.usda.gov |
| | Cation-exchange capacity | Essential nutrients | Nrcs.usda.gov |
| | Depth to restrictive layer | Root growth | Nrcs.usda.gov |
| | pH | pH | Nrcs.usda.gov |
| | Percent organic matter | Essential nutrients | Nrcs.usda.gov |
| | Percent calcium carbonate | Essential nutrients | Nrcs.usda.gov |
| Vegetation | Percent tree cover | Canopy cover | Nlcd.gov |
| | Percent shrub cover | Canopy cover | Landfire.gov |
| Disturbance | Time since wildfire | Years since last fire | Mtbs.gov |
| | Wildfire frequency | Total number of fires | Mtbs.gov |
| Location | Longitude | Centroid x-coordinate | ESRI tool |
| | Latitude | Centroid y-coordinate | ESRI tool |

Table 1—3 Plants species selected for distribution modeling. All species occur in Idaho and are accepted forage for mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*). Scientific name, common name, and life form are included.

| Scientific name | Common name | Life form |
|---|---|---|
| *Pseudoroegneria spicata* | Bluebunch wheatgrass | grass |
| *Poa secunda* | Sandberg bluegrass | grass |
| *Festuca idahoensis* | Idaho fescue | grass |
| *Calamagrostis rubescens* | Pinegrass | grass |
| *Carex spp.* | Sedge | grass |
| *Lupinus spp.* | Lupine | forb |
| *Balsamorhiza sagittata* | Arrowleaf balsamroot | forb |
| *Achillea millefolium* | Common yarrow | forb |
| *Geranium viscosissimum* | Sticky purple geranium | forb |
| *Mahonia repens* | Creeping Oregon grape | shrub |
| *Artemisia tridentata ssp. vaseyana* | Mountain big sagebrush | shrub |
| *Purshia tridentata* | Antelope bitterbrush | shrub |
| *Symphoricarpos albus* | Common snowberry | shrub |
| *Amelanchier alnifolia* | Saskatoon serviceberry | shrub |
| *Physocarpus malvaceus* | Mallow ninebark | shrub |
| *Populus tremuloides* | Quaking aspen | tree |
| *Prunus virginiana* | Chokecherry | tree |
| *Pseudotsuga menziesii* | Douglas-fir | tree |
| *Salix spp.* | Willow | tree |
| *Pinus contorta* | Lodgepole pine | tree |

Table 1—4 A summary of the average AUC values and number of selected environmental variables (EV) for plant species distribution models with distal and proximal variables, and models with proximal only variables. Plant species are grouped by life form. All plant species occur in Idaho and are accepted forage for mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni* ).

| | Distal and Proximal | | Proximal Only | |
|---|---|---|---|---|
| Species | AUC | # EV | AUC | # EV |
| *Grasses* | | | | |
| Bluebunch wheatgrass | 0.71 | 4 | 0.67 | 6 |
| Sandberg bluegrass | 0.73 | 23 | 0.70 | 7 |
| Sedge ssp. | 0.78 | 5 | 0.75 | 3 |
| Idaho fescue | 0.79 | 18 | 0.72 | 4 |
| Pinegrass | 0.93 | 7 | 0.94 | 6 |
| *Forbs* | | | | |
| Common yarrow | 0.69 | 18 | 0.67 | 4 |
| Lupine ssp. | 0.73 | 11 | 0.68 | 5 |
| Arrowleaf balsamroot | 0.79 | 10 | 0.78 | 7 |
| Sticky purple geranium | 0.86 | 7 | 0.85 | 6 |
| *Shrubs* | | | | |
| Mountain big sagebrush | 0.81 | 18 | 0.79 | 8 |
| Common snowberry | 0.86 | 12 | 0.84 | 4 |
| Creeping Oregon grape | 0.85 | 18 | 0.80 | 6 |
| Saskatoon serviceberry | 0.88 | 6 | 0.87 | 1 |
| Antelope bitterbrush | 0.92 | 18 | 0.88 | 9 |
| Mallow ninebark | 0.96 | 7 | 0.96 | 5 |
| *Trees* | | | | |
| Willow ssp. | 0.77 | 10 | 0.76 | 2 |
| Chokecherry | 0.78 | 1 | 0.78 | 1 |
| Douglas-fir | 0.88 | 4 | 0.87 | 4 |
| Quaking aspen | 0.89 | 5 | 0.86 | 3 |
| Lodgepole pine | 0.97 | 11 | 0.96 | 5 |

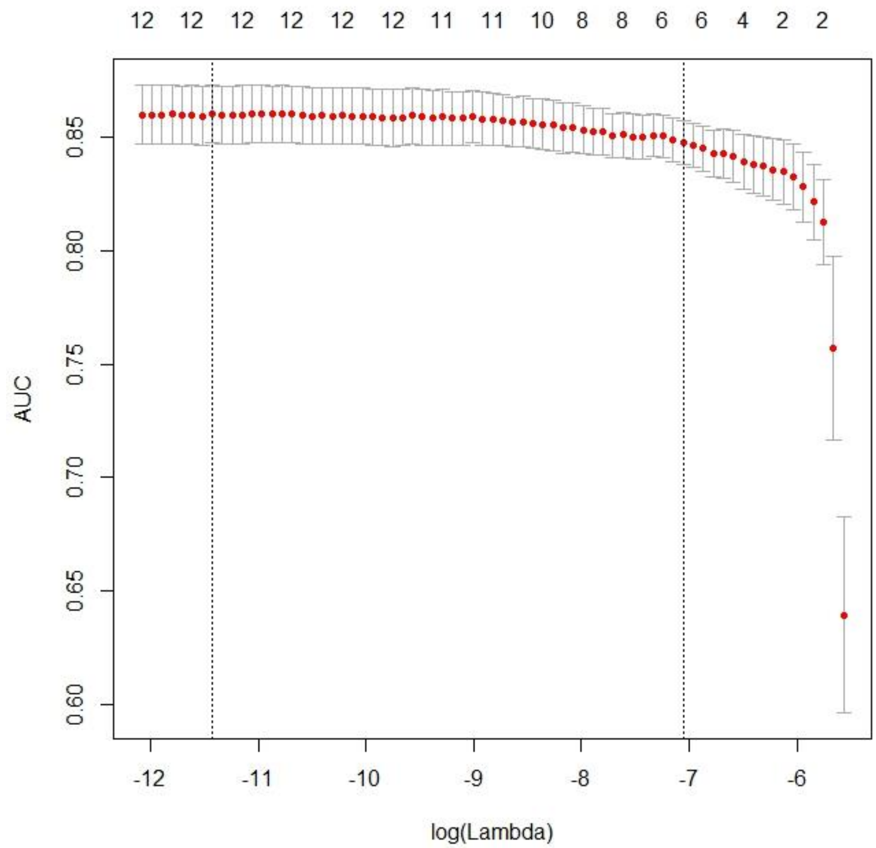


Figure 1—1 Cross validation curve for the model containing only proximal environmental variables for predicting sticky purple geranium (*Geranium viscosissimum*) presence. Graph contains validation curve (red line), average AUC (y-axis), log of the penalty value (lambda; x-axis) and number of selected environmental variables for each penalty (top). Left vertical dotted line represents the penalty value and number of selected environmental variables with the greatest predictive accuracy. Right vertical dotted line represents the penalty value and the number of selected environmental variables within one standard error of the greatest predictive accuracy.

## Chapter 2 : Modeling summer habitat selection by Rocky Mountain elk (*Cervus elaphus nelsoni*) in north-central Idaho.

### Abstract

Rocky Mountain elk (*Cervus elaphus nelsoni*) populations in the Clearwater River Basin in north-central Idaho have declined due to increasing human occupancy, habitat alterations, and increased predation. Growing evidence suggests summer nutrition is especially critical for individual fitness and population dynamics. To understand how Rocky Mountain elk select summer habitat to optimize nutritional needs, lactating females were collared in the Clearwater River Basin to monitor body condition and reproduction. Using GPS locations and resource selection functions (RSFs), I evaluated a series of habitat variables to identify key indicators of summer habitat selection on the Craig Mountain Wildlife Management Area (CMWMA). I found that in the months of July and August, elk selected for habitats that were predicted to support sticky purple geranium (*Geranium viscosissimum*), that were more frequently burned, and that had greater 30-year normal minimum precipitation and available soil water supplies. Elk also exhibited less selection for habitats with greater shrub canopy cover. The presence of herbaceous plant species and wildfire disturbance were the most informative variables for predicting summer habitat selection by elk on the CMWMA. Management strategies that re-open matured forest canopies which are currently limiting herbaceous understory vegetation, will be useful for enhancing the nutritional quality of elk summer habitat. Considerations for non-native plant infestations in areas of highly recurrent and severe wildfires will also be important.

