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FROM FLAMES TO FORAGE: HOW WILDFIRE AFFECTS ELK BEHAVIOR

AND ABUNDANCE

by

Megan M. Whetzel

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2023

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ABSTRACT

From flames to forage: How wildfire affects elk behavior and abundance

by

Megan M. Whetzel, Master of Science

Utah State University, 2023

Major Professor: Dr. Larissa L. Yocom
Department: Wildland Resources

The western United States is currently witnessing rapidly shifting fire regimes, and wildfire activity is projected to continue to change into the future. Increases in annual area burned and increases in area burned at high severity represent threats for some species and opportunities for other species, including some plants and wildlife. My thesis focused on how elk (*Cervus elaphus nelsoni*) behavior and habitat selection are altered in the years following fire. I studied the complex interactions between wildlife habitat selection, herbivory, space-use, and post-fire vegetation regrowth in two ways. First, I examined changes in the time elk spent foraging within burned habitats of different severities and vegetation communities by using Hidden Markov Models (HMMs) to assign behavioral states (e.g., ‘foraging’ or ‘resting’) based on positional data from GPS collars and ran these results through a predictive modeling framework. As time since fire increased, elk probability of being in a foraging state was less dependent on severity, but was more influenced by vegetation type. Elk were more likely to be in a foraging state in aspen habitat when compared to juniper or conifer, and foraging probability in aspen peaked much later than conifer. In my second assessment, I investigated whether recent

fire severity moderates the influence of vegetation biomass alone in attracting elk to a site by placing 40 camera traps, stratified by fire severity (unburned, low, moderate, and high severity), in three wildfire burn scars that burned in 2018 in east-central Utah. I found that with increasing fire severity, herbaceous biomass was the largest indicator of elk abundance. Elk abundance decreased when there were high amounts of shrub burned at higher severities. My findings suggest that elk are an example of a species that will benefit from increasing fire activity, particularly in higher severity burned areas where herbaceous biomass or aspen regeneration is plentiful. In an era of climate change and changing fire regimes, elk preference for fire scars in the years post-fire could indicate elk population resilience even after larger and more frequent wildfire events.

(80 pages)

PUBLIC ABSTRACT

From flames to forage: How wildfire affects elk behavior and abundance

Megan M. Whetzel

The Rocky Mountain elk (*Cervus elaphus nelsoni*) is an ecologically and culturally important wildlife species in the Intermountain West, but it is facing habitat changes caused by increasing fire activity. Wildfire frequency is projected to continue to change into the future, yet increases in annual area burned and increases in area burned at high severity may actually represent opportunities for some species. Large herbivores like elk may benefit from increased access to regenerating areas where forage abundance and quality are often elevated. Therefore, effective management of wildlife populations may depend on quantifying how large ungulates, like elk, alter their behavior in the context of rapidly shifting fire regimes. In order to evaluate elk foraging activity in previously burned areas, my research examined differences in severity and habitat types. I used two sampling methods to understand elk behavior and habitat selection post-fire. First, I ran a Hidden Markov Model (HMM) on GPS collar data to assign one of three behavioral states ('resting', 'foraging', or 'commuting') to each of the approximately 730,000 elk positions located in a previously burned fire perimeter. I statistically tested whether the probability of an elk position being assigned a 'foraging' state depended on fire severity and time since fire, while controlling for other potential behavioral drivers (remote-sensed vegetation type, cover, and productivity). I then used camera data from 40 camera traps, stratified by fire severity (unburned, low, moderate, and high severity), to monitor elk use of burned areas. Results suggest that elk probability of foraging in burned areas

peaks 3-4 years post-fire in conifers, but peaks between 7-9 years in aspen. Also, elk have higher probabilities of being in a foraging state in areas where aspen is burned at high severity. From camera data, I found that the post-fire abundance of herbaceous biomass is the strongest driver of elk abundance, and abundance is highest at higher burn severity. Combined, this research provides information on wildfire's influence on elk behavior and abundance and can help inform management decisions for elk on increasing fiery landscapes in the western United States.

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Megan M. Whetzel

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CHAPTER 1

INTRODUCTION

For about a hundred years, from the late nineteenth to the late twentieth century, land management practices and fire suppression efforts reduced fire frequency across the West (Abatzoglou & Williams, 2016). A reduction in burn frequency led to a buildup of fuels in ecosystems that had historically burned regularly and a loss of heterogeneity in ecosystems that burned infrequently (Graham et al., 2010). In recent years, fire activity has been increasing in much of the western United States (Hagmann et al., 2021).

Although the proportion of wildfires burned at high severity has not increased significantly at the scale of the western US, more area is burning at high severity in recent years due to the overall increase in area burned (Parks & Abatzoglou, 2020). In some regions, such as the U.S. Southwest, wildfires are burning at higher average severity than what was typical within the historical fire regimes of the ecosystem (Haffey et al., 2018, Singleton et al., 2019). Non-native cheatgrass (*Bromus tectorum*) invasion in sagebrush-steppe ecosystems of the Great Basin has caused more frequent fires than was seen in historical regimes (Balch et al., 2013). The state of Utah experienced the same century of fire exclusion as the rest of the West, causing changes in species composition and fuel loads. While Utah has not experienced as many negative effects as other states in the West, wildfire activity is projected to increase in the future (Jakus et al., 2017). We are thus witnessing a rapidly shifting fire regime across the western U.S.

In addition, climate change effects may alter post-fire vegetation dynamics. Warming temperatures in the Rocky Mountains are decreasing seedling recruitment post-

fire, which could indicate decreased resilience of forests to fire (Stevens-Rumann et al., 2018). By modifying fire frequency and severity, climate change will indirectly influence plant assemblages by shifting community composition towards predominantly early seral and fire adapted species (Coop et al., 2020). Therefore, indirect climate change effects through changing fire regimes or altered post-fire conditions may have vast impacts on ecosystems West-wide.

These changes in wildfire frequency and size will increasingly impact wildlife across the western United States. Fires affect animals by altering habitat structure and function and disrupting normal foraging patterns. Whether or not wildlife use a patch post-fire depends on fire severity, re-colonization dynamics, and community structure (Lyon et al., 2000). Previous studies on pronghorn (*Antilocapra americana*), elk (*Cervus* spp.), deer (*Odocoileus* spp.), and bison (*Bison bison*) have found that burned areas are generally beneficial to ungulate populations, and ungulates have increased population densities post-fire because of enhanced forage options (Lyon et al., 2000).

Fire disturbance is an important driver of herbivore movement and habitat selection patterns because it influences the spatiotemporal distribution of forage quantity and quality. Wildlife select habitat based on several factors, including perceived risks, available resources, and abiotic conditions (Matthiopoulos et al., 2015). Vegetation communities contain a mix of both highly nutritious species and those that provide little to no nutritional value to herbivores. Wildlife prefer high-quality forage plants to maximize protein and energy uptake (Cook et al., 2016, Tollefson et al., 2010). Post-fire landscapes can attract wildlife as fire changes the structural makeup of ecosystems by promoting the regrowth of higher quality or more abundant vegetative species (Eby et al.,

2014, Raynor et al., 2015). In turn, herbivores impact plant populations. For example, elk preferentially consume young aspen as it is a nutritious option for browsing herbivores, but elk can consequently reduce post-fire aspen regeneration through intense herbivory (Endress et al., 2012; Maxwell et al., 2019). Since fire disturbance can alter ecosystem structure and generally improve the quality (Eby et al., 2014, Greene et al., 2012) and quantity (Allred et al., 2011) of vegetation communities, wildlife, and particularly large ungulates like the Rocky Mountain elk (*Cervus elaphus nelsoni*), may benefit by actively selecting for burned areas. As many western ecosystems experience growing fire events, it is of increasing importance to know whether fire legacies and their impact on vegetation communities can explain large ungulate behavior, or if there are other environmental drivers at play.

In addition, much attention has been given to research on animal space-use and movement both in and out of the context of wildfires. Wildlife surveys are conducted one of two ways; Lagrangian, or sampling using telemetry through Global Positioning System (GPS) collars or Eulerian, where sampling occurs over a fixed space and time. While both methodologies have benefits in terms of what behavior and space-use they can uncover, research involving both perspectives is not as prevalent (but see Bassing et al., 2022; Phillips et al., 2019). By focusing on both individual- and place-based perspectives in this study, results can be projected across a larger spatial scale and can provide information on elk space-use in western fire-prone ecosystems.

The goal of my research was to evaluate whether phenological drivers, like the Normalized Difference Vegetation Index (NDVI) can explain elk behavior and density or if fire history can provide additional understanding of their space-use. This research also

provided me with an opportunity to use two different methodologies to investigate my hypotheses. In Chapter 1, I used Hidden Markov Models (HMMs), an individual-based method, to analyze the spatial context of elk foraging behavior before and after wildfire events across the state of Utah. Using HMMs to study elk behavior has not been widely implemented and I expected elk probability of foraging to strongly correlate with vegetation regrowth post-fire. In Chapter 2, I investigated how camera trap data, a place-based method, can provide metrics of wildlife abundance in post-fire areas at a smaller spatial scale. The results from these analyses will provide answers to wildlife and land managers on how to manage elk populations in an increasing fiery world.

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CHAPTER 2

DOES FIRE HISTORY DRIVE FORAGING BY A LARGE UNGULATE?

Abstract

The western United States is currently witnessing increasing fire activity, and wildfire frequency is projected to continue to change into the future. Increases in both annual area burned and in area burned at high severity may actually represent opportunities for some species. Large herbivores in particular may benefit from increased access to regenerating areas where forage abundance and quality are often elevated. Effective management of wildlife populations may therefore depend on quantifying how large ungulates, like elk (*Cervus elaphus nelsoni*), will alter their behavior in the context of rapidly shifting fire regimes. In order to evaluate the hypothesis that elk engage more in foraging activity in previously burned areas, I analyzed GPS data from 449 collared elk across the state of Utah by using a Hidden Markov Model (HMM) to assign one of three behavioral states ('resting', 'foraging', or 'commuting') to each elk position.

I then ran a generalized additive model (GAM) to predict elk foraging behavior as a function of vegetation classes and severity categories. I found that, as time since fire increased, elk probability of being in a foraging state was less dependent on severity, but was more influenced by vegetation type. Post-fire, elk were more likely to be in a foraging state in aspen habitat when compared to juniper or conifer, and foraging probability in aspen peaked much later than conifer. This study provided evidence that the timing and intensity of peaks in post-fire foraging behavior are consistent with what we know about post-fire forage availability, and that post-fire increases in vegetation

quality and quantity may indicate that burned ecosystems can support larger populations of elk in Utah. Further research should investigate effects of prescribed versus wildfire effects on habitats as these processes may not achieve the same effects.

Introduction

Fire activity has been increasing in much of the western United States in recent years (Hagmann et al., 2021), and more area is burning at high severity due to the overall increase in area burned (Parks & Abatzoglou, 2020). Increasing fire events can impact both plants and animals across the landscape (Lyon et al., 2000). Most large herbivorous species in western North America live in areas that historically burned regularly, yet a century of fire suppression altered natural fire regimes and led to widespread changes to habitat (Keane et al., 2002). The current increases in fire frequency may alter the interactions between herbivores and the landscape they live in (Jager et al., 2021).

