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Modeling broad-scale patterns of elk summer resource selection in Montana using regional and population-specific models

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Abstract

Understanding animal distribution is important for management of populations and their habitats. Across the western United States, elk (*Cervus canadensis*) provide important ecological, cultural, and economic benefits and the sound management of their habitats is of vital importance. In western Montana, National Forest lands are managed in part to provide and protect elk habitat needs, and summer elk habitat is managed with consideration to motorized routes. We evaluated the relative importance of nutritional resources, access routes, and other landscape attributes on elk summer resource selection at multiple spatial scales, and compared resource selection among nine different southwestern Montana elk populations to determine the applicability of generalized regional models for informing habitat management recommendations. First, we developed nine population-specific and two regional summer resource selection models. Second, we evaluated the predictive performance of each model within and among elk populations using cross-validation scores to identify the best model. We found that in all populations nutritional resources, best represented using normalized difference vegetation index (NDVI) metrics, were the most important factors associated with elk summer resource selection. Access routes affected resource selection in all populations; however, the influence of access routes was relatively modest as compared with nutritional resources. Of the access route covariates we considered, density of all routes (i.e., routes open and closed to motorized use) explained most variation in summer elk resource selection. Validation of population-specific resource selection models among populations revealed that in many cases model predictions extrapolated to areas outside of the development area had modest to poor predictive performance, especially as distance from the modeled population increased. Thus, caution should be used when extrapolating resource selection

⁵ Retired.

models based on a single study population to other populations. Regional models of resource selection predicted resource selection across populations better than population-specific models, particularly when constructed by pooling data from multiple populations, and we recommend these types of models be used to inform regional habitat management policies. Our results suggest that managers should expand any current management paradigm for elk summer habitat that is focused on limiting access route density to also consider nutritional resources as an important component of elk summer habitat.

KEYWORDS

elk nutrition, GPS telemetry, habitat management, habitat selection, NDVI, resource selection function, road effects

INTRODUCTION

Understanding the relationships between organisms and their environments is an essential aspect of ecology, and important in guiding management of wildlife habitats (Morrison et al., 2012). However, the relationship between wildlife and their habitats is not static, as various landscape-level processes, such as fire (Allred et al., 2011; Fisher & Wilkinson, 2005), grazing by domestic herbivores (Torstenson et al., 2006; Yeo et al., 1993), reintroduction of carnivores (Mao et al., 2005), and anthropogenic disturbances through road building (Benítez-López et al., 2010), logging (Fisher & Wilkinson, 2005), and recreation (Bettinger et al., 1999; Czech et al., 2000; Thiel et al., 2007), can change the direction and strength of wildlife–habitat relationships. Additionally, individuals of the same species may have different selection patterns (Estes et al., 2003; Gillingham & Parker, 2008). As such, models explaining wildlife resource selection are constantly being created and adapted by management agencies in an attempt to improve wildlife and habitat management, and respond to changes in the habitat conditions.

Ungulates are important wildlife species to consider with regard to resource selection given their important ecological impacts (Wisdom et al., 2006). Herbivory by ungulates may have direct and indirect impacts on vegetation and plant community structure, even leading to alternative stable states (Marshall et al., 2013, 2014; Wolf et al., 2007). Indirect effects of ungulate herbivory can also have large influences on vegetation community structure through changes in nitrogen balances and cycling (Hobbs, 1996; Rexroad et al., 2007; Schoenecker et al., 2004; Singer & Schoenecker, 2003; Ter Beest, 2005), soils (Hobbs, 1996; Ter Beest, 2005), litter accumulation and composition (Hobbs, 1996; Rexroad et al., 2007), and disturbance regimes (Hobbs, 1996). Following the reintroduction of top predators, both density and

behaviorally driven trophic cascades associated with changing ungulate distributions have been documented, often working in concert with climate, soils, human activity, and hydrology (Fortin et al., 2008; Hebblewhite et al., 2005; Kauffman et al., 2013; Marshall et al., 2014; Ripple & Beschta, 2012). These direct and indirect effects can have dramatic impacts on plant community structure and composition, and thus impact the quality and quantity of nutritional resources available to ungulates.

The nutritional resources available to ungulates on summer range are of particular importance as females must meet the nutritional demands of lactation, while also accruing fat reserves for the winter (Cook et al., 1996, 2013; Monteith et al., 2014; Spitz et al., 2019). During this critical summer period, nutritional resources slowly decrease as plants advance through phenological stages (Baker & Hobbs, 1982; Monteith et al., 2011; Ranglack & du Toit, 2015). Landscape processes, including wildfire and livestock grazing, may influence nutritional resources available to ungulates and create a mosaic of nutritional resources across the landscape. Depending on the intensity and timing of grazing or wildfire, these processes may increase or decrease ungulate nutritional resources (Allred et al., 2011; du Toit, 2011; Fuhlendorf et al., 2009; Odadi et al., 2011; Ranglack & du Toit, 2015). Additionally, insect infestations and plant diseases can reduce the available nutritional resources (Allen & Segarra, 2001; Hewitt, 1977). This distribution of nutritional resources across the landscape is likely an important factor affecting elk summer habitat selection (Rowland & Wisdom, 2015).

Until recently, elk (*Cervus canadensis*) summer range habitat management on western North American public lands broadly (Rowland et al., 2000), and specifically in Montana (MDFWP and USDA Forest Service, 2013), focused primarily on the management of route density as

it relates to habitat effectiveness (Christensen et al., 1993; Lyon, 1979, 1983; Rowland et al., 2000). Habitat effectiveness for elk measures the actual elk use of an area in relation to the expected use of that area if no access routes were present. As such, roadless areas are designated as 100% effective for elk, while areas with route densities of 1 km/1.61 km² are considered to be 75% effective, 2 km/1.61 km² as 50% effective, etc., as actual elk use of those areas is estimated to be less than potential use (Lyon, 1983). This concept focuses on elk distribution across the landscape with an underlying recognition that effective use of summer habitats is required for optimal fat accumulation, thus acknowledging the importance of nutritional resources on the landscape (Cook et al., 1996, 2013; MDFWP and USDA Forest Service, 2013; Monteith et al., 2014; Rowland & Wisdom, 2015; Spitz et al., 2019), but the direct management actions are focused on access routes. While elk preference for areas away from access routes is generally accepted, particularly during the fall hunting seasons (Forman & Alexander, 1998; Montgomery et al., 2013; Ranglack et al., 2017; Rowland et al., 2000, 2005), these specific guidelines do not explicitly reflect many other potentially important factors in elk resource selection, such as nutritional resources, topography, and predation (Allred et al., 2011; DeVoe et al., 2019; Edge & Marcum, 1991; Montgomery et al., 2012; Ranglack & du Toit, 2015; Spitz et al., 2019).

Using fine-scale location data from nine elk populations in southwest Montana collected during 2005–2014, our goal was to evaluate the effects of nutritional resources, access routes, and landscape covariates on elk summer resource selection to provide recommendations for elk summer range habitat management. First, we developed and validated population-specific resource selection models. Then we combined data across all populations using two different methods to develop regional resource selection models. We validated population-specific and regional models within and among populations to understand the amount of variation in selection patterns among populations and determine the utility of models to inform regional management recommendations. We predicted elk would select for areas with higher nutritional resources and fewer access routes; however, we predicted the relative influence of these factors may vary among populations as a function of landscape attributes and resource availability.

