

A century of changing fire management alters ungulate forage in a wildfire-dominated landscape

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Received 5 September 2018

Forestry practices such as prescribed fire and wildfire management can modify the nutritional resources of ungulates across broad landscapes. To evaluate the influences of fire and forest management on ungulate nutrition, we measured and compared forage quality and abundance among a range of land cover types and fire histories within 3 elk ranges in Montana. We used historical fire data to assess fire-related variations in elk forage from 1900 to 2015. Fire affected summer forage more strongly than winter forage. Between 1900–1990 and 1990–2015, elk summer range burned by wildfire increased 242–1772 per cent, whereas the area on winter range burned by wildfire was low across all decades. Summer forage quality peaked in recently burned forests and decreased as time since burn increased. Summer forage abundance peaked in dry forests burned 6–15 years prior and mesic forests burned within 5 years. Forests recently burned by wildfire had higher summer forage quality and herbaceous abundance than those recently burned by prescribed fire. These results suggest that the nutritional carrying capacity for elk varies temporally with fire history and management practices. Our methods for characterizing nutritional resources provide a relatively straightforward approach for evaluating nutritional adequacy and tracking changes in forage associated with disturbances such as fire.

Introduction

Forest management can affect the availability and distribution of nutritional resources for wildlife populations. Grazing, prescribed fire, wildfire exclusion and timber management modify ecological processes and manipulate vegetation (Wondzell and King, 2003; Fisher and Wilkinson, 2005; Noss *et al.*, 2006; Long *et al.*, 2008; Allred *et al.*, 2011). Multiple studies have found that variability in the nutritional resources for ungulates affects pregnancy and survival rates (Monteith *et al.*, 2013; Cook *et al.*, 2013, 2016; Proffitt *et al.*, 2016), as well as ungulate distributions (Bailey *et al.*, 1996; Wilmshurst *et al.*, 1999; Sawyer and Kauffman, 2011; Ranglack *et al.*, 2016).

Environmental heterogeneity creates a spatial and temporal matrix of nutritional resources that affects ungulate distributions at both fine and broad spatial scales (Boyce *et al.*, 2003). Disturbances such as livestock grazing, timber harvest, and fire create and maintain landscape heterogeneity. In the western United States, timber harvest on public lands has declined in recent decades (U.S. Department of Agriculture, Forest Service, 2016). In contrast, the area burned by wildfire annually in the

United States has increased since 1995 (Stephens and Ruth, 2005; Dennison *et al.*, 2014) and is projected to further increase due to fuel load accumulation associated with historic fire suppression (Keane *et al.*, 2002; Ryan *et al.*, 2013) and global climate change (Dale *et al.*, 2001; Brown *et al.*, 2004). In addition to wildfire, prescribed fire is increasing as a method of reducing excessive fuel loads and restoring historic fire return intervals. However, whether prescribed fires adequately mimic natural conditions remains a matter of contention (Koyama *et al.*, 2012; Ryan *et al.*, 2013), and prescribed fires may have positive or negative effects on ungulate nutritional resources (Peck and Peek, 1991; Long *et al.*, 2008).

Fire presents a particularly important yet complex consideration in the management of ungulate habitat. In addition to creating landscape heterogeneity, fire affects wildlife nutritional resources by altering the composition, abundance, and quality of forage plants (Keay and Peek, 1980; Fisher and Wilkinson, 2005; Sachro *et al.*, 2005; Van Dyke and Darragh, 2007; Long *et al.*, 2008; Lord and Kielland, 2015; Sittler *et al.*, 2015; Romme *et al.*, 2016). In the Rocky Mountains, where fire is a common natural disturbance, many plants are adapted to fire, and post-

fire regrowth may include more abundant forage forbs and graminoids, including fireweed (*Chamerion angustifolium*), lupine (*Lupinus* spp.), bluegrass (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*) and needlegrass (*Stipa* spp.). These post-fire plant communities typically provide ungulates high-quality nutrition due to changes in plant species composition (Proffitt *et al.*, 2016), increased nitrogen availability (Greene *et al.*, 2012; Raynor *et al.*, 2015), and the relatively high nutritional value of young plant tissues (Christensen, 1977; Van de Vijver *et al.*, 1999).

Despite these generalities, effects of fire on plant communities and nutritional resources vary widely depending on site-specific deterministic and stochastic factors including land cover type (Sachro *et al.*, 2005), fire severity and intensity (Lord and Kielland, 2015), season of burn (Hobbs and Spowart, 1984), time since fire (Van Dyke and Darragh, 2006), elevation and aspect (Greene *et al.*, 2012), ecosystem nutrient richness (Van de Vijver *et al.*, 1999), and forest development after large wildfires (Romme *et al.*, 2016). For example, fire may increase (Rowland *et al.*, 1983), decrease (Van Dyke and Darragh, 2006), or cause no change in (Greene *et al.*, 2012) forage plant digestibility, which plays a key role in the ability of ungulates to assimilate available nutrients. Similarly, nutritional increases following a fire can vary from a few months (Hobbs and Spowart, 1984; Van de Vijver *et al.*, 1999) to several years (Lehmkuhl *et al.*, 2013; Proffitt *et al.*, 2016) or may not occur at all (Pearson *et al.*, 1995). These diverse results often stem from site-level differences that may not reflect landscape-scale processes of nutritional availability relevant to wildlife populations, underscoring the importance of large-scale studies in quantifying the effects of fire on nutritional resources. Landscape-scale studies of the relationship between fire and ungulate nutritional resources are lacking, and extrapolating results of plot-level studies fails to provide a complete landscape-level understanding (Hobbs, 2003; Pastor, 2011). A landscape-scale examination of the

effects of fire on ungulate forage and nutritional resources may provide a more comprehensive understanding of these effects at a scale relevant to habitat management.

A fundamental issue for managers of plant–herbivore systems is determining how many animals an ecosystem can support. However, the concept of an ecological carrying capacity in stochastic environments may not be useful for describing plant–herbivore relationships (Hobbs and Swift, 1985; McLeod, 1997; Taper and Gogan, 2002). Fire and fire management regimes may alter nutritional carrying capacity over time, resulting in variations in the abundance of animals the ecosystem can support. Additionally, herbivores may influence forage quality and abundance through changes to soil moisture, soil temperature, light conditions, and nitrogen content and availability in plants (McNaughton, 1979; Ruess and McNaughton, 1987; Coughenour, 1991; Jaramillo and Detling, 1992; Milchunas and Lauenroth, 1993; Hobbs, 1996; Singer and Harter, 1996). Thus, understanding the effects of fire on plant–herbivore dynamics is also critical for identifying the magnitude of variability in available nutritional resources over time, and maintaining healthy ungulate populations and ecosystems.

Improved estimates of the effects of fire on forage are needed to infer the nutritional and potential demographic consequences of fire and fire management for ungulate populations. Our goals were to use a landscape-level spatial modelling approach to evaluate the effects of wildfire and prescribed fire on ungulate forage abundance and quality within the Bitterroot Valley of west-central Montana and to assess the potential wildfire-related variations in ungulate forage during the past century. We predicted that fire variably affects the distribution and abundance of nutritional resources depending on the type of forest, seasonal patterns and time since fire, and that increasing wildfire activity in the Rocky Mountains during the last decades resulted in an overall positive effect on the nutritional resources for ungulates.

Methods

Study area

The study was conducted in the Bitterroot Valley in west-central Montana and included the ranges of 3 elk (*Cervus canadensis*) populations: the North Sapphire population in the northern Bitterroot Valley, and the East Fork and West Fork populations in the southern Bitterroot Valley (Figure 1). We sampled vegetation in the North Sapphire range during 2014–2015 and in the East Fork and West Fork ranges during 2012–2015. The extents of each study area were defined by the annual range of the corresponding elk population, which were constructed using a 5-km buffer around Global Positioning System (GPS) collar elk location data.

The range of the North Sapphire population encompassed 2482 km² in the lower reaches of the Bitterroot River. The East Fork population range encompassed 3971 km² in the East Fork of the Bitterroot River, as well as a portion of the Big Hole Valley to the east. The West Fork population occurred across 1990 km² in the West Fork of the Bitterroot River. Mean annual precipitation ranged from 284 mm on the valley floor to 1919 mm on mountain summits, and mean temperatures for July and January were 17.1 and –4.4°C, respectively (PRISM Climate Group, 2016). Elevation ranged from 942 to 3290 m.