Forage is critical to herbivores, and many of their behaviors are influenced by the need to obtain sufficient quantity and quality of forage. Fire effects on forage quality and quantity are generally positive (Snobl et al., 2022), but change over time (Proffitt et al., 2019). Post-fire vegetation community structure, species composition, and productivity are affected by many factors, including pre-fire vegetation, fire severity, and time since fire (Halpern, 1988, Falk et al., 2022). In post-fire landscapes, successional changes in vegetation structure and composition are highly influenced by fire severity (Stevens-Rumann & Morgan, 2019). Changing conditions impact vegetation regrowth, and consequently, available forage for wildlife. Some plant species will have insufficient seed dispersal or seedling survival rates to regenerate in high-severity patches. In locations

without tree regeneration, early successional species - including some forbs, grasses, and shrubs - may dominate the landscape. No matter what initially regrows at a site after fire, a post-fire landscape is rapidly shifting as successional processes play out.

The presence of palatable forage species influences wildlife movement and resource selection, and can help explain how animals use space. Burn severity and time since fire are thought to be important post-fire drivers of foraging in herbivores (Sachro et al., 2005, Snobl et al., 2022). High-severity patches may have little value for large ungulates immediately following a fire, but animals may use other unburned or lower severity areas for foraging or protection while forage regrows (Calhoun et al. 2022, Preprint). Many animals that immediately fled a burned area may return soon after fire because of familiarity with the area (Kreling et al., 2021, Morrison et al., 2021) and because forage may have improved. When returning to burned areas, grazing and browsing herbivores may put increased pressure on post-fire vegetation communities as plants regrow. For example, after prescribed fires, intense browsing by animals changed plant growth and development in treated conifer stands (Endress et al., 2012). This browsing can thus cause shifts in available vegetative species in ecosystems. Assuming that large herbivores, like elk (*Cervus elaphus nelsoni*), choose when and where they are actively foraging to maximize their fitness, their behavior could be an indicator of forage conditions, and hence of the dynamic ecological consequences of fire.

Elk are an ecologically, culturally, and economically important large ungulate species and have long been managed as a game animal across the West. In the state of Utah, elk use habitats ranging from sagebrush to high elevation forests and migrate across large elevation gradients to maintain access to forage throughout the year. Because of

their high mobility, elk likely receive little direct negative impacts from wildfire (such as injury or mortality). Indirect effects of fire, through changes to forage quantity and quality, have generally been found to be positive for elk (Biggs et al., 2010, Canon et al., 1987, Long et al., 2008). In particular, elk have a heavily-studied, complex relationship with aspen - a keystone species in many western ecosystems - and wildfire (Hessl, 2002, Hessl & Graumlich, 2002, White et al., 1998). Aspen regenerate after disturbance events like fire and re-sprout prolifically through asexual suckers. While lengthened time periods between fires and herbivory pressure have reduced aspen populations (Loope & Gruel, 1973, Rehfeldt et al., 2009), the increase in wildfire activity on the landscape in the Intermountain West may provide favorable conditions for aspen, and therefore for elk. Other vegetation communities may also provide higher forage quality and quantity for elk post-fire (e.g., sagebrush; Van Dyke & Darragh, 2007). Elk foraging behavior after fire may indicate the potential for fire-related demographic and distributional effects for both the elk and the vegetation communities where they forage. This is especially important in the context of climate change and a legacy of fire suppression, both of which are driving an increase in the frequency, intensity, and extent of wildfires across many large herbivore ranges.

Animal movements may reveal behavior, and these behaviors change through time. To characterize elk behavior, I fit Hidden Markov Models (HMMs) to elk movement data (Langrock et al., 2012). I used the HMMs to segment elk movement into three distinct behavioral states, which I classified as resting, foraging, and commuting. This study represents novel research on understanding behavior and spatially dynamic wildfire-related variables in Rocky Mountain elk.

Post-fire vegetation community structure, species composition, and productivity (and therefore post-fire forage quantity and quality) are influenced by fire severity and time since fire. I hypothesized that quantity of forage for elk (abundance of forbs, grasses, and browse species like young aspen), as well as forage quality, are minimal immediately after fire, but peak in the early years post-fire as early successional species colonize and re-sprouting species such as aspen produce clonal suckers. I predicted that elk are less likely to be in a foraging state within a fire perimeter immediately after a fire but the likelihood of being in a foraging state will increase two to five years after a fire because of forage regeneration. I also predicted that higher fire severity would cause a delayed, but more pronounced, peak in foraging activity compared to lower severity burned areas. Lastly, I predicted that foraging in aspen-rich habitats will be associated with earlier and more pronounced peaks, as this preferred forage species is expected to become abundant shortly after a fire, but grow out of browsing range, or be suppressed by less palatable competitors, as time since fire increases. By using a study species like elk to determine fire impacts on space-use behavior, I aimed to quantify how large, browsing ungulates may fare in an increasingly fiery world.

Methods

Hidden Markov Models (HMMs) have been extensively applied in movement ecology to assign behavioral states (e.g., ‘foraging’ or ‘resting’) based on available positional data (Franke et al., 2004, Patterson et al., 2009, Langrock et al., 2012). HMMs are prevalent in ecological applications because they can be used to analyze telemetry data, as long as data (i.e., animal locations) are collected at standard time intervals and without error (McClintock & Michelot, 2018). HMMs are state-space models made up of two components, a known or observed data series, and an unknown (latent) sequence of discrete behavioral states (Langrock et al., 2012). By assuming that the true state at any given time is a function of only the previous state and possibly other independent drivers (typically environmental or temporal), and given the (user-defined) number of possible states, HMMs estimate the probability that the animal was in a given behavioral state at each location. HMMs thus allow us to use GPS tracking data to examine the relationship between the probability of foraging and fire.

Study Area

The study area encompassed the entire state of Utah, USA. Elk are present in multiple ecoregions across the state, including sagebrush (*Artemisia* spp.) steppe shrublands, pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodlands in the Great Basin and Colorado Plateau, and Rocky Mountain gambel oak (*Quercus gambelii*) and bigtooth maple (*Acer grandidentatum*) woodlands. They also use aspen forest, mixed-conifer forests, sub-alpine spruce-fir forests and montane riparian systems in the Wasatch and Uinta ranges of the Rocky Mountains. Elk habitat in Utah includes elevations ranging

from 1,500 to 3,100 meters above sea level.

Movement Data

Rocky Mountain elk GPS data were made available through the Utah Division of Wildlife Resources (UDWR) database. Elk locations were recorded every two hours, year-round until either elk mortality or collar failure. Individual elk used in this analysis were tracked for anywhere between a month to four years. GPS data were cleaned according to protocol set forth in the ‘*amt*’ package (Signer et al., 2019) in Program R (R Core Team, 2022). The data were then separated into bursts, consisting of a sequence of consecutive 2-hour GPS positions. A burst ended when a location was missing (time gap of more than 2 hours) and a new burst started when the next string of consecutive locations began.

HMM Analysis

I fit a single Hidden Markov Model to the entire dataset with three behavioral states. I labeled these as: resting, foraging, and commuting and used step lengths and turning angles as data streams. I used a Gamma distribution for step lengths and a von Mises distribution for turning angles. The fitting procedure for HMMs requires reasonable initial parameters for the three behavioral states. I visually explored the distribution of step lengths in the data to determine reasonable initial parameter values for use in the HMM. The first state, or ‘resting’, was set with gamma with mean = 10 m, standard deviation = 20 m, and a zero-mass parameter = 0.5 (indicating I expected a relatively high probability the elk would not move); and von Mises with mean = 0 rad and concentration = 0.01. The second state, or ‘foraging’, was set with gamma with mean = 300 m, standard deviation = 1,000 m, and zero mass parameter = 0; and von Mises with

mean = 0 rad and concentration = 0.25. The third state, or 'commuting', was set with gamma with mean = 1,000 m, standard deviation = 1,000 m, and zero mass parameter = 0; and von Mises with mean = 0 rad and concentration = 0.9 (corresponding to positive directional persistence). I then fit the model using the '*momentuHMM*' (McClintock & Michelot, 2018) package in program R. I then used the Viterbi algorithm to assign each point a behavioral state based on the highest probability of each of the three states.

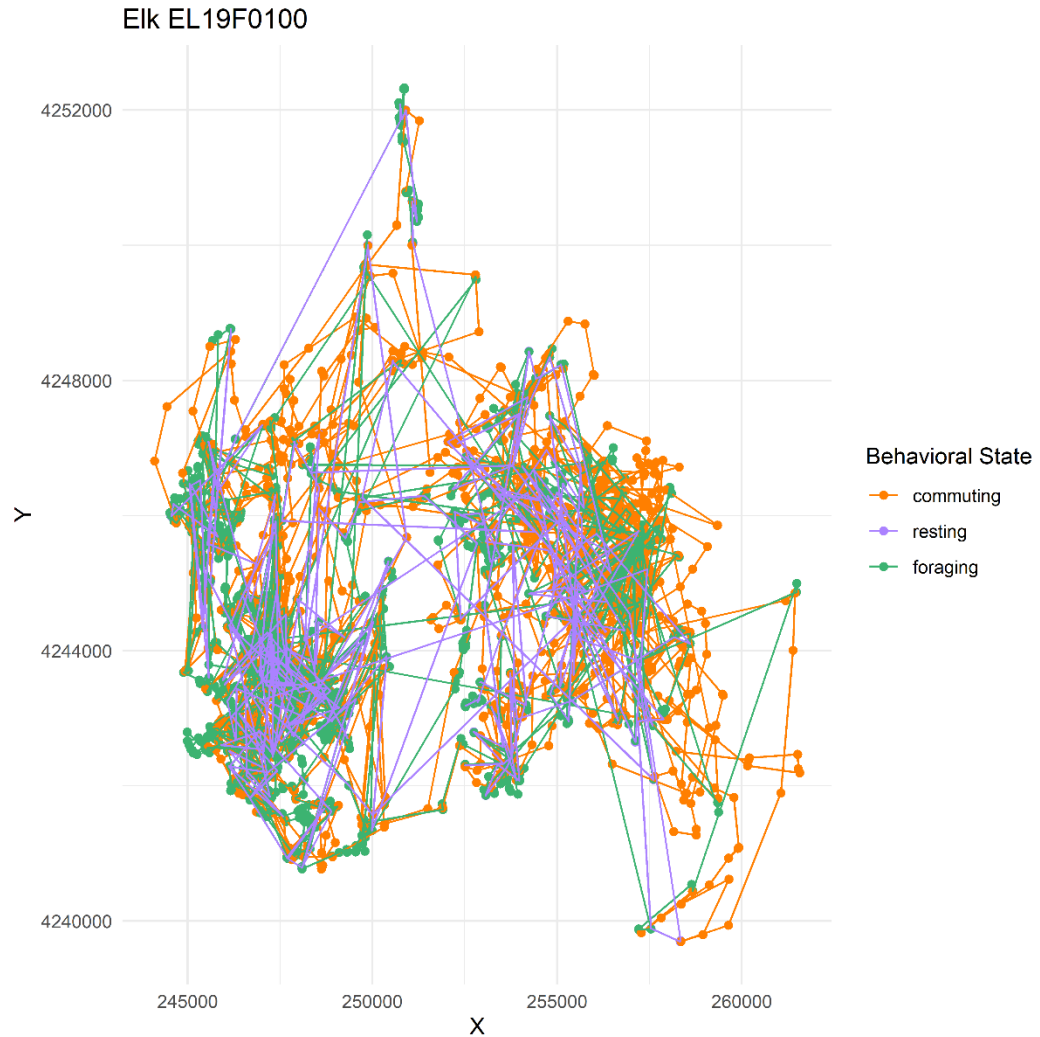


Figure 1: Example of movement tracks for one elk (female; collared in 2019) taken from the HMM output – note every location (in UTM Zone 12) and track are color-coded to reflect the highest probability of being in one of three behavioral states assigned by the Viterbi algorithm.