METHODS

Study area

The study area included the summer ranges of nine elk populations in southwest Montana (Figure 1). Vegetation

types across these summer ranges include a mix of montane forest (e.g., aspen [*Populus tremuloides*], Douglas fir [*Pseudotsuga menziesii*], lodgepole pine [*Pinus contorta*]), open sage-grassland (e.g., big sagebrush [*Artemisia tridentata*], bluebunch wheatgrass [*Pseudoroegneria spicata*], Idaho fescue [*Festuca idahoensis*]), and upland grasslands, meadows, and unvegetated areas, but the relative proportions of these habitat types vary among the populations. Climate in these ranges is characterized by short, cool summers. Mean July–August temperature and precipitation varied across the summer ranges from 13.3 to 16.7°C and 70.5 to 99.5 mm (PRISM Climate Group, 2015). Elevation, access route densities, and indices of nutritional resources varied among the populations' ranges (Table 1). All elk ranges included a mix of public (primarily United States Forest Service [USFS] or National Park Service) and private lands, with the majority of each summer range being located on public land. Mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) also occupy the elk summer ranges. Wolves (*Canis lupus*), mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*) are the elk predators in the system, and grizzly bears (*Ursus arctos*) also occupy the summer ranges in the eastern portion of the study area. For full descriptions of these areas, see Shideler et al. (1994), Gude et al. (2006), White et al. (2012), and Proffitt et al. (2013, 2014).

Data collection

During 2005–2014, we captured and radio-collared adult female elk from nine populations in southwestern Montana on their winter ranges using helicopter net-gunning or chemical immobilization. Elk populations were selected for capture and radio-collaring as part of several different projects related to wolf–elk interactions, elk brucellosis, or elk survival investigations, each operating under Institutional Animal Care and Use Committee approved capture and handling protocols. Collar functionality differed among populations and years, and all collars contained GPS receivers that collected 12–48 locations per day for a minimum of 1 year. Because our goal in this project was to synthesize data collected across a large spatial scale, we pooled data from these nine elk populations to create a regional elk location dataset (Appendix S1).

Data preparation

We developed resource selection functions using a used–available framework (Johnson, 1980; Manly et al., 2007).

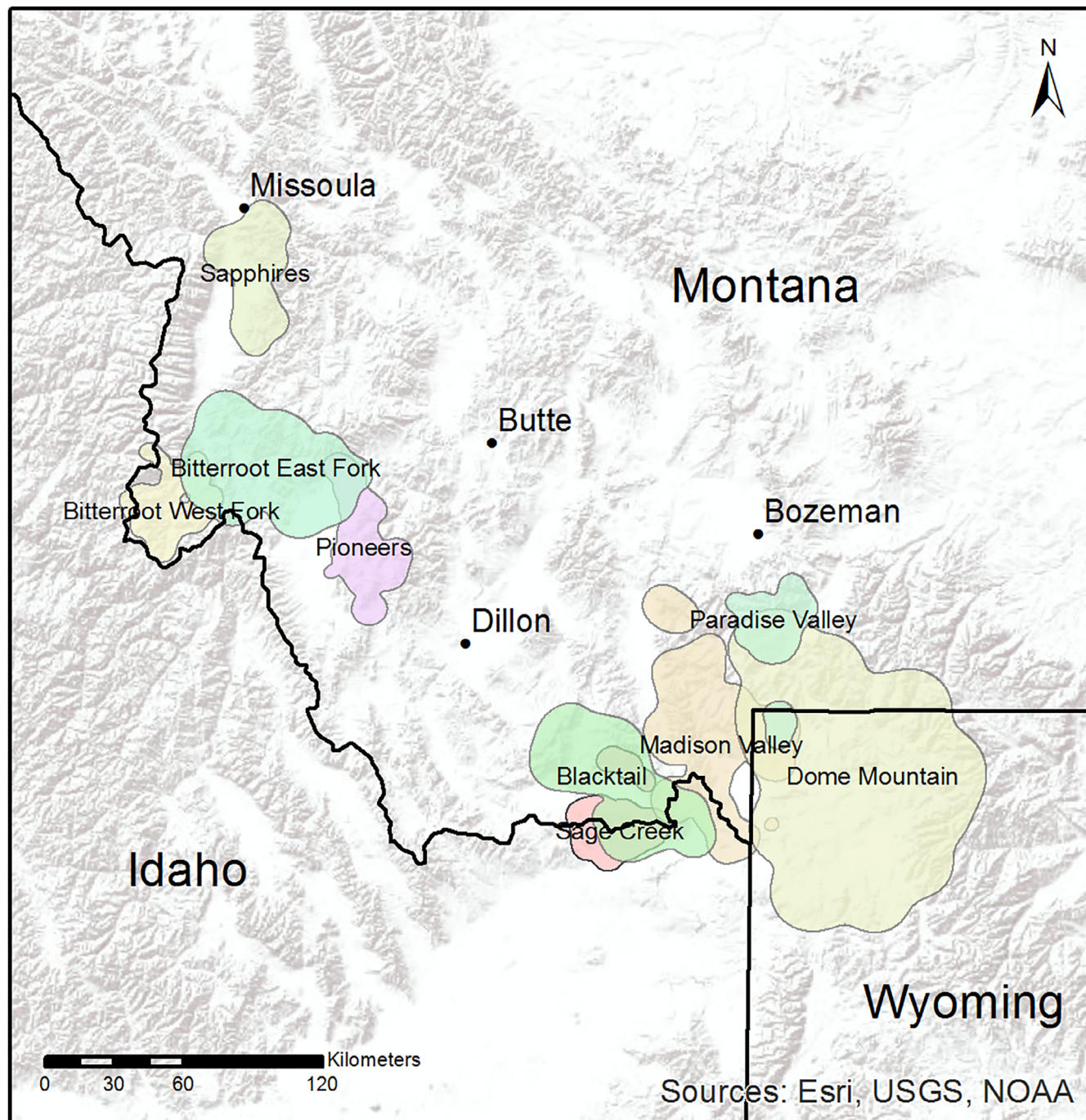


FIGURE 1 The study area included nine elk population summer ranges in southwest Montana, USA.

We treated summer locations collected from the GPS collars as the used sample. We selected July 1 as the summer start date to exclude any potential movements from calving to summer range, as >95% of elk birthing events occur by the end of June (Cross et al., 2015). We selected August 31 as the summer end date to correspond to the period before the archery hunting season began. We randomly selected four used locations per individual per day to ensure that sample sizes were equal for all individuals regardless of collar scheduling, to reduce spatial

autocorrelation in the data (Hansteen et al., 1997), and to avoid potential bias in habitat use that can be the result of systematic data selection (e.g., collecting locations at 0000, 0600, 1200, and 1800). All collars were scheduled to drop-off after 1 year. However, this did not occur for a small number of individuals. As such, we only used data from the first summer each individual was collared to avoid overweighting those few individuals with two summers of data. For the Bitterroot East Fork and Sapphire populations, there were 2 and 14 individuals respectively

TABLE 1 Landscape attributes and weather (mean with SD in parentheses) at nine elk population summer ranges within the southwestern Montana, USA, study area.

