The Journal of Wildlife Management 83(4):801–816; 2019; DOI: 10.1002/jwmg.21638

Research Article

Elk Forage and Risk Tradeoffs During the Fall Archery Season

JESSE D. DEVOE,[1] *Montana Cooperative Wildlife Research Unit, 205 Natural Sciences Building, Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*

KELLY M. PROFFITT, *Montana Department of Fish, Wildlife and Parks, 1400 South 19th Street, Bozeman, MT 59718, USA*

MICHAEL S. MITCHELL, *U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, 205 Natural Sciences Building, Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*

CRAIG S. JOURDONNAIS, *MPG Ranch, 1001 South Higgins Avenue, Missoula, MT 59801, USA*

KRISTIN J. BARKER, *Montana Cooperative Wildlife Research Unit, 205 Natural Sciences Building, Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*

ABSTRACT During late summer and fall, elk (*Cervus canadensis*) need access to adequate nutrition to support physiological requirements for reproduction and overwinter survival. The archery hunting season often occurs during this period and can affect distributions of elk as they seek areas that minimize perceived harvest risk. Areas that confer lower harvest risk may provide relatively low-value nutrition, resulting in a potential tradeoff between minimizing risk and accessing adequate forage. We used radio-collar data collected from female elk during late summer and fall (Aug–Oct) and estimated resource selection models to evaluate the extent of this potential risk-nutrition tradeoff. To evaluate if elk exposed to a greater hunting risk altered selection for forage resources, we assessed the relationship between individuals' selection coefficients for forage and the proportion of their late-summer-fall home range accessible to hunters (our metric of hunting risk). Our results indicate that during the archery season, elk with higher-risk home ranges selected more strongly for areas farther from motorized routes than elk with lower-risk home ranges. Regardless of the level of risk, however, elk maintained or increased selection for areas with higher forage quality, suggesting that elk did not compromise access to nutritional resources during the archery season. Elk with higher-risk home ranges were also exposed to the poorest nutrition and increased their selection for areas with higher forage quality more strongly than elk with lower-risk home ranges during the hunting season. Elk with lower-risk home ranges had access to the highest nutrition, which may be due to the availability of concentrated sources of high-quality forage from irrigated agricultural areas on private lands that restricted hunter access. Resource agencies interested in encouraging elk to remain on public lands during the hunting seasons might consider closing motorized travel during the archery season to increase security on public lands, limiting hunter pressure on public lands, improving forage quality on public lands, and working with private land owners to enhance hunter accessibility and restrict elk access to high-quality forage resources. © 2019 The Wildlife Society.

KEY WORDS archery, *Cervus canadensis*, hunter access, Montana, nutritional resources, resource selection, risk, security.

In temperate climates, the availability and distribution of nutritional resources during summer and fall are important factors influencing ungulate survival, reproductive performance, and distributions (Cook et al. 2013, 2016; Monteith et al. 2014; Long et al. 2016; Proffitt et al. 2016*a*). This time period is critical for female ungulates to accrue sufficient body fat to support demands of lactation and calf-rearing, become pregnant in fall, and survive the nutrient-limited winter (Cook et al. 2004, 2013; Monteith et al. 2014). The availability of adequate forage abundance and quality (digestibility) are important for elk (*Cervus canadensis*) to meet these nutritional demands, with high-quality forage playing an essential role (Cook et al. 2004, 2013, 2016). The onset of the archery hunting season in late summer and fall (late Aug or early Sep) may influence resource selection and distributions of ungulates as they seek areas with less hunting pressure (Kilpatrick and Lima 1973, Conner et al. 2001, Vieira et al. 2003, Cleveland et al. 2012, Ranglack et al. 2017). This behavioral strategy may negatively affect the nutritional condition and, ultimately, survival and reproduction of ungulates, if access to nutritional resources is limited or reduced as animals alter their movements to reduce harvest risk (Hebblewhite 2006, Davidson et al. 2012, DeCesare et al. 2014).

The risk-related effects of the archery season on elk selection for forage has received little attention even though

Received: 25 November 2017; Accepted: 5 December 2018

[1] *E-mail: jessedevoe@gmail.com*

nutrition during this time period is crucial, particularly for female elk (Cook et al. 2004, 2016; Bender et al. 2008). Elk are expected to select areas of higher nutritional value when risks of using those areas are low (Pyke 1984, Ferrari et al. 2009, Godvik et al. 2009). When elk perceive high mortality risks, they may select areas of inferior nutritional value in favor of increased security benefits, implying a potential tradeoff between forage and risk (Morgantini and Hudson 1985, Hernández and Laundré 2005, Hebblewhite and Merrill 2009, Lone et al. 2015). Although a strong tradeoff between forage and risk during the hunting season may reduce an elk's chance of being harvested (Lone et al. 2015), it may also incur longer-term consequences to survival or reproduction through reduced nutritional condition (Cook et al. 2004).

During the archery season, elk select for areas providing security from harvest (Conner et al. 2001, Vieira et al. 2003, Proffitt et al. 2016*b*, Ranglack et al. 2017). Security areas typically offer hiding cover, which obscures the animal from view or allows it to swiftly escape danger (Skovlin et al. 2002), or isolation from hunter activity, such as areas away from roads open to vehicle travel (Montgomery et al. 2013, Proffitt et al. 2013, Ranglack et al. 2017). Selection by elk for security areas, and the potential forage-risk tradeoff, may vary depending on the level of hunting pressure and the availability of areas providing security (Conner et al. 2001; Proffitt et al. 2013, 2016*b*; Ranglack et al. 2017). Many landscapes in the western United States have freely accessible public land adjacent to private lands that often restrict the access of hunters, providing a variety of opportunities for elk to increase security during the hunting season (Conner et al. 2001, Vieira et al. 2003, Cleveland et al. 2012, Proffitt et al. 2013). Although elk may choose to remain on public lands during late-summer and fall (i.e., summer-fall), some elk may move to, or remain as permanent residents on, areas restricting hunter access where hunter density and harvest risk may be lower (Burcham et al. 1999, McCorquodale et al. 2003, Proffitt et al. 2016*b*). The nutritional consequences of these varying strategies during the archery hunting season are unknown.

Traditional management of elk habitat is based on providing security on public land through management of motorized travel routes and hiding cover to balance elk survival and provide hunter opportunity (Christensen et al. 1993). These management plans, however, have focused primarily on male elk during the rifle season (Hillis et al. 1991) even though hunting seasons in many areas are designed to manipulate survival of female elk in efforts to increase or decrease elk populations. In Montana, USA, statewide sales of archery hunting licenses have increased 98% from 21,758 in 1985 to 43,071 in 2014 (Montana Fish, Wildlife and Parks, unpublished data). The continued increase in hunters afield during the archery season may affect distributions of elk more than previously recognized in habitat management plans. Additionally, increased harvest pressure during the archery season may affect hunter success during the rifle season by redistributing elk to areas less accessible to public hunters, thereby limiting the effectiveness of traditional harvest and population management strategies (Burcham et al. 1999, Haggerty and Travis 2006). Increased use and extended stay of elk on areas restricting hunter access may result in increased damage to crops and property and the potential dissatisfaction of private land owners (Bunnell et al. 2002, Haggerty and Travis 2006) and elk hunters seeking opportunity on public lands (Lewis et al. 2014). These conditions create challenges for managing elk populations through traditional harvest methods, particularly for elk populations that exceed management population objectives. Land management agencies recognize the effect of the archery season on the redistribution of elk (Canfield et al. 2013, United States Forest Service [USFS] 2016); however, agencies seek a better understanding of the role the archery season plays in selection of security and foraging areas by female elk, particularly on landscapes with highly variable hunter accessibilities.

To assess the nutritional consequences of risk-related effects of archery hunting on female elk, we evaluated summer-fall resource selection in a population occupying a landscape with varying nutritional resources and levels of hunting risk. We tested 3 hypotheses: the archery season does not substantially affect selection for security and forage by elk; elk do not trade off forage and risk during the archery season because elk can select areas providing forage and security regardless of hunter accessibility; and elk trade off forage for increased security during the archery season, and the strength of the tradeoff increases as hunter accessibility increases (i.e., harvest risk). We tested these hypotheses by developing resource selection functions for female elk using 2 years (2014–2015) of radio-collar location data and evaluating the effect of the archery season on selection of forage and security resources across varying levels of hunter accessibility.

STUDY AREA

Our study area encompassed 2,482 km^2 in the northern Sapphire Mountains and Bitterroot River valley of west-central Montana and included summer-fall (31 Jul–19 Oct) range of the North Sapphire elk population during 2014 and 2015 (Fig. 1). Land ownership was a matrix of publicly accessible state (5%), federal (54%), and corporate timber lands (3%) that dominated the higher elevation summer range and privately owned residential and agricultural lands (38%) that dominated the valley bottom winter range. Development along the study area's wildland-urban interface had increased during the previous 20 years. Mean annual precipitation ranged from 284 mm on the valley floor to 963 mm on mountain summits, and mean temperatures for July and January were 17.1°C and -4.4°C, respectively (PRISM [Parameter-elevation Regressions on Independent Slopes Model] Climate Group 2016). During the summer-fall period, annual precipitation and temperature averaged 128 mm and 10.1°C, respectively. Elevations ranged from 942 m to 2,505 m, and topography varied from flat bottomland to gentle foothills giving way to steep mountain slopes. Lower elevation areas were primarily irrigated and non-irrigated agricultural land composed of pasture grasses, corn, or leguminous forbs; sagebrush (*Artemisia tridentata*)

