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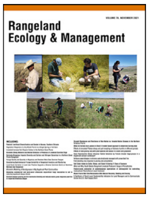

Forage Quality and Quantity in Migratory and Resident Mule Deer Summer Ranges[☆]

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ABSTRACT

The quality and quantity of forage available to reproductive female ungulates during the summer can influence body condition and lactation, ultimately influencing herd production. The energetic costs of migration can influence individual fitness, thus understanding the mechanisms that drive some individuals in a partially migratory population to migrate, while others remain on winter range year-round, has important conservation and ecological implications. We examined differences in forage quality and quantity between migratory ($n = 19$) and resident ($n = 17$) summer home ranges for a population of mule deer *(Odocoileus hemionus)* in the John Day Basin of northeast Oregon. During 2018, we collected vegetation measurements three times throughout the summer (mid-May, mid-June, mid-July) to determine changes in dry matter digestibility (DMD; %) at three different phenological stages (emergent, mature, and cured) for three forage classes (grass, shrub, forbs). On the second visit, at the peak of the growing season, we collected biomass and cover data to determine differences in forage quantity for each forage class between the migratory and resident summer ranges. In mid-June 2019, we revisited a subsample of sites (migratory [$n = 5$]; resident [$n = 5$]) to estimate interannual variation. Migratory deer had access to overall higher quality forage at higher-elevation summer ranges. Forbs had the highest forage quality on both summer ranges. Forage quality declined across the entire study area as moisture declined and vegetation senesced. Shrub forage quality was higher (DMD = 54.1%) on resident ranges than migratory ranges (49.7%; $P = 0.001$). Grasses had higher biomass (26.1 Mg/ha) and cover (50.1 %) than forbs (19.2 Mg/ha; 34.7% cover) or shrubs (20.6 Mg/ha; 6.7% cover) across the entire summer range. Overall, migratory deer had access to higher-quality forage throughout the summer, yet resident deer had access to higher-quality shrub browse. This trade-off in forage availability may partially explain the persistence of a partially migratory population as a bet-hedging strategy on a landscape where low moisture availability and episodic drought and disturbance create variable foraging conditions.

Introduction

Populations in which many, but not all, individuals migrate are referred to as *partially migratory* (Chapman et al. 2011). For partially migratory behavior to be maintained within a population, there is likely a form of demographic balancing taking place (Lundberg 1988). For example, individuals may adopt a migratory or resident strategy depending on body condition or age (Acolas et al. 2012) or will switch between strategies based on resource availability (Eggeman et al. 2016). Partial migration is documented in some populations of several ungulate species across North America, including mule deer *(Odocoileus hemionus)*, elk *(Cervus elaphus)*, pronghorn *(Antilocapra americana)*, and moose *(Alces alces)* (e.g., Nicholson et al. 1997; Ball et al. 2001; White et al. 2007; Barker et al. 2019). Migration behavior in ungulates represents a trade-off between potential benefits of moving to higher quality habitat, which can ultimately increase reproductive success, and the risks associated with moving through unfamiliar territory (i.e., predation, vehicle collision, anthropogenic barriers, and climatic weather events) during the migration process (White 1983; Nicholson et al. 1997).

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Individuals that do not move to a different summer range but remain on the same range year-round forego the potential for better quality habitat and gains in biomass but conserve energy and reduce movement-associated risks (Hebblewhite and Merrill 2009). Previous studies have also demonstrated that ungulates can adopt selection strategies at more than one scale (Boyce et al. 2003; Johnson et al. 2006; Hebblewhite et al. 2008). The scale of selection for an animal may be at the plant, patch, vegetation community, or landscape level. Understanding how forage productivity differs at two different scales for migratory and resident deer can help draw generalizations about what could be driving the divergent movement behavior of a population.

Ungulate migration is driven by the seasonal pursuit of higher quality forage (i.e., higher dry matter digestibility [DMD]; White 1983). Beginning in the spring, individuals follow phenological gradients or “green waves” (i.e., following herbaceous vegetation moisture [Moeslund et al. 2013]) to maximize forage quantity and quality throughout the growing season (Fryxell 1991; Hebblewhite et al. 2008; Hebblewhite and Merrill 2009). Forage quality is highest in new plant growth and declines as the plant matures due to the conversion from easily digestible, nutritious plant cells to dry, fibrous plant material (Van Soest 1982). One proposed mechanism for partial migration in ungulate populations is the forage maturation hypothesis (FMH), which predicts that migratory ungulates will follow phenological gradients to maximize energy intake (Fryxell and Sinclair 1988). Individuals will migrate to areas that offer a balance between forage quality and quantity. Energy intake is not solely a function of forage quality and quantity but also a function of rumination (Fryxell 1991; Hebblewhite and Merrill 2008). For every high-quality bite, less rumination is needed to deliver nutrition to the body. The animal thus spends more time foraging, which can improve body condition and ultimately increase fitness (White 1983). In addition, the individual must select an area with adequate forage quantity to sustain its physiological functions. Adding to the complexity, the distribution of forage quality and quantity varies depending on scale of measurement, starting with plant functional groups all the way to the landscape level (Merems et al. 2020). For example, shrub species may offer a more concentrated source of nutrition but often do not occur as frequently as forbs across the landscape. Therefore, when assessing forage quantity, it is imperative to evaluate forage biomass and vegetation cover. When these two metrics are combined, they describe the vertical structure of forages on the landscape (i.e., forage bulk density).

Summer forage, particularly late-summer forage, is critical in supporting reproductively viable ungulate populations (Merrill and Boyce 1991; Rolandsen et al. 2017; Cook et al. 2018). Summer forage is essential for adult females as it provides nutrition and enables them to meet their energetic demands of lactation for fawns, to build body fat reserves and then maintain the next pregnancy through the winter (Cook et al. 2004). Lactation can have significant costs to an individual; if the required nutrition to produce milk is not consumed, then a deer will metabolize its own body reserves to maintain offspring growth (Landete-Castillejos et al. 2003). In the fall, females may not enter estrus if they are in poor body condition (i.e., low weight and body fat). Collectively, nutritional limitations on females during summer-autumn can limit overall herd production (Cook et al. 2004; Proffitt et al. 2016). Migrants and residents forage in different areas during summer, which may influence an individual’s access to adequate quantity (biomass) and quality (digestibility) of forage (Rolandsen et al. 2017; Baker et al. 2018), ultimately influencing fecundity or survival rates (Cook et al. 2004, Proffitt et al. 2016). Annual variability in climatic factors such as rainfall influence plant phenology and forage availability, which can impose constraints on ungulate reproduction, particularly in semiarid environments (Ogutu et al. 2014). Thus, comparing the quality and quantity of forage available on migrant and resident summer ranges and between years can provide insights into mechanisms driving partially migratory populations of mule deer.

