

Fire history influences large-herbivore behavior at circadian, seasonal, and successional scales

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Abstract. Recurrent environmental changes often prompt animals to alter their behavior leading to predictable patterns across a range of temporal scales. The nested nature of circadian and seasonal behavior complicates tests for effects of rarer disturbance events like fire. Fire can dramatically alter plant community structure, with important knock-on effects at higher trophic levels, but the strength and timing of fire's effects on herbivores remain unclear. We combined prescribed fire treatments with fine-scale location data to quantify herbivore responses to fire across three temporal scales. Between 2001 and 2003, 26 stands of fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) were thinned and burned; 27 similar stands were left untreated as experimental controls. Analyzing female elk (*Cervus canadensis*) locations across 21 yr (1996–2016), we found crepuscular, seasonal, and successional shifts in behavioral responses to fire. Elk displayed “commuting” behavior, avoiding burns during the day, but selecting them at night. Elk selection for burns was strongest in early summer and the relative probability of elk using burns peaked quickly (5 yr post burn) before gradually returning to pre-treatment levels (15 yr post burn). Our results demonstrate that fire history has complex, persistent effects on herbivore behavior, and suggest that herbivores benefit from heterogeneous landscapes containing a range of successional stages.

Key words: behavioral plasticity; *Cervus canadensis*; commuting behavior; discrete choice; large herbivores; resource selection; temporal scale; ungulates.

INTRODUCTION

Explaining the role environmental conditions play in determining species' distributions is a central goal of ecology (Grinnell 1917). Many of these conditions change predictably through time, and when these changes appear in sequence they can elicit complex behavioral patterns even from simple organisms. For example, many zooplankton taxa respond to light by moving deeper in the water column to reduce mortality risk from visually oriented predators, while decreasing light intensity evokes upward movement (Lampert 1989). Alternation between these complimentary behaviors affords zooplankton reduced diurnal risk of predation and the metabolic benefit of increased access to warm food-rich waters at night when predation risk ebbs (Lampert 1989). Comparable seasonal shifts in behavior are also common across a wide range of taxa (e.g., migration; Dingle and Drake 2007). Consequently, individual behavior can shift significantly within diel and seasonal cycles. These conflicting patterns create a challenge for the study of animal behavior; simultaneously analyzing multiple behaviors violates common statistical assumptions (Lele et al. 2013) and can result in the estimation of a “mean” behavior, which misrepresents a species' ecology (Gillingham and Parker 2008). Because behaviors are nested in space and time (Johnson 1980), fine-scale behavioral cycles have the potential to

obscure patterns at coarser temporal scales. Interpreting the effect coarse temporal changes like landscape disturbance have on animals therefore depends on explicitly testing temporal dynamism in animal behavior at finer scales (Godvik et al. 2009, Lone et al. 2017).

Wildfire is a recurrent disturbance that exerts pervasive effects on the structure and function of many terrestrial systems (Bond and Keeley 2005). Among these effects, fire disrupts climax vegetation by facilitating the establishment of early seral stages that provide nutritious forage for large herbivores (Fryxell 1991). Consequently, energy and protein available to herbivores often increase following fire, peak after several years, and then gradually decline as succession progresses (Long et al. 2008b). As a consequence of this alteration of the nutritional landscape, the ecosystem-structuring effects of fire are expected to extend upward across trophic levels and to shift animal distributions in space and time (Pulliam 2000). The importance of understanding fire's ecological role has only increased over the past century of climate change, fire suppression, and proliferating invasive plants (Pechony et al. 2010). Multi-scale responses of herbivores to burns have rarely been documented, leaving a critical gap in our ability to anticipate the strength, direction and duration of the effect of fire history (i.e., post-fire successional changes on forage availability and vertical structure) on animal distributions.

Despite post-fire nutritional benefits, there are also reasons herbivores may avoid recently burned areas. Herbivores must balance the acquisition of resources against energetic expenditure and predation risk (Lima et al. 1999). Openings

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in vegetation like those created by fire, disease, or silviculture reduce vertical structure that can provide herbivores refuge from heat stress and coursing predators (Long et al. 2014, Lone et al. 2017). Furthermore, these benefits and costs associated with burns are temporally dynamic: the importance of thermal-refuge, for example, may vary over the course of a day, while plant phenology drives changes in the nutritional landscape across seasons, and succession extends across years. Thus, if the primary benefit herbivores derive from burns is nutritional, then we would predict their use of burns to be strongly associated with foraging periods, the early growing season (i.e., before exposed forage begins to senesce), and more recently burned areas. In contrast, during periods of rest or late growing season, individuals may avoid or be indifferent to burns, particularly if use of these areas imposes concomitant costs.

Here, we test these predictions with data from a large herbivore, elk (*Cervus canadensis*). Past work in our system has focused on quantifying short-term changes in post-fire forage composition and found that burned areas had higher available nutrition in spring (May–June) with nutritional resources increasing 2–5 yr post burn (Long et al. 2008b). Because post-fire nutritional benefits are linked to early seral stages, these benefits should persist over only a portion of the overall successional process, but are still expected to be long-lasting relative to the lifespan of individual elk (e.g., 25 yr; Skovlin et al. 2002). Reduction of vegetative structure by fire can simultaneously reduce the risk posed by ambush predators and increase prey's vulnerability to coursing predators like humans, thus creating different diel patterns in the risk associated with burned and unburned stands (Lone et al. 2017). Elk are often described as crepuscular foragers (Frair et al. 2005, Naylor et al. 2009) and our study population has two primary predators: diurnal human hunters and cougars *Puma concolor*, a largely nocturnal ambush predator (Wang et al. 2015). Human hunting at our study site occurs only in autumn, but elk are subject to year-round anthropogenic disturbance that is likely perceived by elk as an indicator of risk (Frid and Dill 2002). Outside the hunting seasons, anthropogenic disturbance is largely tied to roads or recreational use (Naylor et al. 2009).

