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Mule deer selection of fuel reductions is restricted by site fidelity and structured by circadian and seasonal patterns

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ABSTRACT

Forests in the western US have undergone a profound transformation over the last 100 years due to chronic fire suppression and a cycle of extensive timber harvest followed by little silvicultural activity. Forested landscapes in this region are now dominated by intermediate age, denser stands of coniferous trees that reduce transmission of light and precipitation to the understory, with potential consequences for ungulate nutrition. We used a 20-year dataset of mule deer locations (560 animal-years of data) to evaluate long-term patterns of selection of forest stands that had been thinned and burned compared to untreated reference stands. We evaluated within home-range (3rd order) selection at 3 temporal scales (hourly, daily, annually) and landscape-scale (2nd order) use annually. We found that annual selection of treated stands during summer generally increased with two peaks, once immediately after treatments were applied and again 15 years later. Mule deer also showed strong seasonal and temporal patterns in selection of treated forest stands. Deer selected treated stands at night in July and August immediately after treatments. After 4–6 years, mule deer selected treated stands both during the day and at night in May, July, and August, but with stronger selection at night. We hypothesize that preference for treated forest stands were driven by differences in forage quantity and quality among forest stands. Vegetation surveys during years of peak selection showed that treated stands had significantly higher biomass and digestible energy of neutrally selected forage and lower biomass of avoided forage species, although there was no difference in biomass of preferred forage species. A subset of female mule deer with multiple years of data did not shift home ranges to overlap with treated forest stands over time (2nd order use) but did show increasing selection over time for treated forest stands within their home ranges (3rd order). Our results show that thinning and burning of forest stands can benefit mule deer both immediately and for up to 15 years after treatment and that researchers should evaluate temporal and seasonal patterns in studies of habitat selection. Given the diverse habitat needs of mule deer, treatments would be most beneficial if they were scattered across large landscapes and staggered in time to provide a diversity of forage and cover types.

1. Introduction

Forests in the western United States have undergone a profound shift in successional dynamics and stand composition during the last 100 years (Covington et al., 1994). Widespread logging has eliminated most late successional forests and suppression of natural wildfire has upended disturbance regimes (Lydersen et al., 2013; Naficy et al., 2010). Continued fire suppression, combined with sharp declines in timber harvest and other forest management on public lands since the 1990s, have shifted much of the landscape toward intermediate age forest stands (approximately 30–90 years old before stem exclusion occurs) with dense structure (Knapp et al., 2013; Merschel et al., 2014; Naficy

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et al., 2010). Moreover, intense summer drought from climate change has increased vulnerability of these dense forest stands to large stand-replacing wildfires that are uncharacteristic of historical fire regimes (Halofsky et al., 2020; McDowell et al., 2020).

Current forest and climate conditions requires action from land managers to minimize the risk of catastrophic wildfire, and adapt to climate change (Charnley et al., 2017; Halofsky et al., 2020; McDowell et al., 2020). Forest management of this magnitude will require both intensive and extensive stand-level timber and fuels management (Field et al., 2020), and in recognition of this challenge the US Forest Service has approved more than $3 billion of fuels-reduction funding for the period of 2022–2026. Much research has been conducted on the effects of various forest treatments on future fire risk (Kalies and Yocom Kent, 2016; Thompson and Calkin, 2011), but understanding the effects of forest treatments on wildlife populations is critical to maintain healthy wildlife populations (Stephens et al., 2021).

Ungulates are a culturally and economically important component of forest wildlife communities throughout the western US. Extensive landscape-level treatments have the potential to dramatically change available nutrition for ungulates (Rowland et al., 2018), and large changes in nutrition can in turn affect the population dynamics of ungulates (Cook et al., 2004; Hopcraft et al., 2010). Mid-sized ungulates such as mule deer (*Odocoileus hemionus*) must select the highest-quality forage available to maximize fitness and can be affected by changes in forage quality, even if overall forage biomass remains unchanged (Forrester and Wittmer, 2013). Spring and summer forage in particular have been shown to be critical for ungulates during gestation and lactation and for improving body condition prior to winter (Cook et al., 2013; Heffelfinger et al., 2020). Forage conditions on summer ranges can affect individual fitness by mediating changes in fawn survival and fecundity of adult females (Hurley et al., 2014; Merems et al., 2020), the two vital rates that are typically most important for population dynamics of mule deer (Gaillard et al., 1998). Summer forage can also impact the survival rate of adult females in some areas (Schuyler et al., 2019), a vital rate that can have large impacts on population growth if it varies (Gaillard et al., 2000, 1998). Mule deer and other ungulates prefer the higher quality forage that grows after low intensity disturbance (Cook et al., 2016; Visscher and Merrill, 2009). Available forage for ungulates is lower in intermediate age forest stands (Cook et al., 2016) and fire suppression has also been linked to lower forage quality for ungulates (Proffitt et al., 2019, 2016) while disturbance such as timber harvest has been shown to increase the quality and quantity of ungulate forage (Hull et al., 2020; Proffitt et al., 2016). These findings show a high potential for fuel treatments to benefit mule deer populations and evidence suggests that mule deer do select forest areas that have been burned or thinned (Bergman et al., 2014b; Roerick et al., 2019).

Several factors are likely to constrain ungulates' ability to fully exploit new forage resources after forest treatments. These factors include predation risk (Lowrey et al., 2019; Sinclair and Arcese, 1995), competition with other ungulates (Beck and Peek, 2005; Coe et al., 2001; Johnson et al., 2000), and site familiarity and memory (Forrester et al., 2015; Jakopak et al., 2019; Morrison et al., 2021a). Mule deer exhibit strong site fidelity even in the face of disturbance and changing landscapes (Brown et al., 2020; Morrison et al., 2021a; Sawyer et al., 2019), and this may constrain the ability of mule deer to exploit changes in forage resources that fall outside of their home ranges or migratory routes (Morrison et al., 2021a; Switzer, 1993). As a result, large scale changes in the spatial distribution of high-quality forage (e.g. large scale forest treatments) will likely have larger impacts on ungulates with high site fidelity that are unlikely to move across the landscape to exploit new resources or avoid recently degraded habitat (Morrison et al., 2021a).

Constraints on habitat selection (e.g., site fidelity, nutritional requirements, predation risk, thermal stress) (Stewart et al., 2002) can result in strong temporal patterns of habitat use as animals attempt to forage during periods where risks and/or costs are lowest. Analytical methods that pool locations over seasons or only use locations from certain time periods may obscure selection patterns that have a strong seasonal or circadian structure (Long et al., 2008; Spitz et al., 2018). This is especially true if individuals are selecting particular vegetation types only during certain times, or if animals spend the bulk of their time engaged in non-foraging behaviors (Bose et al., 2018). These temporal patterns are also likely to change over time as succession changes the availability of forage (Spitz et al., 2018). Understanding these short and long term temporal patterns of selection are critical to understanding the effects of forest treatments on mule deer and other ungulates, but most previous research on the response of mule deer to prescribed burning and thinning have been short-term studies and/or have mostly ignored temporal selection patterns (Klinger et al., 1989; Long et al., 2008).

We studied long-term responses of mule deer to thinning and burning of forest stands and examined circadian and seasonal patterns of selection. Our objectives were to determine to what degree mule deer selected forest stands that were thinned and burned (treated stands) relative to untreated stands of the same forest type, and to evaluate whether patterns of selection were structured by time of day, season, or age of forest treatments both before and after forest treatments. We used over two decades of location data to test several hypotheses regarding selection of treated stands by mule deer including: (1) mule deer would preferentially select treated forest stands over untreated stands at the 3rd order level (hereafter treatment preference hypothesis), (2) 3rd order selection of forest stands by mule deer would vary with time of day (i.e., nighttime vs. daytime hours) and across seasons (hereafter structured selection hypothesis), (3) strength of 3rd order selection for treated stands would change over the course of the study and coincide with forage availability (hereafter successional selection hypothesis), and (4) mule deer would not change 2nd order use by shifting their home ranges in response to forest treatments (hereafter site fidelity hypothesis).

2. Methods

2.1. Study area

The Starkey Experimental Forest and Range (hereafter Starkey) is a 101-km^2 research area managed by the United States Forest Service in northeastern Oregon. Elevations at Starkey range from 1120 m to 1500 m and the topography is mostly moderately sloping uplands with several drainages. Starkey consists of a mixture of vegetation types that include forest, grasslands, and thin-soil meadows with relatively low vegetative cover (Burscu et al., 2014). Forest types vary depending on soil type and moisture, and include ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), Douglas-fir/grand fir (*Abies grandis*), western larch (*Larix occidentalis*)/lodgepole pine (*Pinus contorta*), and less common forest types of grand fir/Engelmann spruce (*Picea engelmannii*) and grand fir/subalpine fir (*Abies lasiocarpa*) (see Rowland et al., 1997 for full site description). Starkey is enclosed by a 2.4-m high fence that prevents the movement of ungulates into or out of the research site and is divided into five distinct ungulate enclosures; our study was conducted in the 77.6-km^2 main study area. Starkey supported populations of coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) and had several mountain lions (*Puma concolor*) that included Starkey as part of their home range. The elk (*Cervus canadensis*) population in Starkey varied from 4.2 to 7.6 elk/km^2 (Oregon Department of Fish and Wildlife, *unpublished data*), with the highest elk densities at the beginning (1996–1997) and end (2012–2016) of the study. There were also 400–500 domestic cattle (*Bos taurus*) present inside Starkey each summer due to a grazing allotment. Cattle arrived in the study area around June 15 and the entire herd moved in a deferred rotation grazing system among five pastures inside the main study area. Cattle pastures were separated by barbed wire fences that did not impede the movement of mule deer, elk, or carnivore species. Female mule deer home ranges averaged 6.0 $\pm$ 0.71 km^2 in the summer (Brown et al., 2020) and mule deer density averaged roughly 1.95 deer/km^2 throughout the 22-year

study period, with a slight decline in density from 1997 to 2005 and evidence of a steeper decline from 2006 to 2018 (Oregon Department of Fish and Wildlife, unpublished data).