### Introduction

The Clearwater River Basin in north-central Idaho has been significantly altered by highway and reservoir construction, increased fire suppression and decreased timber harvest, predator reintroductions, and infestations of non-native plant species (ERG 2013, CBC 2017). Vegetation has departed from natural conditions as much as 40% (ERG 2013, CBC 2017). Consequently, once-abundant Rocky Mountain elk (*Cervus elaphus nelsoni*; hereafter elk) populations have declined. To address population declines and other long-standing conflicts regarding the depletion of natural resources in the Clearwater River Basin, a partnership of 21 groups was formed (i.e. the Clearwater Basin Collaborative;  CBC), including federal and state agencies, private land owners, tribal nations, county commissioners, conservation groups, recreation groups and producers of livestock, agriculture and timber (ERG 2013, CBC 2017).

Restoration of elk populations in north-central Idaho has since been a primary goal of the CBC (CBC 2017). Specific objectives require the monitoring of elk habitat use, nutritional status, and population conditions with initial efforts directed towards summer range. Inadequate summer nutrition has shown to decrease elk body mass and condition, delay breeding times, and reduce pregnancy rates, overwinter survival, and juvenile recruitment (Cook et al. 2001, 2004, 2016, White et al. 2010). The CBC initiated monitoring efforts by targeting lactating females to assess reproductive status and body condition as indicators of summer nutritional quality. Multiple capture events were conducted between December 2012 and January 2013, of which 82 female elk were collared across the Clearwater River Basin (Hetzner Hagle 2016).

The elk population on the Craig Mountain Wildlife Management Area (CMWMA) has been monitored as one of four distinct populations. In 1992, when the Idaho Department of Fish and Game (IDFG) first acquired the Peter T. Johnson management Unit, the population comprised approximately 500 individuals, and by 2012, tripled in size (Barrett 2014). A survey conducted in 2013 however indicated signs of habitat limitation (IDFG 2014). Female elk nutritional conditions were suboptimal and juvenile recruitment exhibited a marked decline (IDFG 2014). Calf-cow ratios (17:100) were less than half of what was observed in 1996 (37:100; IDFG 2014). Low recruitment and poor nutritional conditions may be indicative of summer habitat limitations, therefore the need to assess habitat selection and nutritional quality, as well as alteration of habitat by non-native plant species, has become a management concern (IDFG 2014).

Resource selection functions (RSFs) can quantitatively assess habitat selection using GPS locations of collared animals by comparing characteristics of used and available habitat (Nielson and Sawyer 2013, Boyce et al. 2016). Used habitat refers to areas with documented animal locations, which may be quantified and described based on type of use (i.e. forage, escape, security, or calving; Krausman 1999, Manly et al. 1993, 2002). Available habitat refers to areas that are accessible or have been encountered by animals during a given temporal period (Manly et al. 1993, 2002). Habitat selection therefore describes how an animal chooses to use or forgo available habitat.

In this study, I examined summer habitat selection by elk on the CMWMA using GPS collar locations. I evaluated different measures of habitat (vegetation, topography, soil characteristics, and disturbance) to predict the relative intensity of elk use and to identify key drivers of summer habitat selection. I hypothesized that summer habitat selection by elk can be estimated using predicted probabilities of forage species occurrence. To test this, I compared RSFs using three variable categories: 1) predicted probabilities of accepted forage species presence, 2) environmental variables important to plant growth and 3) environmental variables important to elk use. I predicted RSFs containing probabilities of accepted forage species presence would provide as accurate, if not better, predictions of elk use as those containing environmental variables, because plant species presence is the direct result of environmental gradients. Therefore, I assumed the probabilities of accepted forage species presence could be used as surrogates for environmental variables, with the idea that model parameters could be reduced, and highly correlated variables (e.g. temperature and elevation) could be avoided.

## Methods

### *Study area*

The CMWMA in north-central Idaho comprises approximately 50,585 hectares of public land bordering eastern Washington and Oregon (Figure 1). Bound by the Snake and Salmon Rivers the area provides critical year-round habitat for many wildlife species (Barrett 2014). The CMWMA is a montane ecological system with vegetation characterized by a rolling forested plateau on top and deeply dissected canyon grasslands following the river breaks (Barrett 2014). Temperatures vary substantially with elevation and season—e.g. an average January low of 22.3°F may be found at higher elevations (1808 m) whereas July temperatures frequent over 100°F in the river canyons (240 m; Barrett 2014). Mean annual precipitation ranges from 340-508 mm falling primarily as snow and spring rains (Barrett 2014). This area is also prone to severe thunderstorms, which in combination with a changing climate has increased the occurrence of wildfires, departing from a historic fire return interval of 5-10 years in the canyon grasslands, to now four wildfires (each >20,000 hectares) in the last ten years (Barrett 2014).

*Elk locations, sample units, and habitat use-availability*

To capture summer habitat selection by elk on the CMWMA, I compiled July and August GPS locations that were recorded in 2014 and 2015. Habitat nutritional conditions in June and September are also likely important, but elk locations and habitat selection may be influenced by calving in June, and hunting in September, thus they were not included in my analysis. My sample units were spectrally similar polygons developed by Aycrigg et al. (2017) which represented more similar vegetation characteristics within polygons than between. Polygons were developed by segmenting 2015 1m resolution NAIP imagery based on red, green, blue, and near-infrared spectral values (http://www.insideidaho.org, Aycrigg et al. 2017). To quantify used and available habitat, I spatially joined elk locations with the polygons and used the minimum bounding geometry tool, convex hull, in ArcGIS 10.3 (ESRI, Redlands, California) to define summer range. I identified polygons within the defined summer range as used—if elk locations occurred within the polygon—or available, otherwise.

*Variables*

I generated three categories of variables to assess habitat selection across polygons. The first category was probabilities of accepted forage species presence (%). I selected plant species that are accepted forage by elk and occur on the CMWMA (Kufeld 1973, Korfhage et al. 1980, Baker and Hobbs 1982, Edge et al. 1987, 1988, Mancuso and Moseley 1994—updated with J. Barrett and L. Danly 2015, NRCS 1999, Alldredge et al. 2002, Innes 2011, Cook J. and R. 2016). I also included yellow star thistle (*Centaurea solstitialis*) because it is the most prevalent non-native plant species. I estimated the probability of presence for each plant species in each polygon using lasso (Tibshirani 1996) logistic regression and the line-point intercept vegetation data and environmental variables generated in chapter one. Further, I identified the top three models (one grass, one forb, one shrub) relative to their influence on elk summer habitat selection via univariate analyses, and used these three species and their associated probabilities of presence as variables for my first variable category. My second variable category included environmental variables that are important to plant growth (i.e., plant variables) which were the most commonly selected environmental variables in chapter one. My third category included a subset of environmental variables from chapter one that have been commonly used in similar resource selection applications, and are important to elk habitat selection (i.e., elk variables).

*Resource selection functions*

Using GPS locations, I generated counts for the number of elk locations within polygons and estimated RSFs using Poisson and negative binomial (NB) regressions. I assumed the size of each polygon had a relative effect on the number elk locations within, thus I included polygon area as an offset term in each model. Therefore, I used variable categories to predict the relative intensity of elk use (i.e. the number of elk locations within polygons relative to polygon area) and evaluated differences between highly used polygons and non-used polygons (i.e. habitat selection). I fit Poisson RSFs using the glm( ) function from the ‘stats’ package in R and NB RSFs using the glm.nb( ) function from the ‘MASS’ package (Venables and Ripley 2002, R 2017). For each RSF and variable category I compared: 1) model coefficients and standard errors, 2) model fit using the AICc and BIC selection criterion, and 3) actual count values (i.e. the number of elk locations within polygons) versus model-predicted values. Due to the multiplicative nature of the log link function, Poisson and NB regressions place coefficients on the natural log scale (Beaujean and Morgan 2016). Therefore to interpret coefficient effects I defined a percent change in the expected counts as

$$\text{Percent Change in Expected Counts} = 100\times [\exp(b \times \Delta)-1]$$

where b was the regression coefficient and $\Delta$ was the amount of change in the variable; which I chose $\Delta = 1$ for a one unit change in the variable (Beaujean and Morgan 2016).