Based on the hypothesis that herbivore use of burns is driven by forage benefits, we predicted that (1) elk selection for burns would be strongest at previously documented peaks in feeding activity (i.e., around sunrise and sunset); (2) seasonal elk selection for burns would be strongest in spring before forage begins to senesce; and (3) elk would choose burns for a period that is long relative to the lifespan of individual elk (i.e., ≥ 15 yr post-burn, the scope of our analysis). Alternatively, predation risk or thermal costs may force temporal trade-offs that moderate herbivore use of burns and limit the benefits herbivores derive from post-burn forage. Under this hypothesis, we would expect elk selection for burns to shift with temporal patterns in predator activity or temperature: elk should select burns at night, but avoid them during the day. To test these predictions we used an experimental design that included replicated prescribed burns and 21 yr of animal-location data (1996–2016; 6 yr pre-burn, 15 yr post-burn) to quantify the effects of fire on elk behavior across three temporal scales: circadian, seasonal, and successional. First, we used selection ratios to identify circadian and seasonal patterns of

selection (Fig. 1A). To do this, we took the mean of selection ratios calculated for each individual. Second, we used discrete choice modeling to test of the magnitude and duration of elk behavioral responses to fire history at the successional scale (measured as years since burn) while accounting for the circadian and seasonal structure identified in our analysis of selection ratios (Fig. 1A; Manly et al. 2002).

METHODS

Study area

In 1987, the U.S. Forest Service erected 64 km of 2.4-m woven wire fence to create an ungulate enclosure at the Starkey Experimental Forest and Range in northeastern Oregon, USA (Starkey; Fig. 1B; Rowland et al. 1997). With a main study area containing 7,768 ha, the enclosure is mostly forested with grasslands and meadows where soils are too wet or shallow to support trees (Long et al. 2008b). Between 2001 and 2003, 26 mesic stands of fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) were mechanically thinned and burned as part of a large-scale fuels reduction effort, whereas 27 similar stands were left untreated as an experimental control (Fig. 1B; Long et al. 2008a,b). Between 1996 and 2016, pre-birth-pulse elk density varied from 4.2 to 7.6 elk/km² (Oregon Department of Fish and Wildlife, ODFW, unpublished data; for methods, see Noyes et al. 1996, 2002). Elk density was highest at the beginning (1996–1997) and end (2012–2016) of the study. High female harvest led to a steady decline in elk density 1997–2002 and densities remained low 2003–2010 before increasing 2011–2016 (ODFW, unpublished data).

Telemetry Location Data

Female adult (≥ 2 yr of age) elk in Starkey were captured during 1996–2016 and outfitted with long-range navigation system, version c (LORAN-C, 1996–2006; $n = 432$; Carrel et al. 1997) or Global Positioning System (GPS, 2003–2016; $n = 282$) collars in accordance with IACUC 92-F-0004. On average, 34 collars were deployed annually (minimum = 18, maximum = 60; Appendix S1). LORAN-C collars collected location data on a rotating schedule relying on an internal receiver to triangulate positions relative to fixed radio-tower beacons (Dana and Hindman 1989). GPS collars acquired, at minimum, hourly locations for each animal. We excluded data from LORAN-C collars that collected $< 85\%$ of expected locations and all GPS collars successfully collected $\geq 85\%$ of scheduled fixes, limiting our concern over habitat-induced bias (Hebblewhite et al. 2007). We subset GPS and LORAN-C location data to a consistent hourly schedule and analyzed all locations collected from 1 May to 19 August of each year. This period was chosen to follow departure from the winter range and to precede hunt seasons, which introduced a change in the magnitude and spatial distribution of human disturbance (Wisdom et al. 2005). We did not account for changes in elk behavior surrounding parturition because this change in behavior is relatively brief (typically < 6 d; Vore and Schmidt 2001), especially compared to the calving window (typically 6 weeks, but sometimes months longer; Cook et al. 2004, Keller et al. 2015).