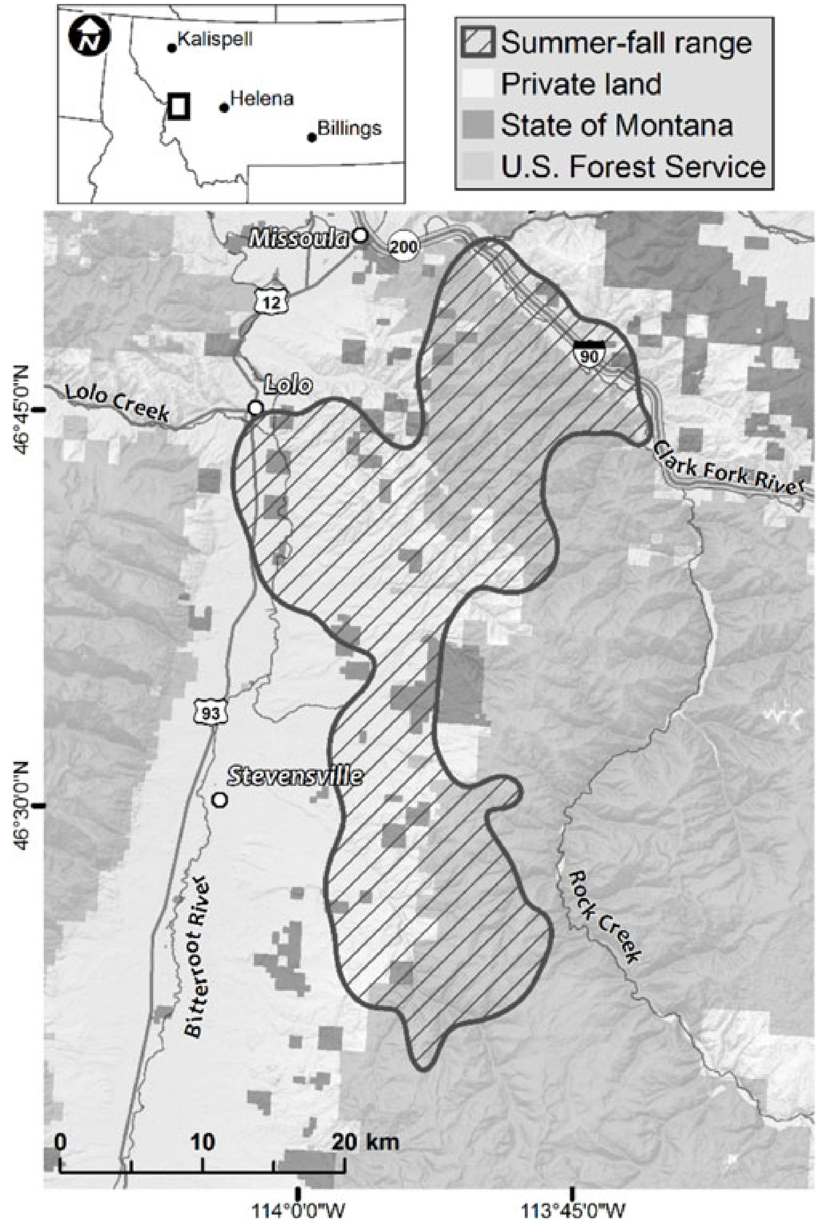

Figure 1. The North Sapphire female elk population summer-fall (31 Jul–19 Oct) range in the northern Sapphire Mountains and Bitterroot Valley of west-central Montana, USA, 2014–2015.

steppe and grassland with Idaho fescue (*Festuca idahoensis*), rough fescue (*Festuca campestris*), and bluebunch wheatgrass (*Pseudoroegnaria spicata*); and riparian wetlands. Higher elevation areas were predominately dry open coniferous forests with ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) and moist mixed coniferous forests with lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*), and subalpine fir (*Abies lasiocarpa*). Patchily distributed wildfires and timber harvests have produced areas varying in successional stages.

Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) were sympatric with elk in the study area. Carnivores that occupied the study area included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), gray wolf (*Canis lupus*), coyote (*C. latrans*), and American black bear (*Ursus americanus*). One established wolf pack inhabited and additional wolves occasionally traversed the study area. We assumed the influence of non-human predators (notably wolves and mountain lions) was consistent across the time periods of our study. No collared elk were killed by non-human predators during or after our study, indicating non-human predation was likely minimal. In addition, wolf densities were low in the study area, so we expected minimal effects of wolves on elk behavior compared to human predators (Proffitt et al. 2009, Middleton et al. 2013).

The core of the annual range for the North Sapphire elk population was within Montana hunting district 204. Montana Fish, Wildlife and Parks measured population trend using aerial surveys each spring. The population steadily increased from 600 in the late-2000s to a high of 1,051 in 2016 owing to a combination of high calf recruitment and limited female harvest. Archery hunting took place during a 6-week season in September and early October, and harvest of brow-tined male or antlerless elk was allowed with a general hunting license. A 5-week rifle hunting season followed the archery season during late October and November. Hunters with a general elk hunting license were allowed to harvest brow-tined male elk, and hunters 12 to 15 years old were allowed to harvest antlerless elk. Additionally, 30 and 100 hunters successful in drawing limited special permits were allowed to harvest antlerless elk in 2014 and 2015, respectively. Archery and rifle season regulations were consistent on both public and private lands. Antlerless-only elk damage hunts also took place on some private properties before, during, and after the archery and rifle hunting seasons. Although damage hunts occurred prior to the archery season beginning in 2015, we assumed that behavioral responses of elk to these harvests were minimal or temporary given the isolation, irregularity, and rarity of the hunts (Cleveland et al. 2012) and based on anecdotal observations by the authors. During the 2 years of our study, there was an annual estimated average of 7,205 hunter-days and 108 elk harvested. Hunters harvested an annual average of 14 elk in the archery season, 84 in the rifle season, and 10 in late-winter damage hunts. Female elk comprised 53% of the harvest in 2015.

METHODS

Data Collection

We captured 41 female adult ($\geq$1.5 years old) elk in February 2014 and an additional 3 elk in February 2015 using helicopter net-gunning or chemical immobilization (i.e., carfentanil and xylazine). We captured all elk in accordance with animal welfare protocols approved by Montana Fish, Wildlife and Parks (FWP19-2013). We outfitted elk with Iridium remote upload global positioning system (GPS) radio-collars (Lotek Wireless, model IridiumTrackM 3D, New Market, Ontario, Canada) programmed to record a location every 2 hours, transmit a mortality notification 6 hours post-mortality, and drop off after 2 years.

Analysis Design

We classified location data as pre-archery (i.e., 1 month prior to a buffer of 5 days before the start of archery season) and archery (i.e., 5 Sep–20 Oct in 2014 and 4 Sep–19 Oct in 2015) to represent times of relatively low and high risk of harvest, respectively. We used only 1 year of data for each elk; for elk with 2 years of data, we randomly selected 1 of the years to assure independence. We removed locations with low spatial precision (i.e., dilution of precision values $>$10; D'Eon and Delparte 2005). After removing these locations, the mean fix success rate of individual elk was 98.9% (range = 94.9–99.9%) across individual collars. We randomly selected 5 locations per individual per day to reduce spatial autocorrelation in the data (Hansteen et al. 1997) and standardize the number of locations per animal.

Our modeling approach consisted of 4 basic steps: determine a single, best-supported model of resource selection by elk during summer-fall using pooled data from all individuals; use the best-supported model to estimate resource selection functions for individual elk (Johnson 1980); estimate exposure of individuals to harvest risk as the proportion of each individual's summer-fall home range accessible to public hunters; and relate harvest risk of individuals to selection coefficients to determine if the forage-risk tradeoff varied for elk exposed to different levels of hunter access.

To determine the single, best-supported model, we first pooled used locations for all individuals and selected available locations at a ratio of 1:5 from within the population's summer-fall range, which we defined using a 95% kernel density estimator contour based on locations combined across all individuals. This method avoids the complexities associated with averaging selection coefficients across individual models that would likely vary considerably in covariate structure (Sawyer et al. 2007, Proffitt et al. 2016*b*). We chose the 1:5 used-available ratio to accurately describe the distribution of resources within the summer-fall range and to aid in model convergence (Northrup et al. 2013). We excluded land cover types that provided no resources to elk (e.g., rivers, lakes). We used generalized linear regression in Program R (R Development Core Team, Vienna, Austria) to estimate resource selection models as a function of standardized risk, forage, and landscape covariates selected based on review of elk studies and our hypotheses of habitat relationships (see Model Covariates; Table 1). We then evaluated the level of empirical support for the covariates within several model tiers (see Model Selection) to reduce the number of covariates, improve the fit of models in successive tiers (Franklin et al. 2000), and select the best-supported model for fitting to each individual's used-available dataset (see Forage-Risk Tradeoffs).

Model Covariates

We evaluated 5 risk covariates representing security areas elk could use to avoid harvest mortality during the archery period: canopy cover, distance to cover, distance to motorized routes, and 2 variations of security patches. We used percent canopy cover from LANDFIRE (www.landfire.gov, accessed 21 Jul 2016) to describe areas elk may use as hiding cover (Rowland and Wisdom 2012). We defined distance to cover as distance (m) to areas with canopy cover $\geq$40% to describe areas elk may use that allow them to swiftly move to secure areas with hiding cover (Canfield et al. 2013, Proffitt et al. 2016*b*). We defined distance to motorized routes as distance (m) to roads (2-track, dirt, or paved) or trails designated as open to public motorized travel, respective to each pre-archery and archery period (McCorquodale 2013). On USFS lands, we classified routes based on current National Forest travel management plans implemented to regulate motor vehicle use on roads (2-track, dirt, and paved) and trails. We assumed areas farther from motorized routes represented areas with reduced hunter pressure and greater security for elk than areas closer to motorized routes. We defined the 2 security patch covariates based on current National Forest management plans for providing elk security (Hillis et al.

Table 1. Covariates, functional forms, and hypothesized direction of selection considered for modeling resource selection by female elk during summer-fall in the North Sapphire population, west-central Montana, USA, 2014–2015. Pseudothreshold forms are a natural log transform.

Covariate	Functional form (hypothesis)	Reference
Risk variables		
Canopy cover	Linear (+), pseudothreshold (+)	Rowland and Wisdom (2012), Ranglack et al. (2017)
Distance to cover (>40%)	Linear (−), pseudothreshold (−)	Canfield et al. (2013), Proffitt et al. (2016*b*)
Distance to motorized route	Linear (+), pseudothreshold (+)	McCorquodale (2013), Ranglack et al. (2017)
Security patch	Binary (+)	Hillis et al. (1991), Christensen et al. (1993)
Security patch with cover (>30%)	Binary (+)	Hillis et al. (1991), Christensen et al. (1993)
Forage variable		
Forage abundance	Linear (+), pseudothreshold (+)	Cook et al. (2004, 2013, 2016), Proffitt et al. (2016*a*)
Forage quality	Linear (+), pseudothreshold (+)	Cook et al. (2004, 2013, 2016), Proffitt et al. (2016*a*)
Landscape variables		
Land cover type	Categorical	
Slope	Linear (+), pseudothreshold (+), quadratic (+/−)	Skovlin et al. (2002); Proffitt et al. (2013); Ranglack et al. (2017)
Archery effect		
Archery period	Binary	

1991, Christensen et al. 1993, Ranglack et al. 2017). Each security patch covariate was binary and included contiguous areas of $\geq$100 ha located $\geq$0.8 km from the nearest road open to motorized travel during each pre-archery and archery period. The second security patch covariate additionally incorporated contiguous areas with $\geq$30% canopy cover and was designed to evaluate whether cover was an important component of security patches.