**Results**

My defined summer range included 77, 536 spectrally similar polygons with an average polygon area of approximately 0.42 hectares. I joined 1,404 GPS collared elk locations from 23 individuals (Figure 2) resulting in 1,145 used polygons. The frequency of elk locations in used polygons ranged from 1 to 15 locations with an average frequency of 1.

I identified 29 plant species as accepted forage for elk on the CMWMA (Table 1). Bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*) had the greatest probabilities of presence for grass species across the defined summer range, yellow star thistle for forb species, and common snowberry (*Symphoricarpos albus*) and mallow nine bark (*Physocarpus malvaceus*) for shrub species (Table 2). Based on the univariate analyses, the top species models for each lifeform relative to the intensity of elk summer use were bluebunch wheatgrass, sticky purple geranium (*Geranium viscosissimum*), and common snowberry. The most commonly selected environmental variables that were important to plant growth (i.e. plant variables) were: 30-year normal minimum precipitation (mm), 30-year normal minimum temperature (°C), soil available water supply (cm), percent tree canopy cover, percent shrub canopy cover, and percent soil organic matter. The most common environmental variables used in similar applications of elk habitat selection (i.e. elk variables) were: elevation (m), slope (°), percent tree canopy cover, percent shrub canopy cover, and wildfire frequency (years; Edge et al. 1987, Unsworth et al. 1998, Hebblewhite et al. 2008, Coe et al. 2011, Proffitt et al. 2013, Hetzner Hagle 2016).

*Model comparison*

Across all variable categories, Poisson and NB RSFs exhibited similar regression coefficients (Table 3). NB RSFs however displayed larger standard errors, indicative of a greater allowance for dispersion (Table 3, Beaujean and Morgan 2016). NB RSFs exhibited better fit measures than Poisson RSFs having lower AICc and BIC values (Table 3). NB RSFs also provided more accurate predictions of the relative intensity of elk summer use, whereas Poisson RSFs greatly underestimated these values (Figure 3).

NB regression allowed for accurate predictions across all variable categories, but some variables were more informative than others. Thirty-year normal minimum precipitation, 30-year normal minimum temperature, soil available water supply, wildfire frequency and the probability of sticky purple geranium presence shared positive correlations with the intensity of elk summer use (Table 3). Whereas percent shrub canopy cover, percent soil organic matter, slope, and the probability of bluebunch wheatgrass and common snowberry presence shared negative correlations with the intensity of elk summer use (Table 3). The greatest effect was exhibited by soil available water supply in which every one-unit increase (cm) resulted in a 97% increase in the intensity of elk summer use (Table 3). The least informative variables were percent tree canopy cover and elevation which exhibited zero effects on the relative intensity of elk summer use (Table 3).

**Discussion**

Growing evidence suggests loss of early-seral habitat and the associated effects from inadequate summer nutrition are contributing to elk population declines (Cook et al. 2001, 2004, 2012, 2016, White et al. 2010). Female elk body condition and reproduction is being assessed, but knowledge of underlying mechanisms driving summer habitat selection is limited. To address this limitation, I developed Poisson and NB RSFs to predict the relative intensity of elk summer use on the CMWMA in north-central Idaho. Using predicted probabilities of accepted forage species presence and environmental variables associated with plant species growth and elk habitat selection, I found that each group of variables provided relatively similar predictions of elk summer use, but some variables were more informative than others.

Elk selected for summer habitat predicted to support sticky purple geranium and exhibited less selection for summer habitat predicted to support bluebunch wheatgrass. Sticky purple geranium is valuable summer forage, highly sought by elk (Kufeld 1973). It is aromatic and protocarnivorous meaning it dissolves insects trapped on its sticky leaf surface and absorbs the extra protein and nitrogen which may explain elk attraction to its leaves (Spomer 1999). Conversely, bluebunch wheatgrass is more valuable as a winter-spring forage during early phenological stages when nutrient content is highest (Buechner 1952, Kufeld 1973, Bryant 1993 Westenkowskow-Wall et al. 1994). During July and August (the time-period of this analysis), bluebunch wheatgrass senesces, crude protein and digestible matter deteriorate, and nutrient quality rapidly decreases with moisture and temperature stress (Cook et al. 1956, Bryant 1993).

Elk also exhibited less selection for summer habitats predicted to support common snowberry. This likely relates to the negative relationship observed with percent shrub canopy cover. Similar findings were observed by Hebblewhite et al. (2008) who examined elk foraging behavior in montane ecosystems in the Canadian Rocky Mountains. They found that elk exhibited strong selection for herbaceous forage in summer months, followed by an increased selection for shrubs in autumn (Hebblewhite et al. 2008). Although I did not examine autumn habitat use, Hebblewhite et al.'s (2008) indication of summer forage selection being driven by more herbaceous species in montane systems where shrub quality is always high, compliments findings of this study

Further, elevation and percent tree canopy cover did not influence elk summer habitat selection on the CMWMA. There was little variation in elevation across the defined summer range likely explaining why it was uninformative. Elevation is commonly used as a surrogate for climate mechanisms driving habitat selection in many elk resource selection studies (Edge et al. 1987, Sawyer et al. 2007, Prokopenko et al. 2017). However, elevation did not capture the relative importance of temperature and precipitation across my defined summer range. Conversely, percent tree canopy cover did vary widely suggesting variable effects may have been masked by others, or that tree canopy cover was simply uninformative over the selected temporal period. Elk also selected areas with gentler slopes, which has been observed in other elk habitat selection studies in Idaho and western Montana (Irwin and Peek 1983, Edge et al. 1987).

Elk selected for habitats with greater 30-year normal minimum precipitation, 30-year normal minimum temperature, and soil available water supply. As exhibited in chapter one, these variables are highly important to plant species distributions, and may be especially critical in summer, indicating where the most nutritious forage will be on the landscape with relation to increasing temperatures and water stressors (Akinci and Losel 2012, Hatfield and Prueger 2015). In July and August, palatable and nutritious herbaceous forage is likely found on the CMWMA in areas with greater precipitation, soil moisture, and cooler temperatures.

Elk selected for areas that were more frequently burned. This finding is similar to previous studies exhibiting elk selection for habitat following wildfire events that shift plant communities towards more nutritious herbaceous vegetation (Proffitt et al. 2016). Wildfire is an important ecosystem regeneration process that provides valuable forage for elk however, suppression activities could lead to decreased nutritional quality in mature forests (Long et al. 2008, Proffitt et al. 2016). Areas with more frequent fire also likely reverse the accumulation of soil organic matter (Neff et al. 2005), therefore if elk are selecting for areas with more frequent wildfire, this may explain the negative correlation observed with soil organic matter.

Lastly, soil available water supply, which is the total volume of water in centimeters available to plants, indicated a strong influence on elk summer habitat selection (STATSGO 2017). Soil variables have not been commonly used in elk resource selection studies, but this finding suggests soil may be an indirect driver. Soil available water supply was an important indicator of plant species presence across all species modeled in chapter one and reveals the longevity of water available to plants. Therefore, summer forage quantity, and likely quality, would be expected to be greater in areas containing greater available soil water supplies (Akinci and Losel 2012, STATSGO 2017).

*Limitations*

One of the greatest challenges in resource selection is defining available habitat (Northrup et al. 2013). Many wildlife species including elk are highly mobile and can alter selections of habitat under circumstantial conditions. For example, habitat selection by elk may be altered in the presence of predators or humans (Creel et al. 2005, Frair et al. 2005, Ciuti et al. 2012, Proffitt et al. 2013). Habitat selection thus involves a series of innate and learned behavioral decisions which are poorly understood by managers and research ecologists (Krausman 1999, Manly et al. 1993, 2002, Ciuti et al. 2012). For my study, I used minimum bounding geometry to spatially define an area of interest (i.e. elk summer range on CMWMA) of which I assigned polygons containing GPS locations as used habitat, and all other remaining polygons as available habitat. This definition of available habitat relies on the number of GPS locations and the time at which locations were recorded. A greater sampling of GPS locations over a longer temporal period would better define available habitat and provide a stronger, ecological basis for elk distributions on the CMWMA.

The detection of elk locations was also limited. GPS locations were only transmitted once-daily. Consequently, elk may have used some of the available polygons without being recorded, which would result in failed detections. Failed detections may have also occurred if elk locations prevented transmission (e.g. in densely forested areas or canyon bottoms). Exclusion of failed detections would affect habitat selection estimates and result in habitat bias. However, among the data used in my analysis there were no indications of GPS collars with sub-optimal fix rates. For future analyses, GPS collars that emit more frequent signals could minimize potential habitat bias.