Topography throughout the Bitterroot Valley varies from flat bottomland to gentle foothills giving way to steep and rugged mountain slopes. Lower elevation areas are agricultural land, grassland, shrubland or

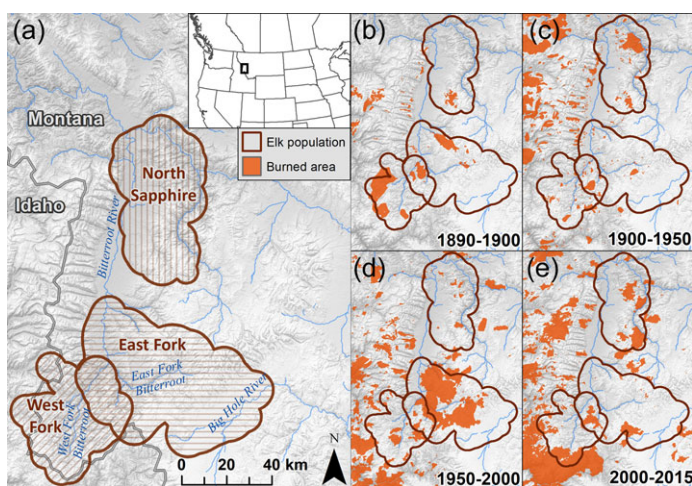


Figure 1 The North Sapphire, East Fork, and West Fork elk population annual ranges (panel a), and the wildfire patterns overlaid on the annual ranges occurring within time spans 1890–1900 (panel b), 1901–1950 (panel c), 1951–2000 (panel d), and 2001–2015 (panel e) in the Bitterroot Valley of west-central Montana, USA. Shaded polygons indicate fires occurring within indicated time spans.

forest. The irrigated and non-irrigated agricultural land is composed of pasture grasses, corn or leguminous forbs. Montane grasslands are dominated by Idaho fescue (*Festuca idahoensis*), rough fescue (*Festuca campestris*) or bluebunch wheatgrass (*Pseudoroegneria spicata*). Shrubland is dominated by sagebrush (*Artemisia tridentata*) or bitterbrush (*Purshia tridentata*), and dry open coniferous forests are dominated by ponderosa pine (*Pinus ponderosa*) or Douglas fir (*Pseudotsuga menziesii*). Higher elevation areas are predominately mesic mixed-coniferous forests with lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*) and subalpine fir (*Abies lasiocarpa*).

Timber harvest and patchy fire history have resulted in habitats in varying successional stages. Timber harvest has declined ~69 and 76 per cent on the Bitterroot and Lolo National Forests, respectively, from averages of 32.5 and 67.4 million board feet cut per year in the 1980s to 7.8 and 21.0 million board feet per year in the 2000s (U.S. Department of Agriculture, Forest Service, 2016). In contrast to declining timber harvest, wildfire activity has been common and is more recently the primary disturbance throughout the Bitterroot Valley. From 1889 to 1949, wildfires burned on average 32 km² annually, decreasing to 16 km² during 1950–1999 (Figure 2). From 2000 to 2015, wildfire activity increased, with large-scale wildfires (>125 km²) occurring in 2000, 2003, 2007 and 2011 and smaller-scale fires occurring annually. During this period, wildfires burned ~2043 km², averaging 159 km² annually. Prescribed fire has been applied intermittently on public lands throughout the Bitterroot Valley, beginning in the early 1990s. During 1990–1999, prescribed fires burned on average 2.5 km² annually, increasing to 6.5 km² during 2000–2015.

Approximately 6000–8000 elk from six different populations currently inhabit the Bitterroot Valley (Edwards et al., 2015). Approximately 2400 elk inhabited the valley in the 1960s, and populations steadily increased to current numbers. The North Sapphire population has steadily increased from 750 in the mid-2000s to a high of 1 051 in 2016 due to a combination of moderate calf recruitment and limited female harvest. The East Fork population peaked at a high of 4135 in 2006, then declined to 3332 by 2012, due to a combination of antlerless elk harvest and increasing predation pressure (Eacker et al., 2016, 2017). As of 2016, the population had increased to 3921. The West Fork population peaked at a high of 1 900 in 2005, then steadily declined to ~722 animals by 2009. Declines were due to a combination of antlerless elk harvest and increasing predation. Elk are sympatric with moose (*Alces alces*), mule deer (*Odocoileus hemionus*), whitetail deer (*O. virginianus*) and bighorn sheep (*Ovis canadensis*). Wolves (*Canis lupus*), coyotes (*C. latrans*), mountain lions (*Felis concolor*) and black bears (*Ursus americanus*) also occupy the study area.

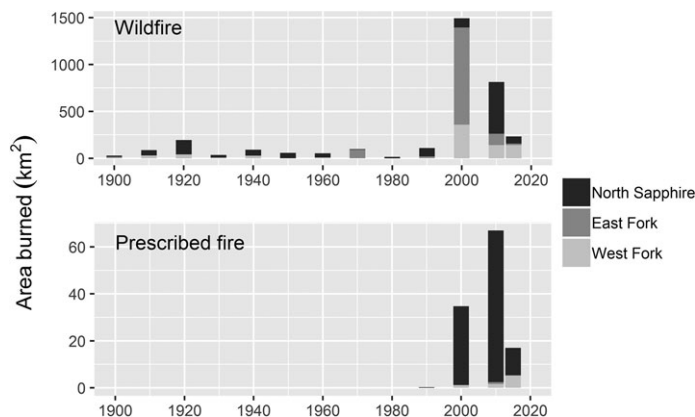


Figure 2 The decadal area (km²) burned by wildfire and prescribed fire within the North Sapphire, East Fork and West Fork elk population annual ranges in the Bitterroot Valley of west-central Montana, USA, 1900–2015. Note different y-axis scales.

Statistical analysis

We used a combined ground and remote-sensing based approach to develop landscape-scale models of summer and winter elk forage quality and abundance for western Montana (e.g. Hebblewhite et al., 2008; Pastor, 2011; Proffitt et al., 2016). We first determined the dominant forage species in the North Sapphire, East Fork, and West Fork elk summer and winter diets. Then we sampled vegetation at locations across a gradient of fire histories to evaluate spatial and temporal effects of wildfire and prescribed fire on forage abundance and quality. Finally, we used historic wildfire data to estimate the potential fire-related variability of forage across the landscape, and summarized fire-related variability in forage during the past 115 years within the 3 different elk summer and winter ranges.

Our approach to quantifying forage was similar to Proffitt et al. (2016), however, in this analysis we treated forage quality (i.e. kcal of digestible energy (DE) per gram of forage) and abundance (i.e. grams of forage biomass per metre²) separately rather than integrate the two in an estimate of digestible biomass. Independently, forage quality directly relates to animal performance, with even small differences in forage quality having large influences on reproductive performance (Cook et al., 2004). Previous work within this study area suggested nutritional limitations on elk reproductive performance (Proffitt et al., 2016). These differences are potentially masked by integration of forage quality and biomass in the estimation of digestible biomass (i.e. high biomass of low-quality forage plants may have high total digestible biomass). Therefore, based on field sampling of vegetation, we first estimated forage quality derived from dry matter digestibility and converted to DE to assess the adequacy of forage quality to support the energetic needs of elk (Cook et al., 2016). Secondly, we investigated variability in abundance of forage.

Elk forage species and vegetation sampling

We used faecal plant fragment analysis from pellet samples collected within each population range to identify the important summer and winter forage species in the diets of Bitterroot elk. We collected 86 composite pellet samples (at least 21 summer and 5 winter samples in each of the 3 population ranges) in 15-day intervals during winter and summer from areas used <24 h prior by GPS-collared elk. 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 season of interest (May–September or December–March). Faecal plant fragment analyses (level B) were conducted at the Wildlife Habitat and Nutrition Laboratory (Pullman, WA, USA) to estimate seasonal diets. We combined all diet samples for each elk population and ranked the top elk forage plant species separately for summer and winter using the species that constituted 95 per cent of the total diet. We screened our plant data (described below) to include only these forage species in estimates of forage quality and abundance.

Within each study area, we estimated plant biomass and species composition at random plots within 12 vegetation cover types based on a proportional allocation sampling design (Krebs, 1989). The 12 cover types included mesic forest systems with three wildfire histories (burned >15 years prior, burned 6–15 years prior and burned ≤5 years prior); dry montane mixed conifer forests with the same three wildfire histories; dry montane mixed conifer forests that were subject to a prescribed understory burn ≤5 years prior (Long et al., 2008); open grasslands, shrublands and woodlands; valley bottom riparian; montane riparian; irrigated agriculture; and dry agriculture. The prescribed understory burn sampling locations were not treated post-fire with weed spraying or forest thinning. We calculated time since burn, and burn age categories, based on the calendar year of the burn and the calendar year of sampling. Our land cover model was developed based on a collection of available land cover products and timing since fire data sources (Appendix A).

At each sampling site, we established a 40-m transect along the contour of the slope. We recorded species composition and percent cover of forbs, shrubs, graminoids and trees <2 m tall at five 1 m² quadrats every 10 m along each transect. Cover estimates were independent of each other, allowing total cover per quadrat to exceed 100 per cent. At the 0, 20 and 40-m quadrat, we established a nested 0.25 m² clip plot and collected all graminoid and forb biomass >1 cm above ground. In 2012–2013, we also clipped all leaves and non-woody stems of shrubs. We dried all samples at 50°C in a drying oven for 48 h and measured dry weight to the nearest gram. We apportioned the dry weight to plant lifeform (e.g. forb, graminoid and shrub) based on the percent cover of each lifeform. In 2014–2015, we made two minor changes to sampling. First, because clipping shrubs was time-intensive and shrubs comprised only a small percentage of the diet, we did not clip shrub biomass but instead estimated shrub biomass from shrub basal diameters (Appendix B). Second, we measured weight of forbs and graminoids separately to more precisely estimate biomass by lifeform.

