



Forest restoration, wildfire, and habitat selection by female mule deer

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ABSTRACT

Decades of fire suppression, logging, and overgrazing have led to increased densities of small diameter trees which have been associated with decreases in biodiversity, reduced habitat quality for wildlife species, degraded foraging conditions for ungulates, and more frequent and severe wildfires. In response, land managers are implementing forest restoration treatments using prescribed fire and thinning to mitigate the risk of catastrophic wildfires and improve habitat conditions for a variety of wildlife species. We monitored habitat selection by female mule deer (*Odocoileus hemionus*) in relation to forest restoration treatments and wildfires in northern New Mexico in 2015. Our specific objectives were to assess changes in forage abundance and determine habitat selection patterns of mule deer in relation to recent wildfires, forest restoration treatments, including duration of the post-treatment recovery, and other habitat characteristics. Herbaceous forage biomass was greater in wildfire-burned areas than in untreated areas or those treated with prescribed burns or thinning. Oak forage biomass was greater in wildfire-burned areas compared to prescribed burns, forest thinning, and untreated areas. However, thinned areas tended to have higher oak forage biomass than untreated areas. Mule deer selected for areas burned by prescribed fire and generally avoided wildfire-burned and thinned areas < 5 years old. Mule deer strongly selected for thinned areas ≥ 5 years old. At both the landscape and home-range scale, grasslands were avoided during most seasons, pinyon-juniper woodlands were selected in winter, and oak vegetation and mixed-conifer forests were selected during summer. Our data suggests that mule deer may benefit from recent prescribed burns and older forest thinning, but the duration of post-treatment vegetation recovery influences the strength and direction of selection. Knowledge of the short- and long-term effects of restoration treatments will provide managers with the means to make more informed decisions regarding implementation of forest restoration and other vegetation treatments intended to benefit mule deer.

1. Introduction

Since Euro-American settlement, the forests in the western United States have been altered by suppression of natural fires, silvicultural practices, human development, and livestock grazing (Covington and Moore, 1994; Belsky and Blumenthal, 1997; Covington et al., 1997; Theobald et al., 1997) resulting in increased tree densities and altered habitat conditions for many wildlife species. This has resulted in less frequent, but high severity, stand-replacing fires. More recently, changing climatic conditions and shifts in phenology have further contributed to more frequent and severe wildfires (McKenzie et al., 2004; Allen et al., 2010; Williams et al., 2010). In response, wildlife and land managers are implementing prescribed fires and forest thinning to reduce the density of small diameter trees and increase the abundance of early successional vegetation to improve habitat conditions for wildlife. Although these restoration projects aim to improve habitat conditions for wildlife species by increasing vegetation productivity and diversity, wildlife responses vary based on species home-range requirements, mobility, and degree of habitat specificity (Chambers and Germaine, 2003).

Many mule deer (*Odocoileus hemionus*) populations throughout the western United States declined during the past few decades (i.e., 1960s–2000s). Suspected causes include changing climatic conditions and reduced forage quality and quantity, suppression of natural fire regimes, predation, human development, and livestock grazing (McNay and Voller, 1995; Clements and Young, 1997; Bleich and Taylor, 1998; Robinson et al., 2002; deVos et al., 2003). Changes in habitat conditions can decrease quality and availability of forage, reduce vegetation cover for protection from predators and weather, and diminish access to water (deVos et al., 2003; Horncastle et al., 2013). Managers often use prescribed fire and forest thinning to remove dead litter, create areas for seedling germination and growth, and increase soil nutrients to bring portions of the landscape back to an early successional state that improves habitat for mule deer (Dills, 1970; Carlson et al., 1993; Kie et al., 2003). Those treatments may provide greater forage availability and nutritional quality (Rowland et al., 1984), thus yielding a positive effect on mule deer populations by improving body condition, fecundity, and survival (Hobbs and Spowart, 1984; Rowland et al., 1984; Kie et al., 2003; Horncastle et al., 2013).

Differences in fire intensity, spatial extent, and post-fire recovery

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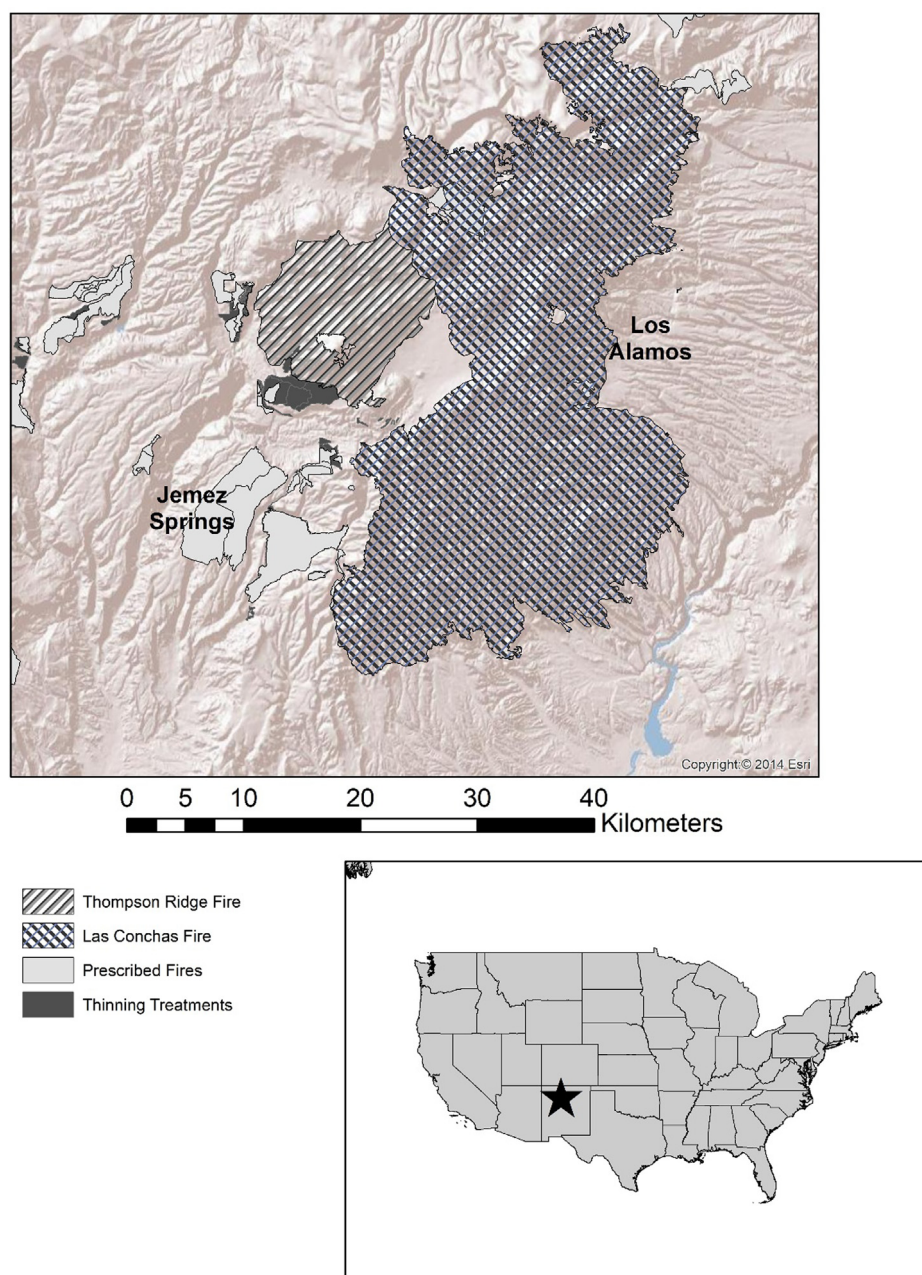