Forage quality is determined by digestibility, protein content, minerals, and tannins (Short 1981; Van Soest 1982). Digestibility is determined by the ratio between the cell walls and the cell content; thus, the less cellulose a cell has, the easier it is digested, resulting in higher nutrition (Van Soest 1982). Plant digestibility is highest when the plants first emerge and then gradually declines due to the thickening of the cell walls as the plant matures (Robbins 1983). Compared with other ruminants, mule deer are selective feeders. Their anatomic features, such as small mouth, rumen, and gut length relative to body size, result in forage selection to achieve relatively small volumes of a high-quality, easily digestible diet (Wallmo 1981). This nutritional niche requires mule deer to be selective browsers rather than grazers. Mule deer primarily consume forbs and shrubs throughout the year, only selecting for grasses when they first emerge (Wallmo 1980; Holecheck 1984). When forbs are green and succulent, they are the most preferred forage for mule deer (Snider and Asplund 1974; Mackie et al. 2003). Shrubs become a critical component of mule deer diet as forbs and grasses senesce and when the ground is covered in snow (Blaisdell et al. 1982). Due to their specialized forage requirements, mule deer also must have a highly varied diet to accommodate their nutritional needs, which vary with seasonal forage availability and density dependence (Carpenter et al. 1973; Geist 1981; Findholt et al. 2004; Stewart et al. 2011; Berry et al. 2019). Variability in summer diets is compounded in a partially migratory population when there are substantial differences in foraging sites due to plant community composition. For example, in sagebrush steppe ecosystems on resident deer summer ranges, antelope bitterbrush *(Purshia tridentata)*, big sagebrush *(Artemisia tridentata)*, yarrow *(Achilles millefolium)*, Sandberg bluegrass *(Poa sandbergii)*, and bluebunch wheatgrass *(Pseudoroegneria spicata)* are major components of a mule deer diet (Willms and McLean 1974). By comparison, buckbush *(Ceanothus cuneatus)*, creeping Oregon grape *(Berberis repens)*, whortleberry *(Vaccinium myrtillus)*, huckleberry (*Vaccinium* spp.), serviceberry (*Amelanchier* spp.), wild strawberry (*Fragaria* spp.), dandelion (*Taraxacum* spp.), and balsamroot (*Balsamorhiza* spp.) comprise the diet of migratory deer in dry forest ecosystems (Huffman and Moore 2003; Hosten et al. 2007; Watkins et al. 2007). Due to the species’ diverse dietary requirements, summer ranges that support the highest diversity of plant species may offer a more optimal selection of forages (Holecheck 1984).

The partially migratory patterns of the female deer that overwinter in the John Day Basin of northeastern Oregon offer a unique Sopportunity to evaluate influences of available nutrition on summer ranges and may provide insight into the mechanisms for differences in migration behavior. The objectives of this research were 1) to determine how forage quality (DMD), quantity (biomass), percent cover, and forage bulk density (plant biomass divided by cover) differed between resident and migratory deer summer ranges; 2) to quantify how forage quality (DMD) changed over the growing season on each range type; and 3) estimate magnitude of the annual variation in forage quality and quantity. We predicted that forage quality would be highest during active plant growth, resulting in higher-quality forage at low elevations early in the summer on the resident ranges and higher-quality forage at higher elevations on the migratory ranges later in the summer (Robinson and Merril 2013; Barker et al. 2019). We also expected that migrators’ summer ranges would have higher forage quantity due to the prolonged access to emergent vegetation (Hebblewhite et al. 2008). Finally, we predicted that annual forage quality and quantity would vary by year due to rainfall and predicted the effect would be stronger on resident ranges due to limited water availability (Marshal et al. 2005). We predicted that migratory and resident individuals would select forages at different scales, such that resident deer would select for higher-quality forages at a finer scale than migratory deer (Wilmshurst et al. 1999; Dussault et al. 2005).

Methods

Study area

The study occurred in the eastern region of the John Day Basin, Oregon, encompassing approximately 409 721 ha of low-elevation sagebrush *(Artemisia tridentata)* steppe and high-elevation dry mixed conifer and ponderosa pine forests of the Blue Mountain Range. The lower elevation shrublands were primary wintering areas for mule deer *(Odocoileus hemionus).* Human land uses at low elevations consisted of privately owned irrigated agriculture and ranching, with low-density rural development (primarily located along the John Day River). Land use at higher elevations included logging and livestock grazing allotments on federal land. There was strong variation in climate and water availability across the 616–2 756 m elevation gradient. Average annual temperatures ranged from -2^{0}C to 33^{0}C, and average precipitation ranged from 30 cm at lower elevations to 78 cm at higher elevations (PRISM Climate Group 2020).

Low-elevation plant communities included sagebrush (*Artemisia tridentata* sp.), antelope bitterbrush *(Purshia tridentata),* snowbrush *(Ceanothus velutinus),* rabbitbrush (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*), western juniper *(Juniperus occidentalis),* fescue (*Festuca* spp.), wheatgrass (*Agropyron* spp.), and bluebunch wheatgrass *(Pseudoroegneria spicata).* Many of the lower-elevation portions of the study area have been impacted by historical overgrazing and wildfire and are invaded by annual grasses, including cheatgrass *(Bromus tectorum),* meduasahead *(Taeniatherum caput-medusae),* and North Africa grass *(Ventenata dubia).* Higher-elevation plant communities contained Ponderosa pine *(Pinus ponderosa),* Douglas fir *(Pseudotsuga menziesii),* quaking aspen *(Populus tremuloides),* grand fir *(Abies grandis),* lodgepole pine *(Pinus contorta),* arrowleaf balsamroot *(Balsamorhiza sagittata),* silky lupine *(Lupinus argenteus),* pine grass *(Calamogrostis candensis),* whortleberry *(Vaccinium myrtillus),* huckleberry *(Vaccinium scooarium*), serviceberry *(Amelanchier alnifolia),* and elk sedge *(Carex geyeri).*

Defining summer ranges

We used spatial location data from a population of mule deer that were captured and radio collared in March 2015 by the Oregon Department of Fish and Wildlife (ODFW) to delineate migratory ($n = 94$) and resident summer ranges ($n = 34$). The deer were considered one population because they shared the same winter range, which occurred on or within 90 km^2 of the Phillip W. Schneider Wildlife Area (PWSWA) and used the same ecoregion (Commission for Environmental Cooperation 1997). The PWSWA was considered critical winter range habitat for a population of 5 500 mule deer and is managed by ODFW. During this study, the population of deer that winter on or nearby PWSWA exhibited partial migration: 75% of the population migrated to higher elevations in the spring and the remaining 25% did not leave the winter range.