*Management implications*

My results suggest the presence of herbaceous plant species and wildfire disturbance were most informative for predicting summer habitat selection by elk on the CMWMA. Wildfire has remained absent from much of the forested plateau resulting in mature grand-fir (*Abies grandis*) and mixed-conifer habitat types with high canopy closures (Barrett 2014, MTBS 2017). Consequently, understory nutrition is limited. It would be useful for managers to adopt habitat strategies that would re-open canopies using prescribed fire or timber harvest to promote natural vegetation regeneration and provide greater herbaceous foraging opportunities for elk on the CMWMA. Conversely, wildfire frequency and area burned has increased in the canyon grasslands over recent decades (Barrett 2014, MTBS 2017). This has caused increased infestations of non-native plant species along the river corridors (Barrett 2014). The predictive plant species distributions models I have developed in this study and in chapter one can be used to help managers predict where non-native plant species might occur, and extrapolate predictions to various climate, wildfire, or environmental related scenarios to determine how their occurrence will influence elk habitat selection and nutritional quality.

Additionally, resource-selection studies have identified elk response to roads, or other human influences, as key indicators of habitat selection (Irwin and Peek 1983, Edge et al. 1987, Unsworth et al. 1998, Coe et al. 2011, Montgomery et al. 2013, Proffitt et al. 2013). Although these variables were not included in my analysis, elk habitat selection on the CMWMA is likely influenced by human presence. The CMWMA is a popular destination for hunting, camping, winter snow sports, and off-highway vehicle riding, with over 402 km of primary and secondary roads (Barrett 2014). Managers could thus include human disturbance variables, such as distance to roads, in the development of habitat selection models as well as consider better measures for quantifying human presence, such as locational use and frequency of use on the CMWMA.

**References**

Akinci, S. and D. M. Losel, 2012. Plant Water-Stress Response Mechanisms. I.M. Rahman, H. Hasegawa (Eds.), Water Stress, Intech (2012), pp. 27-29.

Alldredge, M.W., J. A. Peek, and W. A. Wall. 2002. Nutritional quality of forages used by elk in northern Idaho. Journal of Rangeland Management 55:253-259.

Aycrigg, J. A., T. R. McCarley, E. Strand, T. Johson, R. Long, and M. Lonneker, 2017. Development of a vegetation map for predicting nutritional condition of ungulate habitat in Idaho. Final Project Report, Submitted to the Idaho Department of Fish and Game, Boise, USA.

Baker, D. L. and N. T. Hobbs, 1982. Composition and Quality of Elk Summer Diets in Colorado. The Journal of Wildlife Management 46(3): 694-703.

Barrett, J., 2014. Craig Mountain Wildlife Management Area: Management Plan 2014-2023. Idaho Department of Fish and Game, Clearwater Region, Lewiston, Idaho.

Beaujean, A. A., and G. B. Morgan, 2016. Tutorial of Using Regression Models with Count Outcomes using R. Practical Assessment, Research, & Evaluation 21: 19pp.

Boyce, M. S., C. J. Johnson, E. H. Merrill, S. E. Nielsen, E. J. Solberg, and B. van Moorter, 2016. Can habitat selection predict abundance? Journal of Animal Ecology (85): 11-20.

Bryant, L. D. 1993. Quality of bluebunch wheatgrass (Agropyron spicatum) as a winter range forage for Rocky Mountain elk (Cervus elaphus nelsoni) in the Blue Mountains of Oregon. Ph.D. Thesis. Oregon State University, Corvallis.

Buechner, H. K. 1952. Winter-range utilization by elk and mule deer in southeastern Washington. Journal of Range Management. 5: 76-80.

Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce, 2012. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society, Biological Sciences 279(1746): 4407-4416.

Clearwater Basin Collaborative (CBC) 2017. Wildlife Habitat Restoration Initiative. http://clearwaterbasincollaborative.org/. Accessed 12 December 2017.

Coe, P. K., B. K. Johnson, M. J. Wisdom, J. G. Cook, M. Vavra, and R. M. Nielson, 2011. Validation of Elk Resource Selection Models with Spatially Independent Data. The Journal of Wildlife Management 75(1): 159-170.

Cook, C. W., L. A. Stoddart, and L. E. Harris., 1956. Comparative nutritive value and palatability of some introduced and native forage plants for spring and summer grazing. Utah Ag. Exp. Sta. Bull. No. 385. 39 pp.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. I. M. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 1551:1-61.

Cook, J. G., R. C. Cook, M. Wisdom, M. Rowland, D. Cadwallader, and P. Zager. 2012. Monitoring elk habitat and population responses to early-seral landscape restoration practices in the Clearwater Basin of Idaho. Idaho Department of Fish and Game Technical Report.

Cook, J. G., R. C. Cook, R. W. Davis, and L. L. Irwin, 2016. Nutritional Ecology of Elk During Summer and Autumn in the Pacific Northwest. Wildlife Monographs (195): 1-81.

Cook, J. G. and R. C. Cook, 2016. Forage quality and quantity sampling instructions for elk nutritional resources evaluation, Clearwater Basin, 2016.

Cook, R. C., D. L. Murray, J. G. Cook, P. Zager, and S. L. Monfort, 2001. Nutritional influences on breeding dynamics in elk. Canadian Journal of Zoology (79): 845-853.

Creel, S., J. Winnie Jr., B. Maxwell, K. Hamlin, and M. Creel, 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86: 3397-3397.

Ecosystem Research Group (ERG) 2013. Clearwater Basin Collaborative Selway-Middle Fork CFLRP Project Area Ecological Data Collections and Analysis. Technical Report, Missoula, USA.

Edge, W. D., C. L. Marcum, and S. L. Olsen-Edge, 1987. Summer Habitat Selection by Elk in Western Montana: A Multivariate Approach. The Journal of Wildlife Management 51(4): 844-851.

Edge, W. D., C. L. Marcum, and S. L. Olsen-Edge, 1988. Summer Forage and Feeding Site Selection by Elk. The Journal of Wildlife Management 52(4): 573-577.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales, 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20(3): 273-287.

Hatfield, J. L. and J. H. Prueger, 2015. Temperature extremes: Effect on plant growth and development. Weather and Climate Extremes 10: 4-10.

Hebblewhite, M., E. Merrill, and G. McDermid, 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78(2): 141-166.

Hetzner Hagle, C. R. 2016. Elk summer-autumn habitat selection in the Clearwater Basin of north-central Idaho. MS thesis, Eastern Washington University.

Idaho Department of Fish and Game (IDFG), 2014. Idaho Elk Management Plan 2014-2024. Idaho Department of Fish and Game, Boise, USA.

Innes, R. J. 2011. Cervus elaphus. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/. Accessed Feb 2017.

Irwin, L. L. and J. M. Peek, 1983. Elk, Cervus elaphus, foraging related to forest management and succession in Idaho. Can. Field-Nat. 97:443- 447.

Korfhage, R. C., J. R. Nelson, and J. M. Skovlin, 1980. Summer Diets of Rocky Mountain Elk in Northeastern Oregon. The Journal of Wildlife Management 44(3): 746-750.

Krausman, P.R., 1999. Some Basic Principles of Habitat Use. In: Launchbaugh, K.L., Sanders, K.D. and Mosley, J.L., Eds., Grazing Behaviour of Livestock and Wildlife, Idaho Forest, Wildlife and Range Exp. Sta. Bull. No. 70, University of Idaho, Moscow, ID, 85-90.

Kufeld, R. C., 1973. Foods Eaten by Rocky Mountain Elk. Journal of Range Management 26(2): 106-112.

Long, R. A., J. L. Rachlow, J. G. Kie, and M. Vavra, 2008. Fuels reduction in a western coniferous forest: effects on quantity and quality of forage for elk. Rangeland ecology & management 61:302-313.

Mancuso, M and R. Moseley. 1994. Vegetation Dynamics, Rare Plant Inventory, and Vegetation Monitoring for Craig Mountain, Idaho. Prepared for the U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife. 146pp.

Manly, B. F., L. McDonald, and D.L. Thomas, 1993. Resource Selection by Animals: Statistical Design and Analysis for Field Studies, Chapman & Hall, London. p. 177

Manly, B. F., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson, 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Kluwer Academic Publishers, Dordrecht, The Netherlands.

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(2): 313-325.

MTBS Data Access: Thematic Burn Severity (2017, July - last revised). MTBS Project (USDA Forest Service/U.S. Geological Survey). http://mtbs.gov/data/direct-download. Accessed 9 December 2017.

Natural Resources Conservation Service (NRCS) Wildlife Habitat Management Institute and Wildlife Habitat Council. 1999. American Elk (Cervus elaphus). Available: https://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs143_010000.pdf. Accessed Feb 2017.

