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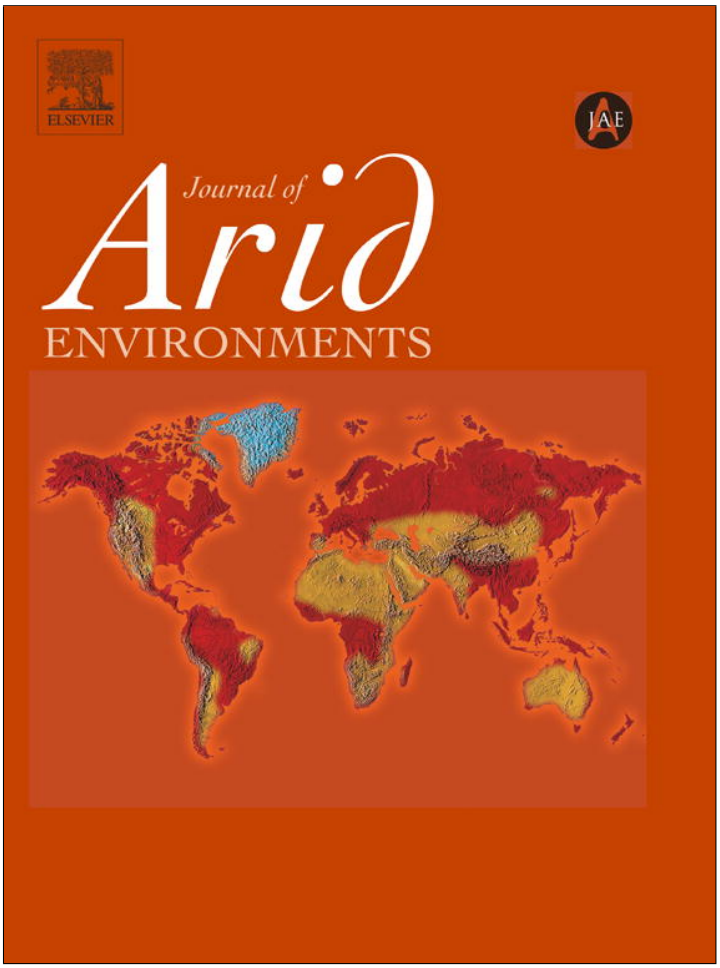

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Short-term vegetation response to wildfire in the eastern Sierra Nevada: Implications for recovering an endangered ungulate

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ABSTRACT

We studied short-term changes in vegetation for two years following a summer wildfire on the winter ranges of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*). Forbs dominated burned areas and shrubs dominated unburned areas. Green forage (new-growth of all forage classes) biomass rebounded quickly; within two years green forage biomass was equal in burned and unburned areas, although total forage biomass remained greater in unburned areas. Plants in the burn had slightly higher crude protein but equivalent digestibility and phenology as plants in unburned areas. This, in combination with the shift toward more forb biomass, likely increased forage quality in burned areas. Forage models developed from ground-based measures of biomass performed better than the NDVI and were able to capture changes in forage composition, emphasizing the importance of field sampling to model vegetation. Based on microhistological analyses of fecal pellets, Sierra Nevada bighorn sheep whose winter ranges were extensively burned consumed more forbs than those with less burned habitat. Visibility was greater in burned areas compared with unburned areas, suggesting that burns may decrease predation risk from stalking predators. In conclusion, wildfire may have beneficial effects for Sierra bighorn by increasing forb availability, forage quality and visibility.