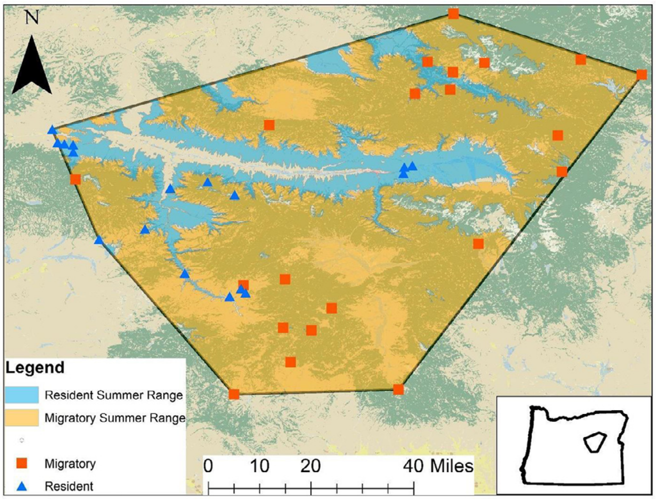

Figure 1. Map of the study area in John Day Basin, Oregon from 2018 to 2019. Orange squares and dotted line are migratory summer range perimeter and field sites ($n = 19$), and blue triangles and solid line are resident summer range perimeter and field sites ($n = 17$).

A deer was considered migratory when its seasonal range was distinctly separate and did not overlap (Brown 1992) the winter range, and the distance between seasonal range edges was > 10 km (migration distance ranged from 27 to 186 km). We determined the extent of each summer range by mapping the GPS locations for the migratory and resident deer separately and creating a minimum convex polygon (MCP) that included all summer locations for each group (Mohr 1947; Chetkiewicz and Boyce 2009; Coe et al. 2018; Fig. 1). We then randomly selected deer from each movement group (migratory $n = 19$, resident $n = 17$) to collect summer range vegetation data.

Vegetation sampling

During the summer of 2018, we compared forage biomass, percent cover, and DMD for three forage classes (shrub, grass, and forb) between individual migratory and resident mule deer summer ranges (see Fig. 1). Individual summer ranges for randomly selected deer were determined by using a 95% kernel home range distribution, which accounts for density of locations and more accurately defines the center of a home range compared with other methods, such as the centroid of a minimum convex polygon (Worton 1989). Each vegetation sampling site was located at the centroid of an individual's summer range. In 2019, we revisited a subset of 10 sites ($n = 5$ migratory, $n = 5$ resident) to collect data on plant biomass, cover, and dry matter digestibility to estimate the magnitude of variation between years.

In 2018, we visited each site three times throughout the summer (mid-May, mid-June, mid-July) to determine changes in dry matter digestibility (DMD) at three different phenological stages (emergent, mature, and cured). We established one transect at each of the 36 sites. Each transect was 30 m long beginning at the home range centroid, and the direction of the transect was randomly generated. During each visit, we took composite samples of the three forage types (forbs, grasses, shrubs) from three 2 × 2 m plots along the right side of transect (at the beginning, middle, and end) for each site visit. On returning visits, we offset the sample plots by 5 m to the right to avoid bias from prior collections.

We only collected plant parts that would be consumed by a deer (e.g., immature stems and leaves, mature leaves, stems, flowers; Spalinger et al. 1986, Hanley 1997). For shrubs, we collected leaves and the current year's growth from all shrubs rooted in the 4 m2 area of the plot. For forbs and grasses, we clipped plants down to 2 cm above soil surface from four 0.0625 m2 subplots within the 4 m2 plots, only taking the current year's growth and leaving any dead standing herbaceous material. In 2019, we repeated the same procedure once, during mid-June, to determine annual variation in DMD. All samples were dried at 50°C in a drying oven for 48 h and analyzed for percent in vitro DMD

(DeGabriel et al. 2008) at Wildlife Habitat Nutrition Lab (Washington State University, Pullman, Washington) for each forage group for the three site visits for all 36 sites.

During the second visit at each site (June 2018), we also estimated maximum forage biomass (Catchpole and Wheeler 1992) and percent cover for all three forage classes to capture peak understory vegetation production (Bates et al. 2006). At each site, we clipped all leaves and nonwoody stems for all shrub species within the 4 m2 plot and clipped grasses and forbs $\geq$ 2 cm above the ground, only taking growth from current growing season, within the four 0.0625 m2 subplots (Buechner 1952). These samples were dried at 50°C in a drying oven for 48 h, and dry weight was recorded. To measure percent cover of forbs and grasses, we used a line intercept method (Canfield 1941) and recorded each species of plant that intersected the transect every 0.5 m and then divided by 60 (30-m transect; Elzinga et al 1998). We calculated shrub cover by tallying the total distance where live shrub canopies intersected the transect (allowing 10 cm between living parts to be counted as same shrub) and then divided by total transect length. Each species' cover estimate was independent, allowing $>$100% total cover at any transect (Canfield 1941). We repeated these same procedures in 2019, during mid-June, to determine annual variation in biomass and percent cover.

To better detect and understand differences in available forage quantity, we measured forage biomass and vegetation cover. While estimating vegetation cover provides a vertical projection of plant dominance or species occurrence, measuring biomass provides information on the volume of forage in a given area (Meese and Tomich 1992; Moleele et al. 2001). When used in tandem, these two pieces of information can describe the vertical structure of forages on the landscape. We created a vegetation production index, called *forage bulk density,* by dividing plant biomass by its respective measurement of vegetation cover.