Neff, J. C., J. W. Harden, and G. Gleixner, 2005. Fire effects on soil organic matter content, composition, and nutrients in boreal interior Alaska. Canadian Journal of Forest Research 35: 2178-2187.

Nielson, R. M. and H. Sawyer, 2013. Estimating resource selection with count data. Ecology and Evolution 3(7): 2233-2240.

Northrup, J. M., M. B. Hooten, C. R. Anderson Jr., and G. Wittemyer, 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. ECOLOGY: Ecological Society of America 94(7): 1456-1463.

Proffitt, K. M., J. A. Gude, K. L. Hamlin, and M. A. Messer, 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. The Journal of Wildlife Management 77(3): 541-524.

Proffitt, K. M., M. Hebblewhite, W. Peters, N. Hupp, and J. Shamhart, 2016. Linking landscape-scale differences in forage to ungulate nutritional ecology. Ecological Applications 26(7): 2156-2174.

Prokopenko, C. M., M. S. Boyce, and T. Avgar, 2017. Extent-dependent habitat selection in a migratory large herbivore: road avoidance across scales. Landscape Ecology 32(2): 313-325.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham, 2007. Habitat Selection of Rocky Mountain Elk in a Nonforested Environment. Journal of Wildlife Management 71(3): 868-874.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. U.S. General Soil Map (STATSGO2). Accessed 9 December 2017.

Spomer, G. C., 1999. Evidence of protocarnivorous capabilities in *geranium viscosissimum* and *potentilla argute* and other sticky plants. International Journal of Plant Science 160(1): 98-101.

Tibshirani, R., 1996. Regression Shrinkage and Selection via the Lasso. Journal of the Royal Statistical Society. Series B (Methodological), Volume 58, Issue 1: 267-288.

Unsworth, J. W., L. Kuck, E. O. Garton, and B. R. Butterfield, 1998. Elk Habitat Selection on the Clearwater National Forest, Idaho. The Journal of Wildlife Management 62(4): 1255-1263.

Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Westenskow-Wall, K. J., W. C. Krueger, L. G. Bryant, and D. R. Thomas, 1994. Nutrient quality of bluebunch wheatgrass re-growth on elk winter range in relation to defoliations. Journal of Range Management 47(3): 240-244.

White, C. G., P. Zager, and M. W. Gratson, 2010. Influence of Predator Harvest, Biological Factors, and Landscape on Elk Calf Survival in Idaho. Journal of Wildlife Management 74(3): 335-369.

Table 2—1 Plant species selected for modeling summer habitat selection by Rocky Mountain elk (*Cervus elaphus nelsoni*) on Craig Mountain Wildlife Management Area (CMWMA) in north-central Idaho. Rank refers to the relative forage value of each plant species to Rocky Mountain elk during summer, as identified by Kufeld (1973).

| Scientific name | Common name | Life form | Rank |
|---|---|---|---|
| *Pseudoroegneria spicata* | Bluebunch wheatgrass | grass | + |
| *Poa secunda* | Sandberg bluegrass | grass | + |
| *Festuca idahoensis* | Idaho fescue | grass | + |
| *Calamagrostis rubescens* | Pinegrass | grass | * |
| *Carex spp.* | Sedge | grass | + |
| *Centaurea solstitialis* | Yellow star-thistle | forb | |
| *Potentilla gracilis* | Slender cinquefoil | forb | - |
| *Lupinus sericeus* | Silky lupine | forb | + |
| *Galium triflorum* | Fragrant bedstraw | forb | |
| *Lactuca serriola* | Prickly lettuce | forb | + |
| *Tragopogon dubius* | Yellow salsify | forb | + |
| *Clarkia pulchella* | Pinkfaries | forb | |
| *Balsamorhiza sagittata* | Arrowleaf balsamroot | forb | - |
| *Achillea millefolium* | Common yarrow | forb | - |
| *Taraxacum officinale* | Common dandelion | forb | + |
| *Geranium viscosissimum* | Sticky purple geranium | forb | * |
| *Geum triflorum* | Old man’s whiskers, prairie smoke | forb | + |
| *Prunus virginiana* | Chokecherry | shrub | + |
| *Symphoricarpos albus* | Common snowberry | shrub | * |
| *Amelanchier alnifolia* | Saskatoon serviceberry | shrub | * |
| *Physocarpus malvaceus* | Mallow ninebark | shrub | + |
| *Berberis repens* | Creeping Oregon grape | shrub | - |
| *Acer glabrum* | Rocky mountain maple | shrub | * |
| *Holodiscus discolor* | Oceanspray | shrub | |
| *Sambucus cerulea* | Elderberry | shrub | * |
| *Vaccinium membranaceum* | Thinleaf huckleberry | shrub | * |
| *Rubus parviflorus* | Thimbleberry | shrub | + |
| *Crataegus douglassii* | Black hawthorn | shrub | |
| *Philadephus lewisii* | Lewis’ mock orange | shrub | |

Summer forage value ranking symbol: - = least valued; + = valued, * = highly valued

Table 2—2 Percent probability of plant species presence summarized across polygons on the Craig Mountain Wildlife Management Area (CMWMA). Mean, minimum, and maximum values are provided. Species are listed by life form. Yellow star thistle was included because it is the most prevalent non-native plant species on the CMWMA.

| Scientific name | Mean | Minimum | Maximum |
|---|---|---|---|
| *Grasses* | | | |
| Bluebunch wheatgrass | 15.58 | 0.34 | 49.96 |
| Sandberg bluegrass | 1.90 | 0.03 | 9.75 |
| Idaho fescue | 10.40 | 0.40 | 64.75 |
| Pinegrass | 3.01 | 0.08 | 53.13 |
| Sedge | 0.45 | 0.06 | 10.59 |
| *Forbs* | | | |
| Yellow star-thistle | 6.61 | 0 | 64.06 |
| Slender cinquefoil | 0.09 | 0.02 | 0.45 |
| Silky lupine | 1.26 | 0.01 | 16.10 |
| Fragrant bedstraw | 0.25 | 0 | 62.07 |
| Prickly lettuce | 0.58 | 0.03 | 6.73 |
| Yellow salsify | 0.33 | 0.02 | 3.53 |
| Pinkfaries | 2.06 | 0 | 50.52 |
| Arrowleaf balsamroot | 2.74 | 0.12 | 13.07 |
| Common yarrow | 2.29 | 0.40 | 20.68 |
| Common dandelion | 0.14 | 0.06 | 0.51 |
| Sticky purple geranium | 0.15 | 0 | 1.89 |
| Old man’s whiskers, prairie smoke | 0.30 | 0.01 | 6.54 |
| *Shrubs* | | | |
| Chokecherry | 0.60 | 0.44 | 1.55 |
| Common snowberry | 6.71 | 1.10 | 39.36 |
| Saskatoon serviceberry | 1.09 | 0.21 | 14.00 |
| Mallow ninebark | 3.34 | 0.01 | 91.78 |
| Creeping Oregon grape | 0.05 | 0 | 2.74 |
| Rocky mountain maple | 0.16 | 0 | 13.54 |
| Oceanspray | 0.47 | 0 | 10.51 |
| Elderberry | 0.09 | 0 | 25.09 |
| Thinleaf huckleberry | 0.33 | 0.03 | 11.45 |
| Thimbleberry | 0.12 | 0.01 | 2.97 |
| Black hawthorn | 1.08 | 0 | 24.60 |
| Lewis’ mock orange | 0.08 | 0 | 15.18 |

Table 2—3 Summary of Poisson and negative binomial (NB) resource selection functions (RSFs) used to model summer habitat selection by Rocky Mountain elk (*Cervus elaphus nelsoni*) on the Craig Mountain Wildlife Management Area (CMWMA). RSFs were modeled using three variable categories (probabilities of accepted forage species presence, plant variables, and elk variables; see text for explanation of categories). Variables, coefficient values, and fit measures (AICc and BIC) are presented for each RSF. Coefficient effects are presented for NB RSFs.