Fuels reduction treatments occurred in the main study area of Starkey from 2001 to 2003, when 26 mesic stands of Douglas fir, grand fir, and grand fir/subalpine fir were mechanically thinned and burned, while 27 similar stands were left untreated as experimental controls (Fig. 1; Long et al., 2008, Spitz et al., 2018). Each stand was thinned and burned with the objective of reducing fuel loads to <35 tons/ha (pre--treatment levels typically exceeded 150 tons/ha) (Bull et al., 2005; Endress et al., 2012). Treated stands ranged in size from 2.5 ha to 214.0 ha, while control stands were 4.0–168.2 ha. Vegetation surveys that documented forb, graminoid, and shrub abundance and digestible energy content of mule deer forage were conducted throughout Starkey in the spring and summer of 2016–2017, including in treated and control forest stands (Merems et al., 2020). We compared the slope, aspect, roughness (Wilson et al., 2007), and topographic position index (TPI) (Weiss, 2001) between the treatment and control units by calculating the mean value of each measure for each forest stand and calculating all values from a digital elevation model (DEM) with a 150 m x 150 m resolution with the terrain function from the `terra` package (Hijmans, 2022) in program R (v 3.6.1) (R Core Team, 2013). We tested the data with a Shapiro-Wolk's test to determine if it was normally distributed and compared the treatment and control unit values with a Welsh's t-test for independent groups with unequal variances.

2.2. Animal location data

Locations of 234 female adult (>= 2 yrs of age) mule deer were collected over a 22-year period (1996–2008) to evaluate pre- and post-treatment responses to fuels reduction. We used long range navigation (LORAN-C) technology to obtain deer locations from 1996 to 2006 (n = 142 collared deer and 338 animal years). Global positioning system (GPS) collars (models 4400 and 4500 Lotek, Newmarket, Ontario, Canada) were used to monitor deer movements from 2007 to 2018 (n = 92 collared deer and 222 animal years).

On average, we collared 22 deer annually (minimum = 5, maximum = 40). The LORAN-C collars obtained location fixes by using an internal receiver to triangulate positions relative to fixed tower locations (see Johnson et al., 1998 for specifications on the performance of LORAN-C collars). Both LORAN-C and GPS collars collected locations on an hourly interval at minimum, except for 2008–2015, when locations were obtained only at 0600 and 1800 h. These years were excluded from hourly and daily selection analyses but were included in analyses of annual selection. We subset all location data to hourly locations and excluded data from LORAN-C and GPS collars that collected < 85 % of scheduled fixes to reduce problems with area-induced bias resulting from low fix success rates (Johnson et al., 1998; Hebblewhite et al., 2007). We analyzed all locations collected from May 1 to August 19 each year, which captured all spring and summer locations after elk had arrived on summer range and excluded locations during hunting seasons within Starkey, which have been shown to alter patterns of ungulate habitat use

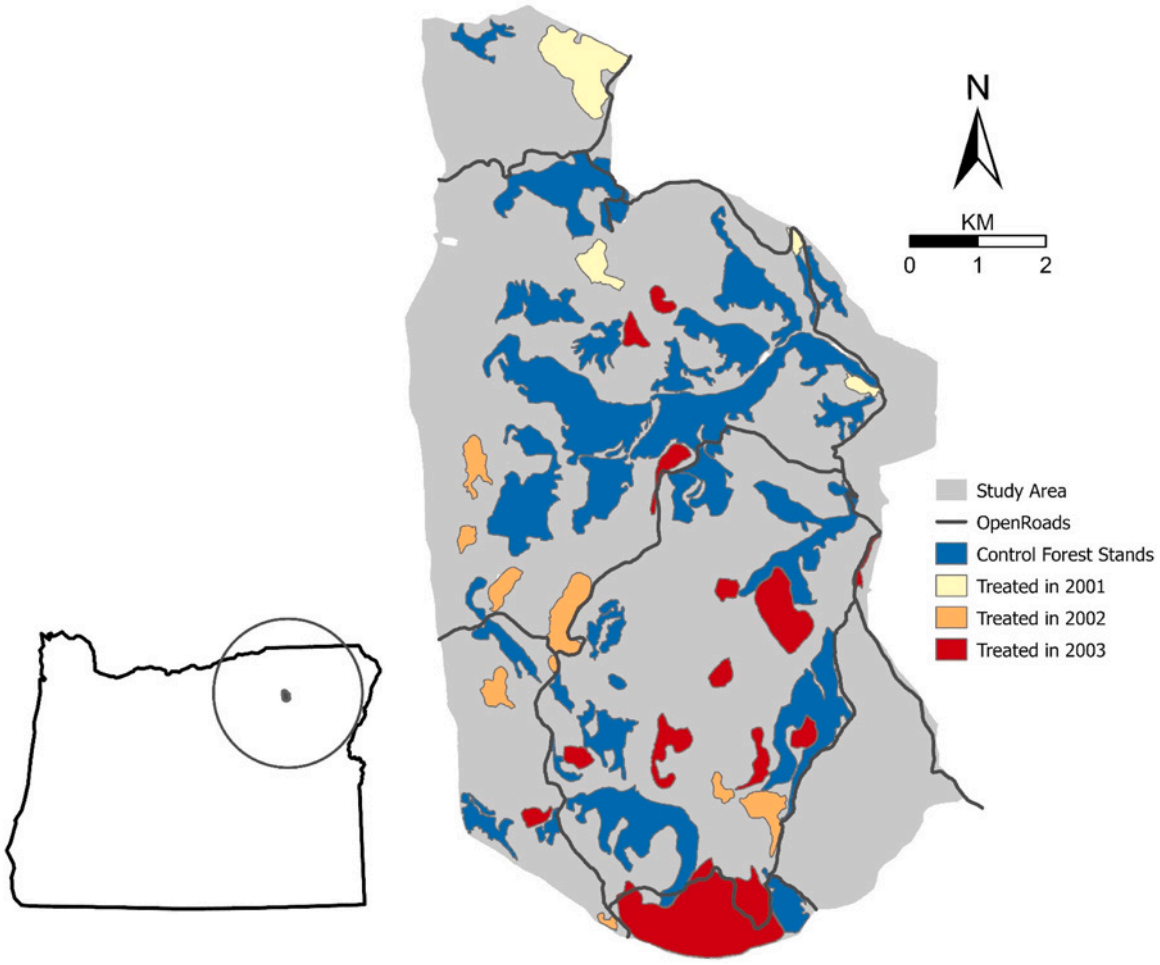

Fig. 1. The main study area in Starkey Experimental Forest and Range (77.6 km^2) in northeast Oregon. The study area is surrounded by an ungulate-proof fence and is traversed by two main roads. Fuels reduction treatments (mechanical thinning followed by prescribed burning) occurred in 26 forested stands during 2001, 2002, 2003 (yellow, orange, red respectively by year), while 27 similar forested stands were designated as experimental controls (blue).

due to increased human disturbance (Brown et al., 2020; Smith et al., 2022; Wisdom et al., 2004).

2.3. Treatment preference, structured selection, and successional selection hypotheses (3rd Order Selection)

Selection ratios of used versus available resource units provided a direct measure of the selection and avoidance of treated and control stands by season and year (Manly et al., 2007). We evaluated mule deer selection of treatment (i.e., thinned and burned) and control (i.e., untreated) stands with a series of univariate analyses to determine hourly (i.e., circadian), daily, and annual patterns of selection. An animal's relative probability of selection for a given resource *i* can be represented by the selection ratio:

$$s(i) = \frac{\%used_i}{\%available_i} \quad (1)$$

with a value of $s(i) > 1$ indicating selection, a value of $s(i) < 1$ indicating avoidance and a value of 1 indicating proportional use (Manly et al., 2007). We defined availability of treatment and control stands, respectively, for each deer in each year as the area of both types of forest stands that overlapped the 95 % isopleth of an adaptive kernel density (Fleming et al., 2015) home range of that individual deer and use as the percent of locations for each deer in each year in treatment and control stands.

We identified three different temporal scales (hourly, daily, and annually) to examine patterns of within home-range selection. We first estimated individual selection ratios for all deer that had at least one location within treatment and control stands (n = 177 deer and 368 animal years) and then calculated a population mean (hereafter population level estimates) with 95 % confidence intervals calculated using the variation in individual selection ratios. We used moving averages to identify trends and reduce the influence of stochastic variation at smaller time scales and seasonal patterns of habitat selection at larger time scales (e.g., Spitz et al., 2018). All rolling mean values were calculated with the `zoo` package for time series analyses in program R v3.6.1 (Zeileis and Grothendieck, 2005).We separated selection ratios into daytime and nighttime periods for analysis of selection at hourly and daily time scales.