Environmental and Temporal Predictors

I extracted multiple environmental and temporal covariates, characterizing each elk location at the time the elk was there – to serve as potential drivers of elk behavior. Time-only covariates included time to dawn and time to dusk (in hours), and the Julian day. Space-only covariates were categorizations of ‘environmental site potential’ (ESP; Landfire, 2016), which uses the biophysical environment to predict vegetation that could

be supported at each pixel. I used this metric because existing vegetation is likely not stable over time and the environmental site potential is more indicative of what was there pre-disturbance and what we can expect to be there post-disturbance. I grouped the numerous ESP categories based on dominant vegetation types that are related to elk foraging ecology in Utah. These included 3 ESP vegetation classes (hereafter “vegetation classes”) – “aspen”, “conifer”, and “juniper”. As with other large herbivores, elk space-use is often driven by the phenological state of forage, where greening-up forage is highly nutritious since it is richer in simple carbohydrates and protein, and has fewer structural and defensive components (i.e., “forage maturation hypothesis”; Hebblewhite et al., 2008) I used Google Earth Engine (Gorelick et al., 2017) to attribute elk positions with spatio-temporally variable covariates (see Table 1). Finally, I also included a snow depth variable from the European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis (Hersbach et al., 2020) as I expected it to decrease the probability of foraging behavior. Snow restricts access to herbaceous forage and hence reduces foraging opportunities.

I downloaded historic fire perimeters (those greater than 1,000 acres) between the years 1985 and 2020 from the Monitoring Trends in Burn Severity (MTBS) database (<http://www.mtbs.gov>, Eidenshink et al., 2007). Fire severity was classified through the differenced Normalized Burn Ratio (dNBR), which is a measure of the ecological change on the landscape due to fire (Keeley, 2009). For each elk position, I extracted fire severity classes (unburned, low, moderate, and high), fire ID, and ignition date from MTBS. From this information, I calculated the time that had passed between the fire and the elk being

observed in the burned area in order to account for changes on the landscape that occur with increasing time post-fire.

I filtered elk points using both temporal and spatial characteristics. I discarded elk points in a fire perimeter within 60 days after the fire ignition, to eliminate the possibility that an elk was in a still-unburned area of the fire, since we did not have fire control dates. I also discarded elk points from elk that never entered a fire perimeter. Finally, I discarded points that were more than 1 kilometer from a fire perimeter. Points that were within 1 km of a fire perimeter were used as “unburned” points. Points that occurred within a fire perimeter before a fire started were also included in “unburned” points. The final dataset had 735,434 locations from 449 collared elk.

Table 1: Overview of covariates used in predictive modeling of HMM results. Sources and resolutions are displayed for each variable

Variable:	Data source:	Temporal resolution:	Spatial resolution:
Snow depth	ECMWF Reanalysis v5	Hourly	11 km
Vegetation class (Environmental Site Potential (ESP))	Landfire	N/A	30 m
Fire severity class (differenced Normalized Burn Ratio (dNBR))	Monitoring Trends in Burn Severity (MTBS)	N/A	30 m

Model Structure and Post-hoc Analysis

I quantified the relationship between the HMM-assigned behavioral states and environmental covariates, including fire history, using a mixed-effects beta-regression GAM (generalized additive model) using the “*mgcv*” package in R (Wood, 2017). My response variable was the HMM-based probability that an elk was foraging at a given

place and time. I wanted to control for factors that are known to influence elk foraging, including time of day and time of year. I used a circular spline for Julian day ('seasonality') and a two-dimensional spline for log-time-to-dusk and log-time-to-dawn ('diurnality'). I also included two categorical random effects: individual elk ID and fire ID. I was interested in the time since fire, vegetation class, and fire severity predictors because of potential relationships with elk foraging probability and these were included as parametric fixed effects. I took the natural logarithm of time since fire, a transformation which creates a high rate of change for small values and a low rate of change for large values. I then modeled $\log(\text{time since fire})$ with a linear and a quadratic term to allow probability of foraging to peak at an intermediate value. I included interactions between the $\log(\text{time since fire})$ terms and the vegetation class and burn severity to allow elk foraging to change differently among these categories. I also included snow depth and the scaled and centered foraging probability in the previous step (to account for temporal persistence of behavior).

Results

HMM Results

Overall, I found that elk had the highest frequency of being in a foraging state compared to the other two states (commuting and resting) (Table 2).

Table 2: Overview of counts and frequencies for each behavioral state assignment within the dataset

Behavioral State Assignment	Count	Frequency
commuting	219,113	0.298
foraging	439,699	0.599
resting	76,622	0.104

Model results

My model explained 40% of the observed variability in elk foraging behavior (Adj. $R^2 = 0.41$, deviance explained = 46.5%). In terms of effect size, the strongest fixed effects were the HMM-based probability that the animal was foraging in the previous step (positive effect; Fig. 2A), followed by the effect of time since fire in moderately burned conifer (Fig. 2B). Elk probability of foraging in unburned habitats was highest in the aspen group, followed by the conifer and juniper (Fig. 2A). Snow depth had a positive effect on elk foraging probability (Fig. 2A). Non-parametric effects (splines) were also important predictors, with the probability of foraging showing a distinct seasonal signal (a peak in early winter followed by a decline until spring, an increase until mid-summer, and then a slight decline during fall; Fig. 3A). There was also a distinct diurnal signal, with a peak in foraging probability during the night (between 23:00 and 02:00), with another peak starting around 15:00 (Fig. 3B).

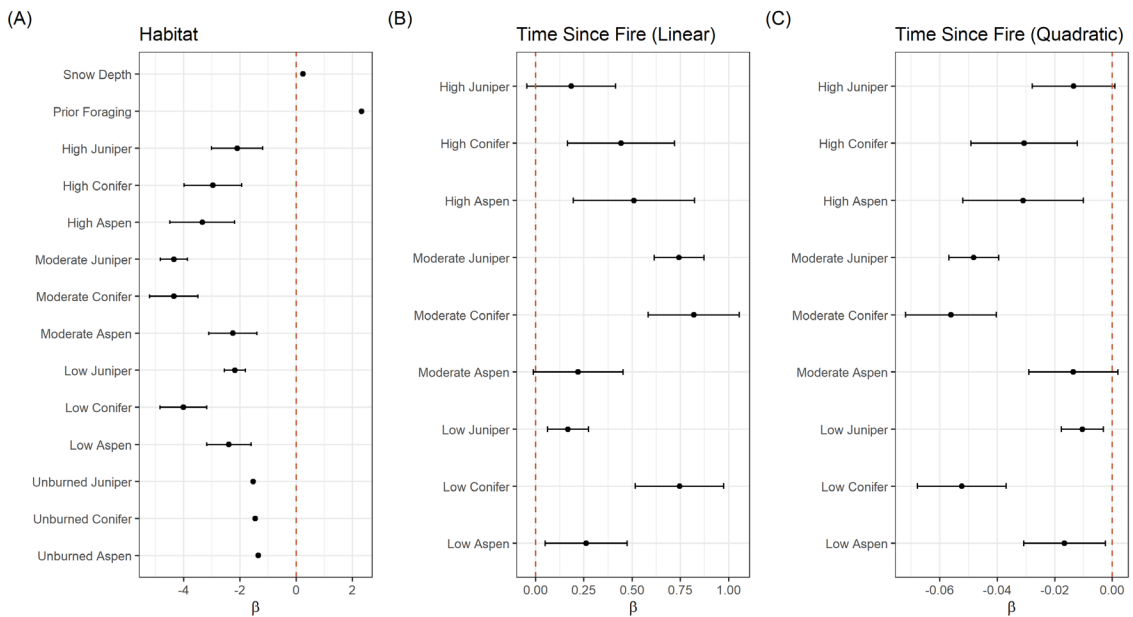


Figure 2: Fixed-effects parameter estimates, and 95% confidence intervals from the fitted generalized additive model for habitat factors (A), the linear term for time since fire (B), and the quadratic term for time since fire (C) note low, moderate, and high correspond to fire severity of each vegetation type.

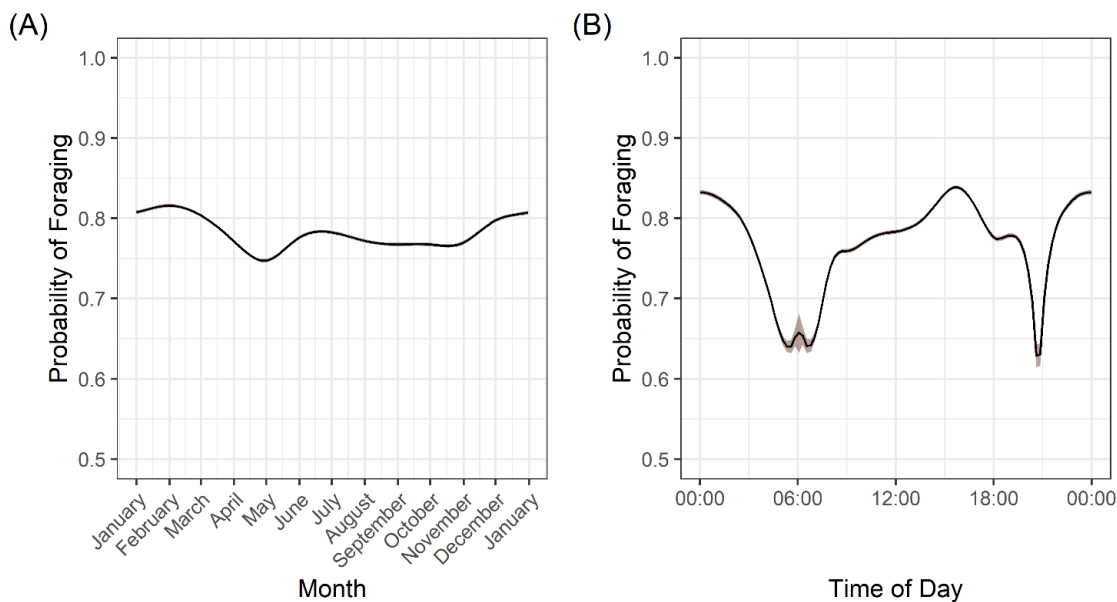


Figure 3: Non-parametric effects with 95% confidence intervals of seasonality (A) and diurnality (B) on the probability of an elk being in a foraging state.