| Variable | Poisson Coef. (SE) | NB Coef. (SE) | NB Coef. Effects |
|---|---|---|---|
| Probabilities of Accepted Forage Species Presence | | | |
| Intercept | -3.68 (0.13) | -3.71 (0.15) | |
| Sticky purple geranium | 0.54 (0.10) | 0.54 (0.13) | 72% |
| Bluebunch wheatgrass | -0.03 (0.01) | -0.02 (0.01) | -2% |
| Common snowberry | 0.0002 (0.01) | -0.01 (0.01) | -1% |
| AICc | 13171 | 12291 | |
| BIC | 13208 | 12337 | |
| Plant Variables | | | |
| Intercept | -14.07 (0.69) | -13.63 (0.80) | |
| Minimum precipitation | 0.30 (0.02) | 0.30 (0.03) | 35% |
| Minimum temperature | 0.07 (0.03) | 0.09 (0.03) | 9% |
| Available water supply | 0.77 (0.08) | 0.68 (0.10) | 97% |
| Tree cover | 0.003 (0.00) | 0.001 (0.00) | 0% |
| Shrub cover | -0.35 (0.13) | -0.44 (0.14) | -36% |
| Organic matter | -0.17 (0.02) | -0.17 (0.02) | -16% |
| AICc | 13073 | 12251 | |
| BIC | 13138 | 12326 | |
| Elk Variables | | | |
| Intercept | -3.96 (0.22) | -3.87 (0.25) | |
| Elevation | 0.0005 (0.00) | 0.0005 (0.00) | 0% |
| Slope | -0.05 (0.00) | -0.05 (0.00) | -5% |
| Tree cover | 0.001 (0.00) | -0.0009 (0.00) | 0% |
| Shrub cover | -0.47 (0.12) | -0.53 (0.13) | -41% |
| Fire frequency | 0.20 (0.04) | 0.23 (0.05) | 26% |
| AICc | 12985 | 12189 | |
| BIC | 13040 | 12254 | |

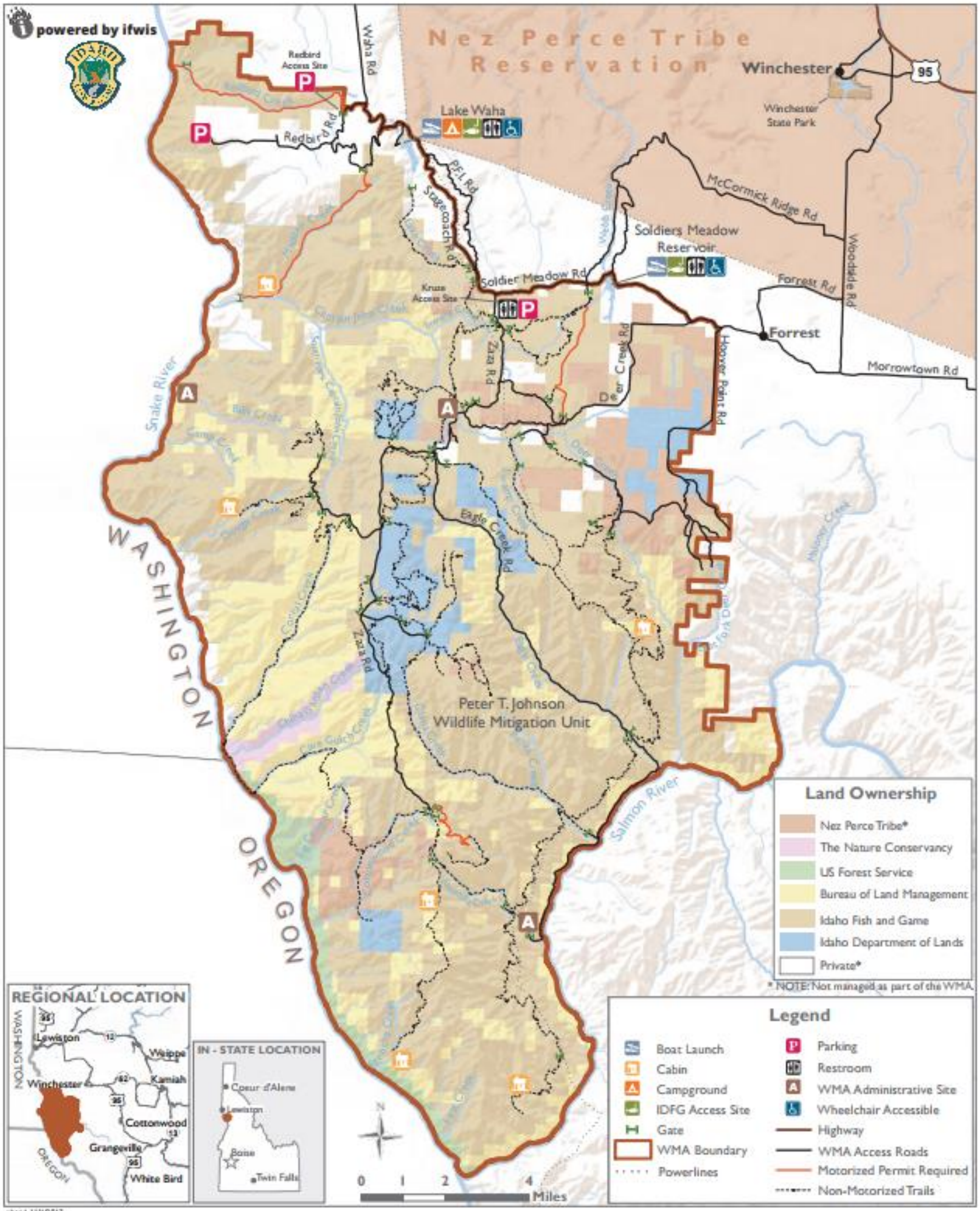


Figure 2—1 Craig Mountain Wildlife Management Area (CMWMA) in north-central Idaho. Map was created by the Idaho Department of Fish and Game. For more information visit: https://idfg.idaho.gov/.

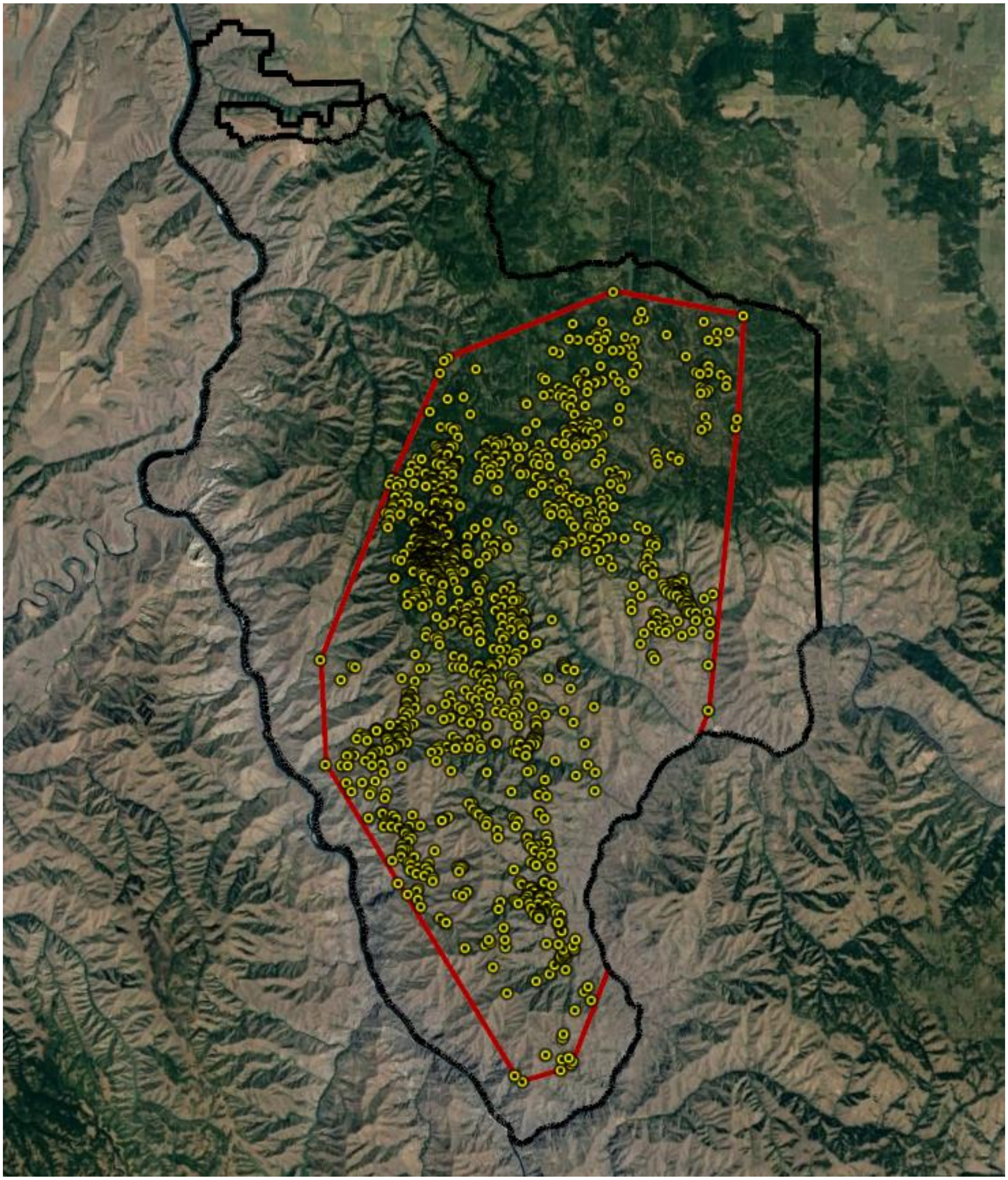

Figure 2—2 GPS locations of Rocky Mountain elk (*Cervus elaphus nelsoni*) during July and August 2014 and 2015 on the Craig Mountain Wildlife Management Area (CMWMA). Red line indicates defined summer range using convex hull minimum bounding geometry tool in ArcGIS 10.3 (ESRI, Redlands, California).