Plant phenology affects plant nutritional availability and needs to be accounted for in plot-based sampling of forage resources. To estimate variation in phenological stage of each forage species, we used two similar approaches. In 2014–2015, we estimated the dominant phenological stage (emergent, flowering, fruiting, mature seed or senescent) of each species at each sampling site. The emergent stage included green plant tissues in the newly emergent, flowering and/or fruiting stages. Plants in the emergent stage were assigned an average forage quality value that was the mean of the newly emergent, flowering, and fruiting stages (see below). In 2012–2013, we estimated the phenological stage of each species at a sample of phenology plots that were stratified across major phenological gradients including elevation, aspect (north, south, flat), and canopy coverage (open and closed). We constrained the phenology data to July 15–August 31 to correspond to the late-summer nutritional period (Cook *et al.*, 2013) and applied the species-specific phenological classifications to all sampling sites (see Proffitt *et al.*, 2016 for details).

Forage quality and abundance

To estimate the quality (i.e. kcal of DE per gram) of forage plant species, we collected samples of forage species during each major phenological stage and estimated dry matter digestibility using sequential detergent fibre analysis (Van Soest, 1982; Wildlife Habitat and Nutrition Lab, Washington State University, Pullman, WA, USA) and an equation developed for wild ungulates (Appendix C; Robbins *et al.*, 1987a; 1987b; Hanley *et al.*, 1992). We then converted dry matter digestibility values to DE (Cook *et al.*, 2016) measured as kcal/g (Appendix C). For each forage plant species, we collected a minimum of three plant samples in each phenological stage. Replicate plant samples were collected from different areas, then combined into one composite sample and dried at 50°C for 48 h. We sampled 32 forage plant species and used literature values from previous studies for remaining forage species to estimate phenological stage-specific DE of species in the elk diets. For each forage species, we applied the same phenological stage-specific DE values to all study areas and all burn classes (Appendix D).

To estimate forage quality within each sampling quadrat at each sampling site, we first rescaled percent cover to include the proportion of each forage species in each phenological stage, such that the total cover for all forage species at each quadrat summed to 1.0. For the summer data, we estimated DE of all forage as the weighted mean of the phenophase-specific DE estimates for each species, weighted by rescaled proportion cover. For the winter data, we applied only the senescent phenological stage-specific DE estimate for each forage species to estimate the mean DE of forage species. Then, we estimated DE per sampling site as the mean of the five quadrat DE estimates within each sampling site, and we refer to this value as the forage quality per sampling site (i.e. mean DE; Appendix C).

To estimate forage abundance (g/m²) at each sampling site, we first apportioned clipped, dry biomass (g/0.25 m²) for each lifeform to each species based on rescaled percent cover (species cover proportional to cover within the appropriate lifeform). Second, we summed biomass of the forage species across each lifeform. Finally, we estimated mean forage abundance at each sampling site by averaging biomass per lifeform across clip plots and scaling up to square metres (0.25 m² × 4 = 1 m²; Appendix C).

Landscape modelling of forage abundance and quality

We developed landscape nutrition models that predicted summer and winter forage quality and abundance. We used linear models to predict forage quality as a function of spatial covariates. We used log-linear models to predict forage abundance as a function of spatial covariates and we treated forb, graminoid and shrub forage abundance as separate models. Abundance was log transformed to meet assumptions of normality for linear modelling. We evaluated eight standardized spatial covariates as predictors of forage quality and abundance: vegetation cover class, elevation, slope, canopy cover, an index of terrain ruggedness (i.e. compound topography index (CTI)), solar radiation index, spring precipitation (PRISM Climate Group, 2016), and Normalized Difference Vegetation Index (NDVI) amplitude (Pettorelli, 2013, Appendix E). We used spring precipitation and NDVI amplitude covariates to account for annual variations in growing season conditions during the 4 years of vegetation sampling. We assumed all covariates were measured without error and we standardized covariates by subtracting their mean and dividing by their standard deviation. We screened spatial covariates for collinearity and included only covariates with a Pearson's correlation coefficient <0.6 and a variance inflation factor <3.0 (Zuur *et al.*, 2010).

We first evaluated if time since fire (i.e. fire history) was an important predictor of forage quality and abundance. We fit two different global models that included all eight standardized spatial covariates. The first model included 12 vegetation cover classes including time since fire categories for mesic and dry forests, and the second model included only seven vegetation cover classes and treated mesic and dry forests of all burn histories as a single mesic forest or dry forest class. We used AIC to select the best model for summer and winter forage quality and abundance. After determining if time since burn should be included in the vegetation cover class covariate, we selected the top ranked forage quality and abundance models using backwards-stepwise model selection, and we used $P = 0.05$ as the threshold for inclusion or exclusion of predictor variables. Here, we employed stepwise selection because we were unsure of which combination of the eight spatial covariates best predicted forage quality and abundance.

We used unstandardized coefficient estimates from the top ranked models to develop spatially explicit predictions of forage quality and abundance. We summed the predicted forb and graminoid forage abundance estimates into an estimate of herbaceous forage abundance. We used R^2 values from the top model to assess model fit. We evaluated the direction and magnitude of covariate effects on forage quality and abundance based on standardized coefficient estimates and sign, as well as comparisons of predictions estimated by holding all covariates at their mean value. Analyses were performed using Program R version 3.3.0 (R Development Core Team, 2016).

Wildfire- and prescribed fire-induced variability in nutritional resources, 1900–2015

To investigate potential effects of wildfire on forage during the past century, we used historical wildfire data and our landscape nutrition models to predict summer and winter forage quality and abundance each decade from 1900 to 2015. Wildfire and prescribed fire history data

included previously compiled data from 1889 to 1985 (Gibson *et al.*, 2014) and data compiled as part of this project from 1985 to 2015 (Appendix A). Prescribed fire history data ranged from 1999 to 2015. For each decade, we developed spatial data representing the time since fire and incorporated these data into our land cover model. Using these decadal land cover products to classify vegetation cover type, we used the estimated coefficients from our top-ranked models to predict forage quality and abundance over time. This approach assumes that sampling conducted during this study represents plant species composition from the past. We present decadal percent of the elk population summer and winter ranges predicted to be within each of four nutritional value classes for lactating female elk in summer and early autumn based on studies performed by Cook *et al.* (2004, 2016): excellent (DE \geq 2.90 kcal/g; no nutritional limitations), good (DE 2.75–2.89 kcal/g; minor nutritional limitations for reproduction and survival), marginal (DE 2.40–2.74 kcal/g; significant limitation on reproduction), and poor (\leq 2.39 kcal/g; significant limitation for reproduction and survival).

We used elk location data collected from 41, 34 and 34 adult female elk in the North Sapphire, East Fork and West Fork populations, respectively, during 2012–2015 to define summer and winter ranges. We captured elk using helicopter net-gunning or chemical immobilization in compliance with the University of Montana IACUC policy # 027-11MHWB-042 611 and Montana Fish, Wildlife and Parks ACUC protocol 19-2013. We estimated population-level summer (July 8–August 31) and winter (January 1–March 31) utilization distributions as the 95 per cent fixed-kernel isopleth, calculated using the reference bandwidth (Worton, 1989). We used the summer and winter range boundaries to estimate forage quality and abundance available to elk in each population over time.

Results

Elk forage species and plant vegetation sampling

We collected 68 summer and 18 winter composite pellet samples from within the study area. A total of 63 species comprised 95 per cent of the summer diets and a total of 17 species comprised 95 per cent of the winter diets of the North Sapphire, East Fork and West Fork elk populations (Appendix F). The most common summer forage species of graminoids were *Poa* spp. and *Carex* spp. and of forbs were *Lupinus* spp. and *Balsamorhiza sagittata*. The most common winter forage species of graminoids were *Festuca* spp., *Poa* spp., *Carex* spp., *Stipa* spp. and *Psuedoroegneria spicata* and of forbs were *Lupinus* spp. and *Balsamorhiza sagittata*.

We sampled vegetation at a total of 752 sites, of which 459, 208 and 111 fell in the North Sapphire, East Fork and West Fork population ranges, respectively. We sampled recently burned forests 12–60 months post-fire and were unable to sample any sites within 12 months of the fire. The most common forage species in each vegetation cover class varied (Table 1).

Elk forage quality

We estimated DE for 34 species in 5 phenological stages using an average of 7 (SD = 2.5, range 3–9) samples collected per species per stage. DE for forage plants varied by plant species, lifeform and phenological stage (Appendix G, Appendix H). Across sampling sites located in different cover classes, the mean DE varied during the summer but did not vary substantially during the winter (Figure 3).

The summer forage quality model that contained vegetation cover classes that included time since fire fit the data better than the model that contained vegetation cover classes without time since fire (Δ AIC = 92.3). The model that included time since fire was therefore used in subsequent analyses of summer forage quality. The winter forage quality model that contained vegetation cover classes that did not include time since fire fit the data better than the model that contained vegetation cover classes with time since fire (Δ AIC = 7.2). The model that did not include time since fire was therefore used in subsequent analyses of winter forage quality analyses.

The top-ranked model predicting summer forage quality included the covariates vegetation cover class, slope, canopy cover, solar radiation and elevation ($r^2_{\text{adj}} = 0.26$; Table 2). Standardized coefficient estimates indicated that summer forage quality varied across vegetation cover classes and burn histories. Summer forage quality was highest in recently burned mesic and dry forests, including dry forests burned by prescribed fire, and irrigated agricultural areas. Summer forage quality was lowest in mesic forests burned >15 years ago and valley bottom riparian areas. Dry forests had 0.3–14.5 per cent higher summer forage quality than mesic forests across comparable fire histories. Within dry forests, summer forage quality was highest in recently burned forests, 8.6 and 4.6 per cent higher than forests burned 6–15 years ago and >15 years ago, respectively. Dry forests treated with prescribed fire within the past 5 years had 2.9 per cent lower and 1.5 per cent higher summer forage quality, as compared with dry forests burned by wildfire within 5 years and >15 years ago, respectively. However, confidence intervals for estimates across fire histories overlapped. Within mesic forests, summer forage quality was highest in recently burned forests, 6.6 and 17.2 per cent greater than forests burned 6–15 years ago and >15 years ago, respectively.