Population	Elev. (m)	Density (km/km ²)		NDVI		Proportion			Jul–Aug	
		Motorized route	All routes	Time Int.	Amp.	Forest	Grassland	Shrubland	Temp. (°C)	Precip. (mm)
Bitterroot East Fork	1960 (318)	0.92 (4.10)	1.34 (4.91)	48.0 (10.9)	42.8 (9.0)	0.70	0.14	0.15	14.8 (1.39)	77.2 (17.8)
Bitterroot West Fork	1948 (278)	0.64 (3.41)	1.04 (4.37)	45.4 (9.3)	40.4 (7.4)	0.84	0.10	0.06	15.3 (1.05)	74.7 (9.7)
Blacktail	2280 (266)	0.65 (3.50)	0.91 (4.10)	58.2 (8.4)	53.7 (8.9)	0.37	0.24	0.37	14.3 (1.13)	84.1 (11.9)
Dome Mountain	2461 (270)	0.17 (1.70)	0.22 (1.98)	53.2 (9.6)	48.8 (8.6)	0.65	0.14	0.19	13.3 (1.26)	88.1 (15.2)
Madison Valley	2359 (305)	0.48 (3.02)	0.81 (3.98)	54.1 (10.5)	49.0 (8.5)	0.57	0.18	0.23	13.9 (1.41)	98.9 (20.0)
Paradise Valley	2300 (398)	0.48 (3.04)	0.83 (3.96)	48.1 (10.4)	45.3 (9.1)	0.61	0.16	0.21	14.1 (2.0)	99.5 (18.6)
Pioneers	2270 (255)	0.71 (3.60)	0.99 (4.21)	45.6 (9.4)	41.8 (8.6)	0.69	0.10	0.19	13.7 (0.8)	85.9 (20.9)
Sage Creek	2227 (244)	0.67 (3.52)	0.86 (3.95)	60.1 (7.3)	54.6 (8.2)	0.45	0.22	0.32	14.7 (0.9)	78.4 (13.7)
Sapphires	1516 (358)	1.66 (5.58)	1.79 (5.82)	40.6 (11.7)	36.1 (7.5)	0.55	0.26	0.19	16.7 (1.5)	70.5 (13.2)

Note: The values presented are based on the minimum spatial scale available for each of the covariates. Weather data are from PRISM Climate Group (2015). “Elev.” is the elevation; “Time Int.” is time-integrated normalized difference vegetation index (NDVI; average values across all years of the study); “Amp.” is NDVI amplitude (average values across all years of the study); “Forest,” “Grassland,” and “Shrubland” represent the proportions of the study area found to be of those land cover types, based on the descriptions found in Appendix S2. In the cases in which the land cover types do not add to 100%, the remaining land cover was treated as “other.” “Precip.” is the precipitation and “Temp.” is the temperature.

that had at least one day with fewer than four locations. In these cases, we used all available data for those days (<4 locations), thus underweighting those individuals in the models. We defined population-specific summer range by randomly selecting one location per day per individual to reduce spatial autocorrelation between the locations, and then building 99% kernel density estimator (KDE) contours using “kernelUD” in the “adehabitat” package in R, using the ad hoc smoothing method. We randomly generated available points at a 1:5 used:available ratio within the population-specific summer range, as this provided adequate available points for model convergence (Northrup et al., 2013) as well as adequately described the distribution of each covariate within the study area. Using the population-specific summer range follows the recommendations of Edge et al. (1986) and MDFWP and USDA Forest Service (2013). This was evaluated by simulating various used:available ratios for each covariate in each of the population-specific summer ranges, following Lowrey et al. (2017).

Covariates

We evaluated 12 covariates describing elk resource selection based on a review of previous elk studies and current metrics used for elk habitat management (Christensen et al., 1993; Hillis et al., 1991; Lyon, 1979; McCorquodale, 2013; Petteorelli et al., 2011; Proffitt et al., 2011). We divided the covariates into three covariate suites representing the potential effects of nutritional resources, access routes, and general landscape attributes on elk resource selection (Table 2). The nutrition suite contained an elk forage quality model developed based on vegetation data collected in the southern Bitterroot Valley of Montana (Proffitt et al., 2016), as well as two remotely sensed metrics of greenness derived from the normalized difference vegetation index (NDVI): NDVI amplitude and time-integrated NDVI. While the influence of forest canopy on NDVI values can limit the usefulness of unprocessed NDVI values in forested areas (Borowik et al., 2013), using NDVI amplitude or

TABLE 2 The covariates included in the analysis of elk summer resource selection in southwest Montana, USA, divided into three covariate suites (nutrition, access routes, and landscape), where square brackets, [], indicate the spatial scales (in meters) that were evaluated (30, 100, 250, 500, 750, 1000 m, all) and curly brackets, { }, indicate the functional forms (L, linear; 2, quadratic; ps, pseudothreshold; all, all) that were evaluated (not applicable to binary covariates).

Nutrition	Access routes	Landscape	
Bitterroot[1000]{L,ps}	Density of All Routes[all]{L,ps}	Forest	Slope[all]{all}
NDVI—Amplitude[≥250]{L,ps}	Density of Motorized Routes[all]{L,ps}	Grassland	Solar Radiation[all]{all}
NDVI—Time-Integrated[≥250]{L,ps}	Security Area	Shrubland	Elevation[all]{all}

Abbreviation: NDVI, normalized difference vegetation index.

time-integrated NDVI partially mediates the issue. NDVI amplitude values represent the increase in NDVI from the start of the growing season to the peak (Bradley & Mustard, 2007), while time-integrated NDVI represents the net primary production during the growing season (Jonsson & Eklundh, 2002; White et al., 2009). The access route suite included three metrics of human disturbance: the density of all access routes, density of motorized access routes, and a binary variable representing elk security areas. Security areas were defined as roadless areas of a given size ($\geq 1, 2, \text{ or } 4 \text{ km}^2$) that are a given distance from the nearest routes ($\geq 805, 1610, \text{ or } 3220 \text{ m}$). These definitions were based on current US Forest Service management strategies. Lastly, the landscape suite contained four landscape attributes including land cover type, slope, elevation, and solar radiation. We evaluated three land cover types: forest, grassland, and shrubland. We treated these as binary variables with all other land cover types in the area (unvegetated, developed, agricultural, etc.) acting as a reference category when all three land cover types were included in the same model. Full details on covariate development are included in Appendix S2.

Although resource selection analyses are typically conducted at the resolution of the available covariate data, animals may perceive and select resource attributes at different spatial scales (Anderson et al., 2005; DeVoe et al., 2015; Laforge et al., 2015). Therefore, we considered each continuous covariate over six different spatial scales (30, 100, 250, 500, 750, and 1000 m). We estimated each spatial scale using moving window averaging to create a new raster with pixel values corresponding to the average values of the moving window size. Examining multiple spatial scales is becoming increasingly important as remote sensing technology advances and the resolution of available data becomes increasingly fine and possibly exceeds an animal's ability to detect differences from one pixel to the next. Additionally, because the relationship between selection and covariates may not always be linear, we evaluated multiple functional forms (linear, quadratic, and pseudothreshold) for each continuous

covariate. Pseudothreshold functional forms were fit using a natural log transformation (Franklin et al., 2000). Binary covariates were only considered at the 30-m spatial scale, to account for telemetry error and the original data structure. We evaluated spatial scale and functional forms for each covariate in an exploratory analysis, unless the most appropriate functional form could be identified a priori from existing literature or the resolution of data did not allow for analysis at certain spatial scales (Table 2).