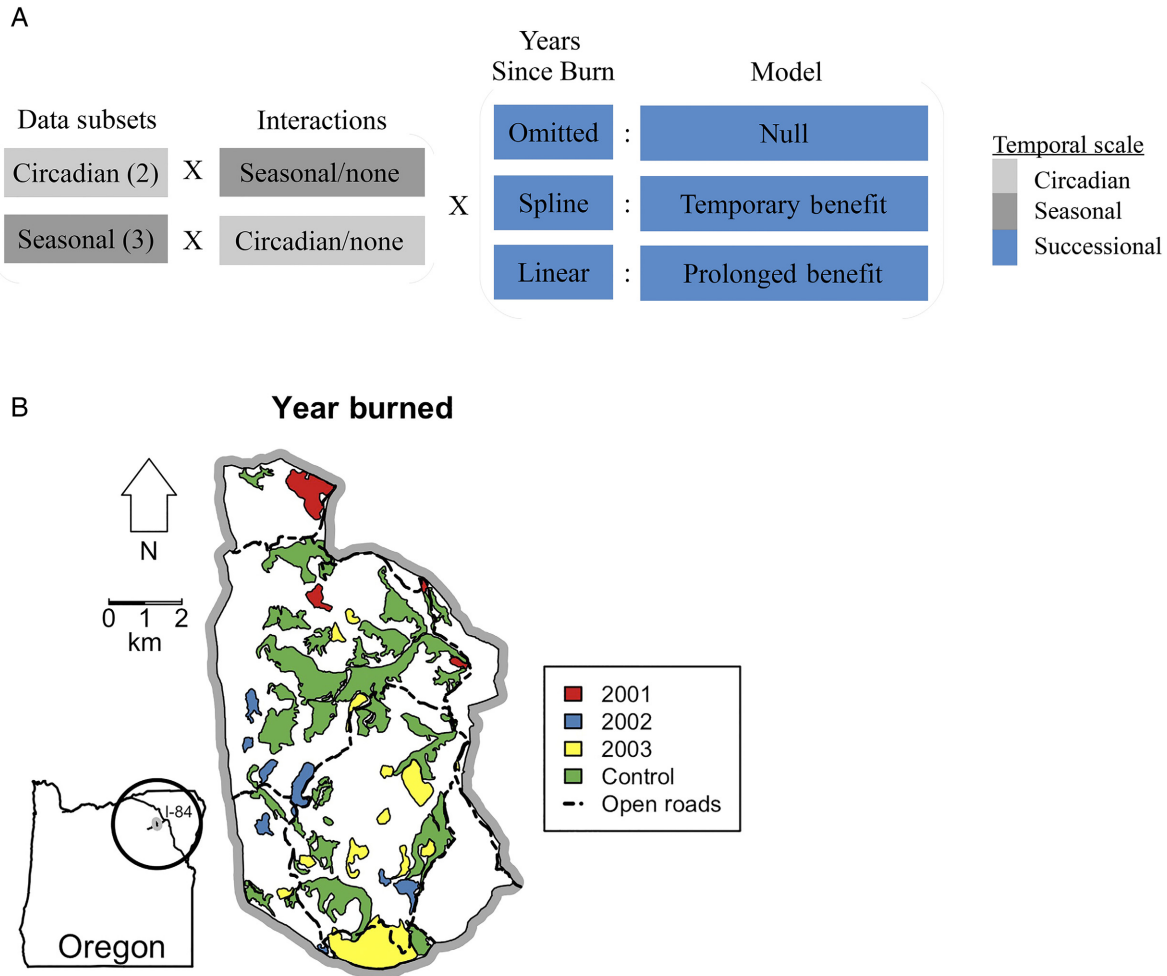


FIG. 1. (A) Schematic of our discrete-choice models quantifying elk (*Cervus canadensis*) behavioral responses to years since fire in north-eastern Oregon, USA. To limit model complexity, we fit models separately to each of five overlapping subsets of our data (two circadian, three seasonal). These divisions were created using categorical variables based on our analysis of circadian and seasonal changes in elk selection ratios for burns (see “Discrete-choice models” for details). Fitting separate models to each subset allowed us to account for seasonal and circadian structure by including interaction terms with our circadian categorical variable in models of seasonal subsets and vice versa. To test the importance of these temporal interaction terms, we also fit a second version of each model that omitted these terms. We fit three core models, each representing a different relationship between elk relative probability of use and years since burn. Thus, the result was six models for each subset (testing three relationships to years since burn, each with and without temporal interactions). The data we fit to these models were collected within (B) the main study area of Starkey Experimental Forest and Range, which is bounded by an ungulate-proof fence (7,768 ha). During 2001–2003, 26 stands of fir (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii*) were treated with prescribed fire (red, blue, yellow). Twenty-seven similar stands were held as experimental controls (green).

Selection ratios

To test for circadian and seasonal patterns in elk behavior, we performed a series of univariate analyses of selection for treatment (i.e., burned during this study) and control (i.e., unburned) locations. An animal’s probability of selection for a given resource i can be represented by a selection ratio

$$s(i) = \frac{\% \text{ use}_i}{\% \text{ available}_i} \quad (1)$$

which answers the question, is resource i used more or less than would be expected by chance (Manly et al. 2002). We interpret values >1 as selection, values <1 as avoidance and

values equal to 1 as indifference. Throughout, we estimated selection ratios by individual that we then combined to calculate a population mean. To identify circadian patterns in behavior, we compared hourly selection ratios for treatment and control locations. To limit the influence of seasonal structure, we calculated hourly selection ratios pooling locations by month within each year. We then tested for seasonal changes in elk selection for burns by calculating daily selection ratios for burns using a symmetrical moving window with a width of 21 d. Based on our analysis of circadian structure, we separated location data into diurnal and nocturnal periods for subsequent analysis of seasonal structure. Because elk were capable of traversing the study area in a matter of hours, we defined availability throughout as the area within Starkey’s main enclosure.

Discrete-choice models

We used discrete-choice models to quantify the phenology of elk's behavioral response to fire at the successional scale (i.e., as a function of years since burn) while accounting for other spatial variables known to influence elk resource selection. Within these models, we also tested the explanatory importance of circadian and seasonal structure identified in our selection ratios analyses. Following Manly et al. (2002) and McDonald et al. (2006), we estimated $C(i)$, the relative probability of use (Lele et al. 2013), sometimes also referred to as the relative probability of selection (Manly et al. 2002, McDonald et al. 2006) for resource unit i , as

$$C(i) = \frac{\exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_p x_{ip})}{\sum_{k \in (U' \cup A)} \exp(\beta_1 x_{k1} + \beta_2 x_{k2} + \dots + \beta_p x_{kp})} \quad (2)$$

where x_{i1} – x_{ip} were resource unit characteristics, β_1 – β_p were the coefficients associated with these characteristics, each unit represented a 30×30 m pixel, and k included the indices for all units in the choice set (i.e., the set of unique used units, U' , and all available units, A). Thus, the relative effect of setting explanatory variable p to value x_i can be estimated as

$$\exp(\beta_p x_{ip}) \quad (3)$$

and interpreted analogously to selection ratios with values >1 interpreted as having a positive effect, values <1 as having a negative effect, and values ~ 1 no effect on the probability of use. The comparative importance of explanatory variables can also be compared using Wald statistics, coefficients divided by their estimated standard errors (Hosmer et al. 2013). The absolute value of Wald statistics represents their relative strength, with positive and negative values respectively indicating increase and decrease in the probability of use.