The top-ranked model predicting winter forage quality included the covariates vegetation cover class, slope, CTI, NDVI amplitude, solar radiation and elevation ($r^2_{\text{adj}} = 0.12$). Standardized coefficient estimates indicated that as compared with dry forests, winter forage quality was similar in mesic forests, grasslands, montane riparian and dry agriculture, and lower in valley bottom riparian ($\hat{\beta} = -0.61$, 95 per cent CI = $-1.01, -0.20$) and irrigated agriculture ($\hat{\beta} = -1.24$, 95 per cent CI = $-1.56, -0.91$). Winter forage quality increased with increasing CTI ($\hat{\beta} = 0.07$, 95 per cent CI = 0.01, 0.14), NDVI amplitude ($\hat{\beta} = 0.07$, 95 per cent CI = 0.01, 0.14), and solar radiation index ($\hat{\beta} = 0.13$, 95 per cent CI = 0.06, 0.19) and decreasing elevation ($\hat{\beta} = -0.21$, 95 per cent CI = $-0.30, -0.11$).

Elk forage abundance

Summer median forb, graminoid and shrub forage abundance were 4.2, 15.4 and 11.8 g/m², respectively, and summer forage abundance varied across vegetation cover classes and burn history (Figure 4). The model that contained vegetation cover classes that included time since fire fit the summer and winter forb, graminoid, and shrub abundance data better than the model that contained vegetation cover classes without time since fire (summer forb: Δ AIC = 34.5, summer graminoid: Δ AIC = 29.2, summer shrub: Δ AIC = 87.9, winter forb: Δ AIC = 31.8, winter graminoid: Δ AIC = 48.8, winter shrub: Δ AIC = 47.3). The vegetation cover class model that included time since fire was therefore used in

Table 1 Number of vegetation sampling plots containing each species for each time since fire category in the Bitterroot Valley of west-central Montana, USA, during 2012–2015.

Dry Forest Burn				Mesic Forest Burn			Species
>15	≤5	Rx ≤5	6–15	>15	≤5	6–15	
75	3	11	36	48	10	32	<i>Carex geyeri</i>
72	5	10	41	10	2	6	<i>Symphoricarpos albus</i>
22	3	1	8	67	17	28	<i>Xerophyllum tenax</i>
63	9	12	36	30	11	1	<i>Calamagrostis rubescens</i>
58	10	10	43	31	9	13	<i>Spirea betulifolia</i>
57	6	11	48	21	3	16	<i>Achillea millefolium</i>
18	5	–	4	56	20	31	<i>Vaccinium scoparium</i>
54	12	8	38	16	8	5	<i>Berberis repens</i>
45	6	1	15	15	9	13	<i>Arnica cordifolia</i>
26	5	2	14	45	13	16	<i>Vaccinium membranaceum</i>
41	2	2	9	6	1	2	<i>Festuca idahoensis</i>
41	4	5	22	16	3	2	<i>Fragaria vesca</i>
41	–	5	21	3	–	–	<i>Physocarpus malvaceus</i>
40	2	2	20	20	–	5	<i>Amelanchier alnifolia</i>
39	6	8	23	17	–	12	<i>Penstemon</i> spp.
16	14	–	24	13	24	39	<i>Chamerion angustifolium</i>
23	2	7	38	6	–	2	<i>Centaurea stoebe</i>
36	3	11	14	4	–	1	<i>Pseudoroegneria spicata</i>
30	5	3	11	34	3	19	<i>Hieracium albiflorum</i>
34	1	3	17	17	1	1	<i>Pseudostuga menziesii</i>
32	1	2	13	9	1	–	<i>Antennaria racemosa</i>
19	1	1	1	32	1	1	<i>Chimaphila umbellata</i>
32	4	4	8	10	–	–	<i>Arctostaphylos uva-ursi</i>
31	1	5	4	3	–	–	<i>Allium cernuum</i>
31	–	4	19	15	–	4	<i>Fragaria virginiana</i>
6	–	–	–	30	5	–	<i>Abies lasiocarpa</i>
29	5	3	7	2	1	–	<i>Balsamorhiza sagittata</i>
27	1	6	9	23	3	–	<i>Carex concinnooides</i>
20	7	1	13	21	5	25	<i>Poa</i> spp.
24	2	2	15	3	–	12	<i>Koeleria macrantha</i>
16	7	–	22	–	2	3	<i>Collinsia parviflora</i>
8	5	–	6	17	9	22	<i>Pinus contorta</i>
17	3	–	21	4	6	–	<i>Eurybia conspicua</i>
20	–	3	8	2	–	–	<i>Poa secunda</i>
5	4	1	20	1	9	3	<i>Epilobium brachycarpum</i>
6	1	–	–	18	5	1	<i>Arnica latifolia</i>
15	9	–	17	13	10	15	<i>Carex</i> spp.
7	3	–	5	14	1	14	<i>Lupinus argenteus</i>
13	–	7	6	10	2	–	<i>Hieracium scouleri</i>

Continued

Table 1 Continued

Dry Forest Burn				Mesic Forest Burn			Species
>15	≤5	Rx ≤5	6–15	>15	≤5	6–15	
2	1	–	13	3	1	12	<i>Salix</i> spp.
1	–	–	5	2	5	13	<i>Anaphalis margaritacea</i>
12	–	8	7	–	–	–	<i>Apocynum androsaemifolium</i>
9	1	1	5	3	2	12	<i>Taraxacum officinale</i>
11	6	–	4	3	5	6	<i>Stellaria</i> spp.
5	6	1	11	–	1	4	<i>Ceanothus velutinus</i>
–	5	–	4	–	8	–	<i>Moehringia macrophylla</i>
5	2	–	2	2	2	8	<i>Arnica</i> spp.
5	1	–	5	7	1	8	<i>Erigeron</i> spp.
–	–	–	–	–	6	–	<i>Gnaphalium macounii</i>

Only the most common (top 20) species in each time since fire category are shown. The Rx ≤ 5 category denotes a forest that was treated with prescribed fire.

subsequent summer and winter forb, graminoid and shrub forage abundance analyses.

The top-ranked model predicting abundance of forb forage during summer included the covariates vegetation cover class, slope, solar radiation and elevation ($r^2_{adj} = 0.17$; Table 2). The top-ranked model predicting summer graminoid forage abundance included the covariates vegetation cover class, CTI, canopy cover, NDVI amplitude, solar radiation and elevation ($r^2_{adj} = 0.22$). Summer predictions of herbaceous forage abundance (combined forb and graminoid model predictions) varied by burn history. Dry forests had 58.7–174.0 per cent greater summer herbaceous forage abundance than mesic forests across comparable fire histories, excepting areas burned within the past 5 years, where mesic forests had 21.7 per cent greater abundance. Within dry forests, summer herbaceous forage abundance was highest in forests burned 6–15 years ago, 44.5 per cent greater than forests burned >15 years ago. Dry forests that were treated with prescribed fire had 39.6 and 46.1 per cent lower summer herbaceous forage abundance than areas burned by wildfire within 5 years or >15 years ago, respectively. Within mesic forests, summer herbaceous forage abundance was highest in recently burned forests, 211.9 per cent greater than forests burned >15 years ago.

The top-ranked model predicting summer shrub forage abundance included the covariates vegetation cover class, canopy cover and solar radiation ($r^2_{adj} = 0.41$; Table 2). Standardized coefficient estimates indicated that within dry forests, summer shrub abundance was highest in areas burned 6–15 years ago and areas treated with prescribed fire. Within mesic forests, summer shrub forage abundance was highest in areas burned >15 years ago and lowest in recently burned areas.