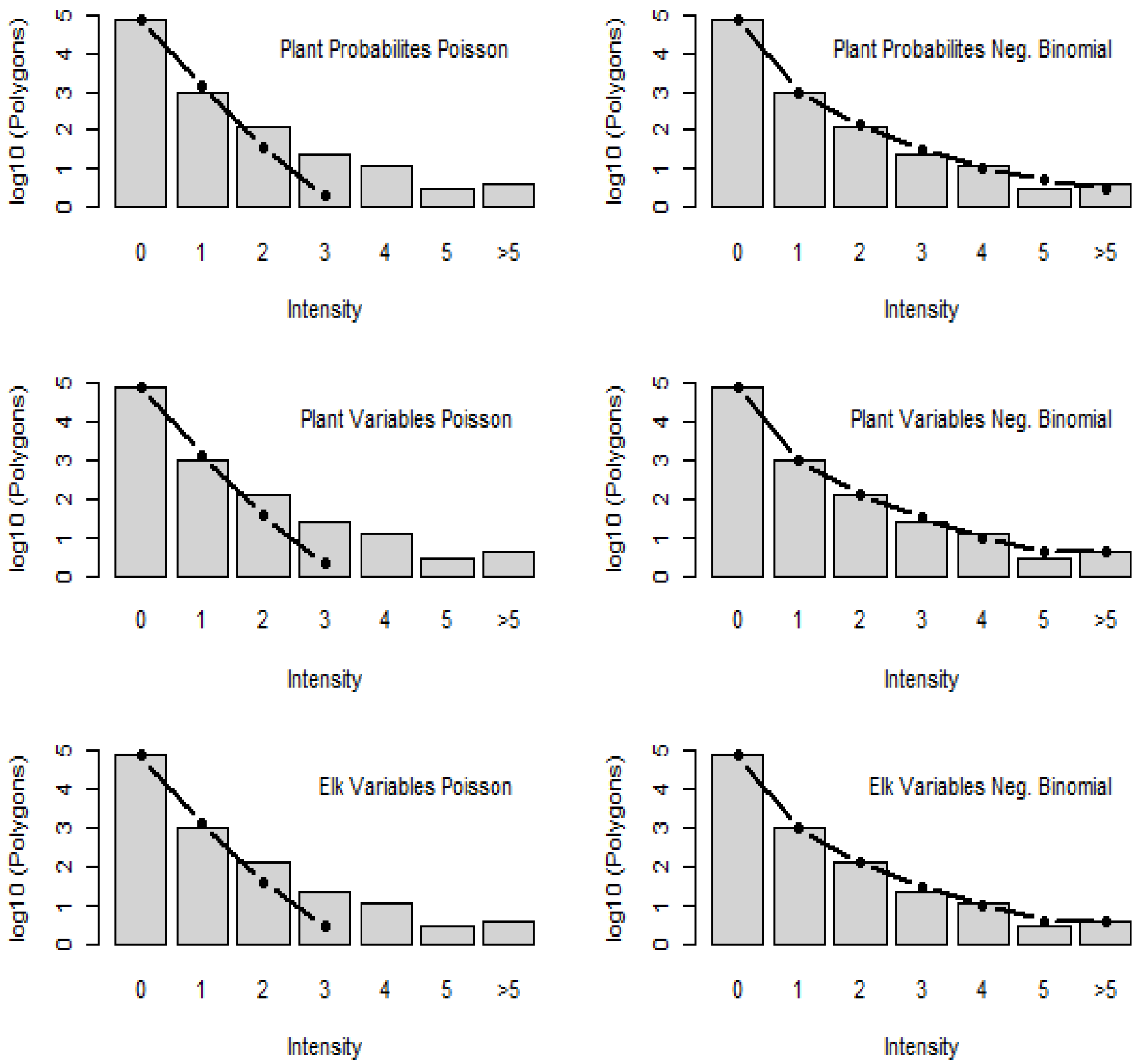


Figure 2—3 Histogram of the number of Rocky Mountain elk (*Cervus elaphus nelsoni*) GPS locations within polygons of the defined summer range on the Craig Mountain Wildlife Management Area (CMWMA) in north-central Idaho. Dotted-dashed lines represent the model predictions for each RSF (Poisson or negative binomial) and each variable category (probabilities of accepted forage species presence, plant variables, and elk variables). Number of polygons (y-axis) are represented on the log10 scale (0, 10, 100, 1000, 10000, 100000) and intensity (number of elk locations within a polygon) are rounded to the nearest integer.

## Appendix 1

Lasso logistic regression outputs for 20 plant species distributions modeled across Idaho. Plant species were selected as accepted forage for mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*). Outputs are grouped into tables by plant species life form (grasses, forbs, shrubs, and trees). Tables include: plant species common name, selected environmental variables, corresponding coefficients, and average AUC values for each species model (one model containing both distal and proximal environmental variables (DP) and a second model containing only proximal environmental variables (P)). Coefficients are exponentiated to be interpreted as odds ratios.

Grass species

| Variable | Bluebunch Wheatgrass | | Sandberg Bluegrass | | Idaho Fescue | | Pinegrass | | Carex ssp. | |
|---|---|---|---|---|---|---|---|---|---|---|
| Model | DP | P | DP | P | DP | P | DP | P | DP | P |
| Intercept | 0.004 | 1.35 | 0.00 | 0.03 | 0.12 | 0.71 | 0.00 | 0.00 | 0.00 | 0.00 |
| Elevation | | | 1.00 | | 1.00 | | | | | |
| Slope | 1.02 | | 0.96 | | 0.99 | | | | | |
| Aspect (cos) | | | 0.99 | | 1.01 | | 1.00 | | | |
| Aspect (sin) | | | 0.99 | | 0.99 | | | | | |
| Wetness index | | | 0.99 | | | | | | 1.09 | |
| Land. curv | | | | | 1.21 | | | | | |
| S. radiation | | 1.00 | 1.00 | | 1.00 | 1.00 | | | | |
| Slope position | | | | | | | | | | |
| Min. precip | | 1.02 | | | 1.01 | 1.03 | 1.00 | 1.03 | | |
| Max. precip | | | 1.02 | | 1.00 | | | | 1.02 | |
| Annual precip | | | 0.99 | 0.99 | | | | | | 1.00 |
| Min. temp[i] | | 1.01 | 0.99 | 0.93 | 1.04 | | | 0.94 | 0.89 | 0.89 |
| Max. temp | | | 1.08 | | | | | | | |
| Water supply | | | 1.16 | 1.13 | 1.02 | | | 1.19 | | |
| Clay | 1.01 | | 1.03 | | 1.02 | | 1.01 | | | |
| Sand | | | | | | | | | | |
| Silt | | | 1.01 | | 1.02 | | | | | |
| Cation ex cap. | | | 0.99 | | 0.96 | | | | | |
| Depth res. | | 0.99 | 0.99 | 0.99 | | | 0.99 | 0.99 | | |
| pH | | | 1.08 | | | | | | 0.79 | |
| Org. matter | | 0.98 | 0.91 | 0.98 | 0.99 | | | | 1.05 | 1.06 |
| Ca. carbonate | | | 0.97 | | 0.90 | 0.99 | | | | |
| Time since fire | | | | | | | | | | |
| Fire frequency | | | 0.98 | | 0.76 | | | | | |
| Tree cover | 0.99 | 0.97 | 0.96 | 0.97 | 0.94 | 0.98 | 1.06 | 1.06 | | |
| Shrub cover | | | 1.11 | 1.09 | | | 0.84 | 0.93 | | |
| Longitude | | | 1.00 | | | | 1.00 | | | |
| Latitude | 1.00 | | 1.00 | | 1.00 | | | | | |
| AUC | 0.71 | 0.67 | 0.73 | 0.70 | 0.79 | 0.72 | 0.93 | 0.94 | 0.78 | 0.75 |