We evaluated support for temporal patterns in elk spatial behavior by fitting a set of a priori models and comparing the results using Akaike information criterion (AIC; Burnham and Anderson 2002). We fit three core models, each representing a different behavioral response to years since burn: our null model omitted years since burn, our “temporary effect” model included years since burn as a penalized spline with a cubic basis to limit model complexity while still allowing for a shape with the predicted initial rapid rise and gradual decline (Thurston et al. 2002), and our “prolonged effect” model included years since burn as a linear term (i.e., indicating that the effect of years since burn had not yet peaked; Fig. 1A). All models included an identical suite of spatial covariates to control for other factors known to influence elk resource selection behavior. Additionally, to test the importance of accounting for circadian and seasonal shifts in behavior, we (1) created circadian and seasonal categorical variables subjectively based on the temporal structure observed in our analysis of selection ratios; (2) divided our data into subsets based on these categorical variables so that we could model circadian and seasonal effects separately (limiting model complexity); (3) fit each resulting subset to two versions of our core models: the first including interactions between spatial covariates and our categorical temporal variables and the second omitting these interactions; and (4)

compared these models using AIC. The resulting subsets included diurnal (day, >30 min after sunrise and >30 min before sunset), nocturnal (night, >30 min after sunset and >30 min before sunrise), spring (1 May–6 June), early summer (7 June–14 July), and midsummer (15 July–19 August). These divisions overlapped, such that, e.g., our “nocturnal” division and “spring” division both included nocturnal spring locations. We used the day and night subsets to test seasonal interactions and used the seasonal subsets to test circadian interactions. Thus, for example, our models testing circadian structure were fit to the seasonal subsets of our data and included interactions between each core covariate and our circadian categorical variable (day/night), i.e.,

$$C(i) = \frac{\exp\left(\beta_1 \times x_{i1} + \beta_{1n} \times x_{i1} \times \text{night} + \dots + \beta_p \times x_{ip} + \beta_{pn} \times x_{ip} \times \text{night}\right)}{\sum_{k \in (U' \cup A)} \exp\left(\beta_1 \times x_{k1} + \beta_{1n} \times x_{k1} \times \text{night} + \dots + \beta_p \times x_{kp} + \beta_{pn} \times x_{kp} \times \text{night}\right)} \quad (4)$$

where “night” is the circadian categorical variable (0/1) and all other terms are as already defined. The interactions we included were constructed so that base predictions referred to diurnal use (for circadian interactions) or spring (for seasonal interactions). Thus, with the “ $\beta_{1n} \times x_{i1} \times \text{night}$ ” interaction as an example, if the β_{1n} term was found to be significant, we could interpret this term as evidence for diel shifts in the relative probability of elk resource use with respect to variable x_1 , with the β_{1n} term indicating the size and direction of the difference in the relative probability of use between nocturnal and diurnal behavior. Thus, the result was five model sets (one for each data subset), each of which contained six a priori models (three relationships to years since burn, each with and without temporal interactions), with base predictions for day, night, spring, early summer, and midsummer, respectively.

We created choice sets for each used location by generating five available locations at the same time step. These locations were randomly selected without replacement from a ring-shaped raster with approximate outer radius 555 m and inner radius 210 m. The outer bound was based on half the 0.9 quantile of observed step lengths, while the inner bound was based on the maximum imprecision associated with our spatial data (to reduce false negatives; Carrel et al. 1997). Both measurements were rounded to conform to the 30×30 m pixels that constituted our sample units. Before selecting available locations, we first excluded all areas inaccessible to elk (e.g., grazing exclosures). To control for other factors influencing elk resource use, we consulted the literature for covariates of established importance at Starkey (Ager et al. 2003, Long et al. 2008a, Coe et al. 2011) and then tested for (but failed to find) correlated variables (pairwise $|r| > 0.6$). Our resulting models controlled for canopy cover (%), cattle presence (daily, 1/0), eastness (sine of aspect), elevation (m), fir (*Abies* spp. or *Pseudotsuga menziesii* dominant, 1/0), northness (cosine of aspect), roads (distance to nearest open road, km), slope (degrees), soil depth (cm), and water (riparian areas defined as sites ≤ 100 m of streams, 1/0). Values for elevation, northness, eastness, and slope were drawn from a digital elevation model, and canopy

values were imputed from LEMMA's generalized nearest neighbor model (Ohmann et al. 2014). All covariates were sampled at a 30×30 m resolution. To improve model fit and facilitate interpretation, we centered and standardized all continuous variables by dividing by two standard deviations (Gelman 2008). We fit all models using Cox proportional hazards regression with models stratified by choice set and clustered on individual. All analyses were conducted in R (R Core Team 2014; Version 3.3.1).