2.4. Hourly habitat selection – structured selection hypothesis

We quantified mean hourly patterns of selection for treated stands across the 24-hour period using a moving average of 3 hours (i.e., each hour's selection ratio was an average that hour's selection ratio with the preceding and following hour's values). We separated these hourly selection ratios by month for each month in the study period (May through early August) to highlight shifts in hourly selection across the months in the study period.

2.5. Weekly habitat selection – structured selection hypothesis

We calculated mean daily selection ratios using a symmetrical moving window of 15 days (i.e., each day's selection ratio was an average of that day's selection ratio with the 7 preceding and following days) and separated daily selection by months to show changes in selection patterns over the spring/summer study period. We compared the mean selection of treatment and control stands and also separated all locations into day and night periods (defined by local sunrise and sunset) to determine if mule deer were exhibiting circadian selection patterns of treated forest stands (e.g. Spitz et al., 2018).

2.6. Annual selection – successional selection hypothesis

We calculated mean selection of treated and control stands across years using a symmetrical moving window of 21 days (i.e., each selection ratio was an average of that day with the preceding and following 10 days) to calculate multiple selection values per year. We then fitted a LOESS (locally estimated scatterplot smoothing) curve to these values to smooth the annual graph of forest stand selection across years and calculated 95 % confidence intervals (Gijbels and Prosdocimi, 2010). The LOESS method uses a low-order polynomial function to fit a curve to a local group of points within a given scatterplot while allowing the local section of the line to take either a linear or quadratic form, combining the simplicity of least squares regression with the flexibility of nonlinear regression (Gijbels and Prosdocimi, 2010). The LOESS curve was fit and confidence intervals for the line were calculated using the `loess` function in the `ggplot2` package in program R v3.6.1 (R Core Team, 2013; Wickham, 2016).

2.7. Changes in Individual 3rd-order selection of treated stands over time

Our goal for this post-hoc analysis was to determine if increases in the selection of treated forest stands were related to individual deer increasing 3rd order selection over time or if changes were more influenced by yearling deer establishing new home ranges that contained more area of treated forest stands than were available in the study area. As a result, we only used data from 2005 to 2016 when treated forest stands were available for selection and excluded 2017–2018 because of the sharp decline in selection at the population level and only included deer with two or more years of data (n = 45 deer and 136 animal years). We quantified whether individual deer were increasing their 3rd order selection of treated forest stands over time by fitting a generalized linear mixed model (GLMM) using a gamma distribution with a log link using the `lme4` package in program R v. 3.6.1 (Bates et al., 2015). We used a gamma distribution because selection ratios were positive and continuous and not log-normally distributed. We calculated mean monthly selection ratios from moving window weekly selection ratios above from May to August for individual deer as the response variable (4 values per deer per year) and included year as a continuous fixed effect. We fit models with a random intercept to account for repeated measures of individual and compared models using Akaike information criteria for small sample sizes (AIC_c). We predicted the selection ratio from this model for 2016 (the year of peak observed selection) and divided this value by the annual selection ratio from 2016 to estimate the proportion of change in population level selection that was accounted for by increases in individual deer selection.

2.8. Site fidelity hypothesis (2nd order habitat use)

To determine whether mule deer were changing 2nd order use for treated forest stands we calculated seasonal (May-mid August) home ranges for deer in the years after treatments were applied ($\geq$ 2004) and the overlap with treated forest stands for each year. We used autocorrelated kernel density estimation (AKDE) in the `ctmm` package in program R (Fleming et al., 2015) to calculate a separate seasonal home range for each year for each individual mule deer that had at least one location in a treatment (n = 45 deer and 136 animal years). We calculated the area of treated and control forest stands within the 95 % isopleth of deer home ranges for each year and individual by clipping the treatment units to each home range with gIntersection from the rgeos package in program R. We tested these area values for normality using a Shapiro-Wilk's test and by examining quantile-quantile plots (Kozak and Piepho, 2018), and log transformed data when necessary. If quantile-quantile plots showed $\leq$3 outliers, we treated the data as normal even if they failed the Shapiro-Wilk's test because this test is sensitive to outliers (Kozak and Piepho, 2018). We tested for changes in the area of both treatment and control stands within individual deer home ranges over time using a repeated measures analysis of variance (rmANOVA) in the `rstatix` package in program R v3.6.1 (Kassambara, 2023).

2.9. Mule deer forage differences in treatment and control stands

We conducted an analysis to determine if the amount and quality of forage differed between treatment and control stands during years of peak selection of treated stands by mule deer (2016–2017, 15–16 years after the first treatments occurred). Earlier years were not included in the analysis because of a lack of vegetation survey data. We used intensive vegetation survey data from 2016 to 2017 to compare the biomass of selected, neutrally selected (i.e., suitable but not preferred, hereafter referred to simply as neutral forage), and avoided forage species, and the digestible energy of preferred and neutral species between treatment and control stands (Merems et al., 2020). Merems et al. (2020) used a clip-and-weigh and double sampling method to estimate biomass of all forage species used by mule deer in Starkey and measured the digestible energy (DE) of those species in each potential vegetation type (see Merems et al., 2020 for full details). We only used data from sampling transects that fell within treated (36 transects) or control (66 transects) forest stands. We calculated biomass per area (kg/ha) to control for different numbers of transects in the treatment and control stands for all selected, neutral, and avoided forage species (Merems et al., 2020). We also compared DE content of forage between treatment and control stands by multiplying species-specific DE values by their corresponding biomass estimates to obtain the total digestible energy (KJ/kg) of each forage class (i.e., forb, graminoid, shrub), and then scaling those estimates by area (KJ/kg per ha) in each treatment and control stand (Merems et al., 2020). We tested for differences in biomass and DE of each forage class between treatment and control stands using linear models with stand type as a 2-level categorical variable; we report effect size for significant results as the percentage difference between the mean values for treatment versus control stands. If residuals from linear models were not normally distributed, we log transformed biomass or DE values. All linear models were run using the `lm` function from the `stats` package in program R (v3.6.1).

3. Results

3.1. Treatment preference, structured selection, and successional selection hypotheses (3rd order selection)

Treatment Preference and Structured Selection: Pre-treatment (1996) hourly selection for control and treatment stands was similar and proportional to availability, with little circadian or seasonal structure