Forb Species

| Variable | Lupine ssp. | | Arrowleaf Balsamroot | | Common Yarrow | | Sticky Geranium | |
|---|---|---|---|---|---|---|---|---|
| Model | DP | P | DP | P | DP | P | DP | P |
| Intercept | 0.00 | 0.01 | 0.01 | 0.04 | 0.02 | 0.07 | 0.00 | 0.00 |
| Elevation | 1.00 | | | | | | | |
| Slope | 1.00 | | 1.04 | | | | 0.99 | |
| Aspect (cos) | 1.01 | | 0.99 | | 1.02 | | 1.02 | |
| Aspect (sin) | | | | | | | | |
| Wetness index | | | | | 1.04 | | | |
| Land. curv | | | | | 0.91 | | | |
| S. radiation | | | | | 1.00 | 1.00 | | |
| Slope position | | | | | | | | |
| Min. precip | | | 1.02 | 1.03 | 1.01 | | 1.03 | 1.06 |
| Max. precip | 1.01 | | | | 1.02 | | | |
| Annual precip | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| Min. temp[i] | 1.09 | 1.05 | 1.15 | 1.23 | | | | 0.92 |
| Max. temp | | | | | | | | |
| Water supply | | | 0.86 | 0.80 | | | | 1.14 |
| Clay | 1.02 | | | | 1.01 | | | |
| Sand | | | | | 0.99 | | | |
| Silt | | | | | 1.01 | | 1.00 | |
| Cation ex cap. | | | | | | | | |
| Depth res. | | | 1.00 | | 1.00 | | | |
| pH | | | | | | | | |
| Org. matter | | | | | 1.05 | 1.02 | | |
| Ca. carbonate | 0.97 | 0.99 | 0.94 | 0.95 | 0.95 | 0.99 | 0.98 | 0.98 |
| Time since fire | 1.03 | 1.03 | | | 1.01 | | | |
| Fire frequency | | | 0.73 | 0.81 | | | | |
| Tree cover | 0.99 | 0.99 | 0.98 | 0.98 | 0.99 | | | 1.00 |
| Shrub cover | | | | | 0.98 | | | |
| Longitude | 1.00 | | | | 1.00 | | 1.00 | |
| Latitude | | | | | 1.00 | | | |
| AUC | 0.73 | 0.68 | 0.79 | 0.78 | 0.69 | 0.67 | 0.86 | 0.85 |

Shrub Species

| Variable | Mountain Big Sagebrush | | Antelope Bitterbrush | | Common Snowberry | | Saskatoon Service-berry | | Mallow Ninebark | | Creeping Oregon Grape | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model | DP | P | DP | P | DP | P | DP | P | DP | P | DP | P |
| Intercept | 0.12 | 0.00 | 0.00 | 0.00 | 143 | 0.01 | 0.01 | 0.00 | 22.5 | 12.2 | 0.00 | 0.00 |
| Elevation | 1.00 | | | | | | | | | | | |
| Slope | 0.99 | | 0.96 | | | | | | | | 1.01 | |
| Aspect (cos) | 0.98 | | 0.96 | | | | | | | | 0.96 | |
| Aspect (sin) | 1.00 | | 0.99 | | | | | | | | 1.01 | |
| Wetness index | | | | | | | | | | | 0.97 | |
| Land. curv | | | | | 0.97 | | | | 0.83 | | | |
| S. radiation | 1.00 | 1.00 | | | 1.00 | | | | 1.00 | 1.00 | | |
| Slope position | | | | | | | | | | | | |
| Min. precip | 1.00 | 1.00 | 0.98 | 0.99 | 1.07 | 1.02 | 1.01 | | | | | 1.02 |
| Max. precip | | | 1.03 | | | | | | 1.02 | | | |
| Annual precip | 1.00 | 1.00 | | | | 1.00 | | | | 1.00 | 1.00 | 1.00 |
| Min. temp[i] | 0.90 | 0.87 | | 0.58 | 1.07 | | | | | | 0.94 | 0.80 |
| Max. temp | | | 1.49 | | | | | | | | 1.02 | |
| Water supply | 1.01 | 1.01 | 1.86 | 0.93 | 1.02 | 1.10 | 1.01 | | 1.04 | | 1.17 | |
| Clay | | | 0.97 | | 1.01 | | | | | | 0.97 | |
| Sand | | | 1.00 | | 0.99 | | | | | | | |
| Silt | 1.01 | | | | 1.01 | | | | | | | |
| Cation ex cap. | 0.99 | | 0.89 | | | | | | | | 0.95 | |
| Depth res. | 1.00 | | 0.99 | 0.99 | 1.00 | | | | | | 0.99 | |
| pH | 0.87 | | 0.79 | | | | | | | | 0.87 | |
| Org. matter | | | 0.91 | 0.97 | | | 1.04 | | | 1.01 | 0.97 | 1.00 |
| Ca. carbonate | 0.90 | 0.92 | 0.81 | 0.68 | 0.99 | | | | | | 0.99 | 0.98 |
| Time since fire | 1.02 | 1.01 | 0.99 | 0.99 | | | | | 0.98 | 0.97 | | |
| Fire frequency | | | | 1.27 | | | | | | | | |
| Tree cover | 0.95 | 0.97 | 0.94 | 0.93 | 1.01 | 1.02 | 1.03 | 1.02 | 1.03 | 1.03 | 1.02 | 1.00 |
| Shrub cover | | | | | | | | | | | 1.10 | |
| Longitude | 1.00 | | 1.00 | | | | 1.00 | | 1.00 | | 1.00 | |
| Latitude | 1.00 | | 1.00 | | 1.00 | | 1.00 | | | | 1.00 | |
| AUC | 0.81 | 0.79 | 0.92 | 0.88 | 0.86 | 0.84 | 0.88 | 0.87 | 0.96 | 0.96 | 0.85 | 0.80 |

Tree Species

| Variable | Quaking Aspen | | Chokecherry | | Douglas-fir | | Willow ssp. | | Lodgepole Pine | |
|---|---|---|---|---|---|---|---|---|---|---|
| Model | DP | P | DP | P | DP | P | DP | P | DP | P |
| Intercept | 0.01 | 0.00 | 0.00 | | 0.01 | 0.00 | 0.05 | 0.00 | 0.00 | 0.00 |
| Elevation | | | | | | | | | | |
| Slope | | | | | | | | | 0.96 | |
| Aspect (cos) | | | | | | | | | 1.06 | |
| Aspect (sin) | | | | | | | 1.03 | | 0.97 | |
| Wetness index | | | | | | | 1.22 | | 1.15 | |
| Land. curv | | | | | | | 0.54 | | | |
| S. radiation | | | | | | | | | | |
| Slope position | | | | | | | 3.94 | | | |
| Min. precip | | | | | | 1.00 | | | 1.04 | 1.03 |
| Max. precip | | | | | | | 1.00 | | | |
| Annual precip | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | | | 1.00 | 1.00 |
| Min. temp[i] | | | | | | | 0.85 | 0.97 | 0.75 | 0.82 |
| Max. temp | | | | | 0.91 | | | | | |
| Water supply | | | | | | | 0.89 | | | |
| Clay | | | | | | | | | | |
| Sand | | | | | | | 0.99 | | | |
| Silt | | | | | | | | | | |
| Cation ex cap. | | | | | | | | | | |
| Depth res. | | | | | | | | | | |
| pH | | | | | | | | | 0.99 | |
| Org. matter | 1.06 | 1.08 | | | 1.12 | 1.12 | | | 1.09 | 1.09 |
| Ca. carbonate | | | | | | | | | | |
| Time since fire | | | | | | | | | | |
| Fire frequency | | | | | | | | | | |
| Tree cover | | | | | | | | | | |
| Shrub cover | 0.93 | 0.91 | | | 0.68 | 0.67 | 0.54 | 0.76 | 0.75 | 0.93 |
| Longitude | 1.00 | | | | | | | | | |
| Latitude | 1.00 | | | | | | 1.00 | | 1.00 | |
| AUC | 0.89 | 0.86 | 0.78 | 0.78 | 0.88 | 0.87 | 0.77 | 0.76 | 0.97 | 0.96 |