Modeling

We standardized all continuous covariates by subtracting the mean and dividing by two times the standard deviation prior to analysis (Gelman, 2008; Lele, 2009). We used a hierarchical approach to model selection (Franklin et al., 2000) to reduce the number of competing models (Burnham & Anderson, 2002). We screened all continuous covariates for multicollinearity using Pearson correlation coefficients. Any covariates that were found to be collinear ($r \geq |0.7|$) were not included in the same model. First, we examined all possible univariate models in an exploratory analysis to determine the most explanatory functional form(s) and spatial scale(s) for each covariate. We considered covariates from all the models within five corrected Akaike information criterion (AIC_c) units of the top model and advanced only these covariates to the next stage, but they were not allowed to occur in the same model as each mother moving forward. This was done as it is possible that some of the less supported functional form/spatial scale combinations from the simple, univariate models may gain more support when combined with other covariates in more complex models. We removed uninformative covariates, if any, from the models being moved forward to the next tier following Arnold (2010). Next, we evaluated all combinations of informative covariates within the landscape suite and determined the best model using AIC_c . For the access route and nutrition suites, we evaluated all informative

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

We fit population-specific models using a conditional logistic regression model, conditioned on year, using “cph” in R v. 3.2.2. We chose this modeling framework to ensure that the available points for each year were evaluated against the used points for that year, as we had annually varying nutrition covariates and a different set of instrumented individuals for each year, as well as to allow for direct comparison with the results of Ranglack et al. (2017), which used data from these same elk herds. A generalized linear mixed model (GLMM) was also considered, as it would not require the GPS data to be subset, instead using random effects on AnimalID and Year to control for differences in sample sizes for individuals and year (Appendix S3). Regional models of elk selection were constructed using two separate approaches: a consensus and a pooled approach. The consensus model was created following the same tiered approach described above, though we forced all the populations to follow a consensus model structure for each tier in a meta-analysis framework. We determined the consensus model structure by ranking each model within a tier among populations and then summing the ranks. The model with the lowest summed rank was moved forward into the next tier, until the final model structure had been fit (Rowland et al., 2018). We determined the consensus model coefficients using the “rmeta” package in R. We combined the results from all the populations for each covariate with equal weighting. The pooled model was created by pooling all the data across populations into a single dataset and following the same tiered approach described for the population-specific models. We created a “herd-year” variable that was unique for each population-by-year combination to use as the strata in the pooled model to ensure that the used points for each population-by-year combination were compared only to the available points for that strata, thus maintaining population-level availability. Resource selection function values for the top models were rescaled to range from 0 to 1 for reporting, representing the relative probability of selection.

Model validation

We validated population-specific models to determine both their internal accuracy and external applicability. Internal accuracy refers to how well the model is

validated using the data for that population, while external applicability refers to how well the model predicts elk resource selection in areas outside where the model was developed. We assessed internal and external accuracy using Spearman’s rank correlations between population-specific models predicted relative use and actual used locations in 10 equal area bins (Boyce et al., 2002). Internal accuracy was assessed using *k*-folds with five random folds (Boyce et al., 2002), with 100 repetitions. To estimate external applicability, we assessed how well each population-specific model predicted relative use in the other eight populations (Wiens et al., 2008). Given that the year of data collection did not always match among populations, we removed the stratification on year when testing the external applicability when necessary, but kept the remaining model structure intact. Lastly, we validated the consensus and pooled models by fitting the model with data for eight of the populations and predicting the use of the ninth as a form of leave-one-out cross-validation. We repeated this process so that each population’s use was predicted using the model fitted with data from the other eight populations.

Post hoc interaction analysis

Given that selection for areas with high nutritional value can overwhelm selection against areas near access routes (Dodd et al., 2007; Gagnon et al., 2007), we conducted a post hoc exercise to examine these impacts. For each of the top models, we included an interaction between the included nutrition and access route covariates. We compared the interaction model to the additive model using ΔAIC_c to determine whether the interaction term improved model fit.

RESULTS

We used a total of 83,946 elk locations collected from 339 individual elk in our analyses (Appendix S1). Of all the elk locations, 62.2% occurred in forested areas, 23.0% occurred in grasslands, and 14.6% occurred in shrublands. Mean elevation of used points was 2180 m (SD = 436). Mean density of motorized routes and all routes (both open and closed to motorized use) of used points measured at the 1000-m scale was 0.658 km/km² (SD = 1.000) and 1.054 km/km² (SD = 1.242), respectively. Mean NDVI amplitude and time-integrated NDVI values of used points were 50.0 (SD = 10.8) and 55.3 (SD = 11.2) respectively. The mean slope of the used points was 13.2° (SD = 8.5).

Population-specific models

The top population-specific models were consistent in that they each contained covariates from each of the nutrition, access route, and landscape covariate suites (Table 3), with the GLMM providing similar results (Appendix S3) to the conditional logistic regression analysis. Presented here so as to maintain consistency with Ranglack et al. (2017). The nutrition covariate was generally the most influential of all the covariates, as well as the only covariate that was consistent in the strength and direction of selection across all populations' top models, with all populations increasing selection for areas with increases in the nutrition covariate (Table 4). The two NDVI metrics, time-integrated NDVI and NDVI amplitude were selected at roughly equal frequency and always in a pseudothreshold functional form, though the specific spatial scale used in each model was more variable. Holding all other covariates in the top population-specific model at their mean, the relative probability of selection (0–1) increased by 123.0% (Bitterroot East Fork), 59.5% (Bitterroot West Fork), 244.8% (Paradise Valley), and 684.7% (Sage Creek) as time-integrated NDVI increased from 35 to 70 (within the range of observed values for all populations). For NDVI amplitude, the relative probability of selection increased by 543.0% (Blacktail), 21.2% (Dome Mountain), 31.2% (Madison Valley), 129.1% (Pioneers), and 44.0% (Sapphires) as NDVI amplitude increased from 35 to 70 (Figure 2).

All of the populations, except Paradise Valley, included one of the route density metrics, with the density of motorized routes being generally more common than the density of all routes. The pseudothreshold and linear forms were included at equal frequency and the largest spatial scale of the covariate was generally preferred (Table 4). The direction of selection for the access route covariates was variable and the strength of selection for or against routes was generally small relative to the strength of selection for nutrition (Table 4). Holding all other covariates in the top population-specific model at their mean, the relative probability of selection (0–1) changed by 16.5% and 13.4% (Bitterroot East Fork), 17.3% and 0.69% (Bitterroot West Fork), and –15.4% and –0.97% (Sapphires) when increasing the density of all routes from 0 to 2 km/km² and 2 to 4 km/km², respectively. Following those same methods for the density of motorized routes, we saw changes in the relative probability of use of –21.9% and –1.41% (Blacktail), 26.6% and 0.90% (Dome Mountain), –4.78% and –5.29% (Madison Valley), –31.2% and –39.8% (Pioneers), and –21.5% and –27.7% (Sage Creek). For the Paradise Valley population, moving from secure to insecure areas led to an increase in the relative probability of use of 55.6% (Appendix S5).

Model selection results showed few generalities in the influence of landscape covariates on resource selection. Abiotic features such as slope and solar radiation were included in all the population-specific models, and elevation was included in all the population-specific models except for the Blacktail population. These were included at both the large or small spatial scale, with little support for intermediate spatial scales. All of the continuous covariates in the landscape models were included in the quadratic functional form. Of the land cover covariates, grasslands were the most commonly included, followed closely by forests. Shrublands were only included in four of the population-specific models. Despite these generalities, the direction and strength of selection for each landscape covariate were variable among the populations (Appendix S6).

Model validation results indicated that each population-specific model was accurate in the area where it was created, though the transportability of the population-specific models to the other populations was variable (Table 5). Each of the population-specific models was unable to accurately predict at least one other population's resource selection, and all but the Paradise Valley model predicted at least one other population's resource selection worse than would be expected at random.

In seven of the nine populations, a post hoc exploratory analysis found a significant interaction between nutrition and access route covariates, resulting in improved model fit based on ΔAIC_c . The top Madison Valley and Pioneers population-specific models did not show support ($\Delta AIC_c \leq 2$) for both the post hoc interaction and original additive model, while the other seven top population-specific models were all improved by including the interaction ($\Delta AIC_c \geq 22$). In areas of higher nutrition (time-integrated NDVI or NDVI amplitude = 70), elk responses to increased route density were generally small. In areas of lower nutrition (time-integrated NDVI or NDVI amplitude = 35), elk responses to increased route density were generally negative. In addition, areas of higher nutrition had positive relative resource selection values across the range of route densities examined (0–4 km/km²), while areas of lower indexed nutrition generally had negative relative resource selection values across all route densities (Appendix S7).