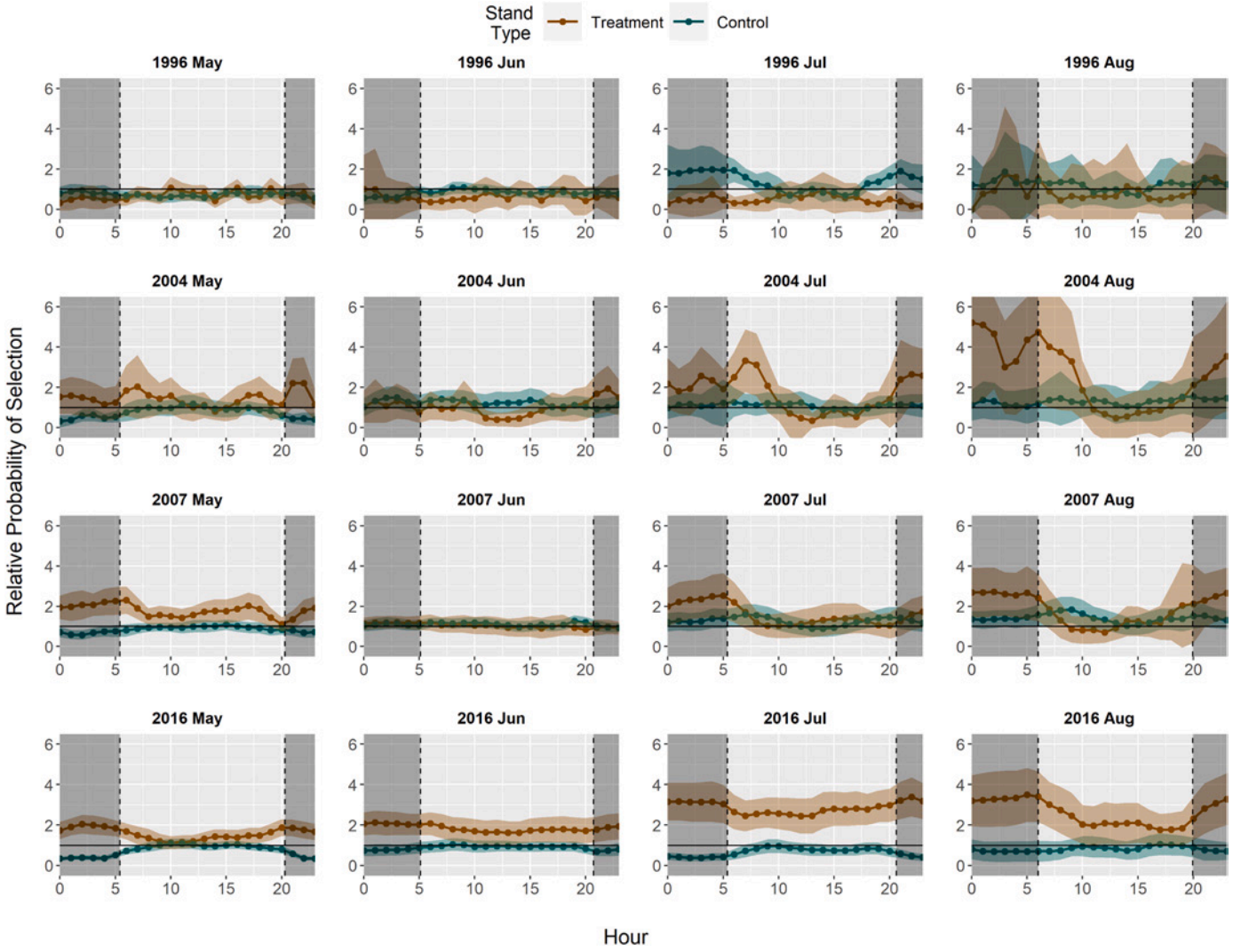

Fig. 2. Hourly selection ratios with 95 % confidence intervals showing selection by mule deer (*Odocoileus hemionus*) for burned and thinned treatment stands (red-brown) and control forest stands (blue-green). The nocturnal period is shown shaded in dark gray while the diurnal period is shown in light gray, and sunrise and sunset are indicated by vertical dashed lines. Average hourly selection for each month (May-Aug) is shown for forest stands before treatment (1996), immediately following the last year of treatments (2004), six years after the first year of treatments (2007), and the year of peak annual selection 15 years after the first year of treatment (2016).

(Fig. 2). Monthly patterns of selection indicated some avoidance of both treatment and control stands, but only during late June and July (Fig. 3). Immediately post-treatment (2004, 1–3 years since treatment) mule deer selected treated stands mostly during nocturnal and early morning periods in July and August (Fig. 2), although variability among deer was high. Daily selection values also reflected this trend, with nocturnal selection peaking in mid-August (Fig. 3). By 4–6 years post-treatment (2007) mule deer showed circadian and seasonal patterns of selection of treated stands. Deer selected treatment units in May during the day and night, used treated forest stands in proportion to their availability in June, and showed selection during the night in July and August in both hourly and daily selection (Figs. 2 and 3). At 13–15 years post treatment, mule deer showed selection during the day and night for treated stands in all months that increased from June through August (Fig. 3).

Successional Selection: Mule deer started selecting treated stands as soon as thinning and burning began followed by a decline in selection from two to four years after the first treatment, although deer were still selected treated stands at a higher level than availability (Fig. 4). After 2005 (4 years since the first stand treatment) selection began to gradually increase, peaking 15 years after the initial treatment (Fig. 4). Use of treated stands during this peak in selection was 2.2 times greater than availability of those stands on the landscape. Prior to treatment, mule deer avoided stands that were scheduled to be thinned and burned, as well as control stands (Fig. 4). However, deer briefly selected for control stands 4–6 years after thinning and burning began in treatment stands before once again avoiding control stands for almost a decade. Mule deer began to select for control stands again during the final year of the study when selection of treatment stands declined to proportional use (Fig. 4).

3.2. Changes in individual 3rd order selection (Within-Home-Range) over time

Individual deer with two or more years of data after 2005 (the year after treatments ended) showed a significant increase in selection of treated stands from 2005 to 2015 (GLMM [Gamma family], Odds $\text{Ratio}_{\text{year}} = 1.38$, 95 % CI = 1.13 – 1.69, $p = 0.002$). The predicted selection ratio in 2016 from this model was 1.81, which accounted for 85 % of the observed peak population selection of treated forest stands of 2.12. However, the 95 % confidence interval for the predicted selection ratio (1.21 – 2.72) overlapped the observed value of 2.12, meaning that all the observed change in selection could be due to increasing 3rd order selection from individual deer. There was individual variation among the sample (Random Effect Standard Deviation = 0.66, Figure A1), with some mule deer showing little predicted change in selection of treated forest stands over time and others showing a increase in selection.

3.3. Site fidelity hypothesis

Data on spatial overlap of home ranges were either normally or log-normally distributed based on the results of Shapiro-Wilk's tests and quantile-quantile plots. Individual mule deer with multiple years of data after 2005 ($n = 45$) showed no increase in the overlap of their home ranges with treated forest stands over time (*rmANOVA*, $DFn = 5$, $DFd = 20$, $F = 0.70$, $p = 0.63$).

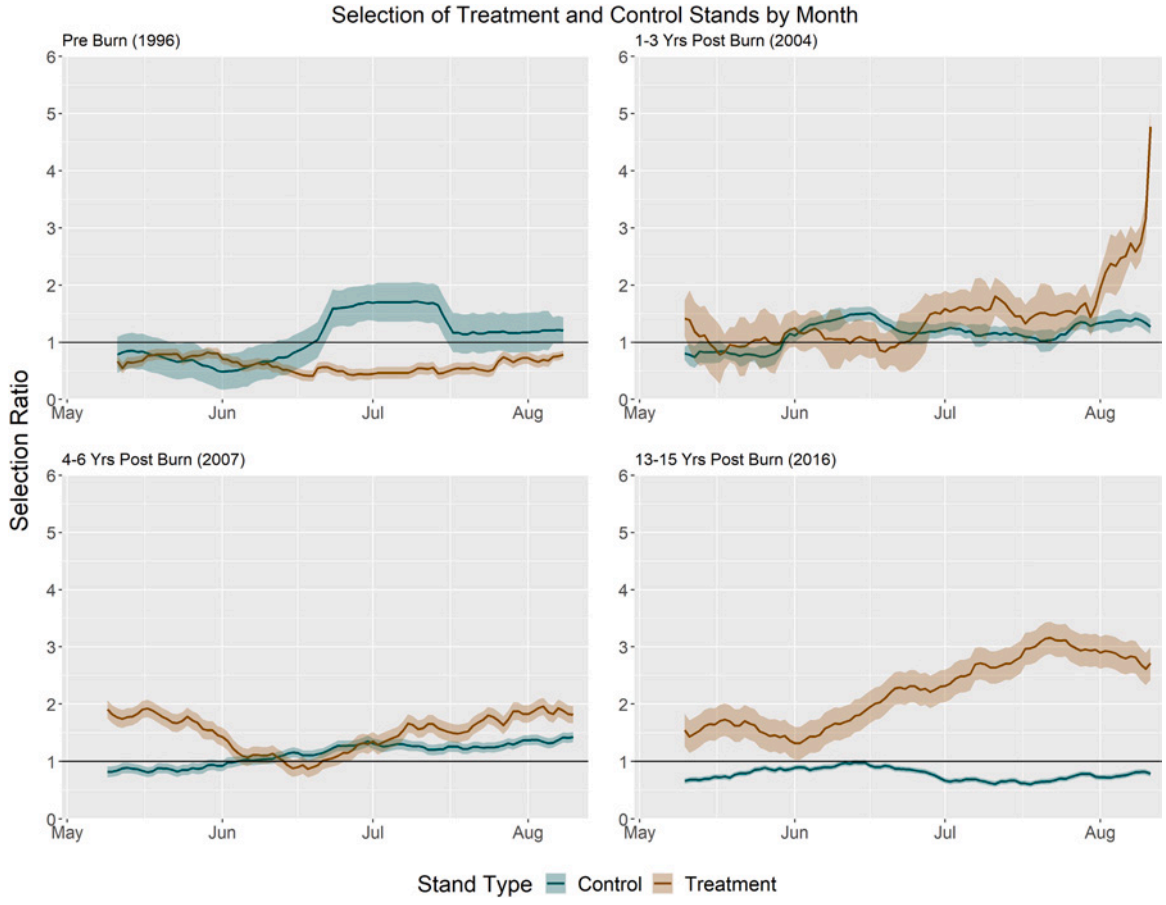

Fig. 3. Weekly selection ratios with 95 % confidence intervals showing selection by mule deer (*Odocoileus hemionus*) for thinned and burned forest stands (red-brown) and control forest stands (blue-green) for all months of a given year for pre-treatment and three different post-burn intervals. Selection ratios were calculated as a seven-day rolling mean and the line at the value of 1 indicates use of treatment stands in proportion to availability.