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1. Introduction

Fire has multiple indirect effects on ungulates through its direct effect on vegetation. Fire affects forage quantity, quality and species composition, and can also change vegetation structure thereby altering behavior and predation risk. Following fire, forage quantity, or biomass, initially decreases but may quickly rebound and often increases beyond the amount of forage in unburned areas (Cook et al., 1994; Sachro et al., 2005), but the timeframe of this transition varies depending on the vegetation community, pre-burn condition or post-fire weather, especially in arid regions (Bennett et al., 2003). In addition to forage quantity, ungulates may be affected by fire-induced changes in forage quality, specifically the digestibility and crude protein within available forage. In response to fire, plants may experience a short-term increase in protein (DeWitt and Derby, 1955; Hobbs and Spowart, 1984) due to a flush of nutrients, including N, from ash (Boerner, 1982). Forage quality may also increase due to a shift in the plant community composition; fires can increase availability of grasses (Cook et al., 1994; Merrill et al., 1980) and forbs (Merrill et al., 1980). Burned areas may also greenup earlier than unburned areas due to increased solar radiation and provide high quality forage early in the season as young plants have more protein and tend to be more digestible than older plants. Overall diet quality, however, is a function of forage quality and availability, as well as diet selection (Hobbs and Spowart, 1984). In addition to altering forage conditions, fire affects vegetation structure, generally resulting in increased visibility (Bentz and Woodard, 1988; Smith et al., 1999). Visibility is important for ungulates such as bighorn sheep (*Ovis canadensis*) because they rely on vigilance behavior to avoid predation, preferring open areas near escape terrain, which allows them to visually detect and flee from predators (Risenhoover and Bailey, 1985). The variation in plant responses to fire and the complex relationships between forage quantity, quality and visibility makes it difficult to predict the effects of fire on ungulates.

The Seven Oaks wildfire of July 2007 provided the first opportunity to evaluate the effect of wildfire on Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; hereafter Sierra bighorn; see Plate 1)

Abbreviations: ANOVA, Analysis of variance; GPS, Global Positioning System; IVDMD, In vitro dry matter digestibility; MODIS, Moderate Resolution Imaging Spectroradiometer; NDVI, Normalized difference vegetation index; Sierra bighorn, Sierra Nevada bighorn Sheep; TM, Landsat-Thematic Mapper.

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Plate 1. Two Sierra bighorn rams foraging in the Seven Oaks wildfire near Independence, California during the winter of 2007–8. Photo credit Todd Vogel.

since being placed on the federal endangered species list in 1999. The effects of this natural wildfire are relevant for Sierra bighorn recovery for two reasons: (1) the large extent of the wildfire may have reduced winter range forage availability in the short-term to detrimental levels and (2) increased understanding of the relationship between fire and Sierra bighorn could be useful in directing future prescribed burns. Prescribed burning has been identified in the Sierra bighorn recovery plan as a management option to combat single-leaf piñon (*Pinus monophylla*; hereafter piñon) encroachment on winter ranges (U. S. Fish and Wildlife Service, 2007). Lower elevation winter ranges are characterized by monocultures of piñon as well as shrublands of sagebrush (*Artemesia tridentata*) or bitterbrush (*Purshia tridentata*). However, in the eastern Sierra Nevada, the spatial extent of piñon encroachment is limited (averaging 4% of lower elevation ranges; Latham, 2010) but variable and the reduction in open habitat has likely caused decreases in forage availability and visibility. The cause of piñon expansion into shrublands is not well understood and geographically variable (Romme et al., 2009). Piñon establishment is not driven completely by fire suppression as previously postulated, but instead the result of a combination of factors including natural range expansion, increased carbon dioxide, fire suppression, and livestock grazing (Burwell, 1999; Leopold, 1924; Romme et al., 2009). Prescribed fires may be an effective strategy to combat piñon expansion (Aro, 1971).

We evaluated the immediate vegetation response to the Seven Oaks Wildfire to test the contrasting predictions that this fire would have either a detrimental impact on Sierra bighorn due to forage reduction or a positive impact on Sierra bighorn by increasing forage quality and visibility. We tested these predictions by quantifying changes in forage quantity, forage quality, and visibility between burned and unburned areas for two years post-wildfire. We used extensive ground sampling to build statistical models of short-term changes in forage biomass, forage class composition and visibility. We were most interested in quantifying changes in green new growth (hereafter green). In addition, we used our ground data to determine how well the normalized difference vegetation index (NDVI) derived from satellite data (Rouse et al., 1973) tracked changes in green forage biomass over time to determine if the NDVI is an appropriate metric for aboveground green biomass for this arid region. The NDVI measures 'greenness' as the difference in the near infrared and red wavelengths and is often used as a surrogate for above ground forage biomass (Pettorelli et al., 2005). If the NDVI correlates well with ground measurements, it could be used to quantify forage biomass responses following fire instead of extensive ground measurements in the future. As an index of forage quality, we compared the crude protein and digestibility of key forage species in burned and unburned regions. Finally, we hypothesized that these changes in forage availability will lead to increased diet quality for Sierra bighorn. We tested this hypothesis by comparing the diet composition estimated from fecal microhistological analyses between two Sierra bighorn herds with contrasting amounts of burned available habitat.