The top-ranked model predicting winter forb forage abundance included the covariates vegetation cover class, slope,

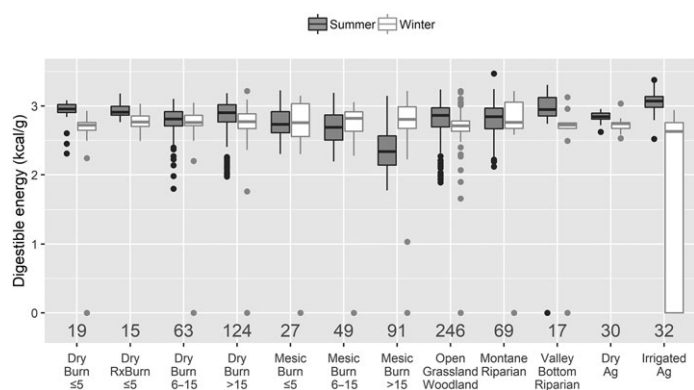


Figure 3 Summer (gray) mean digestible energy (i.e. forage quality; kcal/g) measured within each vegetation cover class in the Bitterroot Valley of west-central Montana, USA, during 2012–2015. Horizontal lines through boxes represent median values, the length of the box represents the middle 50 per cent of observations (IQR), vertical lines represent observations within 1.5x the range of the IQR, and points outside the vertical lines represent observations >1.5x the range of the IQR. Numbers at bottom of plot indicate sample size per cover class. Vegetation cover classes included dry montane mixed conifer forests burned by wildfire ≤ 5 years prior (Dry Burn ≤ 5), 6–15 years prior (Dry Burn 6–15), and >15 years prior (Dry Burn >15), dry montane mixed conifer forests burned by prescribed fire ≤ 5 years prior (Dry RxBurn ≤ 5), mesic forest systems burned by wildfire ≤ 5 years prior (Mesic Burn ≤ 5), 6–15 years prior (Mesic Burn 6–15), and >15 years prior (Mesic Burn > 15), open grasslands, shrublands and woodlands (Open Grassland Woodland), montane riparian, non-irrigated agriculture (Dry Ag), and irrigated agriculture (Irrigated Ag).

canopy cover and solar radiation ($r^2_{adj} = 0.18$; Table 3). The top-ranked model predicting winter graminoid forage abundance included the covariates vegetation cover class, slope, CTI, canopy cover, NDVI amplitude, spring precipitation, solar radiation and elevation ($r^2_{adj} = 0.25$). Winter herbaceous forage abundance predictions (combined forb and graminoid model predictions) varied by burn history. Within dry forests, winter herbaceous forage abundance was highest in forests burned >15 years ago, 278.8 and 123.9 per cent greater than in forests burned ≤ 5 and 5–15 years ago, respectively. Dry forests that were treated with prescribed fire had 74.1 per cent higher and 54.1 per cent lower winter herbaceous forage abundance than areas burned by wildfire ≤ 5 and >15 years ago, respectively.

The top-ranked model predicting winter shrub forage abundance included the covariates vegetation cover class, slope, canopy cover, NDVI amplitude, solar radiation and elevation ($r^2_{adj} = 0.17$; Table 3). Dry and mesic forests of all fire histories had similar shrub forage abundance. Canopy cover was the strongest predictor of shrub abundance, with higher abundance in areas with high canopy cover.

Estimated fire-induced variability in nutritional resources, 1900–2015

We estimated the area of summer ranges to be 775, 1 728 and 645 km² in the North Sapphire, East Fork and West Fork populations, respectively. The total area burned per decade varied during 1900–2015 (Table 4). The area burned during 1900–1990 was small and had little variation across time or populations,

Table 2 Standardized coefficient estimates and standard errors for the top models predicting summer forage quality and forage abundance per lifeform in the Bitterroot Valley of west-central Montana, USA, during 2012–2015.

Covariate	Quality	Abundance		
		Forb	Gram.	Shrub
Intercept	2.86 (0.03)	−0.29 (0.25)	2.59 (0.20)	1.32 (0.30)
Dry Forest Burn ≤ 5	0.13 (0.07)	−0.70 (0.70)	−0.19 (0.53)	−0.62 (0.78)
Dry Forest Rx Burn ≤ 5	0.04 (0.08)	−0.38 (0.77)	−0.63 (0.58)	1.90 (0.87)
Dry Forest Burn 6–15	−0.11 (0.05)	2.23 (0.43)	0.003 (0.34)	2.71 (0.50)
Mesic Forest Burn >15	−0.36 (0.04)	1.21 (0.42)	−1.63 (0.32)	0.58 (0.45)
Mesic Forest Burn ≤ 5	0.07 (0.06)	1.58 (0.62)	−0.07 (0.47)	−2.15 (0.69)
Mesic Forest Burn 6–15	−0.11 (0.06)	0.93 (0.54)	−0.19 (0.43)	1.11 (0.56)
Grass/Open Woodland	−0.13 (0.03)	0.75 (0.32)	−0.46 (0.25)	−1.58 (0.38)
Montane Riparian	−0.03 (0.04)	1.43 (0.43)	−0.82 (0.34)	−0.73 (0.48)
Valley Bottom Riparian	−0.35 (0.08)	0.64 (0.79)	−1.57 (0.62)	−1.85 (0.85)
Dry Agriculture	−0.16 (0.06)	−1.10 (0.61)	−0.24 (0.47)	−3.62 (0.70)
Irrigated Agriculture	0.05 (0.07)	3.12 (0.62)	−1.96 (0.49)	−3.89 (0.69)
Solar Radiation	0.03 (0.01)	0.68 (0.12)	0.35 (0.09)	0.20 (0.13)
Canopy Cover	−0.08 (0.01)	−	−0.59 (0.11)	1.78 (0.15)
Slope	0.02 (0.01)	0.21 (0.12)	−	−
Elevation	−0.08 (0.02)	0.58 (0.16)	−0.71 (0.15)	−
Compound Topo. Index	−	−	−0.13 (0.09)	−
NDVI Amplitude	−	−	0.18 (0.11)	−

Boldface values denote 95 per cent confidence intervals not containing 0. Effects of vegetation cover classes are in relation to the reference (intercept) cover class Dry Forest Burned >15 years prior.

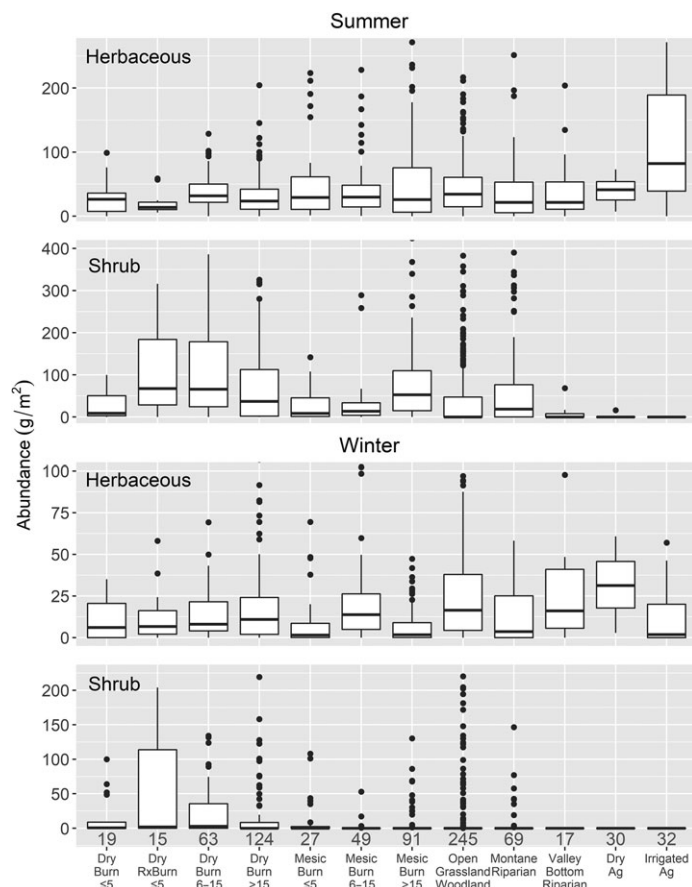


Figure 4 The mean summer and winter herbaceous and shrub forage abundance (g/m^2) measured within each vegetation cover class in the Bitterroot Valley of west-central Montana, USA, during 2012–2015. Horizontal lines through boxes represent median values, the length of the box represents the middle 50 per cent of observations (IQR), vertical lines represent observations within 1.5x the range of the IQR, and points outside the vertical lines represent observations >1.5x the range of the IQR. Numbers at bottom of plot indicate sample size per cover class. Note different y-axis scales. Vegetation cover classes included dry montane mixed conifer forests burned by wildfire ≤ 5 years prior (Dry Burn ≤ 5), 6–15 years prior (Dry Burn 6–15), and >15 years prior (Dry Burn >15), dry montane mixed conifer forests burned by prescribed fire ≤ 5 years prior (Dry RxBurn ≤ 5), mesic forest systems burned by wildfire ≤ 5 years prior (Mesic Burn ≤ 5), 6–15 years prior (Mesic Burn 6–15), and >15 years prior (Mesic Burn >15), open grasslands, shrublands and woodlands (Open Grassland Woodland), montane riparian, non-irrigated agriculture (Dry Ag), and irrigated agriculture (Irrigated Ag).

averaging 17.4, 16.2 and 7.3 km^2 per decade in the North Sapphire, East Fork and West Fork summer ranges, respectively. From 1990 to 2015, the average area burned per decade increased 242, 1772 and 1315 per cent compared with 1900–1990 to 42.1, 287.2 and 96.0 km^2 in the North Sapphire, East Fork and West Fork summer ranges, respectively.

The percent of summer range that had previously burned did not vary substantially for any population from 1891 to 1900 (Figure 5). The average percent of summer range in mesic forests that burned within the past 15 years across populations increased 4.5–16.3 times from 0.8–1.3 per cent during 1891–1990 to

3.6–16.3 per cent during 1991–2015. The average percent of summer range in dry forests that burned within the past 15 years was slightly more variable across populations than for mesic forests, increasing 2.5–26.4 times from 0.7–1.9 per cent to 4.7–18.1 per cent for the same decades.

The proportion of the elk summer ranges comprised of excellent, good, marginal and poor nutritional value classes did not vary substantially during 1891–1990 but did vary in the East Fork and West Fork summer ranges during 1991–2015 (Table 4; Figure 5). Within the North Sapphire, relative proportions of nutritional value classes varied little across the entire time period. Summer ranges of all populations consisted primarily of good and marginal nutritional value classes, although the West Fork population summer range generally had lower overall nutritional value than the North Sapphire or East Fork populations.