Fig. 1. Study area location in the Jemez Mountains, New Mexico.

time influence when and how ungulates use treated areas, resulting in mixed reports on the effects of prescribed burns on ungulates (Carlson et al., 1993). While some studies reported no effect of prescribed fire on forage quality (Wood, 1988) and mule deer habitat use (Long et al., 2008b), others have reported an increase in forage quality 1–2 years post-fire (Dills, 1970; Keay and Peek, 1980; Hobbs and Spowart, 1984; Carlson et al., 1993). Mule deer may benefit from increased forage diversity and abundance if fire is used regularly (e.g., every 4–10 years) and creates a mosaic habitat pattern (Roccafort et al., 2010; Horncastle et al., 2013). Most studies focused on burn effects within 1–2 years after the burn (Dills, 1970; Hobbs and Spowart, 1984; Wood, 1988), with few examining long-term effects of prescribed burns on ungulates and their habitat use (Joly et al., 2007).

Results from research on the effects of thinning treatments are also variable. Some have reported little change in mule deer habitat use or forage availability following thinning treatments (Bergman et al., 2014a; Kramer et al., 2015), whereas others have reported increased

mule deer use of thinned areas (Germaine et al., 2004; Horncastle et al., 2013; Bergman et al., 2014a, 2014b). Overwinter fawn survival in Pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) winter ranges receiving both mechanical and chemical treatments was higher than in untreated areas; however, deer densities did not differ between treated and untreated areas (Bergman et al., 2014a, 2014b). Others have reported an increase in deer abundance and use of thinned and logged areas (Bowman et al., 2010; Horncastle et al., 2013). The differences among studies may be attributed to the time lag between treatment and the period of study, extent of treated areas, or confounding influences of post-treatment climatic conditions on vegetation responses (Kramer et al., 2015).

Understanding ungulate habitat selection in relation to forest restoration treatments is critical to development of successful management strategies for mule deer and more informed design of restoration plans intended to improve forage conditions through creation of uneven-aged habitat mosaics in forested ecosystems. We assessed the

effects of forest restoration treatments and recent wildfires on female mule deer habitat selection in the Jemez Mountains in north-central New Mexico. Our objective was to determine habitat selection patterns of mule deer in relation to recent wildfires, forest restoration treatments, topographic characteristics, water sources, forage biomass, and vegetation types. We also evaluated the influence of mountain lion predation risk on mule deer habitat selection because mountain lions are frequently the primary cause of predation mortality for adult mule deer (Pierce et al., 2004; Roerick, 2017; Cain et al., 2018). Based on previous research, we expected the factors driving deer habitat selection would be scale-specific (i.e., different between landscape and home-range scale) and would vary seasonally (e.g., Collins and Urness, 1983; Nicholson et al., 1997; D'Eon and Serrouya, 2005; Kay, 2018). We expected elevation and distance to roads would be important at a landscape scale, while aspect, slope, edge density, and predation risk would be more important within the home range. In winter, we expected deer to use lower elevations, south facing slopes, and areas with more cover to minimize the effects of lower temperatures and snow. In spring, we expected deer to select burned areas, particularly on south facing slopes due to earlier snow melt and higher quality forage associated with burning. In summer, we expected deer to use areas closer to perennial water sources, at higher elevations, in areas with higher canopy cover to minimize the effects of warmer temperatures. In autumn, we expected that deer would select more open areas and edge habitat to increase foraging opportunities. We also expected deer to select prescribed- and wildfire-burned areas more than unburned areas in spring and summer because of an increase in forage abundance resulting from fire, and we expected stronger selection for wildfire-burned areas compared to prescribed burns. Finally, we expected that mule deer would select thinned areas more than untreated areas, with stronger selection for thinned areas with longer post-disturbance recovery.

2. Materials and methods

2.1. Study area

The study area in the southwest Jemez Mountains of north-central New Mexico is 840 km² and includes land managed by the Santa Fe National Forest, Valles Caldera National Preserve, and Jemez Pueblo (Fig. 1). Elevations ranged from 1600 to 3400 m. The landscape was dominated by pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands at lower elevations (1600–2300 m) and ponderosa pine (*Pinus ponderosa*) forests at intermediate elevations and on south facing slopes at higher elevations (2200–3400 m). Mixed-conifer forests consisting of Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) were prevalent at higher elevations (1900–3400 m). Common forbs and grasses included mullein (*Verbascum thapsus*), purple prairie clover (*Petalostemum purpureum*), mutton grass (*Poa fendleriana*), and fescue (*Festuca* spp.). Common browse species included gamble oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus montanus*), Oregon grape (*Mahonia aquifolium*), and aspen (*Populus tremuloides*).

At lower elevations the average daily high and low temperatures are 29 °C and 12 °C during summer, and 8 °C and –6 °C during winter, respectively (Jemez Springs, NM; 1800 m, 1910–2014; Western Regional Climate Center [WRCC], 2015). At higher elevations, the average daily high and low temperatures are 24 °C and 4 °C in summer, and 4 °C and –13 °C in winter, respectively (Wolf Canyon, NM; 2500 m, 1912–2015; WRCC, 2015). At lower elevations, average annual precipitation is 43 cm (SD = 25 cm), and at higher elevations 58 cm (SD = 25 cm), with the majority of the precipitation coming from monsoon thunderstorms in July and August, and winter snow (lower elevations: 74 cm ± 40; higher elevations: 305 cm ± 97 cm; Jemez Springs, NM; 1800 m, 1952–2012; Wolf Canyon, NM; 2500 m, 1912–2015; WRCC, 2015). Seasons were classified using climographs derived from long-term temperature and precipitation data for the Jemez Springs (1910–2014) and Wolf Canyon (1912–2015) stations (Supplementary

material, Fig. S1) and were defined as: winter (December through February), spring (March and April), summer (May through September), and autumn (October and November).

Elk (*Cervus canadensis*) are the only other native ungulate found in the study area. Predators include black bears (*Ursus americanus*), mountain lions (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). Livestock grazing occurs throughout much of the study area. In addition, the Valles Caldera National Preserve permits fishing, elk and turkey (*Meleagris gallopavo merriami*) hunting, and other recreational activities. The Santa Fe National Forest provides these activities as well as hunting of mule deer, black bear, and mountain lions, firewood cutting, and camping.

The Jemez Mountains study area is comprised of a fire-adapted ecosystem; however, suppression of natural fire has resulted in more frequent and severe wildfires (Allen et al., 2002). Two notable recent wildfires include the Las Conchas Fire of 2011 and the Thompson Ridge Fire of 2013. The Las Conchas Fire burned 63,370 ha in the Santa Fe National Forest, Valles Caldera National Preserve, and Santa Clara and Jemez Pueblos. The Thompson Ridge Fire burned 9698 ha, primarily within the Valles Caldera National Preserve. To reduce catastrophic wildfires, high risk areas were selected to receive low- to mixed-intensity prescribed burns (5986 ha) and mechanical thinning (2380 ha).