We evaluated 2 forage covariates representing nutritional resources for elk during summer-fall (Cook et al. 2004, 2013, 2016; Hebblewhite 2006; Proffitt et al. 2016*a*), including forage abundance (grams of herbaceous forage/m^2) and forage quality (digestible energy/g of forage, kcal/g). We extracted both forage covariates from spatially explicit landscape models estimated from elk diet and vegetation surveys collected during late summer (Appendix A, Proffitt et al. 2016*a*). Briefly, field staff collected 68 summer composite pellet samples for diet analysis to identify important summer forage plant species and sampled 782 vegetation survey locations. Field staff estimated composition, biomass, phenological stage, and percent cover of forage species at each sampling location. We used this information, together with digestible energy estimates of each forage plant species in each phenological stage, to estimate forage abundance and forage quality at each sampling location. Lastly, we developed landscape forage models by modeling forage abundance and forage quality as a function of remotely sensed spatial landscape covariates.

We additionally evaluated 2 landscape covariates to capture general characteristics of the landscape that elk may use: land cover and slope (Skovlin et al. 2002, Proffitt et al. 2013, Ranglack et al. 2017). We classified land cover types into 3 categories: coniferous forests, montane riparian, and valley bottom areas (grasslands, shrublands, riparian, and agricultural areas). We selected these land cover categories to capture variation in habitats used by elk while also providing a reasonable means of estimating animal-specific parameters by lumping relatively similar vegetation community types (Fieberg et al. 2010). We combined riparian with valley bottom areas because riparian areas occurred in grasslands and comprised <4% of the population summer-fall range.

Model Selection

We used 4 model tiers to select a best-supported model based on the pooled data for subsequent use in estimating individual resource selection patterns. We competed models based on corrected Akaike's Information Criterion (AIC$_c$) rankings and advanced models $\leq$4 ΔAIC$_c$ to subsequent model tiers (Burnham and Anderson 2002). We considered only covariates with low multi-collinearity in the same models (Pearson correlation coefficient $|r| < 0.6$).

In model tier 1, we sought to determine the best-supported functional form of each of our continuous covariates. We fit univariate models evaluating different hypothesized functional forms for each continuous covariate (e.g., slope, canopy cover, distance to cover, distance to motorized route, forage abundance, forage quality) that included linear, pseudothreshold (natural log transformation; Franklin et al. 2000), and quadratic forms (Table 1). If necessary, we adjusted covariates considered for the pseudothreshold form by adding a small value to allow log transformation. We advanced the best-supported functional form(s) of each covariate to subsequent model tiers.

In model tiers 2 and 3, we sought to determine the best-supported risk and forage covariates, respectively. In model tier 2, we fit and competed the different risk covariates in models that included a null model, all univariate models, and additive models of all combinations of risk covariates. To avoid potential correlation in binary and continuous covariates, we did not include in the same model 1) the security patches and distance to motorized route; or 2) the security patch variant with incorporated canopy cover and canopy cover or distance to cover. In model tier 3, we fit and competed the different forage covariates in models that included a null model, each univariate model, and an additive model with both forage abundance and forage quality. We advanced the risk and forage covariates from the best-supported models to model tier 4.

In model tier 4, we sought to determine the best-supported model for subsequently applying to individual elk datasets and evaluating the effect of the archery season on potential tradeoffs between forage and risk. We competed all additive combinations of landscape covariates and the most-supported risk and forage covariates from model tiers 2 and 3, respectively.

Forage-Risk Tradeoffs

To assess the effect of the archery season on potential tradeoffs between forage and risk, we first added to the best-supported model from tier 4 a binary archery season covariate (0 for the pre-archery period, 1 for the archery period) as an interaction with each forage and risk covariate. We then fit this best-supported population model to each individual elk's used-available dataset with available locations selected at a ratio of 1:5 from within the individual's summer-fall home range to estimate selection coefficients for individual elk. We evaluated the overall explanatory power and fit of individual models (Shmueli 2010, Sainani 2014) using the le Cessie-van Houwelingen unweighted sum of squares test for assessing overall goodness-of-fit (Hosmer and Lemeshow 1989, le Cessie and van Houwelingen 1991, Hosmer et al. 1997).

To evaluate if the tradeoff between forage and risk varied for elk exposed to different levels of hunter access (i.e., different levels of harvest risk), we first classified hunter access into 2 categories: areas restricted to public hunting (i.e., low risk) and areas accessible to public hunting (i.e., high risk). Areas of restricted public hunting access included private lands that allowed hunting by family and friends, or through any other system that restricted free, equal-opportunity public access. These areas represent places elk may use to increase security during the hunting seasons. Areas accessible to public hunting included public lands and private lands enrolled in Montana's Block Management Program, a program designed to enhance free public hunter access on private lands. We estimated the proportion of the summer-fall home range of each elk that was accessible to hunters, with high values representing areas of high risk. We assessed the relationship between the selection coefficients and the proportion of the home range accessible to hunters using a linear model and interpreted the slope value to represent the effect of hunter accessibility on elk selection.

We interpreted the effect of the archery hunting season on tradeoffs between forage and risk by assessing the direction and magnitude of coefficients for the risk and forage covariates. For the risk and forage coefficients, positive and negative values indicate selection for a resource that is greater and less than expected based on availability, respectively, and values of 0 indicate no selection. For the archery interaction coefficients, positive and negative values indicate a change in selection for a resource that is stronger and weaker during the archery season, respectively, and values of 0 indicate no change in selection.

Based on our hypothesis that elk do not change selection during archery season, we expected to find coefficient estimates with 95% confidence intervals that span zero for risk and forage interactions with archery and no relationship between the interactions and proportion hunter access. Based on our hypothesis that elk do not trade off forage for security when altering selection during archery season, we expected to find coefficient values for the archery × risk interaction indicating increased selection for more secure areas and coefficient values for the archery × forage interaction with 95% confidence intervals that span 0, indicating no change in selection for areas with better forage. We expected that although we may find a relationship between archery × risk interaction coefficients and proportion hunter access, we would not find a relationship between the archery × forage interaction coefficient and proportion hunter access. Based on our hypothesis that elk trade off forage for security during archery season, we expected to find coefficient values for the archery × risk interaction that suggest increased selection for more secure areas (e.g., positive values for distance to motorized route) and negative coefficient values for the archery × forage interaction. We also expected to find a relationship between the archery × risk interaction coefficient and proportion hunter access (e.g., positive relationship between proportion hunter access and distance to motorized route) and a negative relationship between the archery × forage interaction coefficient and proportion hunter access, indicating elk exposed to higher levels of hunter access show a stronger tradeoff between forage and risk.

RESULTS

We collected radio-collar location data from 44 female elk. After constraining the radio-collar location data to the pre-archery and archery periods, we retained 14,855 locations from 41 elk, or an average of 362 (range = 255–370) locations/elk. Five elk died during the 2-year monitoring period. Four mortalities were harvest-related and included 1 archery season harvest, 2 rifle season harvests, and 1 harvest as part of late-season game damage hunts. The remaining mortality was of unknown cause. No mortalities occurred during the pre-archery period.

Used locations varied for the pre-archery and archery periods and available locations varied for the summer-fall across individual elk for the landscape, risk, and forage covariates (Table 2). Summer-fall home ranges of individual elk averaged 50.2 ± 4.3 (SE) km^2 in area. The proportion of the elk home ranges comprising areas accessible to hunters averaged 0.47 ± 0.05 (range = 0.05–0.99). The availability of risk and forage resources within individual home ranges varied with the proportion of the home range comprising hunter-accessible lands (Fig. 2A). More accessible home ranges were on average closer to motorized routes ($R^2 = 0.27$), had lower forage abundance ($R^2 = 0.67$), and had lower forage quality ($R^2 = 0.61$) than elk with less accessible home ranges.

Model Selection

In model tier 1, the best-supported functional forms for each continuous covariate were quadratic slope, linear forage abundance, linear forage quality, pseudothreshold distance to motorized route, pseudothreshold canopy cover, and linear distance to cover (Table 3). In model tier 2, the only supported risk model included pseudothreshold distance to motorized route and pseudothreshold canopy cover. In model tier 3, the only supported forage model included linear forage abundance and linear forage quality. In model tier 4, the only supported model included land cover type, quadratic

Table 2. Average (±SE) of pre-archery and archery used locations and summer-fall available locations across individual female elk ($n = 41$) datasets used in modeling resource selection and tradeoffs between forage and harvest risk during summer-fall in the North Sapphire population, west-central Montana, USA, 2014–2015.

	Used					
	Pre-archery		Archery		Available	
Covariate summary	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Percent in forests	54.7	3.6	43.8	3.8	46.4	3.5
Percent in valley bottom areas	40.7	3.7	52.9	4.3	47.0	3.8
Percent in montane riparian	4.8	0.9	4.4	0.7	6.5	0.4
Mean slope (°)	15.6	0.8	13.2	0.8	15.7	0.7
Mean distance to motorized route (m)	888.8	96.2	888.2	71.8	849.0	76.7
Mean canopy cover (%)	23.7	1.8	20.2	2.0	20.1	1.7
Mean distance to cover (>30%; m)	150.1	16.4	214.4	23.0	200.0	19.5
Percent in security patch	41.8	4.8	44.3	4.3	39.7	3.7
Percent in security patch with cover	37.5	5.0	41.5	4.5	36.5	3.8
Mean forage abundance (g/m^2)	14.8	0.8	15.2	0.6	17.5	0.8
Mean forage quality (kcal/g)	2.78	0.15	2.81	0.17	2.79	0.01

slope, pseudothreshold distance to motorized route, linear forage abundance, and linear forage quality.

Forage-Risk Tradeoffs

We included in our best-supported model the interactions between the archery period and pseudothreshold distance to motorized route, linear forage abundance, and linear forage quality, and we fit the model to each individual's used-available dataset. The mean P-value associated with the goodness-of-fit tests across individual elk models was 0.22 ± 0.05 with 66% of the models indicating no evidence of lack of fit ($P > 0.01$). Standardized selection coefficients indicated that the strength of selection by elk for the risk and forage covariates varied across individuals (Table 4).