Similarly, herbaceous forage abundance per decade did not vary substantially during 1891–1990, but did increase during 1991–2015 (Table 4 and Figure 5). For all elk populations, the highest herbaceous forage abundance occurred in the half-decade 2011–2015. Shrub forage abundance per decade varied considerably across the decades with the highest estimates occurring in 1920, 2015 and 1900 in the North Sapphire, East Fork and West Fork summer ranges, respectively.

We estimated the area of winter ranges to be 400, 441 and 289 km^2 in the North Sapphire, East Fork and West Fork populations, respectively. The total area burned per decade within winter ranges was low ($< 8 \text{ km}^2$) and varied insubstantially during 1891–2015, except 1991–2000 that burned 263 and 70 km^2 in the East Fork and West Fork, respectively.

Winter herbaceous and shrub forage abundance per decade did not vary substantially during 1891–1990 in any of the three elk population ranges (Figure 6). During 1991–2015, herbaceous and shrub forage abundance did not vary in the North Sapphire winter range, but there was some variation across time in the East Fork and West Fork ranges. Because time since fire was not an important predictor of winter forage quality, we did not estimate the effects of past fire history on elk winter forage quality. Overall, fire-related variability in summer forage was greater than winter forage.

Discussion

We used a spatial modelling approach to evaluate the landscape-scale effects of wildfire and prescribed fire on elk nutritional resources in Rocky Mountain forest habitats. Our method provides a straightforward approach for estimating ungulate nutritional resources, tracking changes in nutrition associated with wildfire over time, and identifying summer ranges where nutritional limitations may occur. We found that wildfire and prescribed fire had important yet dissimilar effects on elk forage quality and abundance during summer, and we expect our results to be broadly generalizable to similar forested landscapes in the Rocky Mountains and western United States. Our results show that large-scale spatiotemporal variation in wildfire activity has the potential to alter elk nutritional resources, and that the effects of wildfire on nutritional resources vary across elk populations as a function of terrain and forest cover types burned. Our results also indicate fire most strongly affects elk nutritional resources on summer, not

Table 3 Standardized coefficient estimates and standard errors for the top models predicting winter forage abundance in the Bitterroot Valley of west-central Montana, USA, during 2012–2015.

Covariate	Abundance		
	Forb	Graminoid	Shrub
Intercept	-2.88 (0.23)	2.15 (0.23)	-2.42 (0.29)
Dry Forest Burn ≤5	0.59 (0.61)	-1.37 (0.61)	2.09 (0.77)
Dry Forest Rx Burn ≤5	-1.40 (0.68)	-0.78 (0.67)	1.59 (0.84)
Dry Forest Burn 6–15	-0.39 (0.39)	-0.81 (0.39)	2.30 (0.49)
Mesic Forest Burn > 15	-0.38 (0.34)	-1.68 (0.37)	-0.66 (0.46)
Mesic Forest Burn ≤5	-1.25 (0.54)	-0.44 (0.55)	-0.48 (0.68)
Mesic Forest Burn 6–15	0.30 (0.44)	-1.18 (0.54)	-0.34 (0.62)
Grass/Open Woodland	0.65 (0.30)	-0.78 (0.30)	-0.92 (0.37)
Montane Riparian	-0.58 (0.38)	-1.48 (0.39)	-1.29 (0.47)
Valley Bottom Riparian	-1.29 (0.69)	-1.46 (0.73)	-2.12 (0.88)
Dry Agriculture	-1.39 (0.56)	-0.06 (0.56)	-2.05 (0.69)
Irrigated Agriculture	-1.66 (0.56)	-4.56 (0.58)	-1.70 (0.73)
Solar Radiation	0.53 (0.10)	0.33 (0.11)	0.56 (0.14)
Canopy Cover	-0.54 (0.12)	-0.93 (0.12)	0.66 (0.15)
Slope	0.45 (0.11)	-0.19 (0.12)	0.30 (0.13)
Elevation	-	-0.77 (0.18)	-0.64 (0.21)
Compound Topo. Index	-	-0.25 (0.11)	-
NDVI amplitude	-	0.44 (0.12)	-0.27 (0.15)
Spring Precipitation	-	0.27 (0.13)	-

Boldface values denote 95 per cent confidence intervals not containing 0. Effects of vegetation cover classes are in relation to the reference (intercept) cover class Dry Forest Burned >15 years prior.

winter, ranges. Together with other studies (Cook *et al.*, 2013, 2016; Proffitt *et al.*, 2016), our results suggest that fire-related variability in forage quality has the potential to alter the nutritional resources available for ungulates, and potentially ungulate body condition and demography.

We found that prescribed fires within our study area did not mimic the effect of natural wildfires. In dry forests recently burned by prescribed fire, summer herbaceous forage abundance was lower than in dry forests recently burned by wildfire. Winter herbaceous forage abundance was greater for this same comparison; however, larger uncertainty existed in the estimates. Both summer and winter shrub forage abundance were greater in areas burned by prescribed fire as compared with wildfire; however, shrub forage species had relatively low importance in the diets of elk. Our results are similar to Long *et al.* (2008), who found no difference in herbaceous forage quality, lower herbaceous forage cover, and higher shrub forage cover in coniferous forest stands thinned and burned by prescribed fire as compared with untreated stands.

Our results suggest that dry forests burned >15 years ago likely provide better summer and winter forage opportunities than areas recently treated with prescribed burns. The observed difference in effect of prescribed fire and wildfire may be due to the restriction of prescribed burns to specific times of year, reduced severity of prescribed fire, or other factors purposefully managed to prevent unintentional conflagrations causing collateral damage to adjacent forests, human developments, and

private lands (Ryan *et al.*, 2013). Land managers in the western United States should consider that while prescribed burns may be valuable for other purposes (e.g. reducing excessive fuels, returning forests to a semblance of historical ecological conditions; Arno *et al.*, 2000; Ryan *et al.*, 2013) and may enhance nutritional resources in aspen forests (Canon *et al.*, 1987), wildfires may be more effective for improving summer and winter nutritional resources in coniferous forests. Our study did not evaluate effects of prescribed fire on nutritional resources in grassland, shrubland or open woodland communities, but nutritional resources may or may not be enhanced and selected for by elk in these areas (Jourdonnais and Bedunah, 1990; Peck and Peek, 1991; Vore *et al.*, 2007; Sittler *et al.*, 2015).

Although many studies evaluate the effects of prescribed fire on ungulate nutritional resources in a variety of vegetation communities (Hobbs and Spowart, 1984; Canon *et al.*, 1987; Peck and Peek, 1991; Tracy and McNaughton, 1997; Sachro *et al.*, 2005; Van Dyke and Darragh, 2006, 2007; Long *et al.*, 2008), very few focus specifically on wildfire effects in coniferous forests (Hebblewhite *et al.*, 2009), and none have been conducted at a landscape scale for both summer and winter. Our study provides evidence for differing seasonal effects of wildfire on elk nutritional resources, with generally enhanced summer and diminished winter nutritional resources, but similar to Proffitt *et al.* (2016) the effect varied depending on forest type and fire history. In dry forests, we found an inverse relationship between summer forage quality and abundance (Hebblewhite *et al.*, 2009) within each fire history stage, with recently burned areas exhibiting higher summer forage quality and lower summer forage abundance relative to later fire histories. In contrast, recently burned mesic forests exhibited both higher summer forage quality and higher herbaceous forage abundance relative to later fire histories. The different response of dry and mesic forests may result from differences in light and the availability of soil nutrients. In mesic forests, the dominant environmental factor limiting vegetation is often light, whereas in dry forests, water and nitrogen are most constraining to vegetation (Krueger, 1981; Christy, 1986; Riegal *et al.*, 1991). Wildfires in mesic forests likely increase vegetation growth due to greater light availability from loss of forest canopy. After wildfires in dry forests, vegetation growth is likely still constrained by lack of sufficient water, but the availability of soil nitrogen likely increases resulting in greater plant growth (Gundale *et al.*, 2005).

In general, we found that dry forests had better summer nutritional resources than mesic forests across the same relative fire history, with two potential exceptions. Mesic forests were predicted to have higher summer herbaceous forage abundance in recently burned areas, and higher summer shrub forage abundance in areas burned >15 years ago, compared with dry forests in the same fire history stage. However, because we found shrubs comprised a relatively low proportion of elk diet during summer, areas of higher shrub abundance may not provide appreciably better nutrition for elk than other areas.

Wildfire in dry forests demonstrated a different effect on winter nutritional resources, with areas burned >15 years ago providing the highest and recently burned areas providing the lowest abundance of winter herbaceous forage. Caution should be exercised in the interpretation of our winter results, however. The plant species present in winter diets may be due to elk

Table 4 Area burned by fire (wildfire and prescribed), area of excellent, good, marginal and poor nutritional value classes, and mean herbaceous and shrub forage abundance predicted per decade from 1900–2015 within the North Sapphire, East Fork and West Fork elk population summer ranges in the Bitterroot Valley of west-central Montana, USA.