2.2. Animal capture and handling

We captured 24 adult female mule deer from December 2012 through July 2015 by darting and net-gunning from a helicopter, ground darting, and using clover traps. Deer captured by darting were immobilized with 0.03 mg/kg carfentanil + 0.7 mg/kg xylazine and reversed with 3 mg/kg naltrexone + 1.4 mg/kg tolazoline. Mule deer captured by clover traps and net-gunning were restrained with hobbles during processing. Twelve GPS-Iridium collars (Advanced Telemetry Systems, Inc., Isanti, MN: Model G2110E) and 12 GPS store-on-board collars (Advanced Telemetry Systems, Inc., Isanti, MN: Model G2110B/D) were deployed on adult female mule deer. The collars were programmed to collect a GPS fix every 5–6 h. All collars were equipped with a VHF transmitter and an automatic drop-off mechanism.

From December 2012 to April 2016, 9 mountain lions were captured using trained hounds or cable foot snares. All mountain lions were immobilized with 2.0 mg/kg ketamine + 0.075 mg/kg medetomidine, reversed with 0.3 mg/kg atipamezole and fitted with GPS-Iridium collars (Advanced Telemetry Systems, Inc., Isanti, MN: Model G2110E and Vectronic Aerospace, Berlin: 4 GPS Vectronics Vertex Plus Iridium collars) programmed to record a location every 3 h and transmitted data every 2–3 days. All capture and handling procedures for mule deer and mountain lions followed acceptable methods (Sikes et al., 2016) and were approved by the Institutional Animal Care and Use Committee at New Mexico State University (Protocols #2011–038, 2015–022).

2.3. Multi-scale habitat selection

We estimated female mule deer habitat selection using seasonal resource selection functions (RSFs) at two spatial scales; landscape scale (i.e., within the study area – 2nd order selection) and home-range scale (i.e., within individual seasonal home ranges – 3rd order selection) (Johnson, 1980). The available area for landscape-scale selection was delineated by the 100% minimum convex polygon (MCP) encompassing all mule deer locations. The MCP was buffered by 2 km based on the average daily movement of collared female mule deer; the study area MCP and buffered area was considered the available area at the landscape scale. To determine availability for home-range scale selection, we estimated seasonal 100% MCP home ranges for each individual mule deer. Using ArcGIS, we generated an equal number of random points within the study area MCP (landscape-scale selection) and within each individual seasonal home range (home-range scale selection) to use as our available sample in our RSFs. All locations were

characterized by season, forest treatment status (i.e., prescribed burns, thinning, wildfire-burned, and untreated), vegetation type, distance to perennial water (m), percent tree canopy cover, mountain lion predation risk, edge density (m/ha), herbaceous and woody forage biomass (g/m^2), distance to high-use roads (m), elevation (m), slope (%), and aspect.

We obtained geospatial data on perennial water sources and roads, as well as the spatial extent and ages of wildfires, prescribed burns, and forest-thinning treatments from the Santa Fe National Forest, Valles Caldera National Preserve, and the Jemez Pueblo. We examined mule deer habitat selection in 2015, because that was the only year where the extent and availability of the range of forest treatments and wildfires we intended to test coincided adequately with the distribution of our collared deer. Beginning in 2015, we had sufficient overlap of collared mule deer with prescribed burns and thinning treatments of different post-treatment ages, and as such, we present only 2015 data. Because of an insufficient number of locations in different age categories of wildfires, and due to the limited ages of the more recent wildfires in the study area, we classified all used and available locations as wildfire-burned or not. We categorized prescribed burns as < 2 years old, ≥ 2 years old, and not burned, and thinned areas as < 5 years old, ≥ 5 years old, and not thinned. As part of the standard treatment protocol, most thinned areas received prescribed fire treatment several (e.g., 2–4) years after thinning to remove the residual woody debris, and were therefore classified as thinned. If treatments and wildfires overlapped, the most recent treatment or wildfire was used to classify the location. High-use roads, which primarily consisted of regularly maintained forest roads and paved roads were identified in pre-existing GIS data on road locations. We then calculated the distance (m) from each used and available location to the nearest high-use road and perennial water source in ArcGIS 10.2 (ESRI, Redlands, CA, USA). We obtained tree canopy cover and vegetation type data from the National Gap Analysis Program (GAP; U.S. Geological Survey, 2013) and we reclassified vegetation types by amalgamating pre-existing GIS data from GAP data into broader vegetation type categories that are more specific to mule deer habitat selection (Roerick, 2017), including aspen, grassland, oak, ponderosa pine, pinyon-juniper woodland, and mixed-conifer forest.

We used a $10\text{ m} \times 10\text{ m}$ digital elevation model (U.S. Geological Survey, 2013) to determine aspect, elevation, and slope. We extracted aspect and slope from each $10\text{ m} \times 10\text{ m}$ pixel in the study area. Aspect was converted to northness and eastness. Northness was calculated using the cosine function which converts aspect from a circular variable with values of $0\text{--}360^\circ$ into a linear covariate with values between -1 (south) and 1 (north). Eastness was calculated with the sine function, resulting in values between -1 (west) and 1 (east).

Elevation, slope, percent tree canopy cover, and edge density were assessed within a 35 m radius around each used and available location. We calculated the mean elevation, slope, and canopy cover in each buffered area around each used and available location. We extracted edge between vegetation types from the GAP vegetation GIS layer (U.S. Geological Survey, 2013) using the extract edge tool in Geospatial Modeling Environment (Beyer, 2014). We then calculated edge density (m/ha) within 35 m areas around each location (Said and Servanty, 2005).

To assess biomass of forage available to mule deer, we monitored > 200 vegetation points throughout the study area using methods adapted from Hebblewhite et al. (2008) and Visscher et al. (2006). Vegetation points were distributed by a stratified random design based on vegetation type, treatment type, canopy cover class, aspect, and fire history. At each vegetation sampling point we established either a 100 m or 200 m baseline transect, depending upon the vegetation patch size. Herbaceous biomass was measured with a 0.25 m^2 disc pasture meter every 10 m or 20 m along the transect, depending upon the length of the transect. We developed predictive regression equations to estimate herbaceous biomass from the disc height by clipping vegetation from underneath a sample of disc plots (located 1 m

off of the transect). We then separated clipped herbaceous vegetation into grasses or forbs, dried samples to a constant weight, and determined dry weight biomass. We then used general linear models (GLMs) to determine the relationship between disc height and biomass; the resulting regression equation was then used to estimate biomass for unclipped disc plots (Roerick, 2017). We then calculated the average herbaceous biomass for the entire transect.

Edible biomass (i.e., stems $\leq 5\text{ mm}$ in diameter, leaves, and inflorescence) from oak, mountain mahogany, and Woods' rose (*Rosa woodsii*) was measured in $1\text{ m} \times 2\text{ m}$ plots every 10 m or 20 m , depending upon the transect length. We selected these species because of their importance to mule deer diets and their availability in our study area (Kufeld et al., 1988; Sandoval et al., 2005). Height, basal diameter, and species was determined for all woody stems within each plot. For each browse species, we located stems of varying heights and diameters off of the transect to develop predictive regression equations for edible biomass. For logistical efficiency, clipping samples were collected in areas near existing transects, with the stems randomly selected; however, we ensured our clipping samples represented the stem heights and diameters for each important forage species we encountered on our monitoring transects. Height and basal diameter were measured and all edible biomass was clipped. Leaves were removed and separated from stems so that stem biomass could be included in winter habitat selection models (Visscher et al., 2006). Stems and leaves were dried for four days at 55°C to determine dry weight (biomass) and moisture content. The regression equation was then used to estimate edible forage biomass on stems that were not clipped (Roerick, 2017). The woody forage biomass was summed for each species in each shrub plot, and plot sums averaged for the entire transect.