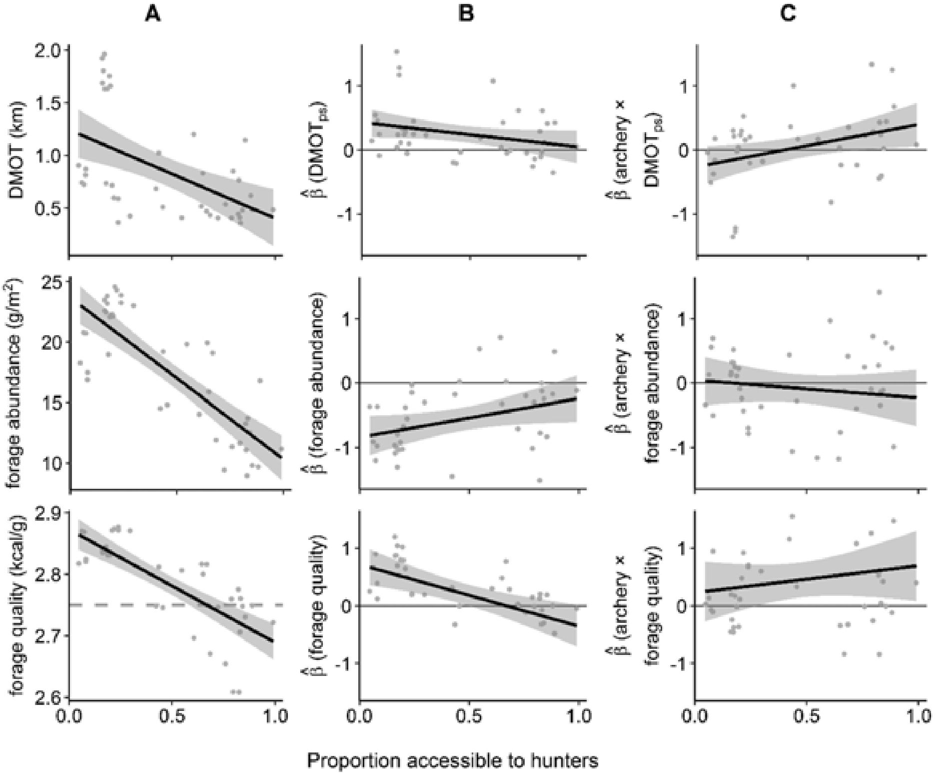

Figure 2. Availability (panel A) and standardized, resource selection coefficients ($\hat{\beta}$; panel B and C) of forage and harvest risk variables for adult female elk occupying summer-fall home ranges with varying proportions of hunter-accessible lands in the North Sapphire elk population, west-central Montana, USA, 2014–2015. Bold lines and shaded areas are simple linear regression lines and 95% confidence intervals, respectively. Panel B represents selection across the late-summer-fall period, where positive and negative values indicate selection for a resource that is greater and less than expected based on availability, respectively, and values of zero indicate no selection. Panel C represents the change in selection with respect to the archery period, where positive and negative values indicate a change in selection for a resource that is stronger and weaker during the archery season, respectively, and values of zero indicate no change in selection. The dashed line indicates the threshold (2.75 kcal/g) of forage quality that is adequate for meeting nutritional requirements of adult female elk (Cook et al. 2004, 2016). Pseudothreshold covariates are indicated with subscripted ps. DMOT = distance to motorized route.

Table 3. Model tier corrected Akaike's Information Criterion (AIC$_c$) rankings comparing models based on pooled used-available locations used to select a most-supported model for subsequent estimation of resource selection by female elk during summer-fall in the North Sapphire population, west-central Montana, USA, 2014–2015. All models within each model tier are presented excepting tier 4 ($n = 16$) showing only the top model and the next most-supported model. The null model had AIC$_c$ = 80,315.0. For each model, we present the number of parameters (K) and AIC$_c$ weight (w_i).

Model tier[a]	Model[a]	K	AIC$_c$	ΔAIC$_c$	w_i
Tier 1: Slope	Slope^2	3	79,776.5	0.0	1.00
	Slope	2	79,889.3	112.7	0.00
	Slope^{PS}	2	80,169.0	392.5	0.00
Tier 1: Forage abundance	Forage abundance	2	79,990.7	0.0	1.00
	Forage abundance^{PS}	2	80,191.8	201.1	0.00
Tier 1: Forage quality	Forage quality	2	80,209.2	0.0	1.00
	Forage quality^{PS}	2	80,228.1	18.9	0.00
Tier 1: DMOT	DMOT^{PS}	2	79,032.7	0.0	1.00
	DMOT	2	79,607.9	575.3	0.00
Tier 1: Canopy cover	Canopy cover^{PS}	2	80,203.2	0.0	1.00
	Canopy cover	2	80,311.2	107.9	0.00
Tier 1: DCOV	DCOV	2	80,291.4	0.0	0.97
	DCOV^{PS}	2	80,298.2	6.8	0.03
Tier 2: Risk	DMOT^{PS} + canopy cover^{PS}	3	78,935.3	0.0	1.00
	DMOT^{PS} + DCOV	3	79,011.5	76.2	0.00
	DMOT^{PS}	2	79,032.7	97.4	0.00
	Security patch + canopy cover^{PS}	3	79,504.8	569.6	0.00
	Security patch + DCOV	3	79,574.4	639.1	0.00
	Security patch	2	79,595.4	660.2	0.00
	Security patch with canopy cover	2	79,615.5	680.2	0.00
	Canopy cover	2	80,203.2	1267.9	0.00
	DCOV	2	80,291.4	1356.2	0.00
Tier 3: Forage	Forage abundance + forage quality	3	79,363.4	0.0	1.00
	Forage abundance	2	79,990.7	627.3	0.00
	Forage quality	2	80,209.2	845.8	0.00
Tier 4: All combinations	Land cover + slope^2 + DMOT^{PS} + forage abundance + forage quality	7	76,575.6	0.0	1.00
	Slope^2 + DMOT^{PS} + forage abundance + forage quality	6	77,064.0	488.4	0.00

[a] DMOT = distance to motorized route, DCOV = distance to cover. Covariate superscripts indicate functional form (2 = quadratic, PS = pseudothreshold, [none] = linear).

Selection varied with the amount of hunter-accessible land within individual summer-fall home ranges and with the archery period (Fig. 2). During the summer-fall (i.e., across both pre-archery and archery periods), elk generally selected for areas away from motorized routes (Table 4) across all levels of hunter accessibility (Fig. 2B). We found some evidence that selection for areas away from motorized routes decreased with increasing hunter accessibility ($\hat{\beta} = -0.4$, $P = 0.07$, $R^2 = 0.06$) during the summer-fall. During the same period, elk generally avoided areas with higher forage abundance, with some evidence that elk with home ranges more accessible to hunters avoided these areas less than elk with home ranges less accessible to hunters ($\hat{\beta} = 0.6$, $P \leq 0.04$, $R^2 = 0.07$). Selection by elk for forage quality decreased with increasing hunter accessibility ($\hat{\beta} = -1.1$, $P \leq 0.001$, $R^2 = 0.23$) during the summer-fall, and elk with

Table 4. Summary of standardized selection coefficients and P-values of terms from the most-supported model used to estimate resource selection of female elk ($n = 41$) during the summer-fall in the North Sapphire population, west-central Montana, USA, 2014–2015. Effects of cover classes are in relation to the reference (intercept) cover class forest.

	$\hat{\beta}$		P	
Term[a]	$\bar{x}$	95% CI	$\bar{x}$	95% CI
Intercept	−3.47	(−4.40, −2.53)	0.02	(0.00, 0.05)
Archery	−0.23	(−1.43, 0.96)	0.15	(0.07, 0.24)
Valley bottom areas	0.02	(−0.06, 0.11)	0.29	(0.20, 0.37)
Montane riparian	−0.99	(−1.17, −0.80)	0.10	(0.04, 0.17)
Slope	−0.30	(−0.39, −0.21)	0.17	(0.07, 0.26)
Slope^2	−0.18	(−0.24, −0.12)	0.16	(0.09, 0.24)
Distance to motorized route^{PS}	0.25	(0.13, 0.38)	0.14	(0.07, 0.22)
Forage abundance	−0.56	(−0.74, −0.38)	0.13	(0.05, 0.21)
Forage quality	0.22	(0.02, 0.42)	0.18	(0.09, 0.27)
Archery × distance to motorized route^{PS}	0.05	(−0.13, 0.22)	0.14	(0.07, 0.21)
Archery × forage abundance	−0.08	(−0.30, 0.13)	0.16	(0.10, 0.22)
Archery × forage quality	0.45	(0.15, 0.74)	0.21	(0.11, 0.31)

[a] Covariate superscripts indicate functional form (2 = quadratic, PS = pseudothreshold, [none] = linear).

home ranges more accessible to hunters showed no selection for or against areas with higher forage quality.

During the archery period, elk selected more strongly for areas away from motorized routes as hunter accessibility of their home range increased ($\hat{\beta} = 0.7$, $P = 0.02$, $R^2 = 0.11$; Fig. 2C); elk with home ranges least accessible to hunters showed no change or a decrease in selection for areas away from motorized roads. During the same period, elk generally did not change their selection for forage abundance (Table 4); however, there was some evidence that elk with home ranges most accessible to hunters increased their avoidance of areas of high forage abundance ($\hat{\beta} = -0.3$, $P = 0.44$, $R^2 = 0.01$). Elk generally increased selection for areas of higher quality forage across all levels of hunter accessibility during the archery period, and there was some evidence that elk more strongly increased selection for these areas as hunter accessibility increased ($\hat{\beta} = 0.5$, $P = 0.35$, $R^2 = 0.01$). Overall, these results support our hypothesis that elk do not trade off forage and risk because elk can select areas providing both security and forage regardless of hunter accessibility. These results refute our hypotheses that selection for security and forage are not substantially affected by the archery season and that elk trade off forage for increased security during the archery season.

DISCUSSION

Forage-Risk Tradeoffs

We found support for our hypothesis that female elk in our study area did not trade off forage and risk during the archery season. The areas providing the most security also provided the highest-quality forage, a critical nutritional resource for female elk during summer-fall (Cook et al. 2004, 2013, 2016). Although elk that experienced more risk (i.e., proportion of public hunter accessibility within their summer-fall home range) changed their selection for security more strongly in response to the archery season, they maintained or increased their selection for high-quality forage (Fig. 2C). This result provides additional support for the importance of high-quality forage on resource selection of female elk during the fall (Cleveland et al. 2012; Ranglack et al. 2016, 2017). It is likely that many of the elk in our study were lactating given high pregnancy rates ($\bar{x} = 0.91$) and calf recruitment rates (26 calves/100 adult females) surveyed during the following winter (2015; Montana Fish, Wildlife and Parks 2017). Our findings may reflect the priority of female selection for forage over risk, particularly for females trying to meet the greater nutritional requirements of lactation (Cook et al. 2004, 2016). Our results also suggest that forage quality may be more important than forage abundance (Cook et al. 2004, 2013, 2016); elk avoided forage abundance across all levels of risk during the summer-fall (Fig. 2B), a response that may be in part due to intermediate or lower abundances having the highest forage quality (Fryxell et al. 1988, Hebblewhite et al. 2008, Hebblewhite and Merrill 2009).