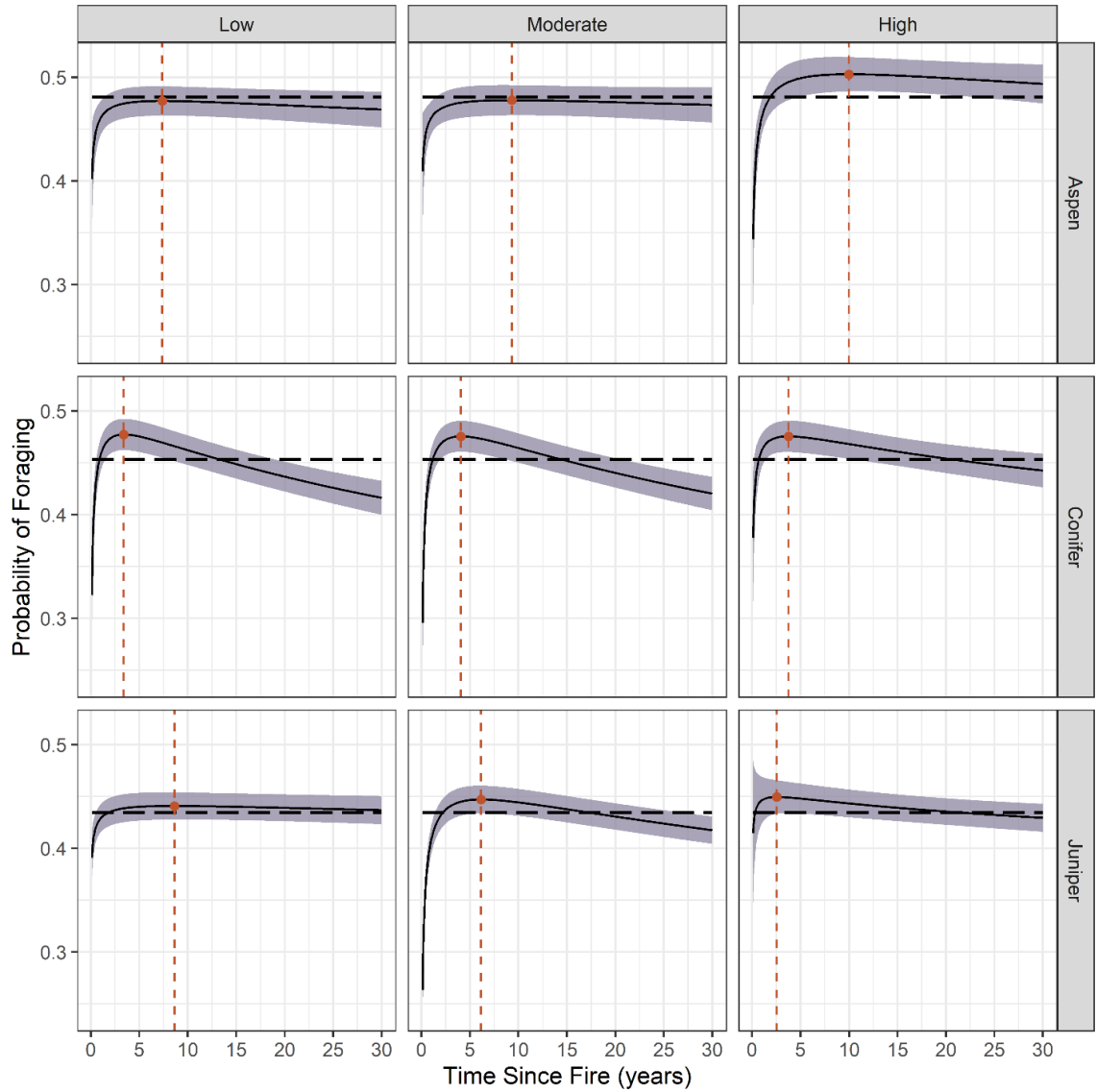


Figure 4: Model predictions of the probability of elk being in a foraging state as a function of time since fire and the categorized environmental site potential vegetation types with 95% confidence intervals where the black dashed line represents the predicted probability of elk foraging in the unburned corresponding vegetation type (i.e., in the buffer around fire perimeters) and the orange dashed line and point represents the year of peak foraging probability; all other covariates were held at their mean for these predictions.

Elk Foraging Probability in Burned Areas

Elk probability of foraging in the unburned vegetation type varied across all three vegetation classes (Fig. 4). In the juniper vegetation class, foraging probability was around 0.43 or 43% of the time. In unburned conifer, the foraging probability was slightly higher around 45%, and was the highest in unburned aspen (near 48%; Fig. 4). In an almost universal trend, elk foraging probability was significantly reduced immediately following a fire. However, elk probability of foraging increased rapidly in the first year after fire (note the positive effects of “Time Since Fire” parameters in Fig. 2B).

In most vegetation and severity class combinations, the probability of foraging increases to the unburned vegetation type in the early years post-fire and in some cases this effect is higher than the unburned vegetation class. This effect was significant in the high severity burned aspen and in all severity classes of conifer (Fig. 4). Also, aspen burned at high severity had the highest overall probability (~50%) of elk being in a foraging state across all severity and vegetation classes. In a general trend, the probability of foraging declines with increasing time since fire and likely eventually returns to a baseline level that is more representative of pre-burn conditions.

When declines in the probability of foraging occurred was different based on vegetation and severity class combinations. The timing on these peaks ranged from two years post-fire in high severity burned juniper to almost 10 years post-fire in high severity burned aspen (Fig. 4). In the aspen vegetation class, the peak in foraging probability occurred later as severity increased. In high severity burned aspen, the peak in foraging activity happened at 9.9 years post-fire. At low and moderate severity, burned aspen experienced peaks at 7.3- and 9.3-years post-fire respectively. When compared to the

other vegetation types, the probability of being in a foraging state in burned aspen remained relatively stable across all severity classes with only small declines. Elk probability of foraging in high severity burned aspen also never fell below the unburned aspen prediction.

In burned conifer, elk foraging probability peaked at the earliest time since fire when compared to aspen or juniper and the timing of the peaks is similar regardless of severity class. Low severity conifer peaked at 3.4 years, moderate peaked at 3.7 years, and high peaked at 3.7 years after fire (Fig. 4). At low and moderate burn severities, the conifer vegetation type experienced noticeable declines in elk foraging probability when compared to the aspen and juniper vegetation types.

In an opposite trend to aspen, the probability of foraging in high severity burned juniper peaked at 2.5 years post-fire – the earliest of all severity and vegetation classes. Moderate severity and low severity juniper peaked at 6.1 years and 8.6 years respectively, which was more like the peaks seen in the aspen class. Similar to low severity burned aspen, foraging probability in low severity burned juniper remained relatively stable across the thirty years after a fire. Elk foraging probability in moderate severity burned juniper declined below the unburned juniper close to 17 years post-fire. The probability of foraging in high severity burned juniper slowly declined after the initial peak and did not fall below the unburned juniper until ~22 years after fire.

Discussion

My results demonstrate the lasting effects that wildfires have on elk foraging behavior as well as how time since fire and burn severity affect this influence. By analyzing an extensive dataset of elk GPS locations using Hidden Markov Models, I was

able to link animal behavior to environmental factors including fire legacies. My results support my hypothesis that foraging likelihood would be low immediately after a fire but would peak in the early years post-fire, likely due to increases in early successional species and aspen producing suckers (Fig. 4). My results show that elk foraging probability was low in the immediate aftermath of a fire across all environmental site potential (ESP) classes (conifer, aspen, and juniper), but also that the timing and magnitude of the ensuing peaks in foraging probability were highly dependent on severity and vegetation class. My findings suggest that fire in aspen, conifer, or juniper dominated ecoregions does alter where and when elk are likely to forage after a burn and has implications for elk population dynamics as severity and vegetation type influence elk space-use and habitat selection.

Elk foraging probability differed slightly throughout the time of year and the time-of-day. Slight decrease in probability of foraging around the month of May likely correspond to elk being in other behavioral states, such as commuting or resting. Decreases in foraging at this time of year might correlate to increases in elk movement and they may thus be categorized as commuting, especially if they are following plant green-up and moving into higher elevations to access forage. The low point in foraging activity might also be representative of elk being in a resting state, particularly if May is an indicator of calving events. Peaks and troughs in foraging activity throughout the day match to expected changes in elk behavior throughout the day. The lows in the probability of foraging near 06:00 and 21:00 follow previous peaks in foraging probability and are likely representative of elk ruminating after hours of foraging.

In unburned vegetation classes, elk had the highest probability of foraging in

aspen, followed by conifer, and then juniper. It is well known that aspen and their associated vegetation communities have higher species diversity (Kuhn et al., 2011), regardless of burn history, and are selected for by elk (Bailey & Whitham, 2002, Hessler, 2002, Spitz et al., 2017), providing context for why high foraging probability is occurring even in unburned aspen. Also, lower probability of foraging in unburned conifer is consistent with the fact that apex conifer-dominated vegetation communities provide little to no forage for elk (Cook et al., 2016). Universally, there were decreases in the probability of foraging immediately after a fire in all vegetation and severity classes. Elk are likely not using areas that have little to no forage availability directly post-fire and so these decreases are representative of that pattern. I also posit that elk are likely foraging elsewhere immediately after higher severity fires such as in unburned areas which may have better vegetation.

While vegetation regrowth post-burn depends partly on time since fire (Fig.4; Bassett et al., 2017) and pre-fire vegetation (Fig. 4; Proffitt et al., 2019), severity is also a large contributor of post-fire variation in vegetation availability. Severity affects regeneration success of species (Parks et al., 2018) and influences successional shifts in vegetation communities (Stevens-Rumann & Morgan, 2019). I predicted that the post-fire peaks in foraging probability would be earlier and more pronounced in aspen stands, since aspen are expected to become abundant shortly after a fire but grow out of browsing range as time since fire increases. I did not find support for this prediction in my results. In every category of fire severity (low, moderate, and high) for the aspen vegetation class, the peak probability of an elk foraging was much later than in conifer (Fig.4). Aspen are a preferred forage option for elk and while aspen do tend to grow

quickly after fire, light availability in their canopy promotes other palatable forbs and grasses, especially as sucker production declines with increasing time after a burn (Bartos & Mueggler, 1981). This is an indication that even as aspen surpass browsing height, understory vegetation provides forage biomass for large ungulates.

In contrast to high severity burned aspen, I found that foraging probability in low or moderate severity burned aspen was never higher than unburned reference aspen. Wildfire disturbance generally has a positive impact on aspen and promotes prolific re-sprouting. In addition, an increase in forage availability associated with numerous regenerating plants post-fire likely explains the higher probabilities of foraging in all severities of burned aspen. I found partial support for my prediction that higher severity fires would cause a delayed peak in foraging activity. High severity burned aspen peaked the latest when compared to conifer and juniper burned at high severity. After high severity fires, increases in available light promotes growth and increases in defensive components (e.g., tannins) in aspen can make them less susceptible to ungulate herbivory (Wan et al., 2014a). Therefore, a potential explanation for why elk foraging probability in high severity burned aspen peaks later is that elk are eating less of the tannin-rich aspen suckers, but they will forage in the aspen stands years later when there is a productive understory of grasses and forbs.

Across all burn severities, foraging probability in conifer showed a sharp initial increase with time since fire followed by a sharp decline. Foraging probability peaked in year 3 for all severity classes after a burn. This result agrees in part with findings from Snobl et al. (2022), who found that forage quantity and quality was increased in conifer forests during year 2 and 3 post-fire, though was not as affected by severity. I found that

while elk do have the highest probability of foraging in conifer forests at this scale post-fire, foraging declines start around 4 or 5 years after fire, regardless of severity. Burned areas can provide unimpeded avenues of movement across the landscape and elk may associate these areas with higher predation risk as there is no overstory cover, regardless of plant abundance or quality. This possible explanation is similar to burn avoidance by white-tailed deer in early years post-fire (Cherry et al., 2017).