All statistical analyses were conducted in R 3.2.5 (R Development Core Team, 2015). We used GLMs to model herbaceous biomass and woody forage biomass across the study area as a function of vegetation type, aspect, slope, treatment type, tree canopy cover, and fire history (Hebblewhite et al., 2008; Roberts et al., 2017). We used forward and backwards stepwise selection to select the most explanatory and parsimonious spatial covariates based on the Akaike Information Criterion (AIC_c) corrected for small sample size (Burnham and Anderson, 2002). We then used these coefficients to estimate forage biomass across all sampling units (i.e., 35 m diameter buffered area around each used and available location) in the study area (Roberts et al., 2017).

To assess differences in herbaceous and woody forage biomass by vegetation type and treatment type, we used ANOVA including all main and interactive effects; Tukey's HSD test was used for post hoc tests.

To estimate predation risk by mountain lions, we first developed seasonal RSFs for radio-collared mountain lions at the landscape scale; available locations for mountain lion RSFs were determined as described for mule deer landscape-scale habitat selection above. Due to the limited number of mountain lions fitted with telemetry collars in any given year, we used all GPS data collected on mountain lions from 2012 to 2016 to develop seasonal RSFs for mountain lions at the landscape scale. Seasons for mountain lions were categorized as summer (May–October) or winter (November–April). Mountain lion locations were characterized by vegetation type, elevation (m), northness, eastness, slope (%), a quadratic term for slope (slope^2), distance to water (m), distance to paved roads (m), and percent tree canopy cover. We developed a set of a priori models based on previous studies of mountain lion habitat selection (Supplementary material, Table S1; Logan and Irwin, 1985; Koehler and Hornocker, 1991; Dickson and Beier, 2002; Pierce and Bleich, 2003). We then used mixed-effects logistic regression using the lme4 package (Bates et al., 2015) with mountain lion ID included as a random effect to model RSFs (Gillies et al., 2006). We used Akaike's Information Criterion (AIC_c) corrected for small sample size to evaluate the relative support for each model (Burnham and Anderson, 2002). We used 5-fold cross-validation (bins = 30; Boyce et al., 2002) to evaluate the performance of the top-ranking models. We used the parameter estimates from the most

supported model in each season to create a RSF map. We then created seasonal kernel density estimates (KDEs) in Geospatial Model Environment with the KDE tool (Beyer, 2014). We created our final predation risk index by taking the product of the seasonal mountain lion RSF and seasonal KDE; these index values were assigned to each used and available points for mule deer.

All predictor variables were standardized prior to analysis. We evaluated predictor variables for multicollinearity using Pearson's pairwise correlation to avoid having correlated variables within the same models (Supplementary material, Table S2). We then developed candidate models a priori based on project objectives and previous studies of mule deer habitat selection (Supplementary material, Table S3; Germaine et al., 2004; D'Eon and Serrouya, 2005; Heffelfinger, 2006; Horncastle et al., 2013; Bergman et al., 2014a, 2014b). We then used mixed-effects logistic regression using the lme4 package (Bates et al., 2015) with mule deer ID included as a random effect to model RSFs (Gillies et al., 2006). We used Akaike's Information Criterion (AIC_c) corrected for small sample size to evaluate the relative support for each model (Burnham and Anderson, 2002). We used 5-fold cross-validation (bins = 30; Boyce et al., 2002) to evaluate the performance of the top-ranking models. Ponderosa pine and grassland vegetation type was used as the reference category for deer and mountain lions, respectively. Not burned was used as the reference level for wildfire and prescribed burns and not thinned was used as the reference level for forest thinning. Variance inflation factors were also calculated for each of the highest-ranking models in each season to further assess multicollinearity. If a combination of predictor variables in a model resulted in a VIF > 5, we eliminated that model from the analysis.

3. Results

3.1. Forage biomass

Herbaceous forage biomass differed by vegetation type ($F_{5,640} = 29.45$ $P < 0.001$) and treatment ($F_{3,640} = 5.10$ $P < 0.001$). Herbaceous forage biomass was 113% to 187% greater in grasslands in comparison to all other vegetation types. Mixed-conifer vegetation had 23% more herbaceous biomass than ponderosa pine and 33% more than pinyon-juniper vegetation (Fig. 2). Wildfire-burned areas had 39–42% more herbaceous forage biomass than prescribed burns, forest thinning, and untreated areas (Fig. 2).

Oak stem + leaf biomass and oak stem-only biomass differed by vegetation type (stem + leaf, $F_{5,193} = 21.45$ $P < 0.001$; stem-only, $F_{5,195} = 22.37$ $P < 0.001$) and there was a vegetation type by treatment interaction (stem + leaf, $F_{5,193} = 6.61$ $P < 0.001$; stem-only, $F_{5,195} = 6.66$ $P < 0.001$). As expected, oak stem + leaf biomass and oak stem-only biomass was 339–473% greater in oak shrublands in comparison to all other vegetation types (Fig. 2). Oak stem + leaf biomass and oak stem biomass was also 32–299% greater in wildfire-burned areas when compared to prescribed burns, forest thinning, and untreated areas (Fig. 2). Oak stem + leaf biomass and oak stem-only biomass was 191–192% greater in oak vegetation burned by wildfires, 99–103% greater in ponderosa pine vegetation burned by wildfires, and 63–70% greater in mixed-conifer vegetation burned by wildfires when compared to untreated areas of those vegetation types. Oak stem + leaf and oak biomass was also 103–104% greater in ponderosa pine wildfire-burned areas when compared to ponderosa pine prescribed-burned areas. Thinned mixed-conifer vegetation had 107–127% more oak stem + leaf and oak stem biomass than mixed-conifer vegetation that was not treated.

3.2. Landscape-scale habitat selection

Elevation, northness, edge density, distance to high-use roads, and covariates describing wildfire, prescribed burns, and forest thinning were in most top models for landscape-scale habitat selection by mule

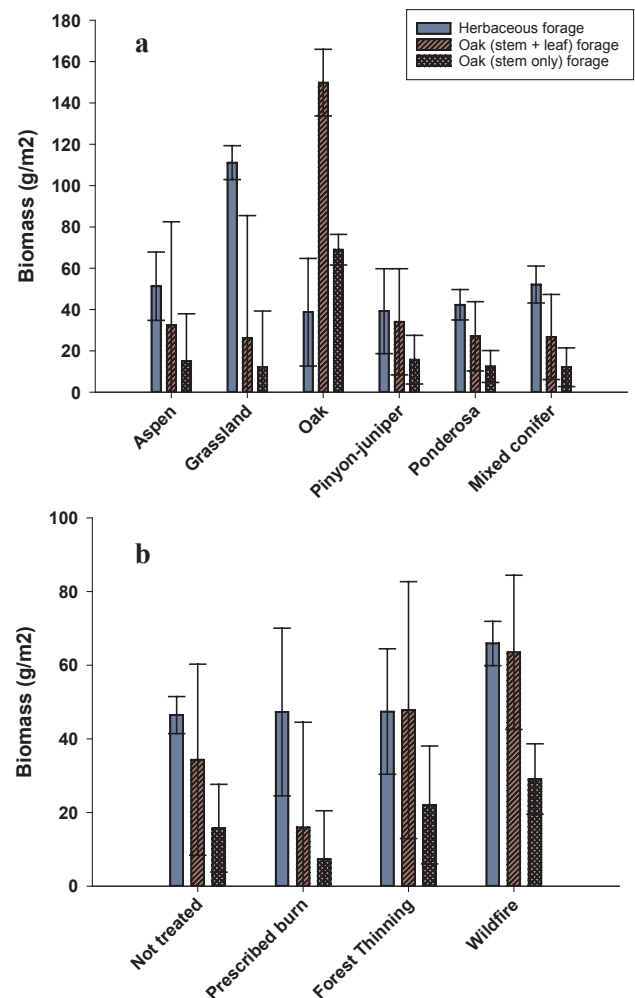


Fig. 2. Marginal means for herbaceous forage, oak stem and leaf, and oak stem biomass (g/m²) in (a) different vegetation types and (b) wildfire-burned, treated, and non-treated areas in the Jemez Mountain, New Mexico, 2012–2015. Error bars represent 95% confidence intervals; confidence intervals that do not overlap are significantly different ($\alpha \leq 0.05$).