RESULTS

Selection ratios

We found strong evidence of circadian and seasonal structure in selection of burned areas by elk. Mean selection ratios for treatment and control locations were initially similar, but diverged following fire (Fig. 2; Appendix S2). Elk selection for burns showed steep crepuscular transitions and seasonal trends 1–13 yr post-burn (2001–2014); strong nocturnal selection for burns during spring and summer weakened later in the year. In contrast, diurnal indifference to burned areas early in the year transitioned to strong avoidance by midsummer (August; Fig. 2). These patterns shifted in our last 2 yr of data, where we saw early-day avoidance transitioning to late-day selection (2015–2016; Fig. 2; Appendix S2). Our final years of data retained greater diel and seasonal structure than we observed pre-burn.

Analyzing diurnal and nocturnal locations separately revealed seasonal patterns in selection that pooling locations across these time periods would have obscured (Fig. 3). Nocturnal selection for burns early in the year was positive in all post-treatment years save the last two. Diurnal selection for burns was inconsistent among years and, when present, was of lower magnitude and shorter daily duration than nocturnal selection. Nocturnal selection for burns peaked in early summer, contrary to our expectations of an earlier peak in spring (Fig. 3). Additionally, prior to 2015, elk showed diurnal indifference to burns in spring, but avoided burns late in the year (August and later; Fig. 3, Appendix S3). Finally, in the last two post-treatment years, elk appeared indifferent to burns at night and began to show diurnal selection for burns.

Discrete-choice models

Our discrete-choice models universally supported the inclusion of circadian and seasonal interactions and the use of a penalized spline to quantify the effect of years since burn on elk use of burned areas ($AIC_w \sim 1$ for all top models, where the AIC weight, AIC_w , is a model's relative likelihood—e to the power of $-0.5 \Delta AIC$ —divided by the sum of relative likelihoods for all models; Appendix S4). At the successional scale, fire did not cause any observable short-term decline in use of burns by elk, but instead was followed by a long-term increase in nocturnal use of burns that peaked quickly (5 yr post burn) before gradually declining to pre-treatment levels over a total of 15 yr (Fig. 4).

Diurnal elk behavior showed strong and consistent avoidance of roads, but nocturnal avoidance of roads was much weaker and bordered on indifference in spring (Table 1).

Similarly, elk's relative probability of using canopy cover was far higher during the day than at night and elk even avoided canopy in spring and early summer. The relative probability of elk using deeper soils was similar at day and night and increased in later seasons. In later seasons, the relative probability of elk using fir also increased and was typically greater during the day than at night. Elk generally selected higher elevations, only using lower elevations during the day in mid-summer. Relationships to northness and eastness also varied temporally, but changes in both direction and magnitude left no clear pattern. Throughout, elk consistently avoided cattle, steep slopes, and riparian areas, but the importance of these relationships varied with time of day and season.

DISCUSSION

Our results are consistent with herbivores deriving nutritional benefits from burns, but contradict the hypothesis that herbivore use of burns is determined solely on the basis of nutrition. Instead, we found support for our alternative hypothesis, that temporal trade-offs moderate herbivore use of burns. For much of the year, elk displayed circadian “commuting” behavior in which their relative selection for burned and unburned areas switched near dusk and dawn. The strongest selection for burns did not, however, coincide with previously reported crepuscular peaks in foraging activity (e.g., Frair et al. 2005, Naylor et al. 2009). This discrepancy suggests that the most important foraging hours for elk in our system are nocturnal rather than crepuscular and that elk in our study relied on unburned areas to reduce daytime costs of thermoregulation, predation risk, or exposure to anthropogenic disturbance. Nocturnal foraging in elk is consistent with previous observations of elk selecting open areas with higher quality forage at night and areas with denser, less nutritious vegetation during the day (Ager et al. 2003, Roberts et al. 2017). Nocturnal foraging and diurnal inactivity are also seen in a close relative of elk, red deer *Cervus elaphus* (Godvik et al. 2009). Rather than being driven strictly by fire, the commuting behavior we observed therefore appears to be part of a more general strategy of alternation between diurnal hiding in vegetative cover and nocturnal feeding in more open areas.

Merrill (1991) reported that elk compensated for landscape-scale disturbance by increasing nocturnal feeding, which emphasizes the plastic nature of these behavioral patterns. This suggests that disturbances like fire play a dual role in providing short-term forage benefits that herbivores enjoy at night, but simultaneously reducing the cover these animals depend on during the day. Unfortunately, in environments with vertical vegetative structure, post-fire increases in temperature, forage quality, and visibility are correlated making it difficult to disentangle the relative importance of potential mechanistic drivers of herbivore behavior (Greene et al. 2012). We were, consequently, unable to distinguish between anthropogenic disturbance, thermoregulation, and predation risk as possible drivers of commuting behavior, and recommend this as a direction for future research.

As predicted, elk seasonal selection for burns declined across summer, consistent with the phenology of senescence, but selection for burns peaked later than expected, in early summer rather than spring. Large herbivores are known to