Statistical analysis

In all models, we tested for differences in biomass (g/m2), percent cover, forage bulk density (biomass/percent cover), and DMD (forage quality) between movement behavior groups (migratory or nonmigratory) using linear mixed effects models. In these models, the response variables were biomass, percent cover, forage bulk density, or DMD. Fixed explanatory variables were forage class (grasses, forbs, shrubs), movement group, year, phenological stage (DMD model only), and all two-way interactions. All models included a random intercept using the site variable with a fixed mean to account for repeated measures, as well as controlling for plot level heterogeneity. We tested for correlations between covariates using Spearman rank-order analyses and considered variables highly correlated when ($|r| \geq 0.60$) (Schober et al. 2018). We did not include any highly correlated variables in our modeling. Forage biomass data were not normally distributed and exhibited a heavy-tailed distribution; therefore, we used the *boxcox* function in the MASS package in R 3.01 (Venables and Ripley 2002; R Core Development Team 2009) to transform the data. All other analyses were performed in R 3.01 using *lme* function in the *nlme* package (Pinheiro et al. 2020).

To detect scale-dependent differences in available forage (Long et al. 2008), we created two forage productivity indexes (FPI) to describe the nutrition per unit area at two different scales: 1) summer range: the area of an individual deer's summer range (FPI1; second order; Johnson 1980) and 2) plant cover: percent cover of available forages at each site (FPI2; fourth order; Johnson 1980), as provided by all forage classes' quantity (biomass) and quality (DMD). The FPIs were calculated using the following formulas:

$\mathrm{FPI1} = ((1 \pm qn\mathrm{forb})^{*} ql\mathrm{forb})) \pm ((1 \pm qn\mathrm{grass})^{*} ql\mathrm{grass})) \pm ((1 \pm qn\,\mathrm{shrub})^{*} ql\mathrm{shrub}))$

$\mathrm{FPI2} = ((1 \pm qn\mathrm{forb})^{*} ql\mathrm{forb})) + ((1 \pm qn\mathrm{grass})^{*} ql\mathrm{grass})) + ((1 \pm qn\mathrm{shrub})^{*} ql\mathrm{shrub}))$ where qn is the biomass (g/m2) of matured plants, ql is the average DMD (%) for each phenological stage by forage class, % is the percent cover of matured plants for each forage class, and area is the area of an individual summer range (km2). Higher index values indicate higher nutrition per unit area for that summer range. The qn term has the addition of a 1 due to the occasions when no biomass was collected for a forage class at a site. We then compared the differences in mean FPI1 and FPI2 between migratory and resident summer ranges using two-sample t-tests with unequal variance assumptions (Welch's *t*-test).

Results

We found differences in available forage between migratory and resident summer ranges. Overall, migratory summer ranges had higher forage quality (DMD) than resident ranges (range type factor; $P = 0.018$, Table 2**,** Fig. 3), however, shrubs on resident ranges had higher DMD than migratory ranges (range type · forage class interaction; $P < 0.001$, see Table 2, Fig. 3). Shrub cover was significantly lower on resident ranges than migratory ranges (range type · forage class factor; $P = 0.028$, Table 3). Shrub biomass ($\bar{x} = 29.9$ g/m2, standard deviation [SD] (22.2) for migratory and 31.4 g/m2, SD (29.9) for resident, see Table 1, Fig. 2) was not significantly different between summer ranges. The forage bulk density index for shrubs was higher on resident than migratory ranges (range type · forage class factor; $P = 0.07$, see Fig. 2, Table 3), indicating that forage on shrubs was more concentrated per unit area. Resident ranges had a higher grass percent cover ($\bar{x} = 60\%$, SD = 27.3) than migratory ranges ($\bar{x} = 40\%$, SD = 16.8) (see Table 1 and Fig. 2) and higher grass biomass ($\bar{x} = 32.2$ g/m2, SD = 30.3) compared with migratory ranges ($\bar{x} = 19.95$ g/m2, SD = 15.4).

Forb mean percent cover (migratory: 42%, SD = 24.7; resident: 29%, SD = 21.8, see Fig. 2), biomass (migratory: 14.9 g/m2, SD = 10.0; resident: 23.4 g/m2 SD = 21.3, and forage bulk density (see Fig. 2, Table 3) was not significantly different between summer ranges.

We found that forage quality (DMD) changed over the growing season. On both migratory and nonmigratory summer ranges, DMD across all sampling dates was similar between forbs ($\bar{x} = 48.7\%$, SD [8.6], see Table 1) and shrubs ($\bar{x} = 49.4\%$ SD [8.3], see Table 1), and both were higher than grasses ($\bar{x} = 40.0\%$, SD [6.7] see Table 1) (forage class factor; $P < 0.001$, see Table 2). Total forage quality was highest for all forage types when plants first emerged and decreased at each subsequent phenological stage ($\bar{x} = 50.8\%$, SD [7.1]; emergent, $\bar{x} = 46.1\%$, SD [10.0]; mature, $\bar{x} = 41.2\%$, SD [6.7]; phenological type factor, $P < 0.001$, see Table 2, Fig. 3); however, forbs had the highest DMD when they were matured (forage class · phenological stage interaction; $P = 0.026$).

We did detect some annual variation between years. Annual variation was not significantly different for biomass, percent cover, or forage bulk density for any forage class (see Table 3). Forage quality was higher in 2019 than 2018 (year factor; $P < 0.001$, see Table 2, Fig. 3). There was no difference in biomass, percent cover, or forage bulk density between years (see Table 3, Fig. 2). There was no difference in the forage productivity indices (FPI) between migratory and resident summer ranges at the summer range scale (FPI1: $t = 0.527$, df = 32.819, 95% CI = −489.572 – 831.397, $P = 0.602$, Fig. 4) or plant cover scale (FPI2: $t = -0.230$, df = 32.392, 95% CI = −372.691 – 296.948, $P = 0.819$, see Fig. 4). Mean elevations for the migratory sites and resident sites were 1 594 m and 1 206 m, respectively. The average rainfall from March to May was 56 mm in 2019, compared with 41 mm during those same months in 2018 (Fig. S1, available online at [insert URL here]).

Table 1
Mean and standard error (SE) for forage quality (dry matter digestibility [DMD]), quantity (biomass; g/m2) and cover (%) of forage classes (grass, shrub, and forb) for migratory (2018: $n = 19$; 2019: $n = 5$) and resident (2018: $n = 17$; 2019: $n = 5$) mule deer summer ranges in the John Day Basin, Oregon.