deer. We observed seasonal differences in mule deer habitat selection in association with seasonal elevation movements. These elevational movements were reflected in seasonal differences in selection of vegetation types and treatments. Mule deer use increased with decreasing distance from high-use roads. Prescribed burns were selected for, while wildfire-burned areas were avoided. Mule deer selected for thinned areas ≥ 5 years old while thinned areas < 5 years old were generally avoided. Mule deer also selected for intermediate slopes and avoided grasslands. 5-fold cross-validation analyses indicated that the most supported model for each season performed well (p : 0.92–0.97) at the landscape scale.

Two autumn models had some support (Table 1); however, the top model had twice the support of the second-ranked model. Both models included elevation, northness, slope², distance to high-use roads, and covariates describing wildfire, prescribed burns, and forest thinning with near identical parameter estimates. The top model also included vegetation type and edge density, while the second-best model included distance to water (Table 1). Based on the model weights and the fact that there were some important differences in selection of different vegetation types, we chose to interpret the highest ranking model. Mule deer selected for lower elevations, north-facing slopes, and areas closer to high-use roads and farther from perennial water. Mule deer avoided pinyon-juniper woodlands and selected for mixed-conifer forests over

Table 1

Five highest-ranking models for seasonal habitat selection by adult female mule deer at the landscape scale (2nd order) in the Jemez Mountains, New Mexico, 2015. Number of parameters (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weights (w_i).

Season	Model ¹	K	AIC_c	ΔAIC_c	w_i
Autumn	Elev + North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	18	3144.29	0.00	0.63
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	13	3145.77	1.48	0.30
	North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	17	3149.01	4.72	0.06
	North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	12	3152.70	8.41	0.01
	Elev + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	12	3154.68	10.39	0.00
Spring	Elev + North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	18	3943.94	0.00	1.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	13	3955.01	11.07	0.00
	Elev + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	12	3962.95	19.00	0.00
	Elev + North + Slope + Slope ² + Veg Type + Roads + Water	13	4008.09	64.15	0.00
	Elev + Slope + Slope ² + Veg Type + Roads + Water	12	4016.75	72.81	0.00
Summer	Elev + North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	18	8698.81	0.00	1.00
	Elev + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	17	8737.23	38.42	0.00
	North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	17	8857.05	158.23	0.00
	Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	14	9072.24	373.42	0.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	13	9077.94	379.13	0.00
Winter	North + Slope + Slope ² + Veg Type + Roads + Water	12	9069.79	0.00	1.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	13	9082.22	12.43	0.00
	Elev + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	12	9088.10	18.31	0.00
	Veg Type + Roads + Water	9	9100.73	30.93	0.00
	North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	12	9104.29	34.49	0.00

¹ Covariates: Elev = elevation, North = northness, Slope = percent slope, Slope² = quadratic term for percent slope, Veg Type = vegetation type, Roads = distance to high-use roads, Wildfire = wildfire-burned areas, RX Burn = prescribed burns, Thin = thinned areas, Water = distance to nearest perennial water source, Edge = edge density.

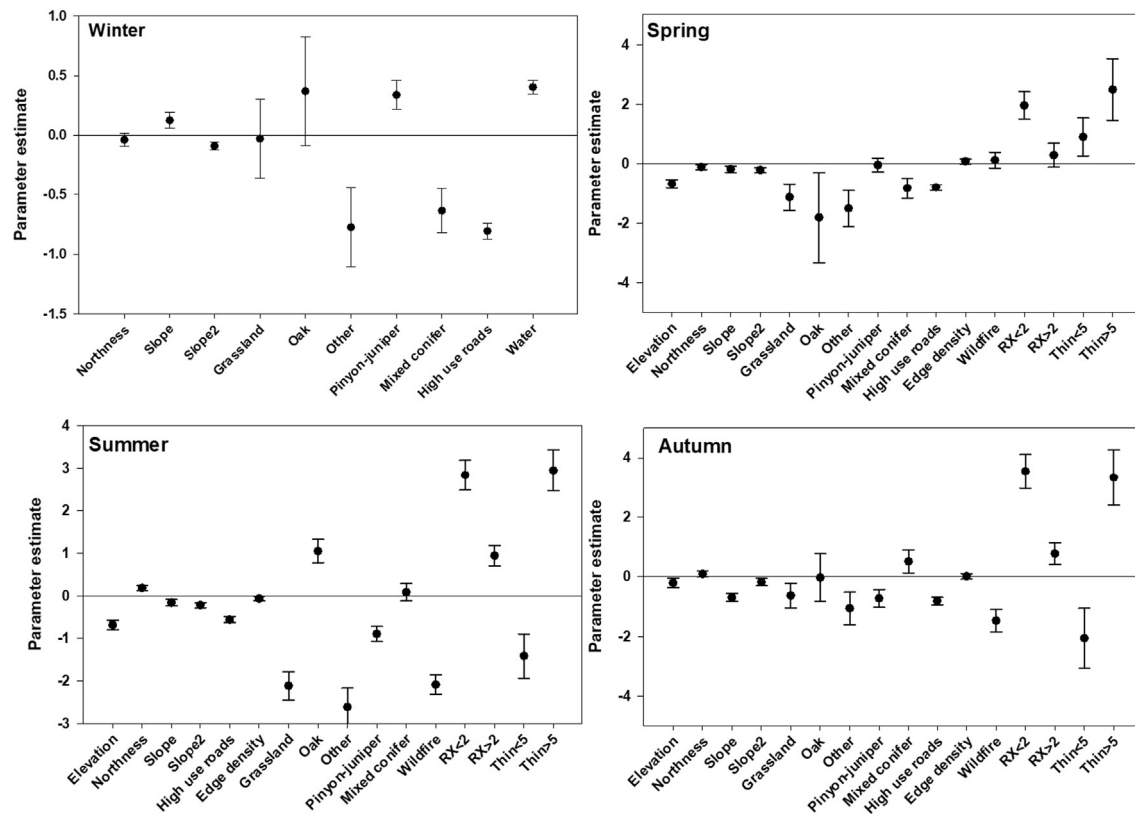


Fig. 3. Parameter estimates from the top models for seasonal habitat selection by adult female mule deer at the landscape scale (2nd order) in the Jemez Mountains, New Mexico, 2015. Error bars represent the 95% confidence intervals. Covariates: Roads = distance to high-use roads, Water = distance to nearest perennial water source, Wildfire = wildfire-burned areas, RX < 2 = prescribed burn less than 2 years old, RX ≥ 2 = prescribed burn greater than 2 years old, Thin < 5 = thinning less than 5 years old, Thin ≥ 5 = thinning greater than 5 years old. Parameter estimates with 95% confidence intervals that do not overlap 0 should be considered significant at $\alpha \leq 0.05$.

ponderosa pine forests. Mule deer avoided wildfire-burned areas and selected for prescribed burns < 2 years old. Mule deer avoided thinned areas < 5 years old, but strongly selected for thinned areas ≥ 5 years old (Fig. 3).