The trends I saw in juniper were opposite to what I saw in aspen. The peak in the probability of foraging decreased with increasing severity in the years post-fire. We may be seeing this effect in the results due to a few reasons. In many areas throughout the Intermountain West, juniper has been migrating into sagebrush and grassland habitat types and it can alter fire regimes where it changes fuel characteristics (Miller & Rose, 1999). Higher severity fires in sagebrush ecosystems have been increasing as mature juniper and pinyon pine presence create better conditions for crown fires (Miller & Tausch, 2000). My results thus lend support to the paradigm that high severity disturbance of juniper could benefit large wild herbivores such as elk due to the removal of juniper leading to better understory forage conditions if native plants are able to reestablish. On the other hand, there is a risk that in the Great Basin, removal of native plants including juniper, sagebrush, or grasses and forbs can lead to invasion of cheatgrass, which declines in nutritional value through the growing season (Cook, 1952) and is not of great importance in elk diets.

Increasing fire activity has been caused partially by the legacy of land management practices, but climate change has also contributed to increased wildfire frequency and increased area burned (Abatzoglou & Williams, 2016; Bond & Keeley, 2005; Li &

Banerjee 2021). Climate has impacted wildfire through lengthened fire seasons, with some western forests experiencing fire seasons extending into fall and winter months (Heidari et al., 2021). By modifying fire frequency and area burned, climate change is expected to indirectly influence plants by shifting community composition towards predominantly early seral and fire-adapted species (Coop et al., 2020). And, in the Rocky Mountains, warming temperatures from climate change are decreasing seedling recruitment post-fire, which could indicate diminishing resilience of forests to fire in a warming climate (Stevens-Rumann et al., 2018).

My results suggest that while elk populations are currently near objectives in Utah (UDWR, 2022), elk are likely to respond well to a future of increasing fire occurrence and severity, especially in aspen stands. Burned areas promote new vegetation growth and appear to lead to increased selection for foraging in the early years after ignition. In particular, burned and unburned aspen had the highest probabilities of foraging by elk overall and those probabilities were consistently high in the thirty years post-fire.

However, more fire on the ground could also correlate to elk having less available cover from predators and therefore a potential impact to populations. Yet, predators causing declines in elk herds has not been documented (UDWR, 2022). While this study did not include on-the-ground sampling for vegetation quantity and quality, I was able to show a link between elk behavior over a much larger spatial scale than previous nutrition or forage studies. My results do suggest elk prefer high severity burned aspen ecosystems, which can put increasing pressure on both sucker survival and population viability (Rhodes et al., 2018, Rogers & Mittenck, 2014, Smith et al., 2016). This is a potentially negative influence for a tree species in decline across much of its western range (Bretfield

et al., 2016, Rehfeldt et al., 2009). While elk have the potential to affect aspen recruitment in the future, increasing fire occurrence will likely help aspen populations. Previous research has shown that aspen recruitment was highest in areas burned 10 to 20 years prior (Reikowski et al., 2022), indicating that the initial regeneration response to fire can benefit aspen viability even as years since the burn increase.

Behavioral state classification

HMMs are becoming more and more prevalent in ecological applications to understand behavior in mobile animals. This is valuable for large mammal research as models are easy to fit and when paired with environmental data, they can be used to infer behaviors and the underlying ecology in a more meaningful way than by only using GPS locations (McClintock & Michelot, 2018). This study has provided insight into behavior and space-use and also employs a predictive modeling framework to determine these behaviors in the context of environmental factors like vegetation phenology, burn history, and snow depth. On the other hand, we should be cautious about interpreting the behavioral states, as they are designated by user-set parameters and serve only as a stand-in for the real behaviors an animal may exhibit during their lifetime. I chose the three main behaviors that are the most common in HMM applications on large ungulates (e.g., muskox; Chimienti et al., 2021, caribou; Franke et al., 2004), but there can be other methods of logging elk behavior, including observational studies or accelerometer data loggers. Nevertheless, pairing HMM state assignments with a predictive analysis can provide insight into wildlife behaviors in changing environments, due to fires, drought, or other large disturbance events. My study provides a foundation for further research on the timelines of animal foraging behavior post-fire and adds to our knowledge on how an

increase in annual area burned and area burned at increasing severities will ultimately impact large-bodied ungulates like the Rocky Mountain elk.

Management implications

To the extent that peaks in foraging behavior accurately reflect post-fire forage availability and elk preference, this study suggests that fire increases both forage quality and quantity and that burned ecosystems may thus support larger populations of elk in Utah. In particular, while I found weak effects of fire severity on most vegetation types, elk appeared to show strong selection for high severity burned aspen, based on high probabilities of foraging up to 30 years after a fire. Given this result, high-severity prescribed burning may be one of the ways in which to achieve preferred vegetation for the Rocky Mountain elk. In general, prescribed burning has been found to increase ungulate preference for habitat, as well as promote regeneration of target species like grasses (Allred et al., 2011) or aspen (Canon et al., 1987). Further research should examine wildfire versus prescribed fire effects on post-fire elk habitat selection and behavior at differing timescales in the context of severity categorizations. My dataset did include prescribed fires, but did not differentiate between wildfires and prescribed burns. Greene et al., (2012) found that prescribed fire did not achieve the same positive effects on post-fire forage biomass and abundance for another ungulate species, the Sierra bighorn sheep (*Ovis canadensis sierrae*). In aspen communities, lower severity prescribed fires may not be as beneficial for reproduction when compared to the effects from higher severity wildfires. It is also unknown whether other high-severity disturbances would have the same positive impact on elk foraging in the years post-disturbance.

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CHAPTER 3

DOES FIRE SEVERITY EXPLAIN ELK ABUNDANCE?

Abstract

Recently, fire activity has been increasing in much of the western United States and wildfire frequency is projected to continue to change into the future. Increases in both annual area burned and area burned at high severity may actually represent opportunities for some species, particularly large herbivores like elk (*Cervus elaphus nelsoni*), through increased access to area regenerating post-fire where forage availability may be improved. Therefore, effective management of wildlife populations may depend on quantifying how elk will alter their space use in the context of increasing fire frequency. In 2018, three fires burned a combined total of 153,00 acres in east-central Utah. To understand how elk abundance is affected by fire legacies, I deployed 40 camera traps, stratified by fire severity (unburned, low, and high), to monitor elk use of burned areas and used the photos to compile elk counts per site. I ran a zero-inflated Poisson count model to predict elk abundance as a function of biomass and severity. I found that the post-fire availability of herbaceous biomass was a major driver of elk abundance, and that this relationship increases with increasing severity. Shrub and tree biomass had a significant effect on elk abundance, but as shrub biomass increased, elk abundance decreased at high severity. Expected elk abundance also increased as tree biomass increased, and the strongest pattern was in unburned sites. Results from this research suggest that increasing patches of higher severity fire in Utah will benefit elk 3 to 4 years post-fire, particularly through the production of herbaceous biomass, and

highlight the need for further studies on elk use of burned ecosystems on a long-term scale.

Introduction

Wildlife select habitat based on perceived risks, available resources, and abiotic conditions (Matthiopoulos et al., 2015). Forage quality and quantity on the landscape are important drivers of wildlife space use. Large herbivores choose habitats with high-quality forage plants to maximize protein and energy uptake (Barboza et al., 2009, p. 35). These habitats provide nutritional resources and have a direct effect on body condition, survival, and thus wildlife populations (Parker et al., 2009). Therefore, areas of high herbivore density can be an indicator of high forage quality and quantity (Mueller et al., 2008). By quantifying patterns of large herbivore presence across space and time, we can gain a deeper understanding of their foraging ecology.

One factor that influences vegetation quality on the landscape is wildfire. In recent years, fire activity has been increasing in much of the western United States (Hagmann et al., 2021). Additionally, more area is burning at high severity due to the overall increase in area burned (Parks & Abatzoglou, 2020). Wildfire's effect on forage quality is dependent on many factors, including pre-fire vegetation communities (Sachro et al., 2005), time since fire (Proffitt et al., 2019), and severity (Snobl et al., 2022). Since burned areas have less canopy cover and therefore receive more sunlight, regrowth may consist of young plants that have higher nutrient loads. After burning, fire can also induce higher protein levels within plants for a few years post-fire (Hobbs & Spowart, 1984). In

many ecosystems, fires shift less desired forage to palatable forbs and grasses, thus improving overall quality for wildlife (Greene et al., 2012).

In post-fire landscapes, successional changes in vegetation structure and quantity are heavily dependent on fire severity and time since fire. Low-severity burned patches are generally characterized by little heat penetration into the soil, and little to no organic material burned in the soil. These factors contribute to better conditions for re-sprouting grasses and forbs. After a fire, forage quantities rise as time since fire increases (Allred et al., 2011, Sachro et al., 2005, Sittler et al., 2019). Forage quantity can also vary by the vegetation communities in which the fire occurs. For example, in conifer-dominated ecosystems, forage abundance was at its highest 6-15 years post-fire (Proffitt et al., 2019), but was highest less than 2 years after a burn in sagebrush systems (Van Dyke & Darragh, 2007).

Forage availability post-fire may also vary based on the regeneration strategies of vegetation communities. Some plant species adaptations, like re-sprouting, help plants thrive in patches of high-severity fires. Because species like aspen (*Populus tremuloides*) can re-sprout through clonal suckers after disturbances like fire, biomass regeneration where aspen are present may be higher at sites of high severity fire when compared to lower severity patches (Bailey & Whitham, 2002). When burned, other vegetation types can have very different responses. For example, mountain big sagebrush (*Artemisia tridentata wyomingensis*) plants recover slowly and are dependent on a seedbank for regeneration post-fire after large fires (Innes & Zouhar, 2018). Yet, quantity and quality of forbs and grasses in sagebrush ecosystems increase after fire (Cook et al., 1994).

Forage quantity and quality can be measured using ground sampling, but remotely sensed methods like the normalized Difference Vegetation Index (NDVI) can also be used as a coarser but broader-scale metric. The main use of NDVI has been as a measure of vegetation greenness and amount across diverse applications, but it has also been used for plant response to disturbance events. In studies on browsing or grazing ungulates, it is used as an indicator of vegetation productivity (Lukacs et al., 2018). In wildlife biology applications, NDVI is used to quantify forage quality and amount to understand wildlife movement, predict wildlife habitat, and explain animal abundance and distribution (Hamel et al., 2009, Mueller et al., 2008, Pettorelli et al, 2011). NDVI has also been used for assessments of fire severity (Escuin et al., 2006) and recovery post-fire (Perez-Cabello et al., 2021). By combining these previous uses, employing NDVI as a metric of forage quality and quantity in post-fire ecosystems can help quantify how wildlife may use the landscape in response to increasing fire events.

Assuming that large herbivores, like elk (*Cervus elaphus nelsoni*), choose when and where they are actively foraging to maximize their fitness, their behavior could be an indicator of forage conditions, and hence of the dynamic ecological consequences of fire. Previous studies have shown that large ungulates actively forage in burned areas in the years post-fire (Sachro et al., 2005, Spitz et al., 2018). For example, elk select for burned areas where graminoid cover is high (Biggs et al., 2010), and elk use burned areas across every season throughout the year (Sittler et al., 2015). Tree species like aspen also attract elk, as young suckers are a nutritious option for browsing herbivores.