2. Study area

Our study area focused on the Sierra bighorn winter ranges of the Mt. Baxter and Sawmill Canyon herds located on the Inyo National Forest in the eastern Sierra Nevada, near Independence, California (Fig. 1). In July 2007, the Seven Oaks wildfire burned 18 square kilometers of Sierra bighorn winter range which included 67% of the Mt. Baxter winter range, including all of the lowest elevation areas and 11% of the adjacent Sawmill Canyon winter range (Fig. 1). These two herds play a critical role in the recovery of Sierra bighorn because they are the largest of all relict populations and they have been the main source for translocations used to restore Sierra bighorn to their historic range (U. S. Fish and Wildlife Service, 2007). Most Sierra bighorn in these herds migrate seasonally, spending summer in the alpine (>3050 m) and winter at lower elevations that provide snow free foraging areas with early exposure to spring greenup.

The Mt. Baxter and Sawmill Canyon winter range pre-fire vegetation comprised 87% sagebrush scrub, 2% piñon woodlands, and 9% cliffs (slope >100%). Common grasses included: *Achnatherum* spp., *Bromus* spp. and *Poa* spp. Winter ranges had a variety of forbs including: *Mentzelia* sp., *Phacelia* spp., *Dichelostemma* sp., *Galium* sp., *Eriogonum* spp., *Tauschia* sp., *Lupinus* spp. and *Linanthus* spp. Shrub genera included *Eriogonum* spp., *Ephedra* spp., *Prunus* sp., *Ceanothus* spp., *Purshia* spp., *Chrysothamnus* spp., *Artemesia* spp., *Lupinus* sp. and *Cercocarpus* sp. No post-fire seeding was done. Total precipitation recorded from the nearest weather station in Independence, California for November through May was 131 mm 2007–8 and 51 mm 2008–9 and the long term average (50 years) is 111 mm (SE = 84; California Data Exchange Center http://cdec.water.ca.gov). Monthly mean temperatures in 2008 were Feb = 8 °C, March = 12 °C, April = 16 °C and May = 20 °C; in 2009 Feb = 7 °C, March = 11 °C, April = 15 °C and May = 24 °C (U.S. National Weather Service, Western Regional Climate Center http://wrcc.dri.edu/). Longer term average (6 years) mean temperatures were February = 8 °C (SE = 0.9), March = 11 °C (SE = 2.1), April = 15 °C (SE = 1.4) and May = 22 °C (SE = 2.0; U.S. National Weather Service, Western Regional Climate Center http://wrcc.dri.edu/).

We delineated each herd's winter range using Global Positioning System (GPS) locations of collared Sierra bighorn collected from November 2007 to May 2009. We added a 500 m buffer around a 100% minimum convex polygon of the GPS collar locations collected within the elevation range 1400 m–2600 m (Fig. 1). There were 4 GPS collared female Sierra bighorn (all from Mt. Baxter) in the winter of 2007–8 and 14 in 2008–9 (8 from Mt. Baxter and 6 from Sawmill Canyon). The Sawmill Canyon herd winter range was 1.2 times larger than the Mt. Baxter Herd winter range and the two herds overlapped by approximately 25%. The elevation distribution and mean were similar between the Mt. Baxter and Sawmill Canyon herds but the distribution of aspects differed slightly. The Mt. Baxter winter range tended more to the southeast and the Sawmill Canyon winter range tended more to the northeast, but both were