	Migratory summer range				Resident summer range			
	201	8	2019	201	8	2019		
Variable	Mean	SE	Mean	SE	Mean	SE	Mean	SE
DMD Emergent								
Grass	47.5	*1.45*	–	–	43.8	*1.24*	–	–
Shrub	52.6	*1.33* –	–	55.3	*1.51*	–	–	
Forb	53.8	*1.25*	–	–	51.6	*1.73*	–	–
Mature	38.9	*0.93*	47.1	*1.54*	36.7	*1.21*	42.1	*3.01*
Grass	42.6	*0.85*	58.2	*5.63*	47.0	*1.72*	67.2	*2.01*
Shrub	46.2	*1.28*	64.3	*4.87*	46.9	*1.65*	63.9	*2.23*
Forb	35.6	*0.62*	–	–	34.3	*1.19*	–	–
Cured	45.4	*1.28*	–	–	46.8	*1.20*	–	–
Grass Shrub Forb	43.9	*1.21*	–	–	41.1	*1.27*	–	–
Percent cover								
Grass	37.2	*4.15*	42.7	*4.70*	53.4	*6.74*	67.0	*11.31*
Shrub	13.4	*2.82*	3.43	*2.30*	6.58	*1.54*	4.05	*2.73*
Forb	33.4	*5.78*	51.0	*8.50*	28.0	*5.38*	30.3	*10.24*
Biomass								
Grass	28.5	*5.69*	11.4	*2.68*	15.7	*4.51*	48.7	*18.92*
Shrub	22.6	*4.50*	14.1	*10.15*	32.5	*9.70*	12.4	*10.46*
Forb	15	*2.71*	14.8	*0.52*	16.8	*3.18*	30.0	*12.66*

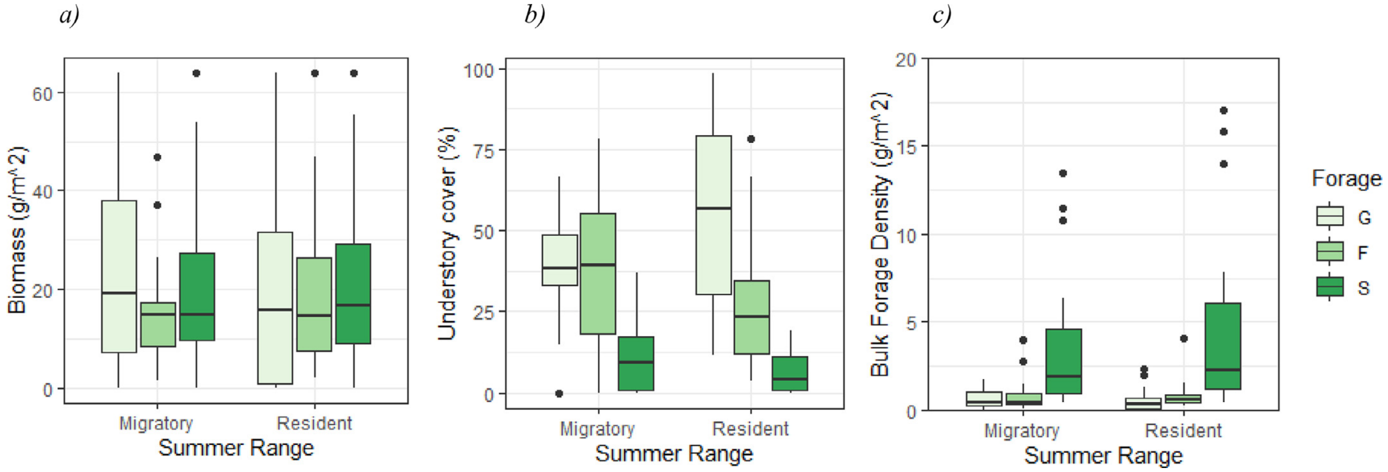

Figure 2. Comparison of (**a**) biomass (g/m2), (**b**) understory cover (%), and (**c**) bulk forage density ([g/m2]/%) for forage classes during mature phenological stage from migratory ($n = 19$) and resident ($n = 17$) summer ranges in John Day Basin, Oregon during 2018–2019.

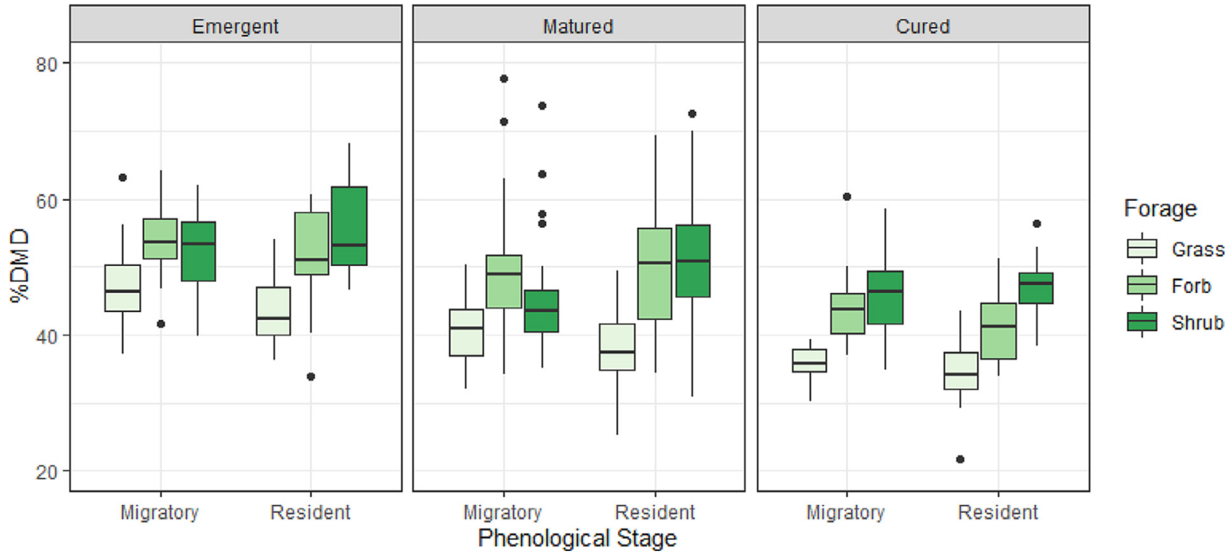

Figure 3. Forage quality (dry matter digestibility, %) for three phenological stages of plants in three forage classes (forb, shrub, grass) for migratory ($n = 19$) and resident ($n = 17$) summer ranges in John Day Basin, Oregon during 2018–2019.