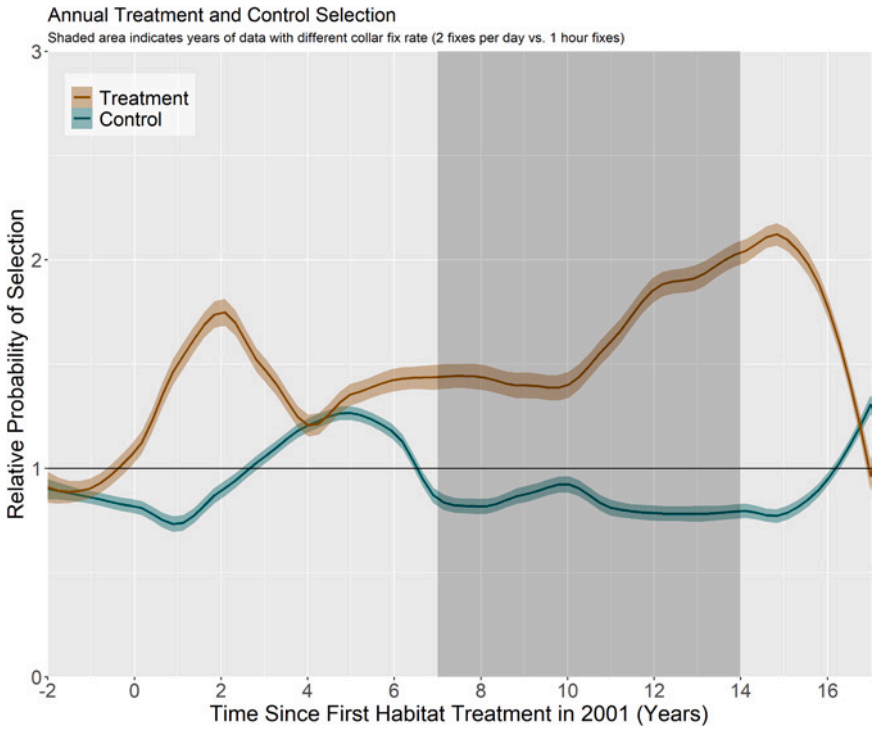

Fig. 4. Annual selection by mule deer (*Odocoileus hemionus*) of treated and untreated forest stands. A group of daily selection values with a 21-day rolling mean were calculated for every year and a LOESS (locally estimated scatterplot smoothing) function was fit through these points with 95 % confidence intervals. Values above 1 indicate selection, values below 1 indicate avoidance, and values with confidence intervals overlapping 1 indicate use in proportion to availability.

3.4. Mule deer forage differences in treatment and control stands

Biomass of selected forage species did not differ between treatment and control stands for forbs ($F = 0.20$, $\beta = 0.85$, $p = 0.65$), graminoids ($F = 0.13$, $\beta = 0.82$, $p = 0.72$), or shrubs ($F = 0.51$, $\beta = 0.79$, $p = 0.48$) (Fig. 5). Some forage plants in the neutral category from Merems et al. (2020) did show a significant difference between treatment and control stands, however. Both graminoid ($F = 4.20$, $\beta = 1.93$, $p = 0.04$; effect size = 93 %) and shrub ($F = 30.43$, $\beta = 14.80$, $p < 0.01$; effect size = 175 %) forage types in this category had higher biomass in treatment units whereas forbs showed no difference ($F = 2.2$, $\beta = 1.24$, $p = 0.14$) (Fig. 5). There were also significant differences between treatment and control stands in avoided forage species. Avoided forbs ($F = 4.21$, $\beta = 0.69$, $p = 0.04$; effect size = −31 %) and graminoids ($F = 3.64$, $\beta = -4.66$, $p = 0.05$; effect size = −24 %) had significantly lower biomass in treatment stands (Fig. 5). Avoided shrubs were only detected on two transects in treatment stands versus 14 transects in control stands, so no statistical test was performed.

Digestible energy of selected forage species also did not differ between treatment and control stands for forbs ($F = 0.22$, $\beta = 0.84$, $p = 0.64$), graminoids ($F = 0.19$, $\beta = 0.78$, $p = 0.66$), or shrubs ($F = 0.64$, $\beta = 0.77$, $p = 0.43$). The digestible energy of neutral forage species was significantly greater in treatment stands for both graminoids ($F = 3.90$, $\beta = 1.89$, $p = 0.05$; effect size = 89 %) and shrubs ($F = 32.93$, $\beta = 131.68$, $p < 0.01$; effect size = 178 %), but not for forbs ($F = 2.22$, $\beta = 13.27$, $p = 0.14$). We did not test for differences in the amount of digestible energy in avoided species between the treatment and control stands since we presumed these species were not used by mule deer.

Differences in both biomass and DE seemed to be caused by the varying abundance of 3–5 common species in each forage category, except for avoided forb species (see Tables A1-A3).

3.5. Physiographic similarities and differences between treatment and control units

We found that there was no difference in the aspect of the treatment and control units (*t-test*, $t = 0.28$, $df = 50$, $p = 0.78$). We did find a difference in slope (*t-test*, $t = -4.38$, $df = 39$, $p = <0.01$) but the effect size was small. The mean slope for treatment units was 5 degrees while the control units were slightly steeper with a mean of 10 degrees. There was also a difference in roughness between the treatment and control units (*t-test*, $t = -4.40$, $df = 39$, $p = <0.01$) although again the effect size was small enough that we did not consider it to have biological significance. Roughness is calculated by subtracting the minimum elevation value of a cell and the 8 cells surrounding it and subtracting this from the maximum value (Wilson et al., 2007). The difference between the mean roughness of treatment (mean = 5) and control units (mean = 10.2) was 5.2 m, which means that across 450 m (3×3 grid of a 150 m x 150 m cell DEM) there was only a 5 m difference between the min and max elevation difference of treatment and control forest stands. We also found that treatment units were closer to ridge top areas than control units that were more mid slope when we compared TPI values (*t-test*, $t = 2.24$, $df = 47$, $p = 0.03$). Given the small elevational ranges at Starkey we did not feel that the 100–150 m elevation difference between near ridge top and mid slope areas were large enough to be biologically significant.

4. Discussion

We took advantage of a large-scale experiment to test how mule deer used forest stands that had been thinned and burned to reduce fuel loads. Mule deer showed strong 3rd order selection for treated forest stands, supporting hypothesis 1 (treatment preference), but this pattern varied in both strength and timing across years. We found partial support for structured selection of treated stands by hour and day across months (hypothesis 2: structured selection), with mule deer showing some differences in selection between day and night soon after stands were treated. Although mule deer generally showed stronger selection

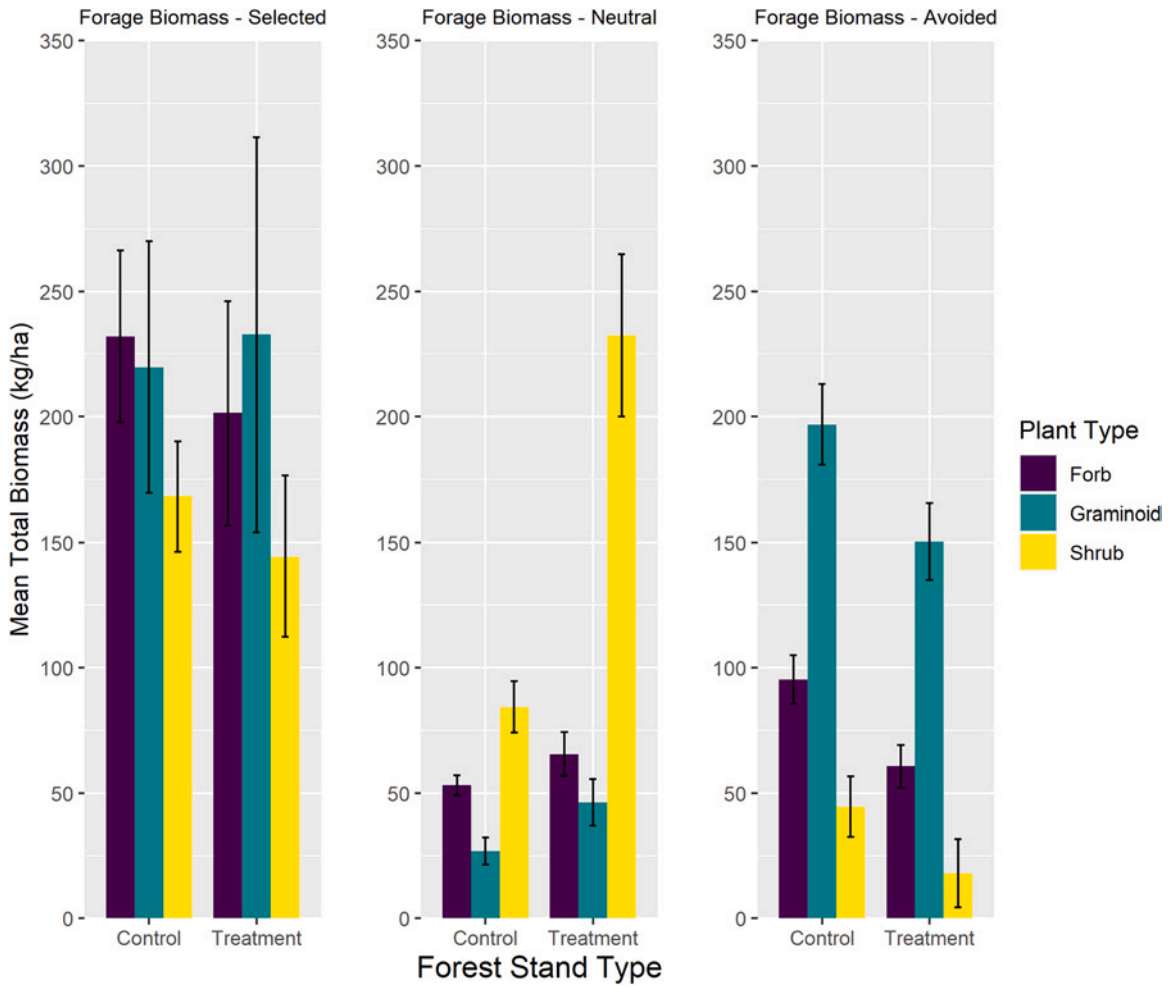

Fig. 5. Mean values of total biomass of forage species that mule deer selected, neither selected nor avoided (neutral), or avoided in the Starkey Experimental Forest and Range. Values are shown for treated and control forest stands, forage species were classified as forbs, graminoids, or shrubs, and the error bars represent one standard error.

for treated stands at night, the overall hourly pattern of selection was sometimes indistinguishable. In contrast, the monthly component of hypothesis 2 was consistently supported, with mule deer showing differences in daily use of treated stands across months both within and among years. Mule deer generally selected treated forest stands more strongly in August than during other months, although deer also selected treated stands in May, early June, and late July one to six years after treatments occurred (Fig. 3). Hypothesis 3 (successional selection) was also supported. Selection of treated forest stands increased immediately following treatment, declined from two to four years after treatments, and then steadily increased until 15 years after treatments (Fig. 4). Finally, we found support for hypothesis 4 (site fidelity). Mule deer showed no evidence of shifting their home ranges (2nd order use) to increase overlap with treated forest stands over relatively short time scales (i.e., 2–4 years) despite increased selection of treated forest stands within their home range (3rd order selection).