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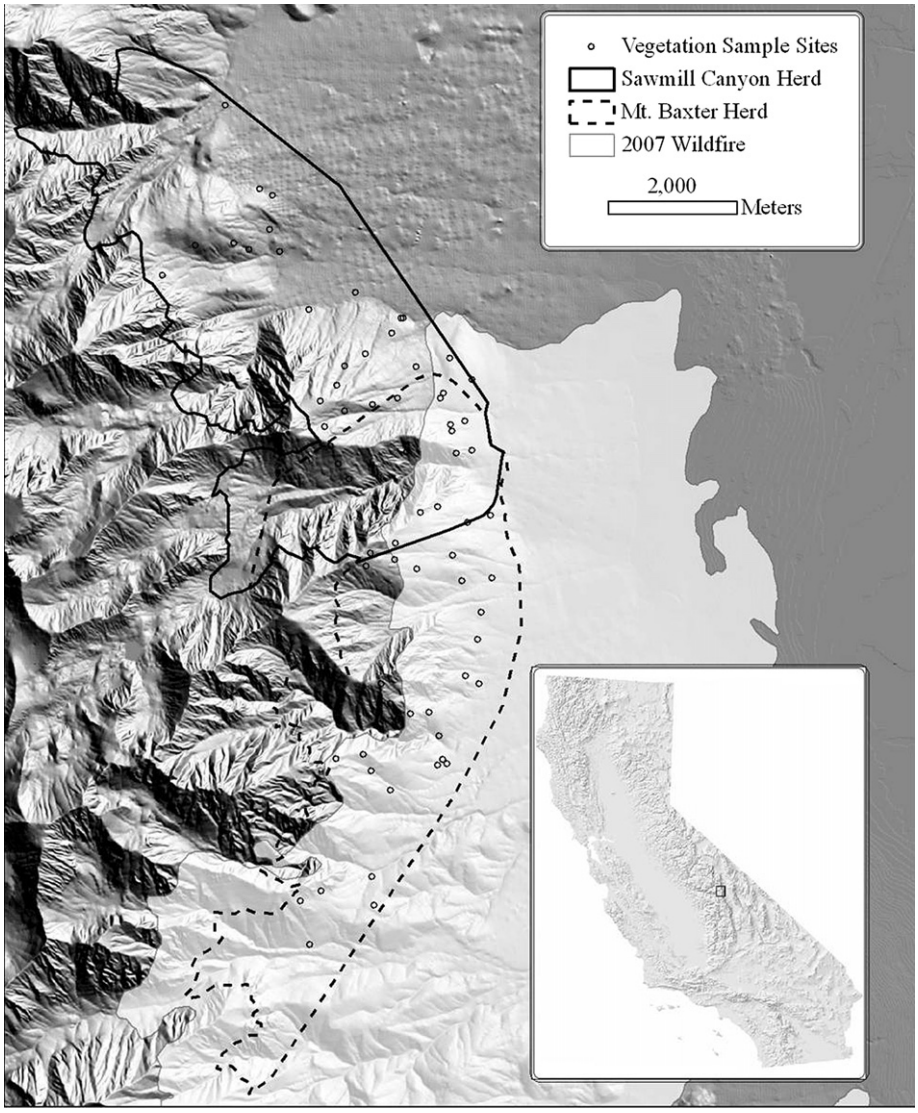

Fig. 1. Sierra bighorn winter ranges for the Mt. Baxter and Sawmill Canyon herds.

dominated by east-facing terrain. The Mt. Baxter winter range aspect was 36% east, 23% southeast, 19% northeast, 9% north, 8% south, and <5% west. Within the Sawmill Canyon winter range the distribution of aspect was 31% east, 29% northeast, 15% southeast, 14% north, 5% south and 6% west.

3. Materials and methods

To quantify the magnitude and duration of changes caused by wildfire, we combined field sampling of vegetation responses following fire into a suite of statistical models (e.g. Hebblewhite et al., 2008). We used a model-based approach to account for differences in aspect between herds and to develop predictive spatial models to understand Sierra bighorn selection (Greene, 2010). We modeled changes in green growth biomass by vegetation class (i.e. grass, forb, shrub) as well as visibility. All models were built with extensive ground sampling data. We evaluated changes in forage quality by measuring digestibility and crude protein and in addition tested for changes in phenology that can impact forage quality (Van Soest, 1994). To determine the potential population impact of burn-induced vegetation changes on Sierra bighorn we assessed changes in diet composition via microhistological analysis between the Mt. Baxter and Sawmill Canyon herds.