Table 2
Predictors of forage quality (dry matter digestibility) in relation to forage type (forb, grass, shrub), migratory or resident range, and phenological stage (emergent, mature, cured) from a linear mixed effect model for a mule deer summer range in the John Day Basin, Oregon, in 2018–2019. The reference level for forage is "grass," "migratory" for movement, and "emergent" for phenological stage. Site was included as a random effect. Total number of observations is $n = 354$. Bold text indicates statistical significance at $\alpha = 0.05$.

Predictors	Estimates	Confidence Interval	*P*
(Intercept)	47.46	45.13–49.79	**< 0.001**
Resident range	−3.58	−6.43 – −0.74	**0.014**
Forbs	6.37	3.41–9.33	**< 0.001**
Shrubs	5.28	2.32–8.24	**< 0.001**
Matured forage	−10.54	−13.41 – −7.67	**< 0.001**
Cured forage	−10.86	−13.85 – −7.87	**< 0.001**
Shrubs * cured forage	2.90	−0.81–6.61	0.125
Shrubs * matured forage	1.10	−2.41–4.60	0.539
Forbs* matured forage	4.00	0.50–7.50	**0.025**
Forbs * cured forage	0.56	−3.16–4.27	0.769
Cured forage * resident range	0.23	−2.80–3.26	0.882
Shrubs * resident range	6.08	3.18–8.99	**< 0.001**
Matured forage * resident range	2.23	−0.64–5.10	0.128
Forbs * resident range	1.35	−1.55–4.26	0.361
Yr (2019)	13.86	11.49–16.22	**< 0.001**

Discussion

Our results show differences in forage availability between migratory and resident summer ranges. As predicted, higher elevation migratory summer ranges had higher quality forage available throughout the summer, likely due to the prolonged access to newly emerging plants (Mysterud et al. 2001), increased water availability, and later plant senescence at higher elevations (Moeslund et al. 2013). Higher forage quality on migratory summer ranges has been observed in other partial migratory ungulate populations as well (Hebblewhite and Merrill 2009). These observations support the theory that the physiological cost of migration is outweighed by the consumption of higher-quality forage, at least in some years, such as we observed (Bischof et al. 2012).

However, from an evolutionary standpoint, both strategies must be beneficial to the species' success at times for partial migration to exist (Kaitala et al. 1993). For example, a study of a partial migratory population in Montana observed a rise in resident elk numbers due to an increase in nutrition provided by irrigated agricultural areas at lower elevations (Barker et al. 2019). This study only captured forage availability for two growing seasons, but it is likely that given a longer timeframe, we would also observe summers in which it is more advantageous to remain on the same range year-round than it is to migrate. For instance, in years when the snowpack melt is delayed, it would be advantageous to be a resident because migratory animals would be limited temporally and spatially to emerging forage, being temporarily held in less suitable foraging areas until the snow melted. However, spring snowpack has been declining in this region; thus, future conditions that favor resident strategies are less likely to occur (Mote et al. 2018).

The resident summer range in this study area is degraded due to recent wildfires, invasion of annual grasses, soil loss, and historic overgrazing (Dittel et al 2018, Oregon Department Fish and Wildlife 2006); therefore, the differences in quality between the two summer ranges may be more pronounced here than what we might see in better quality sagebrush steppe-dominated summer ranges.

Forbs are an essential dietary component for deer, particularly in early summer (Short 1971; Gonzalez-Hernandez and Silva-Pando 1999). The findings from this research exemplify the importance of forbs because they offered some of the highest-quality forage on both summer ranges, particularly during peak biomass. Differences in mule deer herd productivity have been attributed to forb quality and quantity on summer ranges (Pederson and Harper 1978). The availability of a variety of forbs improves mule deer nutrition because the asynchrony of emerging plants will prolong the period in which green, nutritious forage is available (Tollefson et al. 2010). Summer ranges that support a high forb richness and abundance are also beneficial for many other species, such as native bees (Williams et al. 2015), small mammals (Arlettaz et al. 2010), birds, and butterflies (Trathnigg and Phillips 2015).

Although the collective forage quality (DMD) of all forage types pooled was lower on resident summer ranges compared with migratory ranges, shrub forage quality was higher on resident ranges than migratory summer ranges. The mean forage bulk density for shrubs was also higher on resident ranges, meaning that there was more biomass per cubic area when compared with grasses and forbs. In other words, shrub forage provides a denser concentration of nutrition than other forage classes per unit area. A study in the Canadian Rocky Mountains also found that resident elk selected areas with higher shrub biomass and digestible dry matter, emphasizing the importance of shrub communities as a source of quality forage for wildlife at lower elevations (Hebblewhite et al. 2008). Many of the resident sites in the study had large, homogenous stands of older bitterbrush (Appendix A). Bitterbrush is one of the most nutritious forage species for mule deer, particularly during the winter (Bishop et al. 2001; Pierce et al. 2004), but is also valuable during late summer when herbaceous forage has senesced (Austin et al. 1984). High-quality shrub forage on resident ranges may offer one explanation as to why this population of mule deer can support a partial migration strategy. This insight also provides a valuable tool for conservation in sagebrush steppe systems by emphasizing the importance of shrub communities for wildlife nutrition.

Table 3
Standardized coefficients from three linear mixed effects models with a response variable of biomass (g/m2), cover (%), or forage bulk density ((g/m2)/%) in relation to forage type (forb, grass, shrub) and migration behavior (migratory or resident) for mule deer ranges in the John Day Basin, Oregon. Reference levels were "grass" and "migratory" for movement. Site is included as a random effect. Total number of observations is $n = 138$. Bold text indicates statistical significance at $\alpha = 0.05$.