This study provides evidence that mule deer in dry forests used thinned and burned forest stands more than they were available on the landscape. These results are similar to other studies of ungulates that demonstrated selection for areas of timber harvest (Regelin et al., 1974; Wallmo et al., 1972), wildfire (Lewis et al., 2022), controlled burns (Eckrich et al., 2019), or other fuels reductions treatments (Hull et al., 2020; Roerick et al., 2019). Our results are novel for mule deer, however, in demonstrating how selection varied at daily, monthly, and annual time scales. The variable patterns of selection we observed would likely have been obscured by pooling data across months or years and not accounting for temporal patterns of selection, underestimating the importance of forest treatments for mule deer (e.g., Long et al., 2008). Our findings also show the importance of accounting for seasonal variation when evaluating selection of vegetation types, especially on the typical 2–5-year time scale of many mule deer research projects. Together, our results show that time elapsed since treatment, time of day, and month of the year are critical considerations in determining the effects of thinning and burning on mule deer in forested environments.

Forage differences between stands were likely one of the main mechanisms driving higher selection of treatment stands by mule deer. Our results suggest that selection of treated stands peaked at Starkey 15–16 years after initial treatment which is the same time that forb and shrub biomass peaked after burns and timber harvest in similar forests in Washington (14 years) and Montana (15 years) (Hull et al., 2020; Proffitt et al., 2016). The initial peak in selection two years after the first forest treatments and decline in selection to four years after treatments is likely due to the increase in forage quality that can happen immediately after disturbance and peaks 1–5 years after that disturbance (Hull et al., 2020; Proffitt et al., 2016; Visscher and Merrill, 2009). The initial increase in selection may have been responding to the increase in forage quality while the decline between 2 and 4 years post treatment may have been caused by a decline in forage quality before the biomass of forage species had increased enough to be beneficial. Vegetation surveys at Starkey were conducted 15–16 years after the first forest treatments, immediately following the likely peak of forage biomass, and we found higher biomass and available digestible energy of neutral forage species

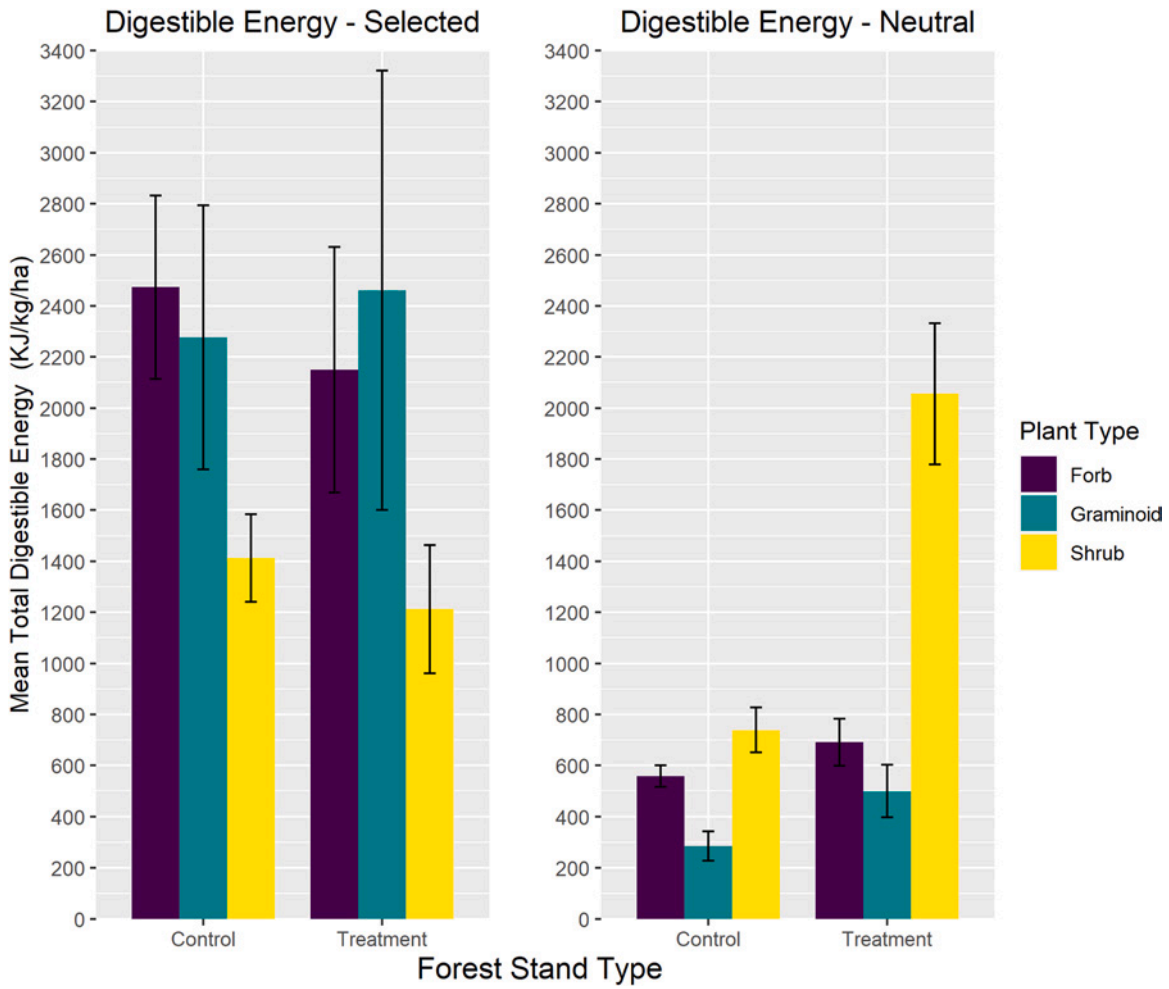

Fig. 6. Total digestible energy of selected and neutral (i.e., not selected or avoided) forage species used by mule deer in the Starkey Experimental Forest and Range. Values are shown for treated and control forest stands, forage species were classified as forbs, graminoids, or shrubs, and the error bars represent one standard error.

and lower biomass of avoided species in the treated stands, whereas biomass and available digestible energy of preferred forage species were similar between treatment and control stands. This suggests the potential for increased foraging efficiency in treated stands because mule deer have more access to neutral forage species and spend less time searching through avoided forage to find both neutral and preferred forage species.

Despite potential increases in foraging efficiency in treated forest stands, exploitative competition with cattle and elk may limit the benefits of forest treatments to mule deer (Stewart et al., 2003). Starkey supported high densities of elk that strongly selected treated stands throughout most of the study period (Spitz et al., 2018) and was part of a grazing allotment for 400–500 domestic cattle. The high abundance of elk and cattle in the study area may have removed preferred mule deer forage before vegetation surveys occurred in some treated stands, especially since high-quality forage species have been found in increased abundance after thinning and burning in other studies (Hull et al., 2020; Lewis et al., 2022; Roerick et al., 2019). Mule deer have a high dietary overlap with elk (Bowyer et al., 2023) and limited dietary overlap with cattle, although dietary overlap between mule deer and cattle increases dramatically after cattle grazing (Bowyer et al., 2023; Damiran, 2006). As a result, foraging by elk and cattle certainly reduced the preferred forage available for mule deer in the study area (Findholt et al., 2004), and mule deer may have derived more nutritional benefits from treated forest stands in the absence of this competition. In areas of the western US with high cattle and elk densities managers should consider the impacts of both exploitative and interference competition of these larger ungulates with mule deer when considering possible benefits of fuel treatments (Bowyer et al., 2023).

Predation can also impact the ability of ungulates to exploit high quality forage in general and forest treatments. However, the high site fidelity of mule deer limits their ability to respond to spatial variation in predation risk (Brown et al., 2020; Huggler et al., 2022; Peterson et al., 2022). Female mule deer increased their movement rates but did not leave their home ranges during intense period of hunting focused on male deer (Brown et al., 2020) and female mule deer exposed to high predation risk from coyotes and mountain lions also did not leave their home ranges but moderated their selection of risk areas within their home ranges (Huggler et al., 2022). Mule deer in Montana avoided predation risk at fine spatial scales instead of reducing selection of forage in risky areas unless forage availability was high (Peterson et al., 2022). These results suggest that mule deer may shift their hourly or even monthly selection of forest treatments to ameliorate predation risk, possibly by constraining their time in areas with good forage by higher predation risk, but large scale changes in 3rd order selection of forest treatments is unlikely unless forage is plentiful and predation risk is high.