3.1. Forage biomass

The goal of our vegetation sampling was to quantify differences in forage biomass between burned and unburned sites. Vegetation sites were located with a stratified, systematic, semi-random sampling design (Krebs, 1989). Sites were stratified based on elevation, aspect, landcover (reclassified as shrub, forest or herbaceous from the regional dominance category of CALVEG: http://www.fs.fed.us/r5/rsl/projects/classification/), slope, and burn status categories. For efficiency, sites were placed systematically along transects from 1500 m to 2500 m every 150 m of elevation change (6 sites/transect). Once the target elevation was reached, the center of each sample site was located using a random bearing and direction. Transects were located systematically every kilometer and tended west but due to the extremely rugged terrain on eastern slopes of the Sierra Nevada, routes were generally selected based on feasibility. Each site was sampled three times a year for

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two years to record early, mid and peak green biomass. Vegetation sampling began in mid-February and lasted an average of 20 days with an average of 21 days in between sampling bouts. For simplicity, we refer to these sampling rounds as March, April and May. Sites were added as snowmelt and time allowed each month so that in the first year there were 21, 48 and 51 sites sampled per month, respectively, and in the second year there were 51, 69 and 69 sites sampled each month, respectively. Eighteen sites were added in the second year based on a proportional allocation of effort from the variance within strata measured in the first year (Krebs, 1989).

Each sample site consisted of eight, 1-m^2 plots laid out in a cross formation with each plot 5 m or 10 m away from the center point with or perpendicular to the fall line. The corners of plots were marked with nails so they could be relocated and photos were taken of every plot at every site visit. At each site we recorded the elevation, slope and aspect. Within each plot we used non-destructive double-sampling in each plot to repeatedly estimate herbaceous biomass by genus in each plot through time (Bonham, 1989). For each genus within a plot we visually estimated the percentage of new growth and the percentage flowering. Ratio estimators were calculated for each observer ($n = 3$), year and vegetation class (i.e., grass, forb, and sub-shrub) to convert field estimates to wet weights. We defined sub-shrubs as small statured woody plants (e.g. *Keckiella* sp., *Phlox* spp., *Monardella* sp., *Galium* sp., *Linanthus* spp.) that were inappropriate to lump with biomass estimation of larger shrubs. After using sub-shrub specific ratio estimators to convert sub-shrub estimates to dry weights, sub-shrub biomass was included into the forb category. Conversion rates (slope of the ratio estimator) varied from 0.83 to 0.93. Nearby plots were clipped to build forage-class specific regression equations to convert wet estimates to dry weights; conversion rates from wet to dry ranged from 0.79 to 0.92. Samples were dried at 100 °C to a constant weight. Missing biomass estimates comprised <1% of all data and <3% of data within any given forage class and were estimated with species-specific multiple linear regressions based on percent cover and percent new and confirmed with field photos of each plot.

We used the comparative yield method (Haydock and Shaw, 1975) to obtain a coarse estimate of total dry shrub biomass (sensu Marshal et al., 2005). We dried samples from 24 clipped plots (6 of each biomass category) at 100 °C to a constant weight to develop a regression model that would convert categorical values into estimates of dry grams. The initial relationship between biomass category and grams of dry green biomass was unexpectedly weak ($R^2 = 0.04$). We uncovered an inverse relationship between biomass category and dry green biomass for bush lupine in which larger bush lupine actually had lower amounts of dry green biomass because of plant architecture. Therefore, we removed lupine from our statistical analysis because it was rare (<3% cover) within the study area and this greatly improved our model fit ($R^2 = 0.40$).

We tested the hypothesis that green forage biomass was initially lower in burned areas, and then rebounded within two years, by developing a set of linear mixed models from ground biomass estimates using Stata 10.0 (StataCorp, 2007). We used univariate analysis to identify significant predicator variables including burn severity, landcover type (shrub, forest, herbaceous), elevation, slope, aspect and time (i.e., year, Julian date, month) variables. Aspect was transformed into a continuous variable using a modified version of Cushman and Wallin's (2002) method by taking −cos(aspect + 35). While southwest aspects are usually the warmest, within our study area, southeast is the most sunny and exposed aspect. By adding 35, southeast aspects represented a value of 1 and northwest aspects were represented by −1. All significant, uncorrelated variables were entered into a full biomass model for each vegetation component; grass, forb, shrub and total biomass. We used backwards manual stepwise regression to remove insignificant variables until all variables maintained in the biomass model were significant (Hosmer and Lemeshow, 2000). Variables were screened for collinearity and biologically relevant interactions and non-linear relationships (through the use of quadratics, $X + X^2$) were investigated and top models were selected based on Akaiki's Information Criterion (AIC; Hosmer and Lemeshow, 2000). The predictive capacity of top models was estimated with a manual calculation of the coefficient of determination by regressing observed to expected values (hereafter referred to as within-sample R^2; Clark, 2007).