	Biomass			Cover			Forage bulk density		
Predictors	Estimates	CI	*P*	Estimates	CI	*P*	Estimates	CI	*P*
(Intercept)	4.05	3.22–4.89	**< 0.001**	37.42	29.40–45.45	**< 0.001**	3.32	0.67–5.97	**0.014**
Forbs	−0.44	−1.54–0.66	0.433	−1.25	−12.04–9.54	0.820	−2.12	−5.78–1.55	0.257
Shrubs	−0.15	−1.25–0.95	0.787	−26.99	−37.77 – −16.20	**< 0.001**	1.59	−2.08–5.25	0.396
Resident Range	−0.56	−1.75–0.63	0.359	18.09	6.70–29.47	**0.002**	−2.31	−6.06–1.44	0.227
Shrubs * Resident Range	0.70	−0.89–2.29	0.389	−26.70	−42.30 – −11.11	**0.001**	4.90	−0.40–10.20	0.070
Forbs * Resident Range	0.80	−0.80–2.39	0.327	−23.52	−39.12 – −7.93	**0.003**	2.41	−2.89–7.71	0.373
Year (2019)	−0.17	−1.00–0.66	0.692	4.14	−3.83–12.12	0.309	−2.07	−4.69–0.55	0.122

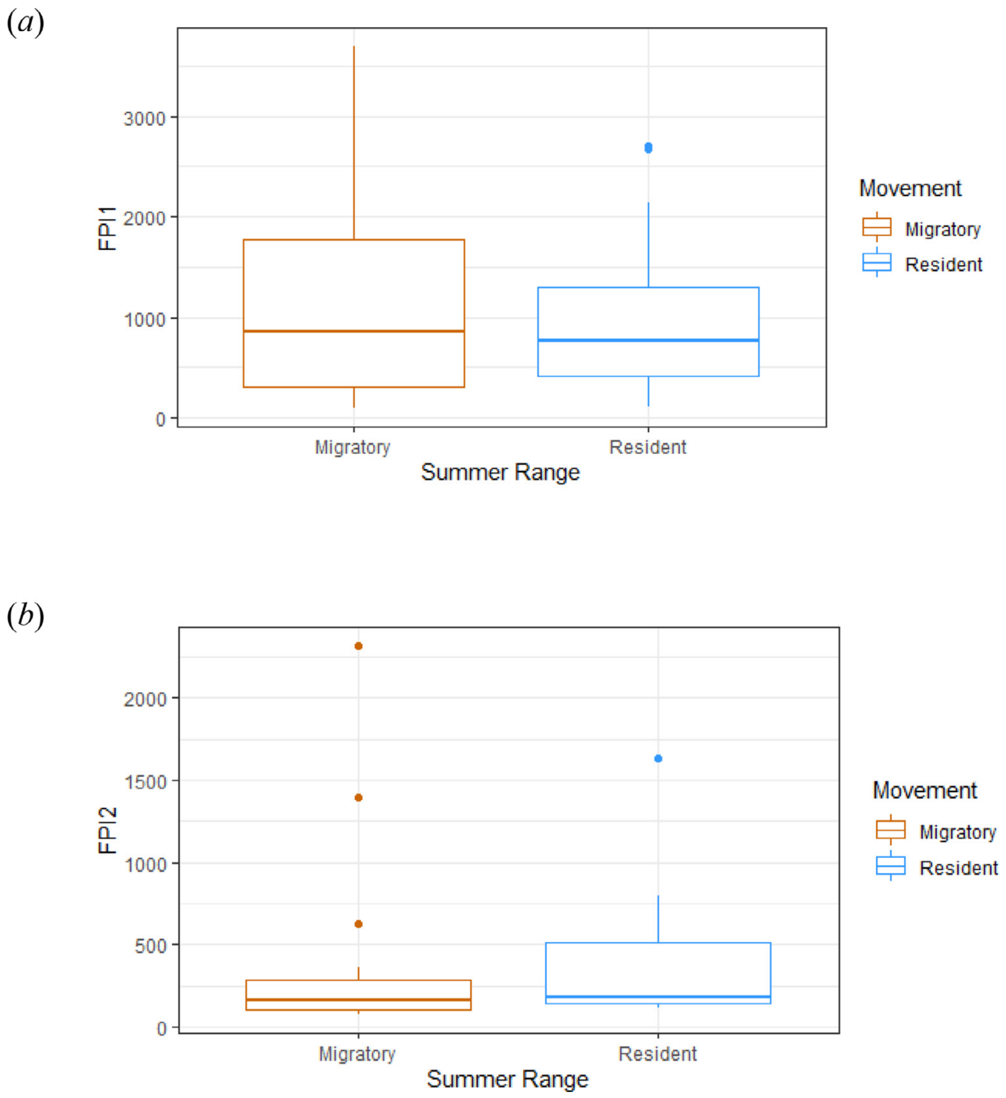

Figure 4. Forage productivity indices (FPI) for migratory ($n = 19$) and resident ($n = 17$) summer ranges in John Day Basin, Oregon during 2018–2019 at the scales of (**a**) an individual deer's summer range (FPI1) and (**b**) the percent cover of available forages at each site (FPI2). FPI1 = [((1+qnforb) • qlforb)) + ((1+qngrass) • qlgrass)) + ((1+qnshrub) • qlshrub))] / area. FPI2 = [((1+qnforb) • qlforb))/%forb] + [((1+qngrass) • qlgrass))/%grass] + [((1+qnshrub) • qlshrub))/%shrub]. Where qn is the biomass (g/m2) of matured plants, ql is the average DMD (%) for each phenological stage by forage class, % is the percent cover of matured plants for each forage class, and area is the area of an individual summer range (km2).

Overall, grasses had the highest biomass, cover, and forage bulk density but had the lowest quality forage on both migratory and resident summer ranges. Grasses have been reported to show relatively low forage quality compared with shrubs and forbs by several authors (Kufeld et al. 1973; Severson et al. 1983; Hanely et al. 1992).

In addition, much of the John Day Basin has been invaded by cheatgrass *(Bromus tectorum),* meduasahead *(Taeniatherum caput-medusae),* and North Africa grass *(Ventenata dubia)* (Dahl and Tisdale 1975; Bansal and Sheley 2016; Jones et al. 2018; Dittel et al. 2018). Thus, the large amount of biomass and high forage bulk density is likely a reflection of the presence of these invasive species. Exotic annual grasses, such as cheatgrass, provide some short-term forage for mule deer when they are first emerging or when there is a fall emergence but has little to no forage value during the rest of the year (Watkins et al. 2007). However, exotic grasses such as North Africa grass and medusahead are high in silica, which makes them unpalatable (Hamilton et al. 2015; Fryer 2017). Both migratory and resident ranges are negatively impacted by the invasion of annual grasses because they outcompete native perennial bunchgrasses and forbs, reducing plant species diversity and ultimately lowering potential forage availability across the landscape (Reid et al. 2008; Litt and Pearson 2013). Forage quality was higher in 2019 than in 2018. This is likely due to differences in spring rainfall that occurred between the 2 yr.