The model for spring with greatest support included elevation, northness, slope², distance to high-use roads, edge density, vegetation type, and covariates describing wildfire, prescribed burns and forest thinning (Table 1). Odds of use decreased with increasing elevation and increasing distance from high-use roads and increased with increasing edge density. Mule deer avoided north-facing slopes and selected ponderosa pine over all other vegetation types. Mule deer selected wildfire-burned areas, prescribed burns < 2 years old, and thinned areas, with stronger selection for thinned areas ≥ 5 years old (Supplementary material, Table S4; Fig. 3).

For summer, there was one supported model that included elevation, northness, slope², vegetation type, distance to high-use roads, edge density, and covariates describing wildfire, prescribed burns, and forest thinning (Table 1). Odds of use decreased with increasing elevation, distance from high-use roads, and edge density. Mule deer selected for north-facing slopes. When compared to ponderosa pine, mule deer selected oak vegetation and avoided pinyon-juniper woodlands and grasslands. In addition, odds of use by mule deer was lower for wildfire-burned areas, higher in prescribed-burned areas, lower in thinned areas < 5 years old, and greater in thinned areas ≥ 5 years old compared to unburned or untreated areas. (Supplementary material, Table S4; Fig. 3).

For winter, the highest-ranking model included northness, slope², distance to high-use roads, distance to perennial water, and vegetation type (Table 1). Odds of use decreased with proximity to high-use roads and were lower nearer perennial water sources. In addition, use was higher in pinyon-juniper woodlands and lower in mixed-conifer stands compared to ponderosa pine forests (Supplementary material, Table S4; Fig. 3).

3.3. Home-range scale habitat selection

Mule deer generally selected for prescribed burns, thinned areas

≥ 5 years old, and intermediate slopes, and avoided wildfire-burned areas and grasslands. 5-fold cross-validation analyses indicated that the most supported models at the home-range scale performed well (ρ 0.74–0.95).

The habitat selection model with greatest support for autumn included elevation, slope², distance to high-use roads, vegetation type, edge density, and covariates describing wildfire, prescribed burns, and forest thinning (Table 2). Odds of use increased with increasing elevation and distance from high-use roads. Mule deer used grasslands and mixed-conifer forests more than ponderosa pine. Additionally, odds of use was lower in wildfire-burned areas, greater in prescribed-burned areas, particularly burns < 2 years old, and greater in thinned areas ≥ 5 years old when compared to unburned and unthinned areas, respectively. (Supplementary material, Table S5; Fig. 4).

The model with greatest support for spring included elevation, slope², distance to high-use roads, vegetation type, edge density, and covariates describing wildfire, prescribed burns, and forest thinning (Table 2). Odds of use increased with increasing edge density and distance from high-use roads and decreasing elevation. Additionally, use was lower in grassland, oak, and pinyon-juniper vegetation types when compared to ponderosa pine. Mule deer use was higher for wildfire-burned areas, prescribed burns compared with unburned areas, and thinned versus unthinned areas (Supplementary material, Table S5; Fig. 4).

The top-ranking model for summer included elevation, northness, slope², vegetation type, distance to high-use roads, edge density, and covariates describing wildfire, prescribed burns, and forest thinning (Table 2). Odds of use was greater in oak and mixed-conifer vegetation and lower in pinyon-juniper vegetation when compared to ponderosa pine. Mule deer also selected for north-facing slopes and areas with lower edge density. In addition, mule deer odds of use were greater in wildfire- and prescribed-burned areas than unburned areas, they avoided thinned areas < 5 years old, and selected for thinned areas ≥ 5 years old (Supplementary Material, Table S5; Fig. 4).

For winter, the highest-ranking model included elevation, northness, slope², vegetation type, distance to high-use roads, and distance to perennial water (Table 2). Odds of use increased with increasing

Table 2

Five highest-ranking a priori models for seasonal habitat selection by adult female mule deer at the home-range scale (3rd order) in the Jemez Mountains, New Mexico, 2015. Number of parameters (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weights (w_i). Models are ranked according to AIC_c from best to worst.

Season	Model ¹	K	AIC_c	ΔAIC_c	w_i
Autumn	Elev + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	17	3866.79	0.00	1.00
	Elev + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	12	3880.10	13.31	0.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	13	3882.10	15.31	0.00
	North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	17	3883.55	16.76	0.00
	Elev + Slope + Slope ² + Predation Risk + Wildfire + RX Burn + Thin	11	3883.64	16.85	0.00
Spring	Elev + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	17	4817.26	0.00	1.00
	Elev + Slope + Slope ² + Predation Risk + Wildfire + RX Burn + Thin	11	4829.63	12.37	0.00
	Elev + North + Slope + Slope ² + Predation Risk + Wildfire + RX Burn + Thin	12	4831.64	14.39	0.00
	North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	17	4834.10	16.85	0.00
	Elev + Slope + Slope ² + Wildfire + RX Burn + Thin	10	4834.61	17.36	0.00
Summer	Elev + North + Slope + Slope ² + Veg Type + High-Use Roads + Edge + Wildfire + RX Burn + Thin	18	11024.89	0.00	1.00
	Elev + North + Slope + Slope ² + Predation Risk + Wildfire + RX Burn + Thin	12	11116.54	91.65	0.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	13	11120.59	95.70	0.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin	11	11121.47	96.58	0.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Can Cover	12	11123.14	98.25	0.00
Winter	Elev + North + Slope + Slope ² + Veg Type + Roads + Water	13	10028.85	0.00	0.99
	Elev + Slope + Slope ² + Veg Type + Roads + Water	12	10037.33	8.48	0.01
	North + Slope + Slope ² + Veg Type + Roads + Water	12	10051.01	22.15	0.00
	Elev + North + Slope + Slope ² + Veg Type + Roads + Edge + Wildfire + RX Burn + Thin	18	10062.58	33.72	0.00
	Elev + North + Slope + Slope ² + Wildfire + RX Burn + Thin + Roads + Water	13	10065.21	36.36	0.00

¹ Covariates: Elev = elevation, North = northness, Slope = percent slope, Slope² = quadratic term for percent slope, Veg Type = vegetation type, Roads = distance to high-use roads, Wildfire = wildfire-burned areas, RX Burn = prescribed burns, Thin = thinned areas, Water = distance to nearest perennial water source, Predation Risk = mountain lion predation risk index, Can Cover = percent canopy cover, Edge = edge density.