Current research on forage availability, nutritional resources, and wildlife diversity after fire is widespread, but there remain few studies that employ place-based

sampling methods to understand large ungulate presence and habitat selection in the context of wildfire. To fill this gap, I used a game-camera array in three fire footprints at years 3 and 4 post-fire to research fire history (including fire severity) and how, when combined with NDVI, improves our understanding of elk habitat use across Utah. I hypothesized that increasing fire severity would improve the quality of herbaceous biomass, the primary forage of elk. I predicted that elk abundance would increase with the quantity of herbaceous biomass, and that this effect would be stronger in high severity sites due to increased forage quality. Above and beyond the fire effect on the quality of herbaceous forage, I predicted that unburned and high severity burns would be least attractive to elk, while low—moderate severity burns would be the most attractive to elk because these sites can incur substantial change, but with little to no loss of nutrients or topsoil that could result in lower quantity or quality of forage. I also hypothesized that for sites with a high percentage of tree cover, NDVI would primarily be measuring canopy biomass. I predicted that elk would not react strongly to changing severity within trees as tree biomass is likely not representative of elk forage.

Methods

Study Areas

The study areas were located on the Manti La Sal and Uinta-Wasatch-Cache National Forests in east-central Utah, USA (Figure 5). In 2018, 3 fires (Bald Mountain, Coal Hollow, and Pole Creek) occurred in this region, burning a combined 153,000 acres. One study area was in the Spanish Fork Canyon, Utah, near Dairy Fork Road and Skyline Drive, and occurred in the footprint of the Coal Hollow fire. The second study area was

near Mt. Nebo Loop Road outside Payson, Utah, where cameras were placed in both the Pole Creek and Bald Mountain fire footprints. Sites on Skyline, Dairy Fork, and Mt. Nebo are characterized by elevations between 2,000 to 2,900 m above sea level and by mixed-conifer, including white fir (*Abies concolor*) and Engelmann spruce (*Picea engelmannii*), and pure aspen stands. Understory forbs and grasses as well as snowberry (*Symphoricarpos* spp.), saskatoon serviceberry (*Amelanchier alnifolia*), wild rose (*Rosa* spp.) and bigtooth maple (*Acer grandidentatum*) are also present.

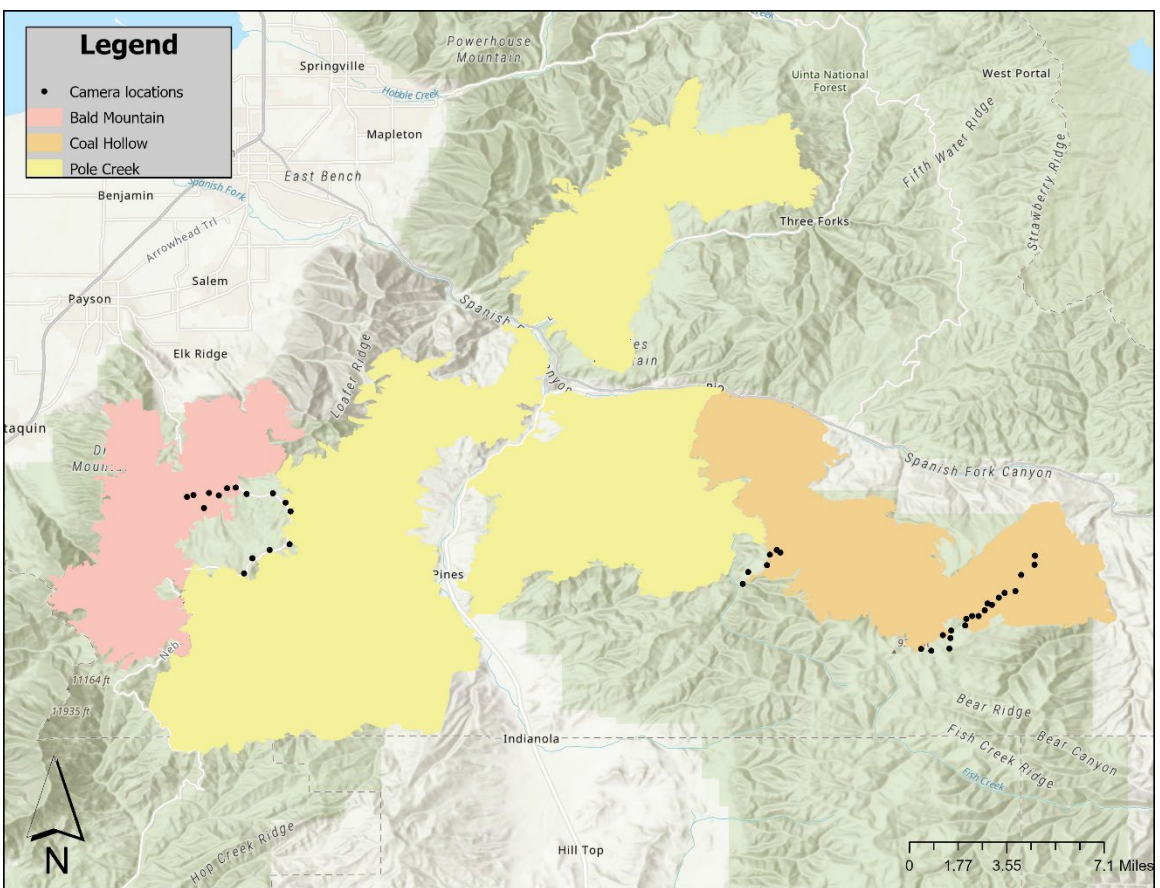


Figure 2. Map of study areas with camera locations and fire perimeters

Field Methods

In May 2021, I selected 40 locations to set up game camera traps. I chose sites based on fire severity layers from Monitoring Trends in Burn Severity (MTBS, <https://www.mtbs.gov>), at least some aspen presence, and proximity of a road (within 500 m) to allow for accessibility and maintenance. I placed 14 cameras in high severity sites, 13 cameras in low severity sites, and 13 in unburned sites. At each site, I set up a Browning Strike Force Pro XD Trail camera near chest height on a tree to provide the best opportunity for capturing large ungulates. I programmed the camera to have a 5 second shutter delay, a normal detection range, and be in power save mode during the night. I selected these settings to prevent excess photos taken of vegetation moving. I placed three metal poles six meters away from the camera; one directly in front of the camera, and the other two poles 1.8 m away to the right and to the left of the middle pole to demarcate a 30-degree 'area of detection' where animal detectability is likely very high. I used these poles to provide a standardized area of 21 m² in order to determine accurate elk counts.

I checked cameras to change SD cards and batteries two times a year, once in May and once in October. However, due to rapid green-up, the camera SD cards would fill up quickly with photos of moving vegetation. In order to combat this, I checked cameras once or twice during the summer months (June through August) to change SD cards or batteries if needed and to avoid long periods of inactivity by full or dead cameras.

Environmental and temporal predictors

Using Google Earth Engine (Gorelick et al., 2017), I linked camera positions with remotely-sensed environmental covariates (see Table 3). I aggregated covariate data from May 1, 2021, until November 1, 2022, to account for the full time that the game cameras were deployed and active. I also used Google Earth Engine to download annual ground cover data from the Rangeland Analysis Platform (RAP; Allred et al., 2021) to quantify percent-cover of herbaceous, shrub, and tree cover. I downloaded the MODIS Normalized Difference Vegetation Index Terra and Aqua products (NDVI; Didan, 2021b, 2021a), which alternate at 8-day intervals for a total of 16-day periods.

I multiplied the NDVI value by the percent cover values to create a proxy for herbaceous, shrub, and tree biomass (these variables will hereafter be referred to as herbaceous biomass, shrub biomass, and tree biomass). I assumed that herbaceous biomass would be an index of forage quantity, that shrub biomass would be an index of alternative forage, and that tree biomass would be an index of protection, thermal refugia, or forage.

I downloaded topographical data (digital elevation model; DEM), including slope, from U.S. Geological Survey's 3D Elevation Program (2019). This variable may affect elk use of an area based on sun exposure or steepness impacting what vegetation grows where or overall accessibility for elk. I also included a snow depth variable from the European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis -Land Hourly (Muñoz Sabater, 2019) as I expected it to decrease the elk presence. Deep snow restricts access to habitats and to the forage that may occur underneath. I downloaded the

fire severity layer for the Bald Mountain, Coal Hollow, and Bald Mountain fire perimeters through the Monitoring Trends in Burn Severity (MTBS) database (<http://www.mtbs.gov>, Eidenshink et al., 2007). Fire severity is classified through the differenced Normalized Burn Ratio (dNBR), which is a measure of the ecological change on the landscape due to a fire (Keeley, 2009). By using previously established CBI severity category thresholds from Miller & Thode (2007), fire severity breaks were calculated through fitting a regression to observed dNBR and CBI plot data (Picotte et al., 2019) within Utah (taken from Kipling Klimas, pers. comm).

Variable:	Data source:	Temporal resolution:	Spatial resolution:
Fire severity (dNBR)	Monitoring Trends in Burn Severity (MTBS)	N/A	30 m
slope (derived)	U.S. Geological Survey, 3D Elevation Program 10-Meter Resolution Digital Elevation Model	N/A	10 m
herbaceous cover (%)	Rangeland Analysis Platform (RAP)	Annual	30 m
shrub cover (%)	Rangeland Analysis Platform (RAP)	Annual	30 m
tree cover (%)	Rangeland Analysis Platform (RAP)	Annual	30 m
NDVI	MODIS Terra and Aqua Normalized Difference Vegetation Index (NDVI)	16-day, (split into alternating 8-day periods with Terra and Aqua)	250 m
snow depth	ECMWF Climate Re-Analysis ERA-5 Land-Hourly	Hourly	11 km

Table 2. Overview of covariates used in model analysis. Sources and resolutions are displayed for each variable.

Data processing

All game camera photos were tagged following an established protocol using the online photo processing software Camelot (<https://camelotproject.org>). Each photo was tagged with the corresponding species, sex, age class, and number of individuals, along with whether each individual was “in” or “out” of the area of detection (delineated by the three metal poles). “In” meant an animal’s body fell halfway or more within the poles. “Out” meant an animal’s body fell somewhere that was less than 50% within the poles or its body was less than 50% between the poles and the camera.

I downloaded the raw data that contained all tagged photos from each site and deployment by using the “export data” tool in Camelot. I checked data to remove duplicate classifications, ensured sex, count, and species of animals accurately matched in photos, and to ensure that sites and deployments matched on each photo. After this, I identified start and end dates for each camera deployment and determined whether there was a malfunction or a camera was knocked down during a camera deployment. A malfunction occurred when the timestamp no longer matched the time of day in the photo. The camera was denoted as being knocked down if the camera no longer faced the poles and a point of reference was not available. I removed the photos after a malfunction or knocked down camera occurred because an accurate time and date stamp could not be ascertained and would not be accurate in count models. I calculated elk counts per camera site in relation to an 8-day NDVI period by summing all counts of elk photos that were tagged as “Elk In” and if the photo fell within the NDVI time frame. For every NDVI period, I ended up with the total count of elk at each site, which I used as the

response variable in my statistical model.