Elk exposed to the poorest nutrition during summer-fall (Fig. 2A), even below the threshold considered to be sufficient forage quality for meeting nutritional requirements of lactating female elk during late-summer and fall (2.75 kcal/g; dashed line in Fig. 2A; Cook et al. 2004, 2013, 2016), also occupied the highest-risk home ranges (i.e., most accessible to hunters). These elk appeared to reduce risk by moving to areas farther from motorized routes during the archery season, a result consistent with other studies (Cleveland et al. 2012, McCorquodale 2013, Proffitt et al. 2016*b*, Paton et al. 2017, Ranglack et al. 2017), and simultaneously increased their selection for high-quality forage. To meet nutritional requirements and compensate for the low availability of nutritional resources, these elk may be increasing use of areas away from roads with greater concentrations of the highest-quality forage, increasing forage intake rates, or selecting high-quality forage at finer spatial scales (Cook et al. 2016). These elk additionally showed relatively weaker avoidance of areas with high forage abundance than elk with lower-risk home ranges across the summer-fall period, indicating selection for forage abundance may have some importance for elk occupying public lands with poor nutritional capacities.

In contrast, elk occupying the lowest-risk home ranges were exposed to the highest-quality nutrition and responded minimally to the archery season in their selection for forage and security resources. This may be due to the high availability of irrigated agricultural areas, which can provide elk with consistent sources of both security and concentrated areas of high-quality forage throughout the summer-fall (Burcham et al. 1999, Middleton et al. 2013). Irrigated agricultural areas in our study area existed only on private properties with restricted hunter access and contained approximately 2–4 times the forage quality than mature dry coniferous forests, grasslands, and shrublands that dominated this landscape (K. M. Proffitt, Montana Fish, Wildlife and Parks, unpublished data). This may also explain the increase in selection for forage quality by elk with intermediate levels of hunter accessibility that used both public and private lands during summer-fall or shifted their distributions from public to private lands at the onset of the archery season.

Alternatively, some movements of elk may be attributed more to changes in the availability of high-quality forage due to late-season senescence of plants than to elk seeking enhanced security (Ager et al. 2003). This may explain the large increase in selection of areas with higher forage quality coinciding with the archery season for the majority of elk in our study. In addition, the authors of this paper have observed large numbers of elk arriving onto irrigated agricultural fields several days or weeks prior to the onset of the archery season. Such behavior would further emphasize the importance of high-quality forage to elk selection during the summer-fall (Cleveland et al. 2012, Cook et al. 2016, Ranglack et al. 2017).

Whereas we did not find tradeoffs between forage and risk during the archery season, we did find evidence that elk occupying high-risk home ranges avoided areas with higher-quality forage during the summer-fall period (Fig. 2B). We suggest this result may be explained by high levels of recreational activities on public lands (USFS 2016). Extensive networks of public roads from past timber harvest activities on this landscape provide important recreational access and opportunities to residents of the adjacent Bitterroot Valley and city of Missoula that include all-terrain vehicle (ATV) riding (authorized and unauthorized), hiking, horseback riding, mountain biking, and pre-hunting season scouting. Elk increase movements, reduce feeding times, and elevate stress levels in response to ATV riding, mountain biking, and hiking (Millspaugh et al. 2001; Preisler et al. 2005; Wisdom et al. 2005, 2018; Naylor et al. 2009). Our results suggest that displacement of elk from forage during the summer may be exacerbated if recreational use on public lands continues to increase in association with the steady growth of the human population (USFS 2016).

Our study provides insight into selection of forage and security during the archery season for an elk population occupying a landscape with highly variable nutritional resources and levels of harvest risk. Our results may or may not be applicable to other populations of elk and likely depend on the availability of security and forage resources and amount of hunting pressure. On landscapes where security opportunities or high-quality forage are more limited, or where greater numbers of archery hunters are present (Cleveland et al. 2012, McCorquodale 2013, Little et al. 2016), elk may demonstrate tradeoffs between forage and risk. Tradeoffs may also occur at larger or across multiple scales of selection (Hebblewhite and Merrill 2009) if elk select home ranges (e.g., second-order selection) in response to the archery season that displace them from accessing forage; however, addressing multiple scales of selection fell outside the scope of this study.

Elk Security During the Archery Season

Managers of public lands should recognize that management of motorized access plays an important role in influencing elk distributions and resource selection patterns, and motorized access management is an important part of achieving harvest objectives. The closure of motorized routes on public lands at the onset of the archery season may provide important security benefits for female elk occupying higher-risk home ranges. We found motorized routes to be the most supported risk variable, similar to other studies of elk response to hunting pressure (Johnson et al. 2004; McCorquodale 2013; Montgomery et al. 2013; Proffitt et al. 2013; Ranglack et al. 2016, 2017), and particularly influential for elk on higher-risk home ranges (Fig. 2C) that also averaged closer to motorized routes (Fig. 2A). These results suggest that closures of motorized routes during the archery season may be useful to effectively balance security resources across landscapes with variable public hunter accessibility.

Shortly after our study ended, the Bitterroot National Forest implemented a new travel management plan that closed approximately 105 km of motorized routes within our study area at the onset of the archery season (USFS 2016). To assess the potential effectiveness in increasing elk security under the travel update, we calculated the average distance to motorized route of the elk summer-fall home ranges under the new plan and compared the results to the previous plan (Fig. 3). The new plan increased the mean distance to motorized routes across all elk home ranges by an average of 104.2 m (range = 0.0–1,339.0 m) and for elk with home ranges comprised of >50% accessible lands by an average of 168.8 m (range = 0.0–1,339.0 m). This increase in security on public lands is likely to benefit elk; however, to effectively balance security across the landscape and provide adequate security for female elk on public lands, further closures may be necessary.

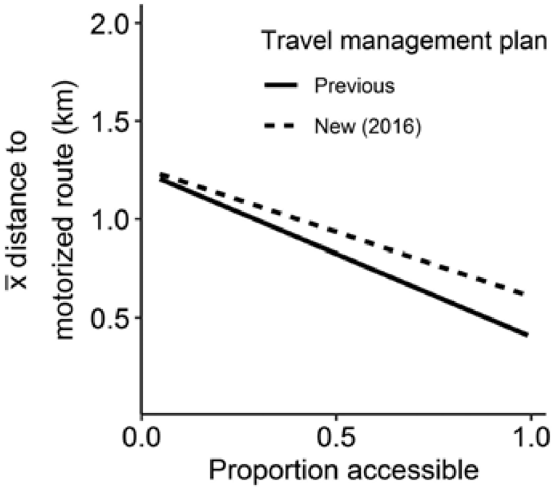

Figure 3. The difference in availability of areas away from motorized routes to female elk summer-fall home ranges with varying levels of hunter-accessible lands between the previous (implemented at the time of this study) and new (implemented beginning 2016) travel management plans of the Bitterroot National Forest, west-central Montana, USA.

MANAGEMENT IMPLICATIONS

Where elk populations occupy a diverse public-private landscape, wildlife managers could consider a combination of public and private land management strategies during the archery season to achieve socially acceptable numbers of elk while providing or enhancing hunter opportunity. Strategies focused on managing forage for elk could include enhancing the availability of and access to high-quality forage on public lands through forest management (e.g., revegetation, timber harvest, thinning, prescribed fire, and wildfire management) and restricting access of elk to irrigated agriculture or other high-quality forage resources on private lands through landowner collaborations. Strategies focused on balancing harvest risk more evenly across public and private lands could include closing motorized routes on public lands at the onset of the archery season rather than the rifle season, when closures traditionally occur, to enhance elk security; reducing hunter pressure on public lands during the archery season by altering season structures (e.g., limiting the number of licenses available to hunters or changing sex and age harvest restrictions); and collaborating with private land owners to integrate less-restrictive goals for hunter access into land owner objectives. These strategies that consider both forage and risk may encourage elk to become more broadly distributed on the landscape and to remain on public lands through to the beginning of the rifle season, allowing managers to increase harvest opportunity of antlerless elk during the rifle season and more effectively manage populations through traditional harvest strategies.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank the landowners that allowed access to their properties during data collection, the aircraft pilots B. Malo, R. Swisher, and T. Throop, the field crew that collected vegetation data, and the hunters who cooperated in returning elk collars and provided harvest information. J. Gude, K. Schoenecker, and 2 anonymous reviewers provided valuable insight through reviews of this manuscript. Financial support for this project was provided by revenues from the sale of Montana hunting and fishing licenses, a Federal Aid in Wildlife Restoration grant to Montana Fish, Wildlife and Parks, Ecosystem Research Group, Montana Department of Transportation, Montana's Outdoor Legacy Foundation, MPG Ranch, Ravalli County Fish and Wildlife Association, Rocky Mountain Elk Foundation, Roseburg Forest Product Company, Burnt Fork Ranch, Missoula Community Foundation, First Security Bank of Missoula, North Sapphire Hunter Opportunity Working Group, and Sun Mountain Lumber.

LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. Journal of Mammalogy 84:1076–1088.

Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2008. Relations between nutritional condition and survival of North American elk *Cervus elaphus*. Wildlife Biology 14:70–80.

Bunnell, S. D., M. L. Wolfe, M. W. Brunson, and D. R. Potter. 2002. Recreational use of elk. Pages 701–740 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

Burcham, M. G., D. W. Edge, and L. C. Marcum. 1999. Elk use of private land refuges. Wildlife Society Bulletin 27:833–839.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, Berlin, Germany.

Canfield, J. E., A. Grove, E. Tomasik, D. Pengeroth, and Q. Kujala. 2013. U.S. Forest Service and Montana Department of Fish, Wildlife and Parks collaborative overview and recommendations for elk habitat management on the Custer, Gallatin, Helena, and Lewis and Clark National Forests. U.S. Department of Agriculture, Forest Service, Bozeman, Montana, USA.

Christensen, A. G., L. J. Lyon, and J. W. Unsworth. 1993. Elk management in the Northern Region: considerations in forest plan updates or revisions. General Technical Report INT-303. U.S. Department of Agriculture, Forest Service, Intermountain Research Station. Ogden, Utah, USA.

Cleveland, S. M., M. Hebblewhite, M. Thompson, and R. Henderson. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. Journal of Wildlife Management 65:926–940.

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 195:1–326.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. 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 155:1–61.

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. Mccorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184:1–45.

Davidson, G. A., B. K. Johnson, J. H. Noyes, B. L. Dick, and M. J. Wisdom. 2012. Effect of archer density on elk pregnancy rates and conception dates. Journal of Wildlife Management 76:1676–1685.