Regional models

The top regional models of summer elk resource selection followed similar patterns to the population-specific models (Table 3). Both the top consensus (Appendix S8)

TABLE 3 Corrected Akaike information criterion (AIC_c) model selection results for the best models explaining elk summer resource selection in southwest Montana and mean cross-validated Spearman rank correlation (r_s).

Population	Top model(s)	K	AIC_c	ΔAIC_c	Mean r_s
Bitterroot East Fork	Time-Integrated NDVI[500]{ps} + Density of All Routes[1000] + Elevation[1000]{2} + Forest + Grassland + Shrubland + Slope[30]{2} + Solar Radiation[1000]{2} + strat(year)	11	287,433	0.00	0.99
Bitterroot West Fork	Time-Integrated NDVI[250]{ps} + Density of All Routes[1000]{ps} + Elevation[1000]{2} + Forest + Shrubland + Slope[30]{2} + Solar Radiation[100]{2} + strat(year)	10	205,859	0.00	1.00
Blacktail	NDVI Amplitude[1000]{ps} + Density of Motorized Routes[1000]{ps} + Forest + Grassland + Slope[1000]{2} + Solar Radiation[250]{2} + strat(year)	8	152,214	0.00	0.99
Dome Mountain	NDVI Amplitude[250]{ps} + Density of Motorized Routes[1000]{ps} + Elevation[30]{2} + Forest + Grassland + Slope[100]{2} + Solar Radiation[100]{2} + strat(year)	10	194,129	0.00	1.00
	NDVI Amplitude[250]{ps} + Density of Motorized Routes[1000]{ps} + Elevation[100]{2} + Forest + Grassland + Slope[100]{2} + Solar Radiation[100]{2} + strat(year)	10	194,130	0.65	1.00
Madison Valley	NDVI Amplitude[250]{ps} + Density of Motorized Routes[1000] + Elevation[30]{2} + Forest + Grassland + Slope[100]{2} + Solar Radiation[100]{2} + strat(year)	11	203,902	0.00	1.00
	NDVI Amplitude[250]{ps} + Density of Motorized Routes[1000] + Elevation[100]{2} + Forest + Grassland + Slope[100]{2} + Solar Radiation[100]{2} + strat(year)	11	203,904	1.31	1.00
Paradise Valley	Time-Integrated NDVI[1000]{ps} + Security Definition I + Elevation[100]{2} + Grassland + Slope[1000]{2} + Solar Radiation[30]{2}	9	197,127	0.00	1.00
Pioneers	NDVI Amplitude[500]{ps} + Density of Motorized Routes[1000] + Elevation[1000]{2} + Forest + Grassland + Shrubland + Slope[100]{2} + Solar Radiation[1000]{2}	11	138,601	0.00	1.00
Sage Creek	Time-Integrated NDVI[1000]{ps} + Density of Motorized Routes[1000] + Elevation[30]{2} + Forest + Grassland + Slope[250]{2} + Solar Radiation[1000]{2} + strat(year)	10	94,242	0.00	1.00
	Time-Integrated NDVI[1000]{ps} + Density of Motorized Routes[1000] + Elevation[100]{2} + Forest + Grassland + Slope[250]{2} + Solar Radiation[1000]{2} + strat(year)	10	94,243	1.15	1.00
	Time-Integrated NDVI[1000]{ps} + Density of Motorized Routes[1000] Elevation[30]{2} + Forest + Shrubland + Slope[250]{2} + Solar Radiation[1000]{2} + strat(year)	10	94,246	4.08	1.00
Sapphires	NDVI Amplitude[250]{ps} + Density of All Routes[750]{ps} + Elevation[1000]{2} + Forest + Grassland + Shrubland + Slope[250]{2} + Solar Radiation[1000]{2}	11	203,681	0.00	1.00
Consensus	NDVI Amplitude[500]{ps} + Density of Motorized Routes[1000]{ps} + Elevation[1000]{2} + Grassland + Shrubland + Slope[100]{2} + Solar Radiation[100]{2}	10	NA	NA	NA
Pooled	Time-Integrated NDVI[500]{ps} + Density of Motorized Routes[100]{ps} + Elevation[30]{2} + Forest + Grassland + Slope[100]{2} + Solar Radiation[30]{2} + strat(herd_year)	10	1,708,407	0.00	1.00

Note: The top models within five ΔAIC_c of the top-ranked model for each population are presented. Covariates: square brackets, [], indicate the spatial scale in meters; curly brackets, { }, indicate the functional form (none, linear; 2, quadratic; ps, pseudothreshold). "K" indicates the number of parameters included in the model. Covariate estimates and standard errors for each of the top models are included in Appendix S4.

Abbreviations: NDVI, normalized difference vegetation index; NA, not applicable.

TABLE 4 Coefficient estimates and 95% confidence intervals (CIs, in parentheses) representing the influence of nutrition and access routes on elk summer resource selection in southwest Montana, based on the top population-specific models.

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

Note: Covariates: square brackets, [], indicate the spatial scale in meters; curly brackets, { }, indicate the functional form (none, linear; 2, quadratic; ps, pseudothreshold). For quadratics, the main effect is listed first. Values in boldface indicate CIs that do not overlap 0. Full model details can be found in Appendix S4. All estimates are standardized with the exception of the consensus model, which is on the original scale.

Abbreviation: NDVI, normalized difference vegetation index.

and pooled (Figure 3) models included covariates from each of the covariate suites, and nutrition had the strongest influence on resource selection (Table 4). The nutrition covariate at the 500-m spatial scale and a pseudothreshold functional form was included in both regional models, but they differed in which nutrition covariate was included. The consensus model included NDVI amplitude and the pooled model included time-integrated NDVI. Holding the other covariates in the top model at their mean, increasing either NDVI amplitude (consensus) or time-integrated NDVI (pooled) from 35 to 70 resulted in an increase in the relative probability of selection (0–1) of 39.1% and 132.6% respectively.

In both regional models, access routes were best represented by the density of motorized routes in a pseudothreshold functional form. The consensus model included this covariate at the 1000-m spatial scale and the pooled model included this covariate at the 100-m spatial scale (Table 3). Both models predicted that motorized routes were negatively associated with resource

selection (Table 4), though this association was stronger for the pooled model than the consensus model. Increasing motorized route density from 0 to 2 km/km² and from 2 to 4 km/km² changed the relative probability of selection (0–1) by -0.97% and -0.05% for the consensus model, and -14.4% and -0.8% for the pooled model.

Similar to the population-specific models, the landscape covariates in the regional models included elevation, slope, and solar radiation in quadratic functional forms. Slope was included at the 100-m scale for both models, but elevation and solar radiation were selected at the 1000-m and 100-m scales, respectively, for the consensus model and the 30-m scales for both covariates in the pooled model. The consensus model included grassland and shrubland, and the pooled model included grassland and forest. The direction of selection for the covariates that were included in both models were similar with the exception of slope and solar radiation (Appendix S6).