Decade	Area (km ²) Burned	Area (km ²) Excellent	Area (km ²) Good	Area (km ²) Marginal	Area (km ²) Poor	Abund. (kg/ha) Herb	Abund. (kg/ha) Shrub
N. Sapphire							
1900	35.4	158.2	349.8	216.1	50.1	171.7	199.5
1910	20.1	164.7	355.0	196.0	58.5	170.9	143.8
1920	71.4	158.4	346.5	214.5	54.7	174.1	321.9
1930	0.3	157.4	350.4	205.2	61.2	171.3	184.8
1940	38.2	171.2	350.7	193.7	58.6	171.0	156.2
1950	4.0	157.9	348.1	207.9	60.3	172.2	199.1
1960	3.0	158.9	351.6	202.1	61.6	170.6	161.9
1970	9.1	163.0	350.1	199.5	61.5	170.3	150.2
1980	10.4	159.7	348.5	204.9	61.1	171.2	182.9
1990	0.0	159.0	351.7	201.8	61.7	170.4	154.0
2000	23.3	166.5	356.9	191.6	59.1	171.3	148.1
2010	102.1	154.2	341.8	229.7	48.4	176.7	236.3
2015	0.8	150.5	343.8	231.6	48.3	177.3	243.0
Mean	24.5	160.0	349.6	207.3	57.3	172.2	190.9
East Fork							
1900	165.1	94.6	692.8	621.4	316.2	139.9	347.0
1910	24.8	105.1	712.9	563.1	343.8	136.1	198.4
1920	13.1	104.5	705.2	568.9	346.3	136.2	217.5
1930	1.2	99.9	704.8	567.9	352.3	135.8	218.2
1940	7.7	101.4	706.7	565.0	351.8	135.7	201.0
1950	1.0	100.5	707.3	564.6	352.5	135.6	209.0
1960	13.8	102.2	712.0	560.1	350.6	135.6	197.8
1970	64.0	99.5	709.3	595.3	320.8	136.5	226.5
1980	0.5	100.9	707.7	563.8	352.5	135.5	198.6
1990	19.6	101.4	716.1	566.7	340.7	136.4	196.6
2000	742.1	346.9	722.4	396.8	258.8	148.9	179.2
2010	119.1	67.1	694.0	716.8	247.0	154.9	390.8
2015	0.3	36.1	663.2	778.5	247.0	155.8	458.4
Mean	90.2	112.3	704.2	586.8	321.6	140.2	249.2
West Fork							
1900	89.1	38.8	192.3	317.3	96.1	112.1	609.0
1910	42.9	45.7	213.2	275.5	110.1	107.5	274.1
1920	8.8	43.5	200.7	291.1	109.1	107.8	410.4
1930	4.2	42.8	199.5	279.4	122.7	106.3	335.1
1940	2.1	42.6	201.2	277.3	123.3	105.5	305.6
1950	0.0	42.2	201.4	277.0	123.9	105.4	300.7
1960	0.0	42.3	201.6	276.5	124.0	105.3	295.2
1970	0.5	42.3	201.6	276.6	123.9	105.3	295.3
1980	3.3	43.4	201.2	275.9	124.0	105.3	294.9
1990	3.8	44.0	201.9	275.1	123.4	106.7	304.4
2000	161.9	81.1	208.8	244.2	110.4	108.8	324.0
2010	56.6	48.3	183.3	306.9	106.0	119.0	447.2
2015	69.6	39.0	184.0	336.4	85.1	123.8	509.4
Mean	34.7	45.9	199.3	285.3	114.0	109.1	361.9

primarily selecting from dry forests burned >15 years ago due to the greater availability of this forest type relative to others on winter range in the North Sapphire and West Fork. Dry forests burned >15 years ago in winter ranges of these populations accounted for 75–99 per cent of the dry forest cover types.

During the past century, the predicted fire-related availability of elk nutritional resources varied across time and by population range (Table 4; Figures 5 and 6). These wildfire-induced changes in nutritional resources can be directly related to the historical large-scale changes in federal wildland fire policy across the

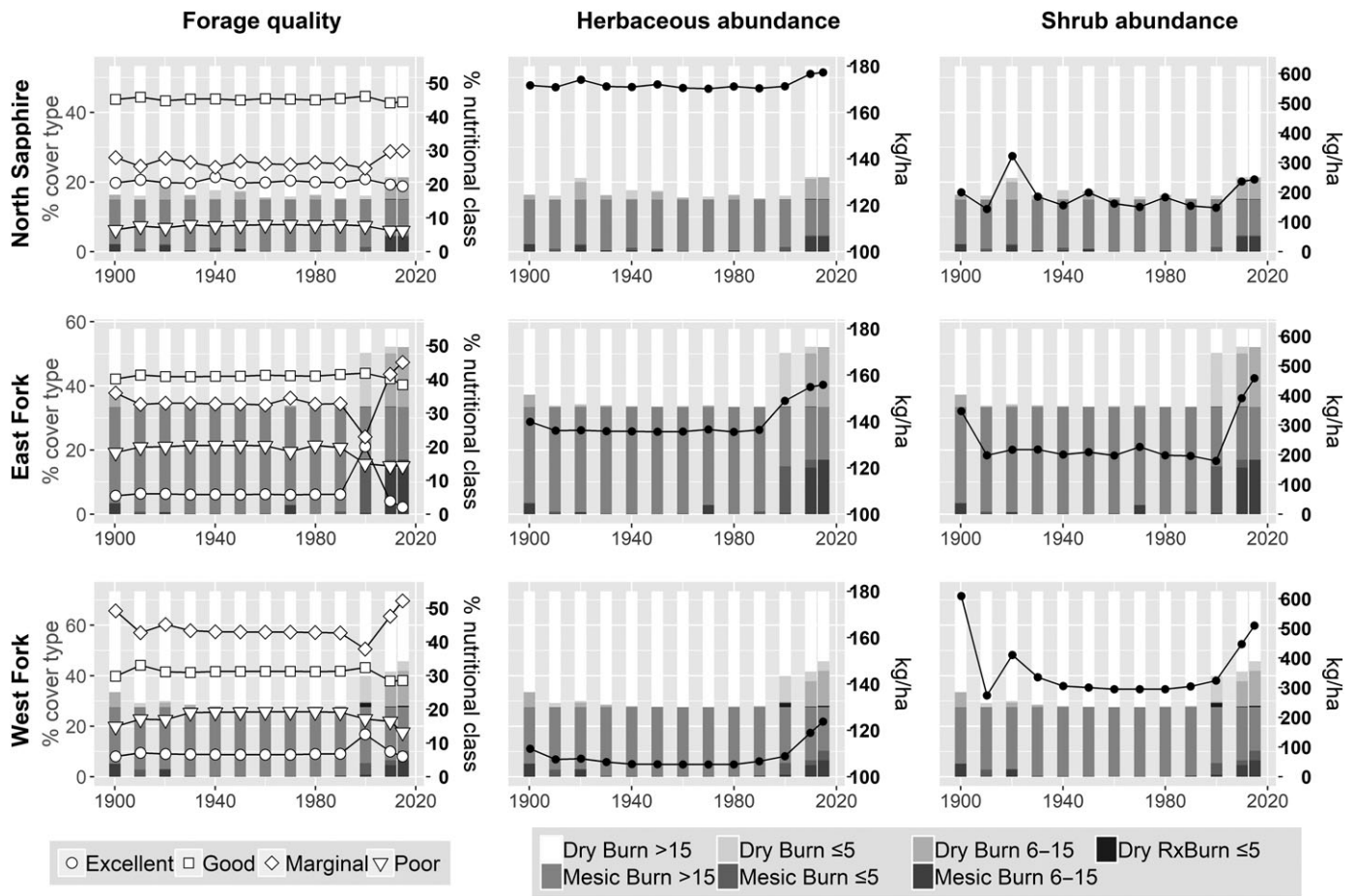


Figure 5 The percent area of dry and mesic forest cover types burned per decade (shaded bars) and predicted percent area of each nutritional value class (white symbols), herbaceous forage abundance (black dots), and shrub forage abundance (black dots) within the North Sapphire (775 km²), East Fork (1 728 km²) and West Fork (645 km²) elk population summer ranges in the Bitterroot Valley of west-central Montana, USA. Note different left-hand (% cover type) y-axis scales. Forest cover types included dry montane mixed conifer forests burned by wildfire ≤5 years prior (Dry Burn ≤5), 6–15 years prior (Dry Burn 6–15), and >15 years prior (Dry Burn >15), dry montane mixed conifer forests burned by prescribed fire ≤5 years prior (Dry RxBurn ≤5), mesic forest systems burned by wildfire ≤5 years prior (Mesic Burn ≤5), 6–15 years prior (Mesic Burn 6–15), and >15 years prior (Mesic Burn >15).

Rocky Mountains (Arno, 1976; Rollins et al., 2001). Prior to modern forestry management, the forests in this study region experienced relatively frequent fires of low to medium severity during 1735–1900, with lower elevation Douglas-fir/ponderosa pine forests (i.e. dry forests) experiencing fire approximately every 10 years and higher elevation subalpine fir and lodgepole pine forests (i.e. mesic forests) experiencing fire approximately every 20–30 years (Arno, 1976). Because of broad-scale wildfire suppression that began in the early 1900s, the frequency, size, and severity of wildfires decreased in this area (Arno, 1976; Rollins et al., 2001) likely resulting in later-successional forest stands with lower ungulate nutritional resources. Beginning around 1975, federal policy began shifting away from suppression strategies that had resulted in fuel accumulation and larger, more severe fires (Arno et al., 2000). The lasting consequences of the suppression era, combined with increasing use of wildfires to maintain or enhance natural resources, is reflected in our study populations with substantial increases in area burned from 1991 to 2015. Similar increases in wildfire during the past 30 years

have been broadly documented across the Great Plains (Donovan et al., 2017). During this period, all populations experienced predicted increases in herbaceous and shrub forage abundance on summer ranges. Winter ranges exhibited fewer fires and had a lower proportion of forest types. Wildfire occurring in the decade spanning 1991–2000 resulted in negative responses in the abundance of herbaceous forage and marginal positive responses in the abundance and quality of shrub forage. Our predictions of change in nutritional resources across the past century do not account for the influence of invasive plants, which have the potential to alter plant community composition and nutrition (Keeley, 2006; Vavra et al., 2007).