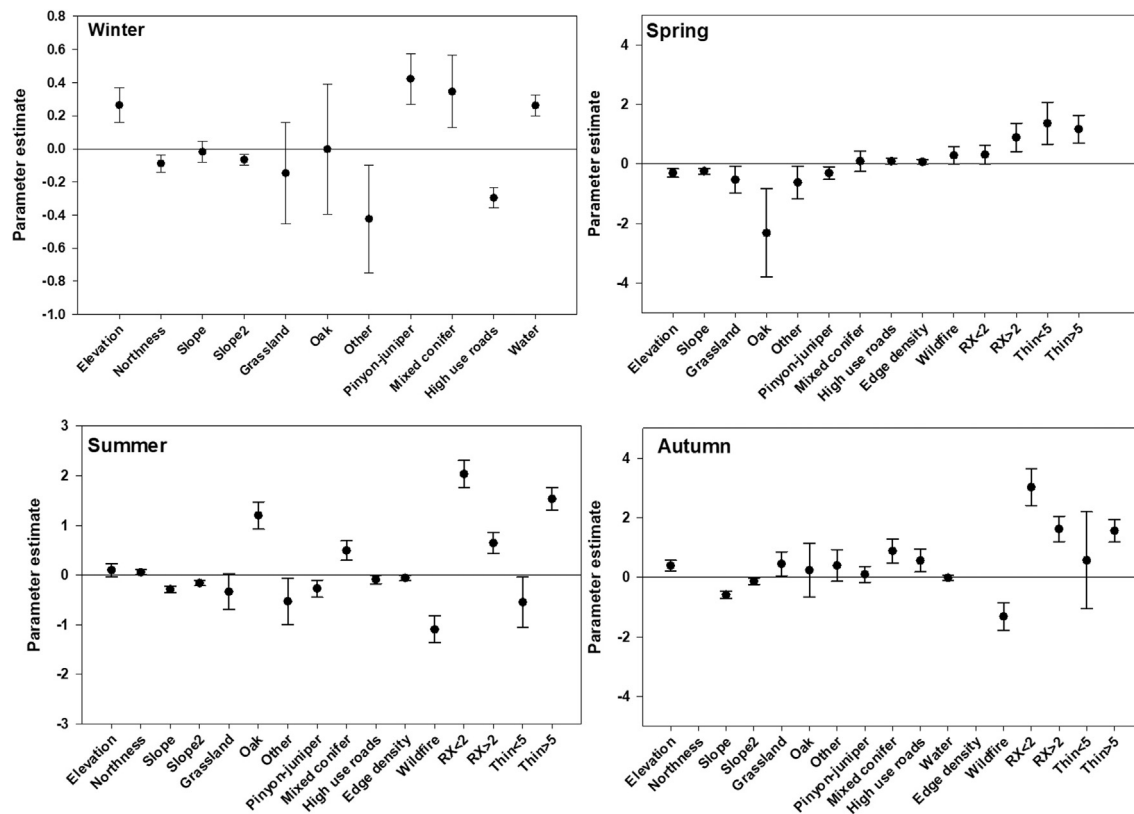


Fig. 4. Parameter estimates from the top models for seasonal habitat selection by adult female mule deer at the home-range scale (3rd order) in the Jemez Mountains, New Mexico, 2015. Error bars represent the 95% confidence intervals. Covariates: Roads = distance to high-use roads, Water = distance to nearest perennial water source, Wildfire = wildfire-burned areas, $RX < 2$ = prescribed burn less than 2 years old, $RX \geq 2$ = prescribed burn greater than 2 years old, Thin < 5 = thinning less than 5 years old, Thin ≥ 5 = thinning greater than 5 years old. Parameter estimates with 95% confidence intervals that do not overlap 0 should be considered significant at $\alpha \leq 0.05$.

elevation and distance to perennial water and decreased with increasing distance to high-use roads. In addition, use was greater in pinyon-juniper and mixed-conifer vegetation in comparison with ponderosa pine (Supplementary material, Table S5; Fig. 4).

4. Discussion

Fire was historically an important natural disturbance in many southwestern ecosystems (Covington and Moore, 1994; Block et al., 2016). Wildfires were frequent in many dry forest types in the Southwest, but generally burned at low intensity. However, with European settlement, natural fires were suppressed and forest structures changed, ultimately resulting in degraded habitat conditions for many wildlife species and less frequent and more severe wildfires (Covington and Moore, 1994; Block et al., 2016). To mitigate wildfire risk, land managers are implementing landscape-scale forest restoration treatments including prescribed fire and thinning. Our results indicate that the influence on mule deer habitat selection during our study varied with the type of disturbance and the duration of the post-disturbance recovery period.

Mule deer selected for prescribed burns in almost all seasons at both spatial scales, with selection being more pronounced for more recent (i.e., < 2 years old) prescribed burns. Prescribed burns generally burn at a lower intensity (Block et al., 2016) and previous studies have reported increased forage quality, especially 2–3 years after the burn (Dills, 1970; Keay and Peek, 1980; Hobbs and Spowart, 1984; Carlson et al., 1993; Masters et al., 1993). Masters et al. (1993) reported that forage production declined after 6 years and suggested prescribed burning every 2–4 years to increase deer forage quality. Previous work in Idaho and Canada have also reported an overall increase in

herbaceous (e.g., forbs and grasses) forage biomass and a decrease in shrubs 2 years after prescribed burns; however, the nutritional impact of prescribed burns generally decreases over time (Canon et al., 1987; Sachro et al., 2005). Our estimates of herbaceous and oak forage biomass did not differ between untreated areas and those treated with prescribed fires. Therefore, the stronger selection of more recent prescribed burns by mule deer in our study may be related to short-term increases in nutritional content rather than the increase in forage abundance reported several years after the burning (Severson and Medina, 1983; Long et al., 2008a; Lashley et al., 2015).

The strong selection by mule deer for older thinned forests (i.e., ≥ 5 years old) and varied selection of more recently thinned areas were likely due to differences in forage and cover, both of which increase with time since treatment. A previous study found mule deer bedding habitat was reduced 50–100% in areas treated with forest thinning followed by prescribed fires that were < 4 years old, but herbaceous forage characteristics (mid-story canopy cover, live ground cover, and species richness) increased 31–66% (Germaine et al., 2004). Furthermore, older thinned areas may also be more heavily used by mule deer because they are often burned several years after thinning to remove residual woody debris left during thinning, which stimulates increased herbaceous forage production and increased nutritional quality (Long et al., 2008a). Similarly, Horncastle et al. (2013) reported that mule deer selected for thinned and burned sites in northern Arizona. The combination of forest thinning, followed by prescribed burns are generally more effective in increasing forage biomass than when either was used alone (Brockway et al., 2002; Schwikl et al., 2009; Stephens et al., 2009; Roccafort et al., 2010; Horncastle et al., 2013). Consequently, mule deer avoidance or lower selection of more recently thinned areas (i.e., < 5 years old) may be a result of the short post-disturbance

recovery time and the influence on woody browse and cover favored by mule deer. Likewise, Long et al. (2008b) reported that fuel reduction treatments including thinning and burning had little influence on resource selection by mule deer in Oregon; however, many of their treatments were < 5 years old.

Mule deer generally avoided the two most recent wildfire areas during our study in contrast to reported extensive use of burned areas by ungulates (Peek, 1974; Keay and Peek, 1980; Wan et al., 2014; Roberts et al., 2017; Kay, 2018). The avoidance of wildfire-burned areas by our deer may have been related to burn severity and recent timing of the fires. The Las Conchas and Thompson Ridge wildfires occurred in 2011 and 2013, respectively, and covered approximately 27% of the study area. Most of the wildfires in our study area occurred within the past 5 years and 33% were high severity, stand-replacing fires. Areas that have had high severity burns may take longer to recover and during this time they provide reduced foraging opportunities and concealment cover due to slow recovery of understory shrubs. The wildfire-burned areas found in the Jemez Mountains study area may not have been old enough to provide the habitat characteristics for which mule deer select. However, elk strongly responded to these wildfire-burned areas due to a rapid increase in herbaceous forage following the wildfires (Roberts et al., 2017). Wan et al. (2014) reported that mule deer in aspen forests of Utah were more dispersed with increasing fire size and severity, but that elk were unaffected. Mule deer did not avoid wildfire-burned areas only during spring, when no effect on selection was detected at the landscape scale, and deer selected for these areas at the home-range scale. During spring, newly emergent herbaceous vegetation would have high nutrient:fiber ratios, and thus, would be attractive to mule deer. However, once herbaceous forage species begin to mature and senesce during summer and autumn, fiber content increases and nutritional value for mule deer declines. Based on their gut anatomy and morphological characteristics, mule deer are less able to efficiently digest low quality herbaceous forage compared to larger grazing species such as elk. The individual and potentially interactive effects of reduced concealment cover, slow recovery of browse species, and high elk use likely contributed to the general avoidance of recent wildfire-burned areas by mule deer.