DeCesare, N. J., M. Hebblewhite, M. Bradley, D. Hervieux, L. Neufeld, and M. Musiani. 2014. Linking habitat selection and predation risk to spatial variation in survival. Journal of Animal Ecology 83:343–352.

D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383–388.

Ferrari, M. C. O., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour 579–585.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 365:2233–2244.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Fryxell, J., J. Greever, and A. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131:781–798.

Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Mysterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90:699–710.

Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37:816–830.

Hanley, T. A., C. T. Robbins, A. E. Hagerman, and C. McArthur. 1992. Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. Ecology 73:537–541.

Hansteen, T. L., H. P. Andreassen, and R. A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Management 61:280–290.

Hebblewhite, M. 2006. Linking predation risk and forage to ungulate population dynamics. Dissertation, University of Alberta, Edmonton, Alberta, Canada.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

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

Hernández, L., and J. W. Laundré. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk (*Cervus elaphus*) and bison (*Bison bison*). Wildlife Biology 11:215–220.

Hillis, J. M., M. Thompson, J. E. Canfield, L. J. Lyon, C. Les Marcum, P. M. Dolan, and D. W. McCleerey. 1991. Defining elk security: the Hillis paradigm. Pages 38–43 *in* Proceedings of a Symposium on Elk Vulnerability. Montana Chapter of the Wildlife Society, Bozeman, Montana, USA.

Hosmer, D. W., T. Hosmer, S. le Cessie, and S. Lemeshow. 1997. A comparison of goodness-of-fit tests for the logistic regression model. Statistics in Medicine 16:965–980.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, Inc., New York, New York, USA.

Johnson, B. K., A. A. Ager, J. H. Noyes, and N. J. Cimon. 2004. Elk and mule deer responses to variation in hunting pressure. Transactions of the North American Wildlife and Natural Resources Conference 69:625–640.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kilpatrick, H. J., and K. K. Lima. 1973. Effects of archery hunting on movement and activity of female white-tailed deer in an urban landscape. Wildlife Society Bulletin 27:433–440.

Krebs, C. J. 1989. Ecological methodology. Harper Collins, New York, New York, USA.

le Cessie, S., and J. C. van Houwelingen. 1991. A goodness-of-fit test for binary regression models, based on smoothing methods. Biometrics 47:1267.

Lewis, M. S., K. M. Proffitt, and M. Thompson. 2014. Selected results from surveys of elk hunters and private landowners regarding elk management in Montana's Hunting District 204. HD Unit Research Summary No. 37. Montana Fish, Wildlife and Parks, Helena, USA.

Little, A. R., S. L. Webb, S. Demarais, K. L. Gee, S. K. Riffell, and J. A. Gaskamp. 2016. Hunting intensity alters movement behaviour of white-tailed deer. Basic and Applied Ecology 17:360–369.

Lone, K., L. E. Loe, E. L. Meisingset, I. Stamnes, and A. Mysterud. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. Animal Behaviour 102:127–138.

Long, R. A., R. T. Bowyer, W. P. Porter, P. Mathewson, K. L. Monteith, S. L. Findholt, B. L. Dick, and J. G. Kie. 2016. Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. Oecologia 181:709–720.

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 and Management 61:302–313.

McCorquodale, S. M. 2013. A brief review of the scientific literature on elk, roads, and traffic. Washington Department of Fish and Wildlife, Olympia, USA.

McCorquodale, S. M., R. Wiseman, and L. C. Marcum. 2003. Survival and harvest vulnerability of elk in the Cascade Range of Washington. Journal of Wildlife Management 67:248–257.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

Millspaugh, J. J., R. J. Woods, K. E. Hunt, K. J. Raedeke, G. C. Brundige, B. E. Washburn, and S. K. Wasser. 2001. Fecal glucocorticoid assays and the physiological stress response in elk. Wildlife Society Bulletin 29:899–907.

Montana Fish, Wildlife and Parks. 2017. North Sapphire Elk Research Project. Montana Fish, Wildlife and Parks, Helena, Montana, USA. http://fwp.mt.gov/fishAndWildlife/diseasesAndResearch/research/elk/sapphire/default.html. Accessed 31 Jul 2017.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1–62.

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

Morgantini, L. E., and R. J. Hudson. 1985. Changes in diets of wapiti during a hunting season. Journal of Range Management 38:77–79.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management 73:328–338.

Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456–1463.

Paton, D. G., S. Ciuti, M. Quinn, and M. S. Boyce. 2017. Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. Ecosphere 8:1–8.

Preisler, H. K., A. A. Ager, and M. J. Wisdom. 2005. Statistical methods for analysing responses of wildlife to human disturbance. Journal of Applied Ecology 43:164–172.

PRISM Climate Group, Oregon State University. 2016. Time series datasets. http://www.prism.oregonstate.edu/. Accessed 21 Jul 2016.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73:345–356.

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. Journal of Wildlife Management 77:514–524.

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

Proffitt, K. M., S. Thompson, D. Henry, B. Jimenez, and J. A. Gude. 2016*b*. Hunter access affects elk resource selection in the Missouri breaks, Montana. Journal of Wildlife Management 80:1167–1176.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecological Systems 15:523–575.

Ranglack, D. H., R. Garrott, J. Rotella, K. M. Proffitt, J. Gude, and J. E. Canfield. 2016. Evaluating elk summer resource selection and applications to summer range habitat management. Montana Department of Fish, Wildlife and Parks, Helena, USA.

Ranglack, D. H., K. M. Proffitt, J. E. Canfield, J. A. Gude, J. Rotella, and R. A. Garrott. 2017. Security areas for elk during archery and rifle hunting seasons. Journal of Wildlife Management 81:778–791.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987*a*. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98–107.

Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987*b*. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology 68:1606–1615.

Rowland, M. M., and M. J. Wisdom. 2012. Blue Mountains elk nutrition and habitat models: second generation models for management. U.S. Department of Agriculture, Forest Service, La Grande, Oregon, USA.

Sainani, K. L. 2014. Explanatory versus predictive modeling. PM&R 6:841–844.

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. Journal of Wildlife Management 71:868–874.

Shmueli, G. 2010. To explain or to predict? Statistical Science 25:289–310.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–555 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. First edition. Smithsonian Institution Press, Washington, D.C., USA.

United States Forest Service [USFS]. 2016. Bitterroot National Forest Travel Management Planning. https://www.fs.usda.gov/project/?project=21183. Accessed 15 Sep 2017.

Van Soest, P. J. 1982. Nutritional ecology of the ruminant. Second edition. Cornell University Press, Ithaca, New York, USA.

Vieira, M. E. P., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. Journal of Wildlife Management 67:717–728.

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2005. Effects of off-road recreation on mule deer and elk. Transactions of the North American Wildlife and Natural Resources Conference 69:1–16.

Wisdom, M. J., H. K. Preisler, L. M. Naylor, R. G. Anthony, B. K. Johnson, and M. M. Rowland. 2018. Elk responses to trail-based recreation on public forests. Forest Ecology and Management 411:223–233.

Associate Editor: Kathryn Schoenecker.

APPENDIX A. ESTIMATION OF FORAGE QUALITY AND ABUNDANCE

We developed spatially explicit, landscape-scale elk forage quality and abundance models for late summer using ground and remote-sensed data. We combined ground vegetation data from a previous study during 2012–2013 (Proffitt et al. 2016*a*) with data collected for the current study following similar methods (K. M. Proffitt, Montana Fish, Wildlife and Parks, unpublished data). These data were collected within the annual ranges of 3 elk populations occupying the Bitterroot Valley that included the North Sapphire population.

Identification of Forage Species

We identified summer (May–Sep) forage species using fecal plant fragment analysis (level B; Wildlife Habitat and Nutritional Laboratory, Pullman, WA, USA) of 68 composite fecal pellet samples (≥21 samples in each of the 3 population ranges). We collected composite pellet samples in 15-day intervals during summer from areas used <24 hours prior by global positioning system (GPS)-collared elk, which included areas used by resident and migratory individuals. This method enabled sampling across a variety of vegetation types and geographical gradients used by elk across the study area. Each composite pellet sample included

10–20 individual pellets selected at random from 10 pellet groups within a 2–5-ha area. We collected only moist samples to ensure pellets were fresh and from the summer season. For each elk population, we ranked the forage plant species identified in the samples based on percent of the diet and considered the species that constituted 95% as forage species (Table A1). We screened our vegetation data to include only these forage species in estimates of forage quality and abundance.

Vegetation Collection

We sampled composition, cover, and phenological stage of plant species during the time of peak vegetative growth (15 Jul–31Aug) at 752 vegetation plots located within the annual range of the 3 elk populations. We proportionally allocated sampling plots to 12 vegetation cover types, then stratified plots within vegetation cover types based on aspect and slope (Krebs 1989). The vegetation cover types included mesic forests with 3 wildfire histories (burned >15 yrs prior, burned 6–15 yrs prior, and burned ≤5 yrs prior); dry montane mixed conifer forests with the same wildfire histories; dry montane mixed conifer forests that were burned by prescribed fire ≤5 years prior (Long et al. 2008); open grasslands, shrublands, and woodlands; valley bottom riparian; montane riparian; irrigated agriculture; and dry agriculture. Each sampling plot consisted of a 40-m transect placed along the contour of the slope with 5 1-m^2 quadrats located every 10 m along the transect and 0.25-m^2 clip plots nested within the 0-m, 20-m, and 40-m quadrats. At each quadrat, we recorded species composition and percent cover of forbs, graminoids, shrubs, and trees <2 m tall; however, we only considered herbaceous (graminoid and forb) species in this study because of the limited importance of shrub species in the diet (Table A1). Estimates of cover were independent of each other, allowing total cover per quadrat to exceed 100%. At each clip plot, we clipped all forb and graminoid biomass >1 cm above ground (however, see differences in sampling methods between 2012–2013 and 2014–2015). We dried samples at 50°C in a drying oven for 48 hours and measured dry weight to the nearest gram. In 2012–2013, we allocated the dry weight to each lifeform (e.g., forb and graminoid) based on the percent cover of each lifeform. In 2014–2015, we made a minor change to sampling that included collecting separate weights of forbs and graminoids to more precisely estimate biomass by lifeform.

To account for variation in nutritional availability due to plant phenology, we estimated the dominant phenological stage (emergent, flowering, fruiting, mature seed, or senescent) of each species at plots using 2 similar approaches. In 2014–2015, we estimated phenological stages at each of the aforementioned sampling plots that were stratified across vegetation type, slope, and aspect. In 2012–2013, we established phenology plots stratified across major phenological gradients including elevation, aspect (north, south, flat), and canopy coverage (open and closed). We estimated phenological stages at each phenology plot during the time of peak vegetative growth and applied the species-specific phenological classifications to all sampling plots (Proffitt et al. 2016*a*).