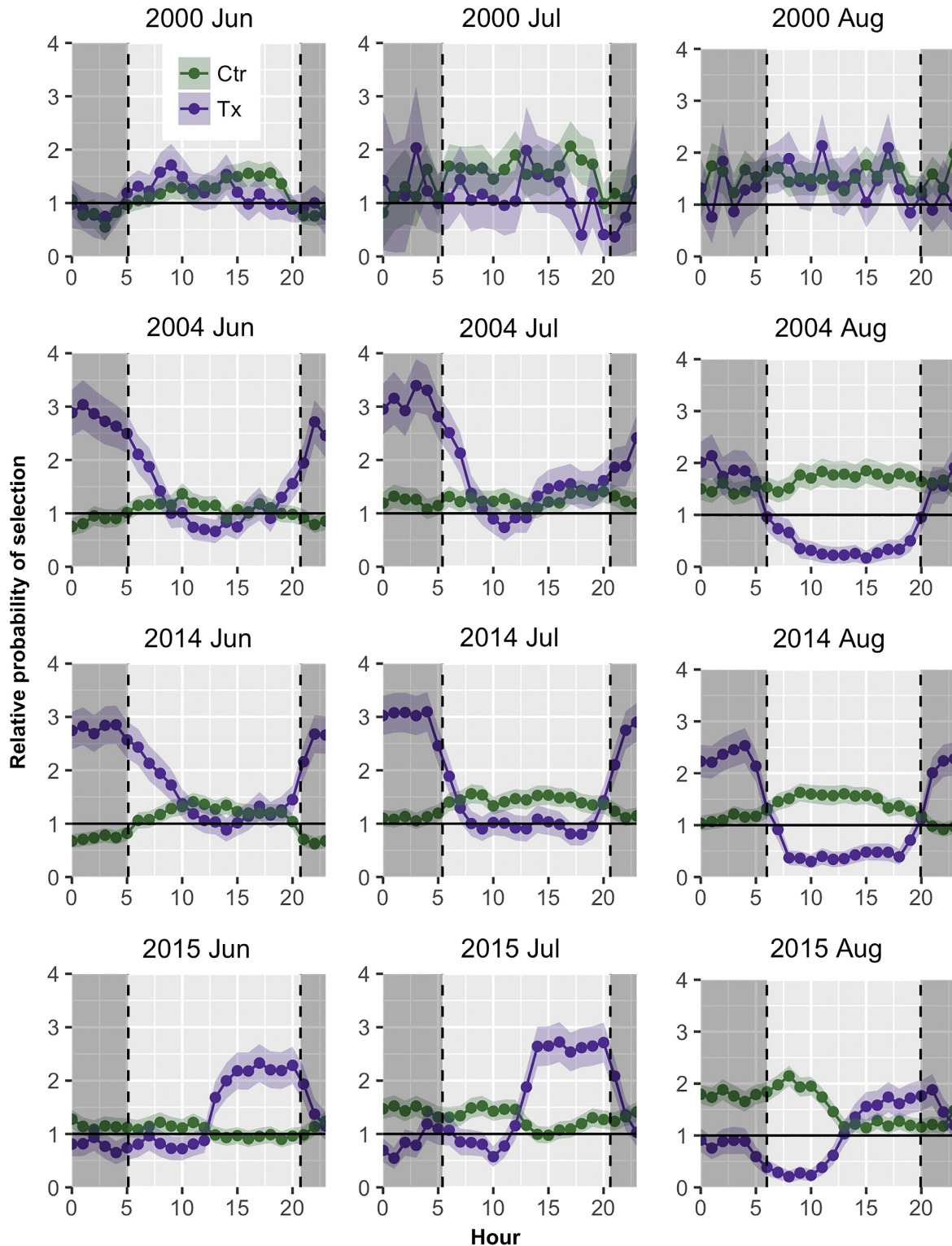


FIG. 2. Hourly selection ratios with 95% confidence intervals of elk (*Cervus canadensis*) for burned treatment (purple) and unburned control (green) locations. The interval between sunrise and sunset is shown shaded in dark gray. Pre-treatment (2000), the relative probability of selection for treatment and control locations was comparable (largely overlapping) with wide confidence intervals near or overlapping indifference (i.e., relatively probability of use = 1) and little circadian or seasonal structure. Post-treatment (2004–2014), elk relative probability of selection for burned and unburned locations diverged with behavior toward burns showing steep crepuscular transitions and seasonal trends; strong nocturnal selection for burns (Jun, Jul) weakened later season (Aug). In contrast, diurnal behavior toward burns moved from indifference to strong avoidance. Steep crepuscular transitions were no longer visible in 2015 (i.e., 12–14 yr post-burn), but these years still contained greater temporal structure than pre-treatment years. Results for all years are presented in Appendix S2.