The influence of the other habitat characteristics we assessed on mule deer habitat selection were mostly consistent with previous research (D'Eon and Serrouya, 2005; Sandoval et al., 2005; Horncastle et al., 2013). Similar to other studies, mule deer generally selected for intermediate slopes (Sawyer et al., 2006; Horncastle et al., 2013). When northness appeared in top-ranking models, mule deer selected for north-facing slopes during summer and autumn; in summer they tend to be cooler and hold more moisture, and therefore have greater potential for more abundant forage. During winter and spring, mule deer generally avoided north-facing slopes when they receive less solar radiation and have deeper snow, reducing forage availability and increasing energy requirements for locomotion (Parker et al., 1984; D'Eon and Serrouya, 2005).

Seasonal changes in selection or avoidance of specific vegetation types were associated largely with seasonal movement along the elevational gradient. In comparison to ponderosa pine, low elevation pinyon-juniper woodlands were avoided in autumn and summer and selected during winter. High elevation mixed-conifer stands were selected during autumn and mid-elevation oak patches were selected during summer. Mixed-conifer stands provided greater herbaceous (i.e., grasses and forbs) biomass, and likely delayed phenology due to their higher elevations and more northerly aspects than other vegetation types, and oak are an important woody forage species for mule deer (Sandoval et al., 2005; Heffelfinger, 2006; Kay, 2018). Mule deer tended to avoid oak vegetation types within their home range in spring, but they strongly selected for oak during the summer, indicating that mule deer may be likely focusing on emergent herbaceous vegetation during spring green-up in mixed-conifer forests, then shifting towards browse in oak-dominated patches later in the summer after fiber

content increases and nutrient content decreases in herbaceous vegetation (Boeker et al., 1972; Heffelfinger, 2006). During winter, mule deer likely shifted to lower elevation pinyon-juniper woodlands to avoid deeper snow at high elevations and because pinyon-juniper stands often provide browse species preferred by mule deer, such as oak and mountain mahogany (Bartmann, 1983; Sandoval et al., 2005; Heffelfinger, 2006). Additionally, covariates for wildfires and forest restoration treatment were not in top models for winter at either spatial scale because most of the fires and treatment-affected areas were in high elevation ponderosa and mixed-conifer vegetation types. High elevation grassland areas were largely avoided or had no influence on selection at either spatial scale.

Availability of perennial water has often been reported to have a strong influence on mule deer habitat selection, particularly at lower elevation arid and semi-arid regions, or during drought in more mesic areas (Germaine et al., 2004; Heffelfinger, 2006; Horncastle et al., 2013). Distance to perennial water was only in our highest-ranking habitat selection models during autumn and winter at the landscape scale and during winter at the home-range scale, and generally had little support during other seasons. When this covariate was important, mule deer selected areas farther from perennial water at both spatial scales. Water is generally abundant throughout our study area; 94–96% of our seasonal study areas were within 1.6 km of a perennial water source, likely decreasing the influence of perennial water on habitat selection by mule deer in our study. Mule deer also have access to numerous ephemeral water sources that persist for varying lengths of time after precipitation events, especially during summer monsoons and winter. Furthermore, mule deer may be obtaining substantial pre-formed water from their forage, and therefore may not need to be as close to water sources to maintain water balance (Cain et al., 2006, 2013). On average, during summer in our study area, herbaceous forage contained 40–42% moisture and woody browse 50% moisture (Roerick, 2017).

Previous studies have found predators influence ungulate habitat selection and often cause ungulates to make trade-offs to reduce predation risk (Creel et al. 2005; Hebblewhite and Merrill 2009; Thaker et al., 2011). Mountain lions can have a large impact on deer populations (Cooley et al. 2008; Knopff et al. 2010; Pierce et al., 2012) and are one of the main predators of mule deer in the Jemez Mountains; they accounted for 9 out of 11 mule deer mortalities during this study (Roerick 2017). Despite this, predation risk was only in a couple of the top-ranking models at the within home range scale, but it was not in any top models at the landscape scale. When predation risk was a significant variable, mule deer selected for areas with low predation risk, however predation risk by mountain lions was not consistently in the highest ranking models, indicating that other habitat characteristics exerted a stronger influence on resource selection at the scales we assessed.

5. Conclusion

Our data suggest mule deer may benefit from prescribed burns and thinned areas after sufficient post-treatment recovery of vegetation has occurred. Mosaic treatment patterns may therefore be beneficial to mule deer by providing forage and cover through different stages of treatments. As restoration treatments continue in the Jemez Mountains, New Mexico, we recommend researchers to continue to investigate the short- and long-term effects of prescribed burns and forest thinning on mule deer. Understanding mule deer habitat selection is critical to the future development of successful management strategies and restoration plans.

Funding

Funding was provided by the Pueblo of Jemez, Santa Fe National Forest, the Valles Caldera National Preserve, Pope and Young Club,

Dallas Safari Club/Ecological Foundation, and the New Mexico Chapter of the Rocky Mountain Elk Foundation.

Acknowledgements

We thank the Texas Tech University Department of Natural Resources Management, the United States Forest Service, National Park Service, the Pueblo of the Jemez, Pope and Young Club, Dallas Safari Club/Ecological Foundation, and the New Mexico Chapter of the Rocky Mountain Elk Foundation for funding and equipment. We thank S. Gifford, G. Kaufman, C. Madalena and the staff from the Pueblo of Jemez; K. Buermeier, S. Harrelson, J. Marshall, B. Riley, A. Silva, E. Taylor from the Santa Fe National Forest-Jemez Ranger District and Santa Fe Headquarters, and J. Banuelos-Silva, S. Compton, M. Peyton and B. Parmenter from the Valles Caldera National Preserve for logistical support. We thank M. Peyton, J. Roerick, K. Humagain, A. Anaya, C. Roberts, J. Naranjo, J. Daly, T. Lubenau, A. Karasov-Olson, M. Levy, R. Passernig, S. Smythe, S. Gaffney, E. Cate, S. Johnson-Bice, A. Gerrits, T. Stonecypher, and L. Howard for field assistance. Mountain lions were captured by B. Jansen and M. Peyton and mule deer were captured by P. Alcumbrac, M. Forsyth, S. Kindschuh, W. Livingstone, K. Mower, M. Peyton, M. Ross, C. Stallings, and E. Watters. Helpful comments from two anonymous reviewers improved an earlier draft of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions

Contributions for this study are as follows: JWC and TMR collected field data on vegetation and mule deer habitat use. TMR, JWC, and JVG assisted with data analyses. TMR wrote the manuscript with help of JWC and JVG. All authors critically evaluated and revised the text.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.05.067>.

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