Site fidelity is another factor that may limit the benefits of forest treatments for mule deer. Previous studies of mule deer at Starkey showed high fidelity to established home ranges (Brown et al., 2020), which is common for mule deer throughout their range (Garrott et al., 1987; Morrison et al., 2021a; Sawyer et al., 2019). Our results showed that mule deer maintained a high site fidelity even when treated forest stands improved forage within and immediately adjacent to their home

ranges. While site fidelity has been found to lead to higher survival in some deer populations (Forrester et al., 2015), site fidelity may also be maladaptive in landscapes that are undergoing higher rates of change than in the past (Merkle et al., 2022). Mule deer exhibit an "always stay" strategy for site fidelity (as opposed to a "win-stay, lose-switch" strategy) (Merkle et al., 2022; Morrison et al., 2021b), and this strategy appeared to restrict their ability to exploit improved forage in treated forest stands. In our study area even mule deer that had home ranges that partially overlapped treated stands showed no evidence of expanding or shifting their home range to encompass more of these forest stands in the years after thinning and burning occurred.

Despite the lack of change in 2nd order use, adult female mule deer in our study showed an increase in selection of treated forest stands within their home ranges over time (3rd order of selection). However, the increase in 3rd order selection over time from our subsample of individual deer was not as large as the increase in annual selection from our population level analysis. This could indicate that the establishment of new home ranges by yearling mule deer also influenced selection at the population level, but this was difficult to determine since few yearlings were collared and so yearlings were not included in our analysis. The importance of increasing 3rd order selection vs. the establishment of new home ranges that select for forest treatments should vary based on population characteristics. Changes in selection within home ranges (3rd order selection) will likely have the most influence on habitat selection at the population level for stable populations with an older age structure, while the establishment of new home ranges (2nd order use) will drive selection patterns in growing populations with more dispersing yearlings. Genetic analyses of mule and black-tailed deer populations show that female yearlings establish home ranges near their birthplace (within 1–3 km), which would allow yearlings to establish new home ranges encompassing fuel treatments or other forest disturbances in areas with many scattered disturbances like our study (Bose et al., 2017; Noble et al., 2016). Unfortunately, we did not have the data to test the hypothesis of yearling home range establishment, and this is an area that would benefit from future research.

Our findings can help managers optimize fuel reductions and thinning treatments to benefit mule deer. Because mule deer showed no change in 2nd order use of treated forest stands forest management will primarily benefit deer whose home ranges already overlap treated areas. Mule deer need security cover for bed sites and avoiding predators (Mysterud and Østbye, 1999) as well as foraging habitat (Ager et al., 2003), which suggests that large blocks of fuel treatments are less likely to benefit mule deer as much as scattered smaller treatments (Bergman et al., 2014a; Hull et al., 2020). Our results also showed that forest treatments benefit mule deer for up to 15 years, which suggests benefits to spacing out treatments in time as well as space. The distribution of smaller forest treatments over space and time may also benefit other wildlife species. Small mammals and many species songbirds either benefit or are not negatively affected by smaller fuel treatments, but are negatively affected by large-scale overstory removal and wildfire, although a few species of songbirds showed declines (Hagar et al., 2004; Kalies et al., 2010; Lance and Phinney, 2001; Leupin et al., 2004; Stephens et al., 2014). Lynx, a Threatened status species under the Endangered Species Act that overlaps mule deer range in the Rocky Mountains, also benefit from a matrix of mature and younger age forest but avoid large areas of forest disturbance and have greater reproductive success in mature forest (Holbrook et al., 2019, 2018).

Forest managers must balance multiple wildlife and forest health objectives when planning forest treatments and are tasked with sustaining high-quality habitat for multiple species over time while also reducing fire risk. Smaller treatments scattered in space and time can benefit both mule deer and other species of wildlife and the benefits to mule deer should last for well over a decade depending on the vegetation and forest types of the area. Periodic vegetation monitoring will be critical to document actual nutritional benefits to ungulates and measure when forage biomass and quality increases after treatments. Our results also show the importance of including temporal and seasonal structure in studies of habitat selection. Studies that focus only on early summer or that combine data across the entire summer period will underestimate both the importance of forest treatments to mule deer, especially where vegetation outside of forested habitats has senesced by late summer, as well as the importance of climate impacts on forage species (Brown et al., 2022; Merems et al., 2020). We strongly recommend that future research on habitat selection include temporal and seasonal structure of habitat use to provide the best information to managers who are balancing several competing objectives.

CRediT authorship contribution statement

Tavis D Forrester: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Ryan A Long:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Darren A Clark:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Michael J Wisdom:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Mary M Rowland:** Writing – review & editing, Methodology, Conceptualization. **Derek B Spitz:** Writing – review & editing, Validation, Methodology, Conceptualization. **Jennifer L Merems:** Writing – review & editing, Investigation, Data curation. **Taal Levi:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition. **Bruce K Johnson:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Joshua B Smith:** Writing – review & editing, Methodology.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data that has been used is confidential.

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The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official USDA or U.S. Government determination or policy. We thank Brian, Dick, Cheryl Borum, Jennifer Hafer, and Bridgett Naylor for data collection and management.

Appendix A

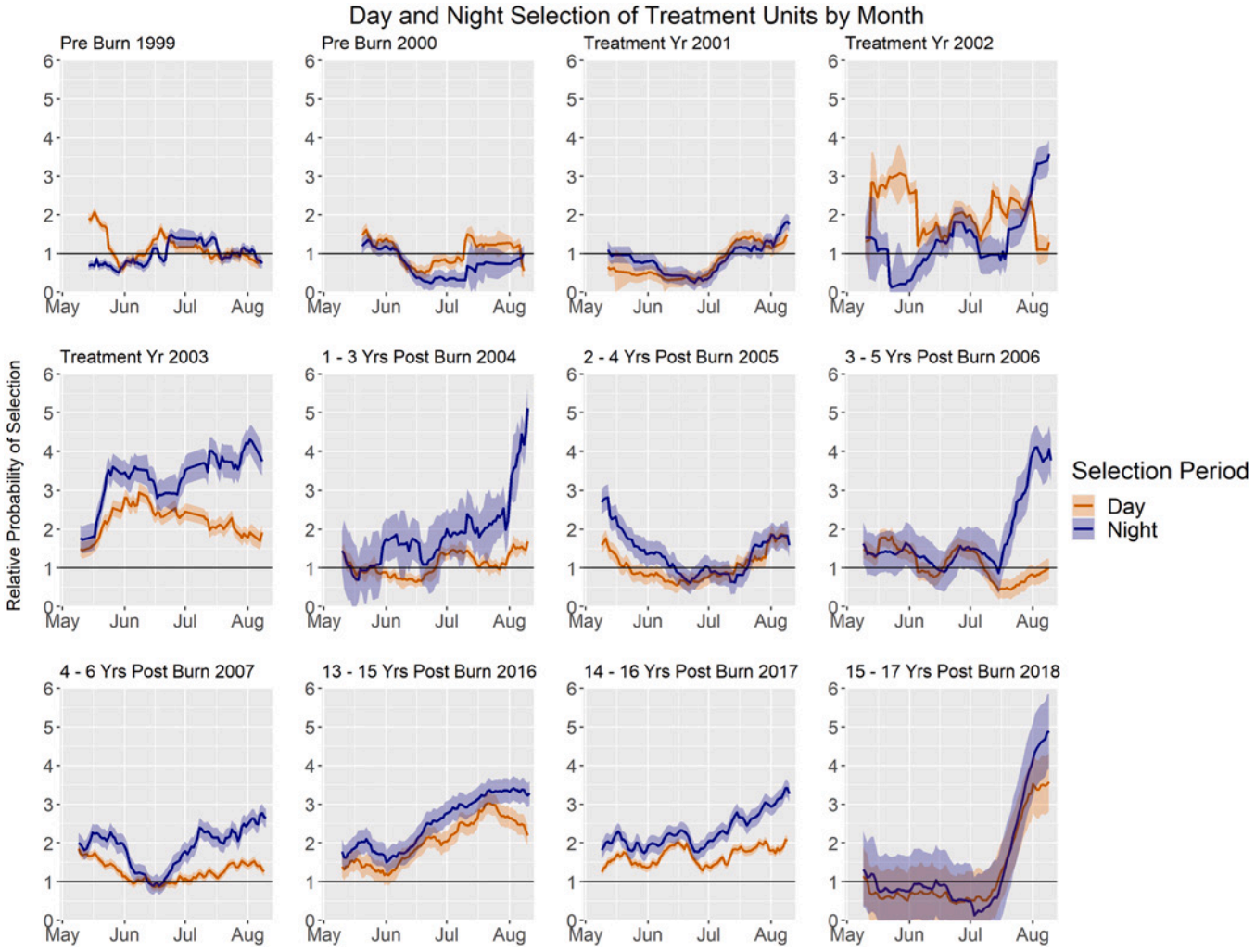

Figure A1. Daily selection ratios with 95 % confidence intervals for diurnal and nocturnal periods for all months of a given year for two years pre-burn (1999–2000), the years of habitat treatments (2001–2003), and all year's post-burn when deer GPS collars were collecting data during all hours of the day (2004–2007 and 2016–2018). The selection ratios were calculated as a 21-day rolling mean and the line at the value of 1 indicates when treatment stands were used in proportion to availability, values with confidence intervals above the value of 1 indicate selection, and values with confidence intervals below the value of 1 indicate avoidance.