Model validation results indicated that each regional model predicted population-specific resource selection

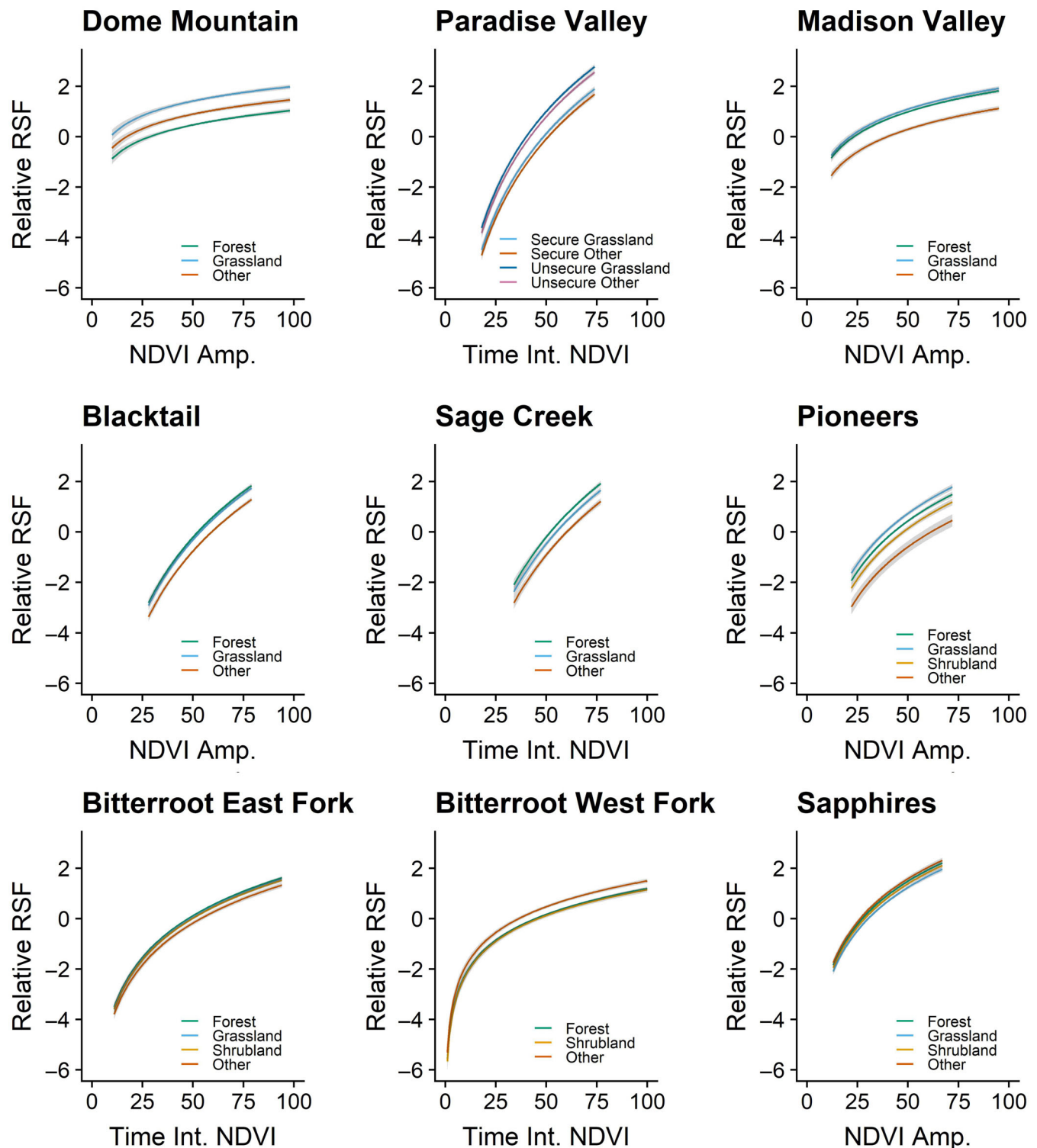


FIGURE 2 Plots for the nutrition covariate included in the top model for each population, presented on the original, non-standardized scale. The plots present the coefficient estimate (line) and 95% confidence interval (shaded) across the available range of the covariate, while holding all other covariates in the model at their mean. The plots are arranged based on geography (roughly east to west) moving from the top left to the bottom right of the plot grid. The y-axis is analogous to the log odds of selection. Note that the x-axis may be different for each of the population-specific models. NDVI amp., normalized difference vegetation index amplitude; Time Int. NDVI, time-integrated NDVI.

well. The consensus model accurately predicted elk resource selection in seven of the nine populations, and the pooled model accurately predicted elk resource

selection in all of the individual populations (Table 5). On average, both regional models significantly and accurately predicted elk resource selection.

TABLE 5 The generalizability of each population-specific and regional top model of summer elk resource selection in southwest Montana was estimated by predicting resource selection for the other populations (subsequent columns) and assessing accuracy of predictions using the Spearman rank correlation coefficient.

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

Note: Values on the diagonal represent the results of the k -fold cross-validation with five random folds and 10 equal area bins, averaged over 100 repetitions. Model generalizability is the mean Spearman rank correlation coefficients for the top model for each population (rows). Population generalizability is the mean Spearman rank correlation coefficient for each population (columns). Values in boldface are significant ($\alpha = 0.05$) and negative values indicate that the model predicted resource selection worse than random.

Given that the consensus model is built by averaging the coefficient estimates and standard errors of the population-specific models in a meta-analysis framework (Appendix S8), it was not possible post hoc to assess if a nutrition and access route interaction improved model fit based on ΔAIC_c . In the exploratory analysis, including a nutrition and access route interaction in the top pooled model improved model fit ($\Delta AIC_c \geq 491$). Similar to the population-specific models, the pooled model showed that at high nutrition values, elk responses to increased route density were generally small, but at lower nutrition values, elk responses to increased route density increased and were negative (Appendix S7).

DISCUSSION

Our modeling of elk summer range resource selection across southwestern Montana suggests that greenness is the primary factor affecting summer elk distribution. We recommend that elk summer habitat management paradigms based on managing motorized route density to maintain elk habitat effectiveness should be expanded to also directly consider nutritional resources. Additionally, our results suggest that population-specific resource selection models may be poor predictors of resource selection outside the area in which they were generated. Broader scale, regional models built through

meta-analysis of population-specific models or by pooling data across populations are more reliable predictors of resource selection across multiple areas and are better suited to inform regional habitat management policies.

Indices of nutritional resources were consistently the strongest predictors of summer resource selection in each of the population-specific and regional models, highlighting the importance of nutrition in elk summer resource selection in this region and the need to incorporate nutritional resource considerations more directly in elk summer habitat management beyond managing route density for habitat effectiveness. The importance of summer nutritional resources on ungulate population dynamics is well documented (Cook et al., 2013; Monteith et al., 2014), and in some ecosystems summer nutritional resources may have a stronger effect on population dynamics than winter severity (Cook, Johnson, et al., 2004). Summer nutritional condition affects elk pregnancy rate, calf growth rate, and overwinter survival (Cook, Johnson, et al., 2004; Cook et al., 2013; Spitz et al., 2019), and may be an important predictor of population growth rate for ungulates (Monteith et al., 2014). In southwest Montana, most studies indicate that nutrition is not commonly limiting elk pregnancy rate or overwinter survival (Cook, Cook, & Mech, 2004; Evans et al., 2006; White et al., 2011), however some populations may experience nutritional limitations that limit productivity (Proffitt et al., 2016). Additionally, the