To determine if the NDVI can be appropriately interpreted as aboveground green forage biomass following fire on winter ranges of Sierra bighorn, we correlated our ground estimates of green biomass with the NDVI. We evaluated the NDVI data from Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra and Aqua satellites and also values derived from Landsat-Thematic Mapper (TM). Although both the MODIS and TM imagery was acquired every 16 days, some images had to be removed due to obvious cloud interference. This resulted in higher temporal resolution with the available MODIS data (14 images at 250 m^2 range) while the TM data had a reduced temporal resolution but higher spatial resolution (6 images at 30 m^2 range). The dates of MODIS imagery used in this analysis were: 2/2/08, 2/18/08, 3/5/08, 3/21/08, 4/6/08, 4/22/08, 5/8/08, 5/21/08, 2/18/09, 3/6/09, 4/7/09, 4/23/09, 5/9/09, 5/22/09. The dates of TM imagery used in this analysis were: 2/16/08, 6/7/08, 2/18/09, 4/23/09, 5/9/09, 5/25/09. We excluded areas with forest landcover class because NDVI in forest regions likely represent tree biomass and not forage availability and in general it is recommended to integrate landcover type information to derive biomass estimates from NDVI (Huete et al., 2002).

3.2. Forage quality

We measured two components of forage quality: digestibility via in vitro dry matter digestibility (IVDMD) and crude protein (Van Soest, 1994). IVDMD was estimated using rumen fluid from domestic sheep following methods of Tilley and Terry (1963). Samples of 8 forage species were collected up to 3 times throughout the growing season from two different elevations (low elevation was 1700 m and high elevation was 2300 m) within burned and unburned areas. Each plant sample was a composite of new green growth from ~5 plants, as availability allowed. Samples were intended to mimic foraging bites and therefore included both leaves and stems clipped to a diameter (~<2 mm) that mimicked observed foraging. We also included 3 samples of old growth *Achnatherum* spp., a dominant forage species (Schroeder et al., 2010), to quantify the magnitude of difference between old and new growth. Samples were dried at 60 °C for 24 h and analyzed for IVDMD and crude protein at the Wildlife Habitat Nutrition Laboratory at Washington State University in Pullman, Washington. We used a simple ANOVA to test for differences between crude protein and IVDMD between burned and unburned sites. To further quantify how much forage quality was driven by elevation, month, year since burning and interactions of these variables, we also developed a linear mixed model with species as the mixed-effect ($N = 124$, genera $N = 8$). Our model building and fitting techniques were similar to those outlined above for biomass.

To measure potential phenological differences caused by the burn, we documented the percent flowering of four target genera: *Purshia* spp., *Dichelostemma* spp., *Achnatherum* spp., and *Mentzeilia* spp. at each of the vegetation sites in May in 2008 and 2009. These species were selected because they were common throughout the study area and we had informally observed Sierra bighorn foraging

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Table 1
Coefficients for top predictive forage models of total new growth dry biomass (green) for the winter ranges of Sierra bighorn during 2008 and 2009.