Model Structure

I fit a zero-inflated Poisson model using the “*glmmTMB*” package (Brooks et al., 2017) in R to quantify the effect that fire severity and other environmental and temporal factors have on elk abundance. The zero-inflated Poisson model is a mix of two processes, a Poisson and a binomial. The Poisson-process part of the model represents elk counts, conditional on the zero-inflation process. The binomial part of the model provides the zero-inflation, allowing more zeros than the Poisson would accommodate. I will refer to the Poisson part of the model as “abundance given occupancy” or “conditional abundance”. I will refer to the binomial part of the model as “occupancy”, although this statistical representation does not exactly match the ecological definition of occupancy. The model shorthand is given by the below equation:

$$E[\text{abundance}] = E[\text{abundance}|\text{occupancy}] \cdot \Pr[\text{occupancy}]$$

My response variable was the count of elk at a camera site per 8-day NDVI period. I will refer to this variable as “abundance”. In the abundance-given-occupancy process, I included the interaction between herbaceous, shrub, and tree biomass and fire severity to test my prediction that elk abundance would be greater at sites with high herbaceous biomass and intermediate fire severity. I also included the slope of terrain taken from the DEM and two random effects: the NDVI period and the camera site ID. In the occupancy process, I included snow depth and a random intercept for site ID. Note that *glmmTMB* models zero-inflation as the probability of excess zeros (i.e., positive

coefficients mean a greater chance of zeros, thus expected abundance decreases with positive coefficients in the occupancy process).

Model Assessment

I measured the goodness-of-fit of my model with the R^2 . I used the function 'r2_zeroinflated()' from the R package *performance*, which calculates an R^2 value based on the residual and total variance (not deviance; Ludecke et al., 2021).

Results

My model explained 98% of the variance in expected elk abundance ($R^2 = 0.98$). The high R^2 value likely reflects the overwhelming absence of elk during winter where zeroes are over-inflated. The strongest fixed effects were tree biomass (positive effect, Fig. 6A), followed by herbaceous biomass (Fig. 6A). Conditional abundance (elk being captured in a photo) was higher between June and December 2021, but was lower between January and April 2022 (Fig. 6B). The effect of snow depth on zero-inflation (i.e., on elk absence) was slightly positive but not significant (Fig. 6C).

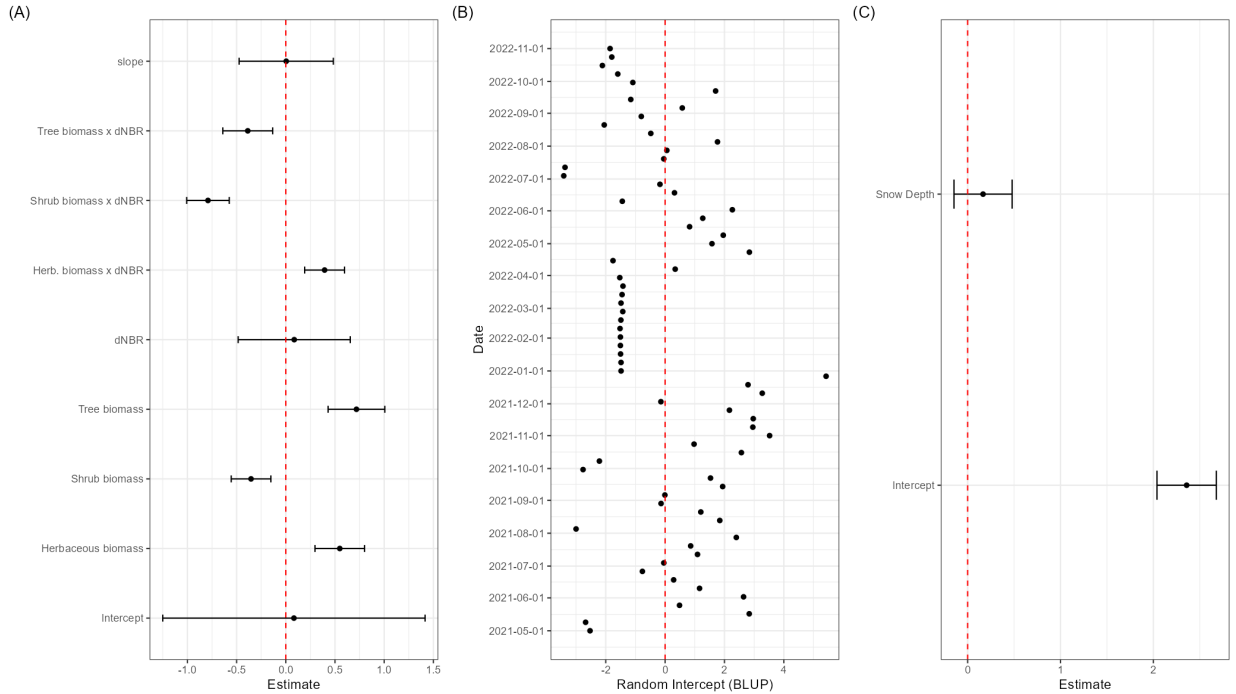


Figure 3. Parameter estimates with 95% confidence intervals for the zero-inflated Poisson model where panels A-B refer to the abundance given occupancy (Poisson) part of the model and panel C refers to the occupancy (binomial) part of the model.

The random effects of site were included in the abundance given occupancy (Fig. 7A) and occupancy processes (Fig. 7B) of the model. Conditional abundance was variable across the landscape and did not show a clear geographical pattern (Fig. 7A).

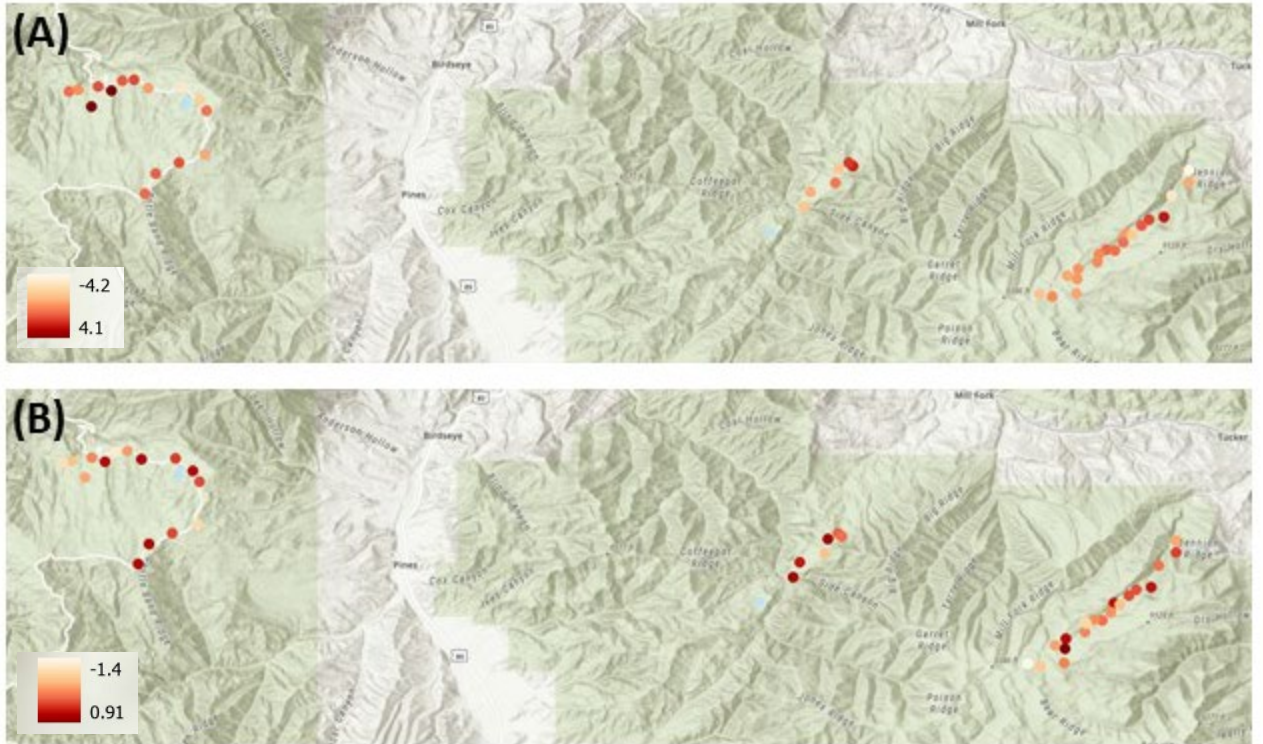


Figure 4. Map of camera sites color-coded by the Best linear unbiased prediction (BLUPs) of the random effect of Site from the (A) occupancy given abundance (Poisson) process and the (B) occupancy (binomial) process. Darker colors correspond to larger BLUPs, or higher abundance of elk, and lighter colors represent lower and potentially negative BLUPs.

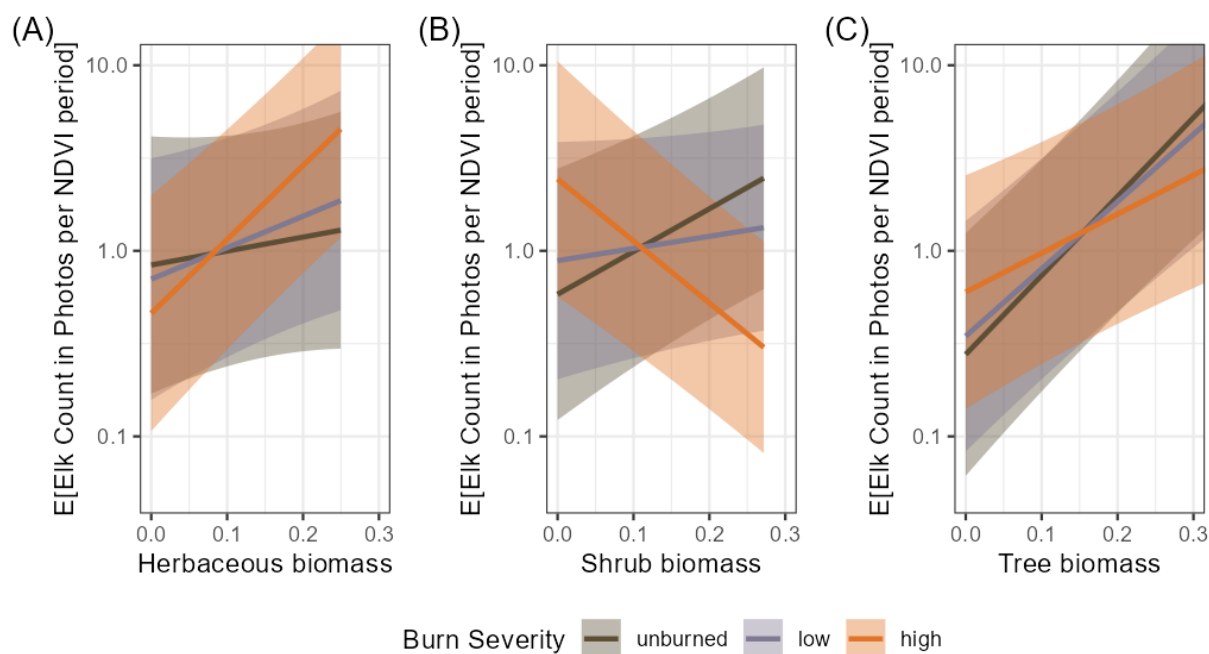


Figure 5. Model predictions of the expected number of elk in photos over an 8-day NDVI period as a function of vegetation biomass and burn severity – note each line (shaded ribbons show 95% confidence interval) indicate the trend in expected elk counts when the severity is set at thresholds taken from CBI and dNBR regressions in Utah (Picotte et al., 2019).

Elk abundance was strongly influenced by burn severity and vegetation biomass.

Sites that had burned at high severity and that currently had higher amounts of herbaceous biomass had the highest number of expected elk photos (Fig. 8A), which did not match my prediction. When sites had burned at low severity, expected elk abundance increased with increasing amounts of herbaceous biomass in all severity categories (Fig. 8A). In unburned sites, expected elk photos increased with higher herbaceous biomass, but the trend was similar to the low severity line (Fig. 8A).