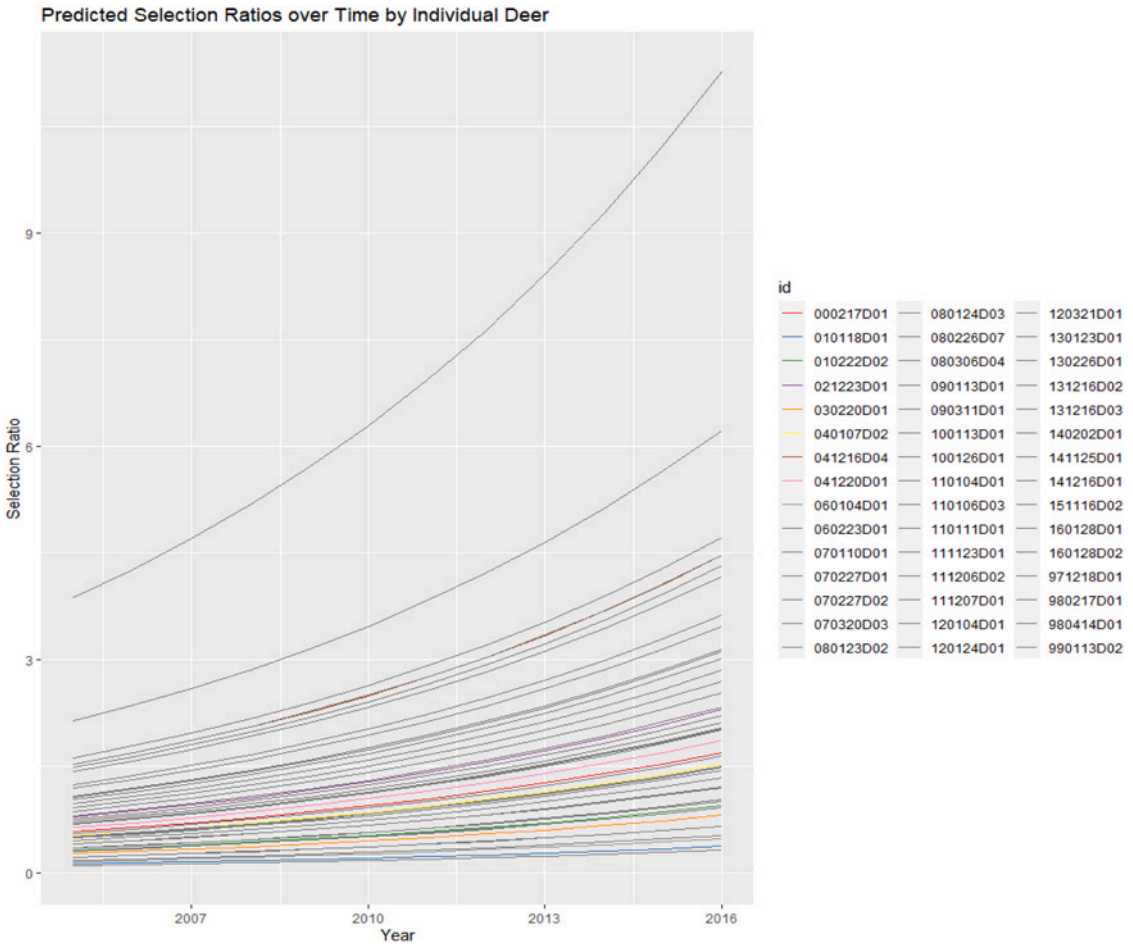

Figure A2. Predicted selection ratios of treated forest stands by individual deer with at least 2 years of location data. The graph covers the time since the first treatment in 2004 to peak population selection of treated units in 2016. Deer IDs are shown in the legend and the graph does not include confidence intervals for increased readability.

Table A1
List of all species of **selected** forage plants with more than 50 occurrences on transects in treated or control forest stands from vegetation surveys conducted in 2016 and 2017. Forage plants are listed for each class of forage (forbs, graminoids, and shrubs). Forest types are listed after each plant species because some plant species were selected in some forest types and neutral or avoided in other forest types. Forest types are Douglas-fir (DF), Grand Fir (G), Grand Fir-Subalpine Fir (GS), Ponderosa Pine (PP), and Grassland (GRSS). Species that had >50 occurrences only in treatment stands are marked with * and species that had >50 occurrences only in control stands are marked with ^.

Forbs			Graminoids			Shrubs		
Common Name	**Scientific Name**	**Forest Type**	**Common Name**	**Scientific Name**	**Forest Type**	**Common Name**	**Scientific Name**	**Forest Type**
Violet	*Viola* spp.	All	Idaho fescue	*Festuca idahoensis*	DF; G; GS	Shinyleaf Spirea	*Spiraea lucida*	All
Heartleaf Arnica	*Arnica cordifolia*	DF; G; GS	Onespike danthonia	*Danthonia unispicata*	All	Common Snowberry	*Symphoricarpos albus*	DF; G; GS
Clover	*Trifolium* spp.	All	Bluebunch wheatgrass	*Pseudoroegneria spicata*	DF; G; GS	Dwarf Rose	*Rosa gymnocarpa*	All
Common Dandelion	*Taraxacum officinale*	DF; G; GS						
Common Yarrow*	*Achillea millefolium*	PP; GRSS						

Table A2
List of all species of **neutral** forage plants with more than 50 occurrences on transects in treated or control forest stands from vegetation surveys conducted in 2016 and 2017. Forage plants are listed for each class of forage (forbs, graminoids, and shrubs). Forest types are listed after each plant species because some plant species were selected in some forest types and neutral or avoided in other forest types. Forest types are Douglas-fir (DF), Grand Fir (G), Grand Fir-Subalpine Fir (GS), Ponderosa Pine (PP), and Grassland (GRSS). Species that had >50 occurrences only in treatment stands are marked with * and species that had >50 occurrences only in control stands are marked with ^.

Forbs			Graminoids			Shrubs		
Common Name	**Scientific Name**	**Forest Type**	**Common Name**	**Scientific Name**	**Forest Type**	**Common Name**	**Scientific Name**	**Forest Type**
Lupine	*Lupinus* spp.	All	Grass inflorescense	*Poaceae* spp.	All	Kinnikinnick	*Arctostaphylos uva-ursi*	All
Hawkweed	*Hieracium* spp.	DF; G; GS	Prairie Junegrass	*Koeleria macrantha*	DF; G; GS	Creeping barberry	*Mahonia repens*	All
VA Strawberry	*Fragaria virginiana*	All	Tall Trisetum	*Trisetum canescens*	All	Huckleberry	*Vaccinium* spp.	All
Smallflower Miterwort^	*Mitella stauropetala*	All	Woodrush^	*Luzula* spp.	All			
Beardtongue^	*Penstemon* spp.	All	Sandberg Bluegrass^	*Poa secunda*	All			
			Geye's Sedge*	*Carex geyeri*	PP; GRSS			

Table A3
List of all species of **avoided** forage plants with more than 50 occurrences on transects in treated or control forest stands from vegetation surveys conducted in 2016 and 2017. Forage plants are listed for each class of forage (forbs, graminoids, and shrubs). Forest types are listed after each plant species because some plant species were selected in some forest types and neutral or avoided in other forest types. Forest types are Douglas-fir (DF), Grand Fir (G), Grand Fir-Subalpine Fir (GS), Ponderosa Pine (PP), and Grassland (GRSS). Species that had >50 occurrences only in treatment stands are marked with * and species that had >50 occurrences only in control stands are marked with ^.

Forbs			Graminoids			Shrubs		
Common Name	**Scientific Name**	**Forest Type**	**Common Name**	**Scientific Name**	**Forest Type**	**Common Name**	**Scientific Name**	**Forest Type**
Common Yarrow	*Achillea millefolium*	DF; G; GS	Geye's Sedge	*Carex geyeri*	DF; G; GS	No avoided shrubs with >50 occurrences		
Woodland Strawberry	*Fragaria vesca*	All	Pinegrass	*Calamagrostis rubescens*	All			
Stonecrop	*Sedum* spp.	All	Sedge	*Carex* spp.	DF; G; GS			
Sweet Cicely^	*Osmorhiza berteroi*	All	Western Fescue	*Festuca occidentalis*	All			
Twinflower^	*Linnaea borealis*	All	CA Brome^	*Bromus carinatus*	DF; G; GS			
Largeleaf Sandwort^	*Moehringia macrophylla*	All	Smooth Brome^	*Bromus inermis*	All			
Silverpuffs	*Microseris* spp.	All						
Mariposa Lily^	*Calochortus* spp.	All						
Tall Willowherb	*Epilobium brachycarpum*	All						
Littleleaf Pussytoes	*Antennaria microphylla*	All						
Tiny Trumpet^	*Collomia linearis*	All						
Douglas's Knotweed^	*Polygonum douglasii*	All						
Mountain Goldenbanner^	*Thermopsis montana*	All						
Mountain Tarweed	*Madia glomerata*	All						

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