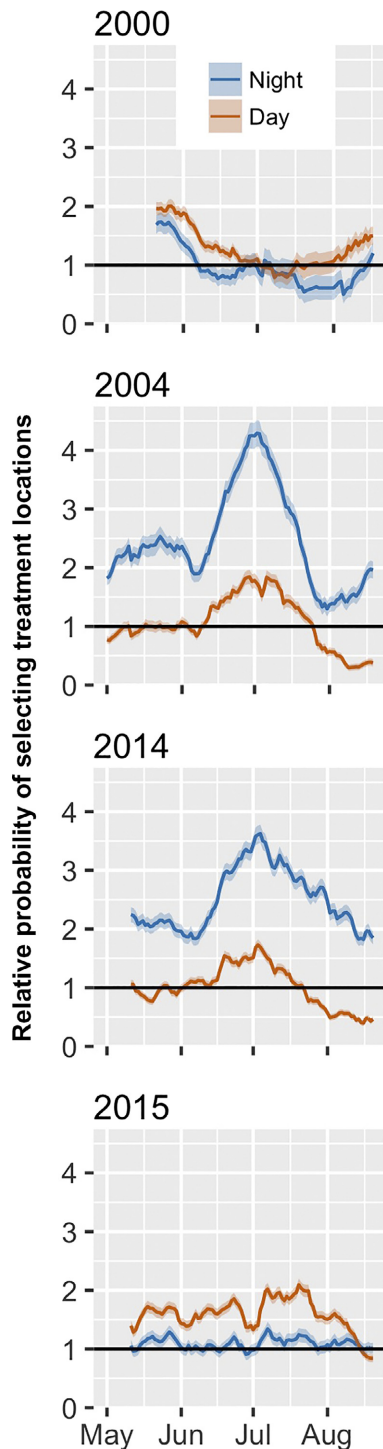


FIG. 3. Daily selection ratios with 95% confidence intervals of elk (*Cervus canadensis*) for burns. Pre-treatment (2000) diurnal (orange) and nocturnal (blue) relative probability of selection appeared consistent and lacked clear seasonal pattern. Following treatment (2004–2014), diurnal and nocturnal relative probability of selection diverged, with nocturnal behavior showing increasingly strong and persistent selection and diurnal behavior showing indifference in spring, weak selection in early summer, and avoidance in midsummer. By 2015 (12–14 yr post-burn), nocturnal selection returned to indifference, approximating pre-treatment behavior, while diurnal selection persisted through mid-August and no longer showed strong late-season avoidance. Pooling diurnal and nocturnal data obscured these patterns. Results for all years are Appendix S3.

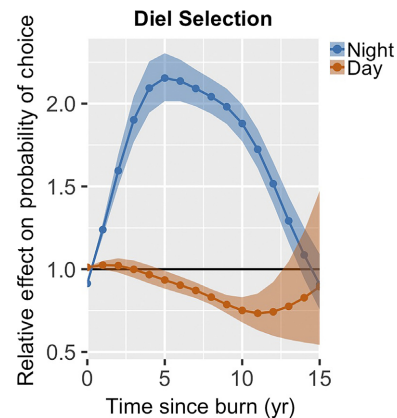


FIG. 4. Predicted relative effect of time since burn on elk (*Cervus canadensis*) resource selection behavior in spring with 95% confidence intervals (0 refers to pre-burn conditions). Separate predictions are shown for diurnal (orange) and nocturnal (blue) elk behavior (based on separate models, see “Discrete-choice models” for details). For up to 14 yr post burn, burns increased the probability of a location being chosen by an elk at night (blue, values > 1). Elk nocturnal choice for burns peaked 5 yr post-fire and gradually declined thereafter. In contrast, during the day, elk were indifferent to recent burns (orange, values ~1), but burns aged 6–12 yr decreased the probability of a location being chosen by elk.

pursue green-up as a means of maximizing nutritional intake (Merkle et al. 2016). Long et al. (2008b) found evidence that reduction in canopy structure following fire accelerated plant phenology at burned sites, perhaps a consequence of increased solar radiation. Phenology, however, also varies across plant communities, and the combined effects of taxa and environmental factors can result in differences in growing seasons that span several weeks (Stewart et al. 2006). Thus, our observation of later than expected seasonal use of burned areas likely reflects variation in phenology among vegetative communities and/or environments that resulted in increased availability of nutritious early-season growth in non-forested areas, especially grasslands.

We do not expect the interpretation of our main results to be affected by changes in elk density over the course of our study, but density may nonetheless play an important role in determining the duration of the successional-scale behavioral responses. As with many species, elk resource selection is density dependent; high densities of animals have the potential to weaken signals of selection as competition restricts use of high quality areas or diminishes the value of these areas through overuse (e.g., van Beest et al. 2014). Furthermore, Stewart et al. (2006) illustrated how net aboveground primary productivity of plant species declines at high ungulate densities, which could offset post-fire nutritional benefits for herbivores. Consequently, fire’s nutritional benefits may be more durable when herbivore densities are lower or intermediate. In fact, large fires typically reduce large-herbivore populations (McMullen et al. 2017). For example, malnutrition drove an estimated 24–37% decrease in Yellowstone’s elk population in the first winter following the 1988 fires (Singer et al. 2004). In our study, a larger proportional decline in density (~44%) began prior to our fire treatments as a result of human hunting (i.e., increased tag numbers in service of other research objectives; Noyes et al. 2002) rather than malnutrition.

TABLE 1. Wald statistics for (A) main terms and (B) interaction terms from top models of resource selection by elk (*Cervus canadensis*).

	Covariate									
	Canopy	Cattle	East	Elevation	Fir	North	Road	Slope	Soil	Water
(A) Model										
Day	24.1	-5.5	11.3	-6.9	15.1	-4.3	33.1	-25.7	20	-2.9
Night	6.1	-9.7	-5.3	3.1	10.6	11.7	10.6	-9.7	17.9	-5.8
Spring	-4.7	—	-7	5.4	0.1	1.5	-0.3	-9.5	-8	-15.1
Early Summer	-3.8	-4.6	-14	5.3	5	3.9	5.7	-11.2	2.6	-8
Midsummer	5.5	-10.3	-5.2	4.6	18	11	10.3	-11.3	17.9	-6.3
(B) Interaction										
Day:Spring	-13.3	—	-5	17.4	-5.3	-1.3	-0.5	9	-18.5	-7.1
Day:Early Summer	-5.4	1	-2.3	10.4	-3.3	-5.2	1.5	1.6	-8.6	-0.3
Night:Spring	-10.1	—	-1.7	1.9	-16.4	-8.3	-5.9	-2.8	-17.1	-10
Night:Early Summer	-9.2	1.6	-6.4	1.1	-9.5	-6.8	-1.2	-2	-11.2	-1.8
Spring:Day	6.6	—	8.5	3.1	1.9	-6.7	16.5	4.8	0.5	9.1
Early Summer:Day	12.9	2.2	17.5	-0.7	-4.1	-12.1	15.1	-2.3	4	5.6
Midsummer:Day	10	5	12.4	-10.3	-7.4	-10.5	16.7	-7	-0.5	3.8

Notes: Results from one top model are shown for each of five data groupings (day, night, spring, early summer, and midsummer locations; see “Discrete-choice models” for details). Covariate abbreviations include cattle (cattle present), elevation, road (distance to nearest road), soil (soil depth), and water (locations ≤ 100 m from streams). All continuous variables were centered and standardized (cattle, fir, and water terms were categorical). Temporal interactions varied by model with models fit to diel groupings (day/night) including seasonal interactions and models fit to seasonal groupings (spring, early summer, and midsummer) including diel interactions. Interactions are listed as the data grouping followed by the interaction term. Dashes indicate omitted terms. Night and midsummer were held as reference categories.