Estimation of Forage Quality at Sampling Plots

To estimate forage quality at each sampling plot, we first estimated the phenological stage-specific digestible energy (DE; kcal/g) of each forage species and then applied those estimates to the phenological stages of forage species observed at each sampling plot. To estimate the phenological stage-specific DE of forage species, we first collected ≥5 plant samples of each forage species in each of the 5 phenological stages. We collected the replicate samples from different areas within the annual ranges of the elk populations and combined the samples into 1 composite sample that was dried at 50°C for 48 hours. We then estimated the phenological stage-specific DE of each forage species using sequential detergent fiber analysis (Van Soest 1982; Wildlife Habitat and Nutrition Lab, Washington State University, Pullman, WA, USA), an equation developed for calculating dry matter digestibility (DMD; %, or grams per 100 grams of forage) for wild ungulates (Equation 1; Robbins et al. 1987*a*,*b*; Hanley et al. 1992), and an equation for converting dry matter digestibility values to DE (Equation 2; Cook et al. 2016). We collected samples for 32 forage species and used literature values from previous studies for remaining forage species (Hebblewhite 2006). We applied the same phenological stage-specific DE values for each forage species at all sampling plots.

$$\mathrm{DMD} = \left[\left(0.9231\mathrm{e}^{-0.0451\times((\mathrm{ADL}/\mathrm{NDF})\times 100)} - 0.03\times\mathrm{AIA}\right)(\mathrm{NDF})\right] + [(-16.03 + 1.02\mathrm{NDS}) - 2.8\times\mathrm{P}], \tag{1}$$

where ADL is the acid detergent lignin (%), AIA is the acid insoluble ash (or biogenic silica content; %) of monocots, NDF is the neutral detergent fiber (%), NDS is the neutral detergent soluble (%), and P is the reduction in protein digestion (%). In the equation, P is estimated as 11.82 × BSA, where BSA is the level of bovine serum albumin (Robbins et al. 1987*b*); BSA is an index of the inhibiting effect of increasing tannins measured in milligrams of BSA precipitated per milligram of dry matter forage. The BSA values were assumed to be zero for graminoids and forbs that typically do not contain significant tannins. For samples missing AIA values, we used the mean phenological stage-specific AIA value of the same species. For samples missing DMD values, we used the mean phenological stage-specific DMD value of the same species.

$$\mathrm{DE} = (\mathrm{DMD}/100)\times\mathrm{GE}, \tag{2}$$

where GE is the gross energy content and estimated as 4.53 kcal/g for forbs and graminoids (Cook et al. 2016).

We then estimated forage quality (i.e., mean DE) at each sampling plot (refer to steps in Fig. A1) by first multiplying each phenological stage-specific proportion cover estimate (step C) by the respective phenological stage-specific DE estimates (step D) and summing across phenological stages to estimate DE of each forage species (step E) at each of the 5 quadrats. We then calculated a weighted mean DE at each quadrat using the proportion cover of each forage species as the weight (step F and G). We lastly averaged DE across the 5 quadrats (step H).

Table A1. The percent composition, rank, and cumulative percent (Cum.%) of the diet of forage species in the summer diet of 3 elk populations (North Sapphire, East Fork, and West Fork) in west-central Montana, USA, 2014–2015. We considered the species comprising 95% of the cumulative diet as forage species. Asterisks indicate general grouping categories of unidentifiable species in diet analysis not used to filter data to forage species.

			North Sapphire			East Fork			West Fork		
Species	**Common name**	**Lifeform**	**%**	**Rank**	**Cum.%**	**%**	**Rank**	**Cum.%**	**%**	**Rank**	**Cum.%**
Poa spp.	Bluegrass spp.	Graminoid	12.1	1	12.1	8.8	4	46.5	11.2	2	37.6
Agropyron spp.	Wheatgrass spp.	Graminoid	8.9	2	20.9						
Lupinus spp.	Lupine spp.	Forb	6.2	3	27.1	12.1	2	28.7	7.2	3	44.8
Carex spp.	Sedge spp.	Graminoid	5.9	4	33.0	16.6	1	16.6	26.4	1	26.4
Verbascum spp.	Mullein spp.	Forb	4.7	5	37.7	0.0	69	99.9	0.0	68	100.1
Bromus tectorum	Cheatgrass	Graminoid	4.1	6	41.9						
Stipa comata	Needle and thread	Graminoid	3.1	7	45.0						
Festuca campestris	Rough fescue	Graminoid	3.1	8	48.1	3.2	10	73.1	0.5	24	95.9
Poa pratensis	Kentucky bluegrass	Graminoid	2.7	9	50.8						
Balsamorhiza sagittata	Arrowleaf balsamroot	Forb	2.6	10	53.4	4.0	9	69.9	5.5	7	67.4
Medicago sativa	Alfalfa	Forb	2.4	11	55.8						
Salix spp. stem	Willow spp.	Shrub	2.4	12	58.1	2.1	14	83.4	1.7	14	87.3
Elymus glaucus	Blue wildrye	Graminoid	2.2	13	60.3						
Centaurea stoebe	Spotted knapweed	Forb	2.1	14	62.5	0.0	54	99.9	0.0	48	100.1
Bromus inermis	Smooth brome	Graminoid	2.1	15	64.6						
Other grass*		Graminoid	1.7	16	66.3	4.3	7	61.7	4.4	8	71.8
Festuca idahoensis	Idaho fescue	Graminoid	1.6	17	67.9	1.7	17	88.8	1.2	16	90.1
Shepherdia canadensis leaf	Canada buffaloberry	Shrub	1.6	18	69.5						
Physocarpus malvaceus leaf	Mallow ninebark	Shrub	1.5	19	71.1						
Calamagrostis rubescens	Pinegrass	Graminoid	1.5	20	72.6						
Other forb*		Forb	1.5	21	74.1	5.5	5	52.0	5.5	6	61.9
Pseudoroegneria spicata	Bluebunch wheatgrass	Graminoid	1.5	22	75.5	9.0	3	37.7	5.8	4	50.6
Composite hair*			1.2	23	76.8	1.1	19	91.3	2.7	11	82.0
Pinus spp.	Pine spp.	Tree	1.2	24	78.0						
Vaccinium spp. stem	Huckleberry spp.	Shrub	1.1	25	79.1	1.3	18	90.2	0.7	21	94.1
Achillea millefolium	Common yarrow	Forb	1.0	26	80.1	0.1	42	99.4	1.8	12	83.9
Phleum pratense	Timothy	Graminoid	1.0	27	81.1						
Cirsium spp.	Thistle spp.	Forb	1.0	28	82.2						
Astragalus spp.	Legume spp.	Forb	0.8	29	83.0	0.3	29	96.8	0.7	19	92.7
Trifolium spp.	Clover spp.	Forb	0.8	30	83.8						
Alopecurus spp.	Foxtail spp.	Graminoid	0.7	31	84.6						
Taraxacum spp.	Dandelion spp.	Forb	0.7	32	85.3						
Koeleria macrantha	Prairie Junegrass	Graminoid	0.7	33	86.0	0.4	25	95.5	0.4	28	97.6
Other shrub leaf*		Shrub	0.6	34	86.6	0.7	22	93.8	0.4	29	98.0
Galium spp.	Bedstraw spp.	Forb	0.6	35	87.2						
Ranunculus spp.	Buttercup spp.	Forb	0.6	36	87.8						
Solidago spp.	Goldenrod spp.	Forb	0.6	37	88.4	0.0	67	99.9	0.0	65	100.1
Other shrub stem*		Shrub	0.5	38	89.0	0.2	39	99.0	0.3	32	98.9
Agropyron cristatum	Crested wheatgrass	Graminoid	0.5	39	89.5						
Equisetum spp.	Horsetail spp.	Forb	0.5	40	89.9	0.4	26	95.9	1.7	13	85.6
Populus spp. stem	Cottonwood spp.	tree	0.5	41	90.4						
Potentilla spp.	Cinquefoil spp.	Forb	0.5	42	90.9	0.0	63	99.9	0.0	60	100.1
Symphoricarpos albus	Common snowberry	Shrub	0.5	43	91.4	0.9	21	93.1	0.4	27	97.2
Berberis repens leaf	Oregon grape	Shrub	0.4	44	91.8	5.5	6	57.5	4.4	9	76.2
Dactylis glomerata	Orchard grass	Graminoid	0.4	45	92.3						
Salix spp. leaf	Willow spp.	Shrub	0.4	46	92.7	0.3	28	96.6	0.5	26	96.8
Zea mays	Corn	Graminoid	0.4	47	93.1						
Phlox spp.	Phlox	Forb	0.4	48	93.4	0.2	33	97.9	0.5	25	96.4
Cornus spp. leaf	Dogwood spp.	unknown	0.3	49	93.7	0.3	31	97.4	0.0	49	100.1
Aristida purpurea	Three-awn	Graminoid	0.3	50	94.0						
Xerophyllum tenax	Bear grass	Forb	0.3	51	94.3	2.8	11	76.0	0.0	69	100.1
Prunus spp. leaf	Chokecherry spp.	Shrub	0.3	52	94.7						
Triticum aestivum	Common wheat	Graminoid	0.3	53	94.9						
Chamerion angustifolium	Fireweed	Forb	0.2	54	95.2	0.6	24	95.1	0.7	22	94.8
Juncus spp.	Rush spp.	Graminoid	0.1	76	98.8	0.9	20	92.2	0.7	20	93.4
Shepherdia canadensis	Canada buffaloberry	Shrub				4.2	8	65.9	0.6	23	95.4
Other shrub*		Shrub				2.7	12	78.6	3.2	10	79.3
Pinus contorta	Lodgepole pine	tree				2.7	13	81.3	5.8	5	56.4
Stipa spp.	Needle grass spp.	Graminoid				1.9	15	85.3	1.6	15	88.9
Bromus spp.	Brome spp.	Graminoid				1.8	16	87.1	1.1	17	91.1
Physocarpus malvaceus	Mallow ninebark	Shrub				0.7	23	94.5	0.2	35	99.5
Ceanothus velutinus	Snowbrush ceanothus	Shrub				0.2	41	99.3	0.8	18	92.0

Estimation of Forage Abundance at Sampling Plots

We estimated forage abundance (g/m^2) at each sampling plot (refer to steps in Fig. A2) by first apportioning clipped, dry biomass from the clip plots (g/0.25 m^2) for each lifeform (step D) to each species (step E) based on rescaled percent cover (species cover proportional to cover within the appropriate lifeform; steps A–C). We then filtered out forage species (step F), summed biomass across lifeform