Rainfall has a positive linear relationship to DMD, particularly in arid environments (Marshal et al. 2005), so we expect that the above-average precipitation in 2019 was a driver of higher forage quality that year. We did not find any differences in biomass between years; however, this is likely the result of low sample sizes as we collected 3x as many samples for forage quality ($N = 354$) than forage quantity ($N = 144$). The future climate for much of the western United States is predicted to have hotter, drier summers (Chambers and Pellant 2008). For this reason, it may be important to incorporate environmental conditions, such as drought, when projecting available forage on the landscape.

Although we did not find statistically significant differences in the forage productivity indexes (FPI) at the summer range or plant cover scales, it is interesting to note how the range of index values were inversely related. When forage productivity was measured at the scale of an individual's summer range (FPI1), there was a higher interquartile range of values for migratory ranges than for resident ranges. Conversely, when the forage productivity was measured at the percent cover of the plants (FPI2), there was a higher interquartile range of values for the resident summer ranges than the migratory ranges. This inverse relationship has been documented in other partial migratory populations where residents displayed stronger selection at the plant level to compensate for the lower availability of higher-quality forage compared with migrants (Wilmshurst et al. 1999) or migrants make forage decisions at larger scales due to the abundance of high-quality forages within their summer range (Hebblewhite et al. 2008).

Dussault et al. (2005) similarly reported resident moose were more selective at finer spatial scales due to lower availability of quality forage. It is important to note several caveats when interpreting our results. First, we were interested in capturing the annual variability between forage quality and quantity, which Srelies heavily on rainfall in the Great Basin (Tang et al. 2015). The winter of 2018 was wetter than average while the summer of 2019 was drier than average; therefore, we were unable to measure variability between years with similar monthly precipitation (**Fig. 5**). Second, we collected data using a single transect at center of a deer's summer range.

This method was effective at capturing major differences between the two movement groups' summer ranges as they were relatively homogenous at larger scales (i.e., sagebrush steppe vs. ponderosa pine ecosystems). However, to detect differences between individual summer ranges from members of the same movement group, we would recommend increasing the number of transects to detect finer-scale differences.

Third, while there appears to be overlap in resident and migratory seasonal ranges (see Fig. 1), the two ranges are distinct and occur in different ecosystems due to the animals' use of different elevation bands within the polygons. Migratory summer ranges are in the high elevations only, and resident summer ranges occur at low elevations. Finally, our measurements reflect forage availability rather than what forages may actually be consumed. Density dependence, intraspecific and interspecific competition, anthropogenic disturbances, and plant palatability are just a few examples of how forage availability does not directly translate into what forages are being consumed (Nicholson et al. 1997; Stewart at el. 2011, Barry et al. 2019).

The partially migratory strategy in ungulates must confer some evolutionary advantage. This study indicates that differences in forage availability between summer ranges may partially explain the mechanism for this strategy in mule deer. It also demonstrates the plasticity within the species that allows either strategy to be beneficial depending on annual variability in biotic and abiotic factors. This study supports the forage maturation hypothesis in that migratory deer had access to high-quality forage. However, the nutritional compensation for not migrating is likely provided by shrub species at lower elevations. Future research is needed to determine how major environmental changes affect the foraging trade-offs of migration behavior across large spatial and temporal scales, particularly as the climate continues to change rapidly.

Management Implications

During summer, the availability of shrub species at lower elevations (resident home ranges) had higher forage quality when compared with shrub species at higher elevations (migratory summer home ranges). We recommend landowners and managers focus habitat restoration and forage utilization monitoring efforts in shrub-dominated areas at low elevations, particularly bitterbrush stands, as these areas provided high-quality forage for resident mule deer during a time of year when all other forages are limited. Conversely, on migratory seasonal ranges, managers should prioritize protecting species diversity for herbaceous plants, particularly forbs as this plant functional group offers the highest nutritional at higher elevations. The more diverse the plant community is, the higher likelihood there is for asynchronous emergence of forbs.

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.

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Appendix A. Most common encountered forage species for migratory and resident summer ranges in John Day Basin, Oregon during 2018–2019. Species are listed in order of greatest to least cover within groups for each seasonal range.

Summer range	Species	Common name	Cover (%)
Migratory forbs	Microseris nutans	Nodding microseris	9
	Epilobium sp.	Willowherbs	4
	Achillea millefolium	Yarrow	4
	Erigonum sp.	Wild buckwheats	2
	Fragaria sp.	Wild strawberry	2
	Lupinus sp.	Lupine	2
	Leucanthemum sp.	Daisy	2
	Myosotis stricta	Forget-me-not	2
Grasses and grasslike plants	*Carex* sp.	Sedges	9
	Poa secunda	Sandberg bluegrass	5
	Pseudoroegneria spicata	Bluebunch wheatgrass	4
	Fescue sp.	Fescue	1
	Bromus tectorum	Cheatgrass	3
	Bromus marginatus	Mountain brome	1
	Elymus elymoides	Squirreltail	1
	Ventenata dubia	North Africa grass	1
Shrubs	*Vaccinium* sp.	Fruiting shrubs	17
	Vaccinium myrtillus	Whortleberry	10
	Berberis repens	Creeping Oregon grape	8
	Amelanchier alnifolia	Saskatoon serviceberry	5
Resident Forbs	*Viola* sp.	Violets	2
	Lupinus wyethii	Lupine	2
	Achillea millefolium	Yarrow	2
	Collinsia parviflora	Maiden blue eyed Mary	2

(*continued on next page*)

Summer range	Species	Common name	Cover (%)
	Sisymbrium altissimum	Tall tumblemustard	2
	Erodium cicutarium	Common stork's-bill	2
	Gayophytum sp.	Evening primrose	2
	Blepharipappus scaber	Rough eyelashweed	2
Grasses	*Bromus tectorum*	Cheatgrass	10
	Poa secunda	Sandberg bluegrass	6
	Taeniatherum caput-medusae	Medusahead	4
	Ventenata dubia	North Africa grass	4
	Festuca idahoensis	Idaho fescue	4
	Bromus japonicus	Japanese brome	4
	Koeleria macrantha	Prairie Junegrass	3
	Elymus sp.	Wild rye	3
	Elymus multisetus	Big squirreltail	3
Shrubs	*Bromus brizaeformis*	Rattlesnake brome	3
	Artemisia tridentata	Big sagebrush	9
	Purshia tridentata	Antelope bitterbrush	6
	Ericameria nauseosa	Rubber rabbitbrush	5
	Chrysothamnus viscidiflorus	Yellow rabbitbrush	4

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