Consequently, elk only reached higher densities toward the conclusion of our study. This increase in elk density may have led us to underestimate the duration of fire history's effects on elk and the relative strength of elk selection for burns in later years. In light of these changes in density, circadian and seasonal patterns in elk behavior may be more pronounced than our results suggest but, based on the maximum density of elk we observed, we expect this effect to be small. It is therefore unlikely that reducing elk densities would significantly prolong these behavioral effects beyond the duration we observed.

Past attempts to evaluate herbivore responses to fire at successional time scales have often found only weak or ambiguous effects 1–5 yr post-fire (Long et al. 2008b, Biggs et al. 2009), leading to speculation that post-fire forage benefits are delayed and manifest at coarser temporal scales. In contrast, the results of our discrete-choice models showed no delay in ungulate selection for burns at night and also indicate that the duration of these benefits (~ 15 yr) is relatively short compared to successional timescales (Skovlin et al. 2002). The relatively short duration of these effects may, in part, stem from rapid regeneration. In our system, prescribed fire greatly reduced the density of older age class trees, but even in the immediate aftermath of fire (2–5 yr post burn), burned and unburned stands had similar densities of several species of young trees (Long et al. 2008b). In addition to reducing understory growth by limiting light, dense stands may discourage ungulate use by impeding movement (Beyer et al. 2016). Still, the persistence of temporal structure in elk behavior through the end of our study contrasts with pre-burn conditions, suggesting that even our 21-yr time series was insufficient to capture the full duration of fire effects on elk behavior in this system.

Additionally, our results emphasize the value of testing and accounting for temporally dynamic behavior, especially in resource selection analyses attempting to draw inference at coarser temporal scales. Elk commuting behavior

exemplifies this problem. Based on the assumption that ungulates like elk are crepuscular foragers, numerous past studies have focused on analyzing locations within an hour of sunrise and sunset (Green and Bear 1990, Long et al. 2008a, Coe et al. 2011). These crepuscular windows were precisely the time periods in which we saw the steepest transitions in resource-selection behavior. In many instances, a series of three locations sampled from either of these windows would illustrate three distinct behaviors: selection, indifference, and avoidance (e.g., August 2004, before, at, and after sunset, respectively; Fig. 2). We propose that these countervailing signals are likely to cancel out, which may explain why past efforts to model large-herbivore resource selection have had difficulty detecting behavioral responses to fire history despite strong theoretical expectations (Long et al. 2008a). Many species have some degree of behavioral plasticity that allows them to respond to changes in environmental conditions, but modeling these capacities remains challenging (Muñoz et al. 2015). This behavioral plasticity often leads to behavioral cycles that have important implications for coexistence of competitors (Monterroso et al. 2014), coexistence of predators and prey (Lone et al. 2017), and adaptation under climate change (Muñoz et al. 2015). For example, Monterroso et al. (2014) found that most members of a diverse carnivore community exhibited substantial plasticity in diel activity patterns and that pairwise temporal overlap in species activity declined as the number of predator species present increased. This in turn supports the hypothesized importance of temporal behavior in allowing the coexistence of similar species (MacArthur and Levins 1967). In the past, the availability of animal location data has limited our ability to resolve behavioral changes, but as the resolution of these data continues to increase (Kays et al. 2015) so too do our opportunities to test our assumptions about these behaviors. We encourage other authors to more explicitly consider the assumption underlying resource selection methods that behavior is constant

through time and to test this assumption when it may be influential.

The circadian and seasonal patterns we observed are only possible within landscapes that are spatially heterogeneous. Individuals may only commute between burned and unburned forest, for example, if these areas occur close together in space. Maintaining landscape heterogeneity should therefore be a consideration when managing fire to benefit herbivore populations (Fuhlendorf et al. 2006). However, changing fire regimes highlight three potential threats to the continuance of this spatial diversity: fires are changing in size, frequency, and severity. Climate-driven changes to fire regimes over the past century have led to increasing worldwide incidence of larger wildfires (Pechony et al. 2010). Fortunately, large fires typically leave a landscape mosaic (e.g., Foster et al. 2017) that may also benefit herbivores by expanding their access to a range of conditions with different attendant risks and rewards. Unfortunately, following anthropogenic fire suppression and the invasion of exotic grasses, the severity of large fires in many landscapes has intensified, resulting in increased landscape homogeneity post-fire (D'Antonio and Vitousek 1992, Turner and Romme 1994). Finally, even as the prevalence of large fires increases, climate-driven changes to fire regimes have reduced fire frequency in many regions, including our study area (Ager et al. 2014). In areas where fire frequency has declined, prescribed fire may prove key to maintaining landscape heterogeneity.

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SUPPORTING INFORMATION

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DATA AVAILABILITY

Associated data are available on Figshare: <https://doi.org/10.6084/m9.figshare.6937736.v1>