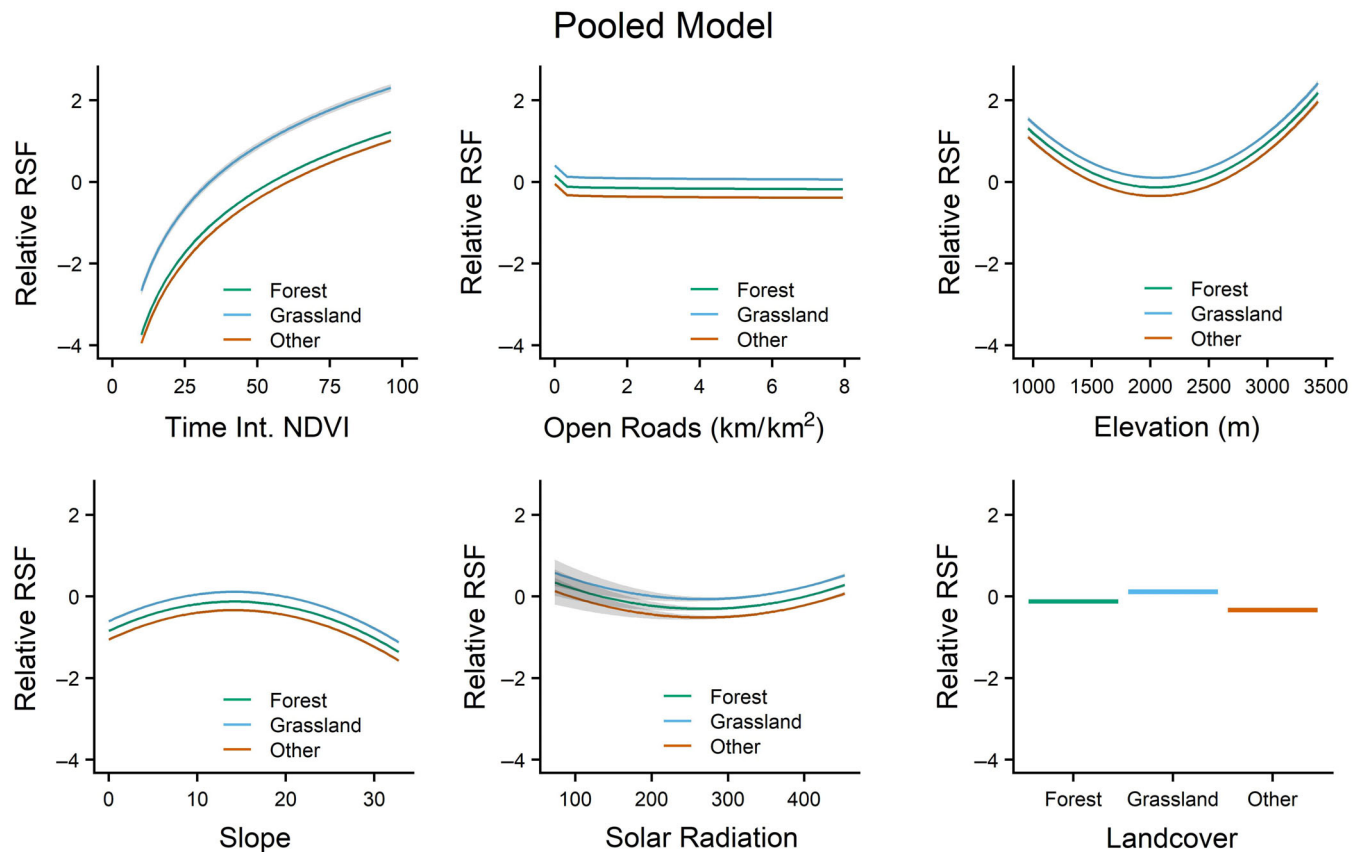


FIGURE 3 Plots for the covariates included in the top pooled regional model, presented on the original, non-standardized scale. The plots present the coefficient estimate (line) and 95% confidence interval (shaded) across the available range for each covariate, with the other variables held at their mean value. The y-axis is analogous to the log odds of selection. NDVI, normalized difference vegetation index; Time Int. NDVI, time-integrated NDVI.

importance of nutrition may persist into the fall hunting season (DeVoe et al., 2019; Ranglack et al., 2017; Spitz et al., 2019). Managers should identify areas where elk are likely to be nutritionally limited and be particularly thoughtful about directly incorporating nutrition into summer habitat management strategies in these areas. This may include directly manipulating nutritional resources through the use of fire (Fuhlendorf et al., 2009; Ranglack & du Toit, 2015), domestic ungulate grazing (du Toit, 2011; Odadi et al., 2011), or timber harvest that opens a mature forest canopy (Cook et al., 1996), while also managing road densities, especially in areas of relatively low nutritional quality.

Our results suggest that NDVI may be a useful index of ungulate nutritional resources, although additional field data are required to fully understand the relationship between NDVI and ungulate forage quality (Borowik et al., 2013). NDVI amplitude and time-integrated NDVI may be indicators of ungulate nutritional resources, and we found that both performed well in our models, with five of the population-specific models and the consensus model containing NDVI amplitude

and the remaining models containing time-integrated NDVI. NDVI is a metric of greenness based on satellite imagery and has become one of the most widely used vegetation indices in ecology (Pettoirelli et al., 2005). We found elk selected for areas that have larger increases in NDVI across the summer growing season, which would be indicative of foraging areas that start the spring at lower greenness levels and increase in greenness as the growing season progresses. Similar patterns have been documented in a wide variety of animal species, making NDVI an easily accessible and useful tool in wildlife ecology (Pettoirelli et al., 2011).

Surprisingly, NDVI indices predicted elk summer resource selection better than a landscape model of forage quality developed within the study area (Proffitt et al., 2016). NDVI is simply an index of greenness rather than a direct measurement of elk forage quality or quantity. Time-integrated NDVI, our most supported nutrition covariate, represents the greenness of the entire growing season. By contrast, the Bitterroot elk forage quality model integrated ground-based measurements of forage species biomass, phenology, and digestibility to estimate

forage quality, then modeled late-summer landscape forage quality as a function of landscape attributes. It may be possible that elk are responding to areas of higher overall productivity instead of nutritional resources only during the late-summer period. Additionally, the Bitterroot model may suffer from issues of extrapolation in that it was developed in the Bitterroot Mountains and may not be a good predictor of nutritional resources in the other study areas. NDVI metrics do not suffer from these same issues of extrapolation. Additionally, landscape nutrition modeling is time- and labor-intensive and may only be conducted at relatively small scale. By contrast, NDVI-derived indices are freely available, cover broad spatial scales, and are updated routinely, allowing agencies to evaluate changes in plant productivity associated with elk summer nutritional resources that may occur due to varying weather/climate and changes associated with natural and anthropogenic impacts (fire, disease and insect outbreaks, silviculture treatments, etc.), making these indices a practical tool for regional or large-scale applications. However, as methods for landscape nutrition modeling advance, these types of landscape nutrition models may ultimately provide additional data that directly estimate forage nutritional resources for a given species (Avgar et al., 2015; Hebblewhite et al., 2008; Pretorius et al., 2011; van Beest et al., 2010).

In addition to the strong effect of nutritional resources on elk summer resource selection, access routes were also included in all models as a predictor of resource selection. The effects of access routes on elk are widely documented (see McCorquodale, 2013 for review), and elk habitat management on public lands in Montana is structured on managing route density to maintain habitat effectiveness (MDFWP and USDA Forest Service, 2013). While our results generally support that elk select for areas away from access routes, we found that the effects of routes on summer resource selection were highly variable. Of the nine top-ranked, population-specific resource selection models we developed, five models included a covariate representing elk selection for areas away from routes and four included a covariate representing elk selection for areas nearer routes. At the regional level, both models predicted elk selection for areas with fewer motorized routes, but the magnitude of the effect was small relative to other factors, particularly nutrition (Table 4). The relative weakness of this preference for areas with fewer routes is contrary to expectations based on existing literature and current management strategies (Christensen et al., 1993; Forman & Alexander, 1998; Lyon, 1979; Montgomery et al., 2013), which largely show the strong negative impacts of roads on resource use, though there is some variation by sex and season. In these same areas, the

impact of access routes on elk habitat selection increased dramatically during both the archery and rifle hunting seasons, suggesting that the influence of roads may vary seasonally, with elk being more tolerant of roads during periods when hunting does not occur (Ranglack et al., 2017).