Elk abundance was most variable across shrub biomass and fire severity (Fig. 6A). Higher amounts of shrub biomass in sites that were unburned correlated to increases in expected elk abundance (Fig. 8B). Sites burned at low severity also had higher

expected elk counts as a function of increasing shrub biomass (Fig. 8B). However, as shrub biomass increased, sites that had burned at high severity had a negative association where expected counts of elk decreased (Fig. 8B). The shrub vegetation was the only vegetation type to have a decline in elk counts as biomass increased.

Burn severity and tree biomass had positive effects on elk abundance (Fig. 6A). Similar to the herbaceous biomass category, the expected number of elk photos did increase as tree biomass increased (Fig. 8C). Unburned sites or those burned at low severity had very similar positive trajectories, with elk counts increasing with increasing tree biomass (Fig. 8C). Sites that burned at high severity also had an increase in elk counts as tree biomass increased, but it was not steep and was similar to unburned shrub (Fig. 8B,C).

Discussion

As the western United States moves into a future of growing fire frequency and area burned at high severity, it is increasingly important to understand how large ungulate populations will change in response. Through the use of a place-based sampling approach, I was able to relate elk abundance to fire severity and vegetation productivity. My results partially support my hypothesis that fire severity would be a major driver of elk presence (Fig. 4), as this was highly dependent on the values of vegetation type and biomass. My results showed that elk abundance increased as herbaceous biomass increased across all levels of fire severity, including unburned, low-moderate, and high-severity. In herbaceous vegetation, expected elk abundance was actually highest after high-severity fire. Expected elk abundance also increased as tree biomass increased, but

the strongest pattern was in unburned sites. High-severity fire did have a negative effect on elk abundance with increasing shrub biomass. My findings suggest that increasing patches of higher severity fire in Utah will benefit elk 3 to 4 years post-fire, particularly through the production of herbaceous biomass.

Herbaceous biomass was a strong determinant of elk abundance due to its positive effect on increasing elk counts across all severity categories. Grasses are the dominant component of elk diet (Christianson & Creel, 2010), though, elk preference and nutritional value of forage species can change dependent on ecosystem (Cook et al., 2016). For example, in sagebrush and aspen habitat, elk largely prefer forbs (Beck & Peek, 2005), but graminoids are strongly selected for on alpine summer ranges (Baker & Hobbs, 1982). Because herbaceous plant communities (e.g., forbs and graminoids) are generally some of the first successional vegetation types to return post-fire (Swanson et al., 2011), elk abundance in year 3 and 4 after a fire is likely tied to availability and preference. And, after higher severity fires, the abundance of canopy light and potential nutrient cycling from downed, dead, woody debris can promote better conditions for sprouting grasses and forbs. My results showed that herbaceous biomass has a positive influence on elk being captured in a photo. Snobl et al. (2022) found that herbaceous abundance in recently burned areas was higher regardless of severity, but my results indicate that higher burn severity actually increases the likelihood of an elk visiting a site, especially where there is high herbaceous biomass. This could be because high fire severity increases the quality of the forage (nutrition). It is also possible that the RAP cover categories misclassified aspen suckers as herbaceous vegetation or shrubs, and so

high-quality aspen suckers that emerged post-fire in high-severity burned areas are being represented in the herbaceous biomass category.

While shrub communities can provide winter forage availability for large ungulates (Hodder et al., 2013), Proffitt et al., (2019) found that shrubs were not an important forage option for elk. My results showed that shrub biomass had both positive and negative effects on expected elk abundance, depending on fire severity. Higher shrub biomass corresponded to decreases in expected elk abundance when sites had been burned at high severity. This finding offers partial support to my prediction that high severity sites would be least attractive to elk because this was the opposite of the trend with herbaceous and tree biomass. Elk abundance and its negative relationship to increasing shrub biomass after high-severity fire is likely representative of elk avoiding shrub-dominated communities, particularly in higher severity burned areas, where regenerating shrubs may be dense and impede movement or not selected for forage, especially when there are other more palatable graminoids present elsewhere. Elk abundance increased with increasing shrub biomass when sites were unburned or had burned at low severity, but this could be an effect from shrubs being browsed simply because of their presence in habitats instead of actual selection (Christianson & Creel, 2010), particularly in summer when shrubs are less selected.

Aspen, spruce, and fir were all common tree species in my study area, but I did not control for species when using the tree cover data from RAP. Elk abundance increased with tree biomass at all severity categories. Conifers and aspen have very different understory community compositions that can affect elk presence. For example, apex conifer-dominated vegetation communities provide little to no forage for elk (Cook

et al., 2016), while aspen are a preferred forage option for elk and more sunlight in their canopy promotes other palatable forbs and grasses, especially as sucker production declines with increasing time after a burn (Bartos & Mueggler, 1981). Aspen were present in the majority of sites and was a criterion for camera site selection, yet other research shows that elk preference for foraging in aspen sites may peak much later following fire than conifer (see Chapter 2). In Chapter 2, I found that elk foraging in aspen peaked between 7-9 years post-fire, dependent on severity. Therefore, while this study shows positive relationships between elk abundance and increasing tree biomass at different severity values, elk abundance may actually be much higher in aspen sites in the future.

I found support for my prediction that elk abundance would not be strongly related to tree biomass, but my metric of tree biomass is likely only measuring canopy and is not representative of what elk are actually foraging in the understory. On-the-ground vegetation sampling would be useful in this study to understand plant species composition. Nevertheless, the positive association of increasing expected elk counts with increasing tree biomass is likely due to these areas providing protection from predators as well as thermal protection. The weaker relationship between elk abundance and tree biomass in high-severity areas could reflect the fact that high-severity fire leaves little live tree biomass, and RAP may be picking up snags or standing dead trees, meaning thermal refugia or protection from predators is unlikely.

Elk are a well-studied large ungulate species across the Intermountain West and are managed for both ecological and hunting purposes in Utah. While wildfire in Utah has not seen the huge increases in frequency and area burned as many other places in the

West, fire activity is still projected to increase. Through this research, I was able to use game cameras to link elk abundance on the landscape to changes in vegetation composition and productivity and fire severity, the latter of which is also projected to rise in future fire events (Parks & Abatzoglou, 2020). Elk abundance at a site is strongly influenced by herbaceous biomass combined with fire severity; a result that supports my hypothesis that burned areas increases forage quality. My model results show that elk abundance was expected to increase most sharply as herbaceous biomass increased in high severity areas, which does not support my initial prediction about high severity patches within fires. I expected higher severity areas to have delayed regrowth because of more potential soil, root, and seedbank damage, but perhaps by conducting this study 3- and 4-years post-fire, those impacts were not as prevalent. And, there is some evidence that elk may prefer high severity patches (Lewis et al., 2022). My interpretations are limited to the timing of this study, which only includes years 3 and 4 post-fire, but this research bolsters previous work on elk ecology and populations post-fire and fills a gap in the post-fire timeline (1-4 years, Biggs et al., 2010; 2-3 and 7-11 years, Sachro et al., 2005; 2-3 years, Snobl et al., 2022; 10+ years, Wan et al., 2014).

Increasing fire activity has been caused partially by the legacy of land management practices, but climate change has also contributed to increased wildfire frequency and increased area burned (Abatzoglou & Williams, 2016; Bond & Keeley, 2005; Li & Banerjee 2021). Climate change impacts will likely have varying effects on forage abundance and quality post-fire depending on site characteristics. However, the results of this study indicate that elk will likely thrive in an increasingly fire-prone future, especially if herbaceous biomass remains plentiful after a fire. In addition, fires of mixed-

severity may provide the most beneficial habitat; elk may prefer heterogeneous habitats of burned and unburned patches which provides access to cover and food (Long et al., 2004). Further long-term studies are needed on what drives elk presence in post-fire ecosystems to provide a comprehensive understanding of elk ecology in the context of forest regeneration. This research suggests that higher severity burned patches with substantial herbaceous biomass presence are expected to provide extended periods of resource availability for elk, especially as beneficial post-burn conditions in lower severity areas likely diminish sooner after wildfire events.

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CHAPTER 4

CONCLUSIONS

My research was conducted in order to examine wildfire effects on elk behavior and abundance in the years post-fire. Elk in the western United States have coexisted with wildfire over evolutionary timescales, but it is important to understand how the current fluctuations in fire severity and area burned will affect ecosystems and wildlife as we move into a future of shifting fire regimes. In the past centuries since European settlers introduced grazing and suppressed natural fire regimes across much of the western United States, several generations of elk have experienced less fire on the landscape and more time in between burns. With fire size, frequency, and area burned at high severity rising over recent decades (Parks & Abatzoglou, 2020), wildlife and their habitats are increasingly affected, yet studies on the behavior and space use of animal populations after fire events are not prevalent in the contemporary literature. Therefore, I aimed to compare and contrast two known wildlife sampling methods to answer questions on elk space-use behavior and abundance in post-fire habitats. The results of this research suggest that elk are a species that will adapt well to burned landscapes in a future of higher intensity and more frequent fire events.

In the second chapter, I first implemented a Hidden Markov Model (HMM) based on an individual-based sampling method (GPS collars) to assign elk behavioral states. By including only the foraging state in the post-HMM analysis, I was able to predict the probability of foraging based on fire and other environmental factors. I then ran a generalized additive model to predict elk foraging probability in different severity classes

and habitat types between one- and thirty-years post-fire. This showed that the timing of peaks in foraging probability was largely dependent on vegetation type and time since fire rather than severity. Consistent with previous research on elk selection post-fire for aspen ecosystems (Canon et al., 1987, Wan et al., 2014) and previously burned landscapes (Biggs et al., 2010, Proffitt et al., 2019), I found that elk were more likely to be in a foraging state in high severity burned aspen. I also found that regardless of fire severity, elk foraging probability peaked 3-4 years post-fire in the conifer vegetation class and declined sharply compared to other vegetation classes as time since fire increased. This suggests that elk use of conifer-dominated habitat after fire is tied to forage regrowth in the early years post-burn.

In the third chapter, I used a camera trap array to capture motion-activated photos of elk to provide insight on elk abundance and use of aspen-dominated systems in the years following fire. I then used those photos of elk to fit a zero-inflated Poisson count model to look at abundance based on fire severity and habitat type. I found that elk abundance (based on counts of elk in camera photos) is positively associated with herbaceous biomass, and abundance is highest with higher amounts of herbaceous biomass and when a site burned at high severity. This is consistent with previous research on elk foraging activity, where grasses (Christianson & Creel, 2010) and forbs (Beck & Peek, 2005) make up the majority of elk diets. However, I also found that as shrub biomass increased, higher severity sites were negatively correlated with elk abundance; a likely indicator of elk avoiding these areas for lack of preferred forage.

This research provided a comparison between two methods of measuring elk space use and behavior in order to determine future management implications for this

ecologically and culturally significant ungulate species. By answering similar questions but with different methodologies, I was able to provide strategies for wildlife and land managers. I recommend that management agencies should prioritize high severity prescribed fire when and where possible or to let fires burn when human life and infrastructure are not at risk. This will not only improve habitat for elk, but high severity burned areas will likely improve forest stand dynamics, and be beneficial for aspen in particular. I hope that methodologies used in this research will be beneficial as a blueprint for further ecological studies on other wildlife species in order to provide insight into animal behavior in response to increasing wildfire events.

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