Although we found that landscape-scale effects of wildfire enhanced summer nutritional resources for elk, actual acquired nutrition may not be represented by our predictions, as nutrition is a function of the interactions between foraging behaviour and availability of nutritional resources (Hobbs and Spowart, 1984; Cook et al., 2016). Foraging behaviour and acquired nutrition may be dependent on a variety of factors, including nutritional

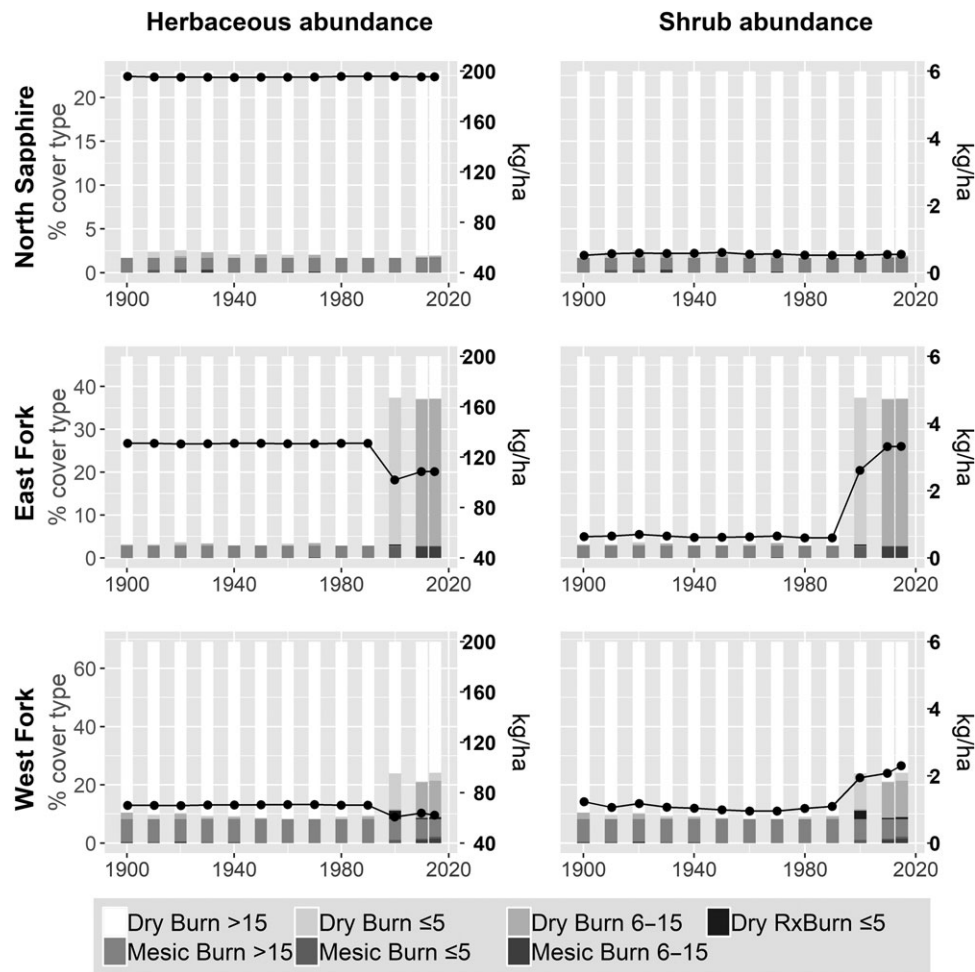


Figure 6 The percent area of dry and mesic forest cover types burned per decade (shaded bars) and predicted percent area of herbaceous forage abundance (black dots) and shrub forage abundance (black dots) within the North Sapphire (400 km²), East Fork (441 km²) and West Fork (289 km²) elk population winter ranges in the Bitterroot Valley of west-central Montana, USA. Note different left-hand (% cover type) y-axis scales. Forest cover types included dry montane mixed conifer forests burned by wildfire ≤ 5 years prior (Dry Burn ≤ 5), 6–15 years prior (Dry Burn 6–15), and >15 years prior (Dry Burn > 15), dry montane mixed conifer forests burned by prescribed fire ≤ 5 years prior (Dry RxBurn ≤ 5), mesic forest systems burned by wildfire ≤ 5 years prior (Mesic Burn ≤ 5), 6–15 years prior (Mesic Burn 6–15) and >15 years prior (Mesic Burn > 15).

resources, predation risk, security cover, availability of irrigated agricultural lands, proximity to roads, or other human disturbances (Rowland *et al.*, 2000; Frair *et al.*, 2007; Hebblewhite *et al.*, 2005, 2009; Middleton *et al.*, 2013). Nutritional resources may also vary more strongly than we predicted depending on the spatial and temporal distribution of other effects that land and wildlife managers should also consider (e.g. changes in vegetation cover types resulting from timber harvest, insect infestation or altered land use from human land conversions). Timber harvest has been an important forest management practice in the Bitterroot Valley and may have important effects on elk nutritional resources and habitat selection not captured in our study (Hebblewhite *et al.*, 2009; Cook *et al.*, 2016). Additionally, variability in weather and precipitation patterns during the past century may have also confounded our predictions.

Our study reveals that ascribing a single, static estimate of nutritional carrying capacity across regions or landscapes with

unpredictable environmental variance may not be justifiable (McLeod, 1997). Given the potential impact of wildfire (as reported here) and timber harvest (Long *et al.*, 2008; Hebblewhite *et al.*, 2009; Cook *et al.*, 2016) to influence the quantity and quality of forage for elk, land and wildlife managers should consider these factors when creating policy for managing populations and balancing population sizes with ecosystem processes. Additionally, management policy to strategically use wildfire for increasing forest heterogeneity and restoring ecosystem function may be enhanced by integrating the important effects of wildfire on seasonal ungulate nutritional resources.

Our findings that summer forage quality and herbaceous forage abundance were higher in irrigated agricultural lands as compared with native grasslands or any forested cover class also have important implications for elk management. Irrigated agricultural areas were predicted to have 22.6 times greater forage abundance and 2.1 times greater forage quality

than dry forests burned >15 years ago, 6.7 times greater forb abundance and 10.1 times greater forage quality than mesic forests burned >15 years ago, and 4 times greater forage quality and 10.7 times greater forb abundance than open woodland areas. This distribution of abundant, high-quality forage throughout the summer in irrigated agricultural areas likely has important effects on elk distributions and may contribute to increased resident elk populations that are not dependent on migratory strategies to access high-quality nutrition during the summer months (Wilmers and Levi, 2013). The presence of abundant, high-quality forage in privately owned irrigated agricultural areas may encourage consistent use of private rather than public lands, and, if hunter access to these private lands is restricted, may limit harvest as an effective tool for regulating elk populations within socially tolerable levels (Haggerty and Travis, 2006; Proffitt et al., 2013). With land use changes and increases in irrigated agriculture across the west (Schwabe et al., 2017), resident elk populations may become common leading to property damage and conflicts with hunters that use public lands. Additional work is needed to determine if habitat treatments strategically implemented on public land may be used as a management tool to increase the abundance of high-quality forage and maintain elk distributions that span both public and private lands.

Conclusion

We used a novel method to characterize landscape-scale variation in plant quality and availability and differences in the way wildfire and prescribed fire affected forage resources for elk within coniferous forests of the Rocky Mountains. Wildfires tended to increase the quality and abundance of nutritional resources, with the highest-quality forage occurring in forests burned within the past 5 years and the highest abundance generally occurring in forests burned 6–15 years ago. Prescribed fires in recently burned forests less strongly increased the quality and more strongly reduced the abundance of nutritional resources than wildfires in same-stage forests. Nutritional resources strongly affect survival and reproduction of ungulates. Resource professionals should consider how stochastic processes such as wildfire affect the availability and quality of forage for elk when setting goals for habitat and population management across dynamic landscapes.

Supplementary data

Supplementary data are available at *Forestry* online.

Acknowledgements

We thank A. Bernhisel, E. Brandell, M. Blankenship, M. DuPre, E. Flynn, J. Meyer-Morey, Z. Poetzsch, L. Sullivan for their work in field sampling. We also thank numerous private landowners for facilitating field sampling efforts. Remote sensing phenology data were provided by the United States Geological Survey EROS Centre.

Conflict of interest statement

None declared.

Funding

Sale of hunting and fishing licenses in Montana; Montana Fish, Wildlife and Parks Federal Aid in Wildlife Restoration grants; MPG Ranch; the United States Forest Service; the Bitterroot National Forest Resource Advisory Council; the United States Department of Agriculture McIntire Stennis program; and the National Aeronautics and Space Administration [Grant number NNX11AO47G].

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