Several factors may be contributing to these observed differences. First, our models focus on elk resource selection of specific locations within established population ranges, as recommended by Edge et al. (1986) and MDFWP and USDA Forest Service (2013), which may already represent population-level avoidance of areas with the highest route densities, as found in Alberta, Canada (Frair et al., 2008). If we evaluated first- or second-order resource selection (Johnson, 1980), we may have found a stronger influence of motorized routes on elk resource selection. Second, motorized route densities have been the target of forest travel management for several decades (Christensen et al., 1993), reducing motorized route density in some areas. The lack of a strong influence of access routes on elk resource selection in our study may indicate that these management actions have been effective and should continue. It is also possible that there is not enough traffic on the routes during summer to influence elk behavior (Gagnon et al., 2007; Johnson et al., 2000; Wisdom et al., 2004). Additionally, routes are frequently built along terrain and riparian corridors that are high-quality habitat for ungulates. These high-quality areas may be selected for by ungulates despite their proximity to motorized routes (Dodd et al., 2007; Gagnon et al., 2007). The results of our post hoc interaction models support this hypothesis, with elk showing little response to route density in areas of high nutritional value, but stronger negative responses to route density in areas of low nutritional value (Appendix S7). Finally, while route density metrics are sensitive to the methods used to generate them, these population home ranges may have lower route densities than what is found on other public lands, leading to smaller than expected responses in elk summer resource selection. Reported motorized route densities on public lands in Idaho, Oregon, USA, and Alberta, Canada, range from 0.13 to 2.54 km/km² (Frair et al., 2008; Gratson & Whitman, 2000; Rowland et al., 2000), while mean motorized route density in our elk population summer ranges is 0.71 km/km² (Table 1).

Our results suggest that caution should be used when extrapolating resource selection functions to new areas beyond the model development area. Although each of our population-specific models had good predictive accuracy in the areas in which they were created, the predictive accuracy of population-specific models beyond the area in which they were developed was sometimes poor

and occasionally worse than random. This can be mostly explained by geography and habitat similarity, as models performed best for populations that were near to where they were generated, or that contained very similar habitat types. As an example, elk resource selection in the Bitterroot West Fork summer range, which is heavily forested and quite different ecologically than many of the more open elk summer ranges for the other populations we studied, was predicted worse than random by half of the other population-specific resource selection models, as well as the regional consensus model. Thus, managers should use caution when extrapolating results of resource selection functions to new areas. These risks are lessened when the models are developed using data from multiple populations, either through the use of consensus or pooled models of habitat selection, or when the new areas are close geographically and similar ecologically to the area where the model was developed.

The regional consensus model performed reasonably well and predicted elk resource selection accurately in every population except for the Bitterroot East Fork and West Fork populations. The consensus model likely performed well because it was based off of a larger dataset that captured a wider range of variability in available habitat than any one population-specific model. However, when the direction of selection varied among populations, as was particularly evident with the varying positive and negative model coefficients for the effects of route density, grasslands, and solar radiation, the averaged effect in the consensus model approached zero (Appendix S8). This highlights a potential weakness of deriving inference or predictions from regional meta-analyses, in that these models may not capture the range of differences in population-specific selection patterns among populations. Elk in different areas have different selection patterns that may arise as a result of different availabilities or different selection patterns (Appendix S8).

The pooled model that was based on a dataset that included all location data from all individuals in all populations performed the most accurately and consistently. In contrast to the consensus model that used model averaging from population-specific models to develop a regional model, the pooled model coefficient estimates were derived from the data without employing any model averaging techniques. All individuals in all sampled populations were weighted equally in the pooled model. Additionally, all covariate values were estimated across the range of availability for the entire region, as opposed to being restricted to what was available in each population-specific summer range. This pooled model supported the conclusions of the population-specific models with regard to the magnitude of the effects of

nutritional resources and access routes. We recommend that, when possible, managers use data pooled from multiple populations to inform regional habitat management policies.

The results of the spatial scale analysis offer few generalities, as there were large differences in the preferred spatial scale among covariates and populations (Boyce, 2006; Laforge et al., 2015). Route density is the exception here, with the largest spatial scale being preferred fairly consistently, with only three models (Pioneers, 500 m; Sapphires, 750 m; Pooled, 100 m) reflecting elk responses to route density at smaller scales. Despite the wide range of variability in the other covariates, precision in the models was improved by the use of various scales. The ecological patterns of selection remained consistent across scales within a population, but certain scales were much more supported than others (Appendix S4), highlighting the value of performing exploratory analyses on scale as part of resource selection function modeling exercises. We recommend resource selection models developed for predictive purposes employ this modeling strategy to improve precision. This becomes particularly important as new remote sensing technologies produce spatial data at finer and finer scales that may exceed an animal's ability to detect such differences. However, if resource selection models are being used for understanding biology only, this may not be necessary as the biological interpretation did not differ among spatial scales.

Although carnivores have the potential to effect elk resource selection, data to evaluate these potential effects were not available in this study. In the presence of wolf risk, elk may shift habitat use toward areas of higher structural complexity (steeper slopes, more cover, etc.; Beschta & Ripple, 2013; Creel et al., 2005; Mao et al., 2005). However, in these areas, elk are more vulnerable to predation by mountain lions (Bartnick et al., 2013; Ruth et al., 2003); thus, elk may ultimately select for habitat types that provide the lowest overall predation risk between these two predators (Atwood et al., 2007; Kohl et al., 2019; Kunkel et al., 1999). However, predator-prey spatial dynamics are complex, with both predator and prey adjusting their space use behavior in response to the other (Kohl et al., 2019; Kunkel et al., 2004; Thaker et al., 2011). Thus, the effects of predators are likely to be variable and ungulates are able to balance the trade-off between predation risk and forage quality (Hebblewhite & Merrill, 2009; Marchand et al., 2015). Given the importance of nutritional resources we demonstrated here, predator impacts are likely less important to overall summer elk habitat selection than nutritional resources, though this balance is likely variable in time and space.

Our findings on the impacts of nutrition and access routes on elk summer resource selection provide additional evidence to the importance of nutritional resources for elk during the summer season. We recommend elk summer habitat management should include an evaluation of elk nutritional resources, as indexed by an averaged NDVI metric. Recognizing areas of higher or lower quality nutritional resources could help inform management decisions regarding the placement of travel corridors, the management of motorized use, and in planning habitat treatments to convert areas of low nutrition into areas of higher nutrition. Nutritional resources may be directly influenced by the use of fire (Fuhlendorf et al., 2009; Ranglack & du Toit, 2015), domestic ungulate grazing (du Toit, 2011; Odadi et al., 2011), or timber harvest that opens a mature forest canopy (Cook et al., 1996). Elk were more likely to select for areas of lower route density, but the influences of route density were variable and route density alone did not drive elk summer resource selection. Therefore, we recommend continued management for reasonable motorized route densities, along with direct consideration of nutritional resources in elk summer habitat management strategies. Finally, caution should be taken when extrapolating the results of resource selection functions to new areas. When possible, managers should use models developed using data from multiple populations, either through the use of consensus or pooled models of habitat selection, and/or use models from areas that are close geographically and similar ecologically to the area where the model will be applied.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Ranglack et al., 2022) are available from Dryad: <https://doi.org/10.5061/dryad.zw3r22895>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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