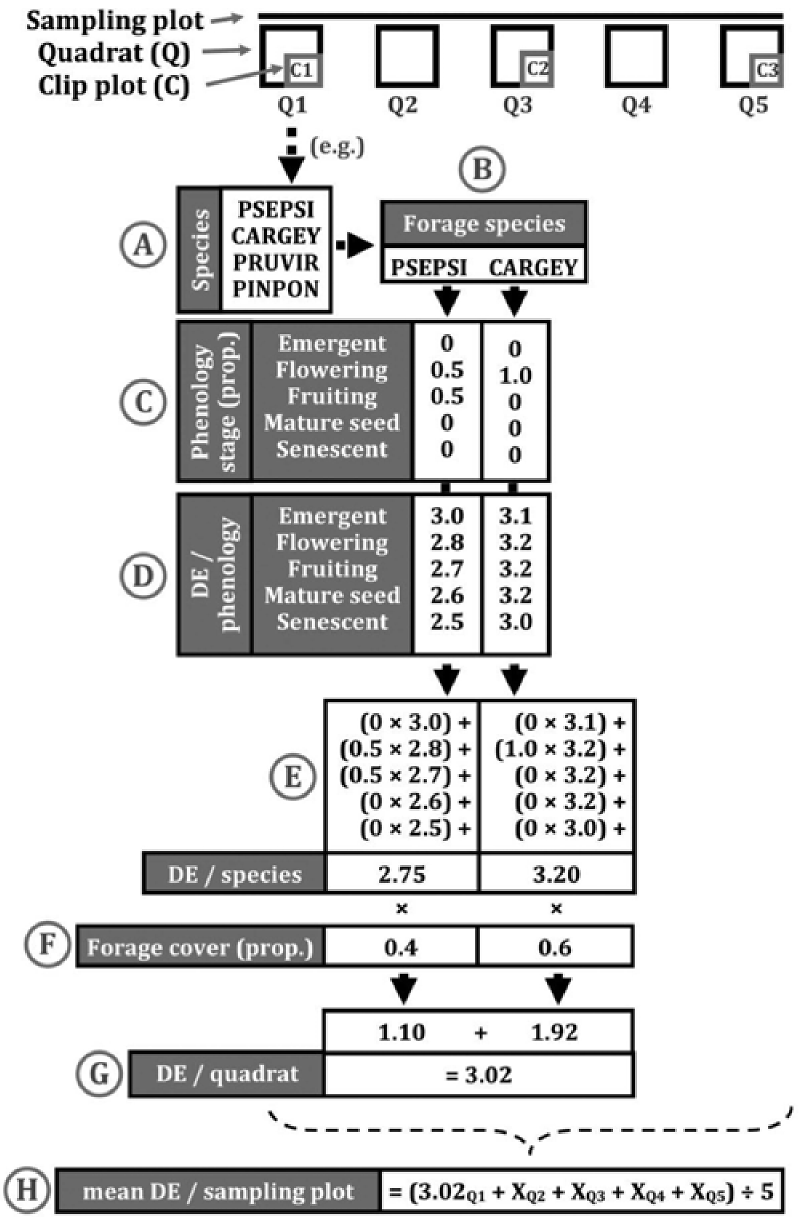

Figure A1. Illustrative methods for estimating mean forage quality (i.e., digestible energy [DE]; kcal/g) at each vegetation sampling plot in the Bitterroot Valley, Montana, 2012–2015. Each sampling plot consisted of 5 1-m^2 quadrats ($Q_{1\text{-}5}$) placed at 10-m intervals and 3 0.25-m^2 clip plots ($C_{1\text{-}3}$) placed in the 0-m, 20-m, and 40-m quadrats. Estimation methods included A) determining plant species present at each quadrat, B) filtering plant species to include only forage species found to be important in the diet of elk based on fecal sample analyses, C) estimating phenological stage-specific proportion cover of each forage species at each quadrat, D) estimating phenological stage-specific DE of each forage species from samples analyzed for nutritional content, E) estimating DE of each forage species based on phenological stage-specific cover and DE estimates, F) estimating proportion cover of each forage species at each quadrat, G) estimating DE at each quadrat by weighting each forage species DE estimate by the proportion cover of each forage species, and H) averaging DE across the 5 quadrats. PSEPSI = *Pseudoroegnaria spicata*, CARGEY = *Carex geyeri*, PRUVIR = *Prunus virginiana*, PINPON = *Pinus ponderosa*.

(step G), and averaged biomass per lifeform across the 3 clip plots (step H). We lastly scaled up to m^2 (0.25 m^2 × 4 = 1 m^2; step I).

Landscape Forage Quality and Abundance Models

We used linear and log-linear regression to predict forage quality and forage abundance, respectively, in 30 × 30-m pixels across the study area as a function of spatial landscape covariates (K. M. Proffitt, unpublished data). We predicted graminoid and forb forage abundance separately. We selected a top model of the most-explanatory covariates for each forage metric using bidirectional stepwise selection of an initial global model of 8 standardized covariates that may influence vegetation growth: vegetation cover type (described in Vegetation Collection above), elevation, slope, canopy cover (LANDFIRE; www.landfire.gov, accessed 21 Jul 2016), compound topography index, solar radiation index (solar radiation calculated using the Area Solar Radiation tool in ArcMap 10.2), spring precipitation (PRISM [Parameter-elevation Regressions on Independent Slopes Model] Climate Group 2016), and normalized difference vegetation index (NDVI) amplitude. All covariates had a

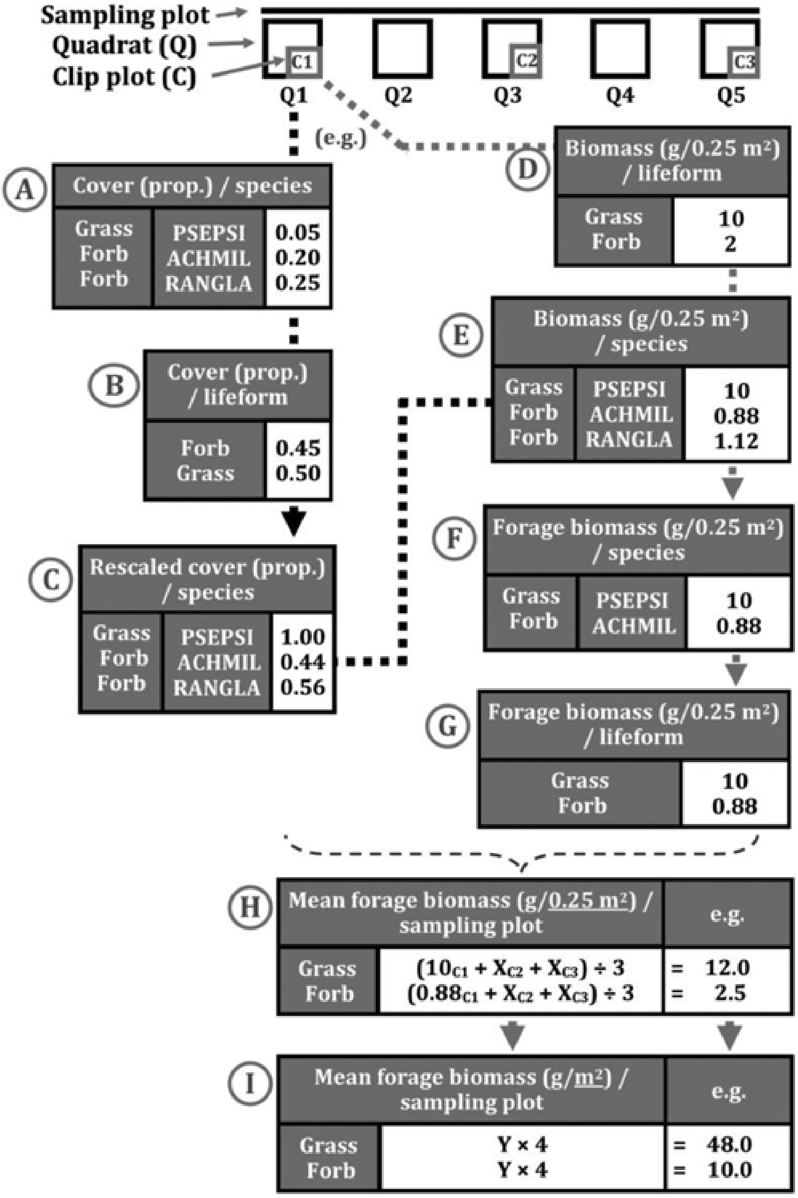

Figure A2. Illustrative methods for estimating mean forage abundance (i.e., biomass; g/m^2) at each vegetation sampling plot in the Bitterroot Valley, Montana, 2012–2015. Each sampling plot consisted of 5 1-m^2 quadrats ($Q_{1\text{-}5}$) placed at 10-m intervals and 3 0.25-m^2 clip plots ($C_{1\text{-}3}$) placed in the 0-m, 20-m, and 40-m quadrats. Estimation methods included A) estimating proportion cover of each plant species at each quadrat, B) estimating proportion cover of each lifeform at each quadrat, C) rescaling proportion cover of each species based on proportion cover of lifeform, D) measuring dry weight (g) biomass of each lifeform from vegetation clipped in clip plots, E) estimating biomass of each species based on rescaled proportion cover of each species, F) filtering plant species to include only forage species found to be important in the diet of elk based on fecal sample analyses, G) summing forage biomass for each lifeform, H) averaging biomass of each lifeform across the 3 clip plots, and I) scaling biomass from g/0.25 m^2 to g/1 m^2. PSEPSI = *Pseudoroegnaria spicata*, ACHMIL = *Achillea millefolium*, RANGLA = *Ranunculus glaberrimus*.

Pearson's correlation coefficient <0.6. The top model predicting forage quality included vegetation cover type, slope, canopy cover, solar radiation index, and elevation ($r^2_{adj} = 0.26$). The graminoid forage abundance model included vegetation cover type, elevation, canopy cover, compound topography index, solar radiation index, and NDVI amplitude ($r^2_{adj} = 0.22$). The forb forage abundance model included vegetation cover type, slope, solar radiation index, and elevation ($r^2_{adj} = 0.17$). We used unstandardized coefficient estimates from the models to develop spatially explicit predictions of forage quality, graminoid forage abundance, and forb forage abundance across the Bitterroot Valley. We summed overlapping pixels of graminoid and forb forage abundance predictions to estimate forage abundance. We extracted predicted values of forage quality and forage abundance to the used-available locations for developing resource selection models of elk.