Predictor variable	Green grass		Green forb		Green shrub		Total green biomass	
	β	P	β	P	β	P	β	P
Burn	−1.4	<0.01	−0.4	0.08	−2.4	<0.01	−1.7	<0.01
Burn × Year	1.5	<0.01	1.1	<0.01	1.7	<0.01	1.8	<0.01
Year	−0.2	0.2	0.6	<0.01	−0.5	<0.01	−0.2	0.02
Month	−1.2	0.04	0.9	<0.01	1.3	<0.01	1.0	<0.01
Elevation	0.022	<0.01	−0.002	<0.01	0.01	0.03	−0.002	<0.01
Elevation^2	−0.000007	<0.01			−0.000003	0.02		
Elevation × Month	0.001	<0.01						
SE aspect	0.9	<0.01	0.4	0.01			0.5	<0.01
Wald χ^2	161	<0.01	534	<0.01	325	<0.01	673	<0.01
Within-sample R^2	0.15		0.42		0.27		0.5	

on them. We used a generalized linear model to test for differences in flowering time between burned and unburned sites. If phenology was ahead in the burn we would expect burn to be a significant predictor variable of percent flowering.

3.3. Diet composition

We tested our hypothesis that burns influenced diet quality by comparing the diet of the 'burned' Mt. Baxter herd (67% of winter range burned) with the 'unburned' Sawmill canyon herd (11% of winter range burned). Fecal samples ($N = 38$) were air dried and microhistological analysis (plant genus level with 25 views/slide and 4 slides/sample at the Wildlife Nutrition Laboratory at Washington State University in Pullman, Washington) to determine diet composition. We used univariate linear regression to quantify the differences in forage class composition between the Mt. Baxter and Sawmill Canyon herds and to identify significant predictor variables to include in multiple linear regression models. All significant variables or interactions were included in top models. Our response variable was the percentage of each forage class (i.e., grass, forb and shrub) in the diet and the predictor variables were herd, year, month, and relevant interactions. We also tested for differences in consumption of each plant genus using Bonferroni's correction for multiple comparisons. Angular transformation did not improve residual distribution so we did not transform the data in order to make coefficients easier to interpret. Model fit was evaluated with the coefficient of determination.

3.4. Visibility

We measured horizontal visibility as an index of predation risk, although this is only one of several possible factors that determine predation risk. Visibility was measured at all 69 vegetation sites using the staff-ball method (Collins and Becker, 2001) at distances of 5 and 15 m. An observer walked a complete circle around a tennis ball on a 1 m tall stick held at the center of the site, systematically stopping and crouching down to 1 m to determine whether the target was visible, obscured by vegetation or obscured by rock. Percent cover was calculated as the number of locations where the target is obscured divided by the total number of locations around the circle. We assumed visibility did not change during the two year study period because all documented vegetation growth was <1 m. To test our hypothesis that visibility was higher in burned compared to unburned sites, we used a linear regression model with predictor variables elevation, landcover class, aspect and terrain ruggedness. Elevation, landcover class and aspect were measured in the field. Terrain ruggedness was calculated from USGS 10 m digital elevation models with an extension developed by Sappington et al. (2005) for use in ArcGIS 9.3 (Environmental Systems Research Institute, California).

4. Results

4.1. Forage biomass

Green forage biomass models indicated that forb and grass biomass rebounded quickly from burning, while after two years shrub biomass in burned areas still lagged behind unburned areas. The biomass of green forage generally decreased with elevation and increased with month, year, and was greater on northern aspects while the effects of burn on forage varied by month and year (Table 1) and burn severity was not significant. The quadratic of elevation was significant in grass and shrub models indicating green biomass was greatest at intermediate elevations. Two interactions were significant: burn × year and elevation × month. The burn × year interaction reflected an increase in biomass in the second year post-fire in burned areas while biomass remained steady in unburned areas. At the lowest elevations some sites reached the peak of new grass growth in April instead of May which is represented by the elevation by month interaction. The best performing model was for total green biomass (Wald $\chi^2 = 673$, within-sample $R^2 = 0.5$). Among forage categories, the best performing model was new forb growth (Wald $\chi^2 = 526$, within-sample $R^2 = 0.42$) followed by new shrub growth (Wald $\chi^2 = 353$, within-sample $R^2 = 0.27$) and new grass growth (Wald $\chi^2 = 172$, within-sample $R^2 = 0.15$).

Mixed models for forage biomass were simplified to a generalized linear format to enable prediction and demonstrate post-fire forage trends (Figs. 2 and 3). These predictions clearly demonstrate the difference in community composition between burned and unburned areas. Forbs made up most of the green biomass in burned areas, while shrubs made up most of the green growth in unburned areas. Total green biomass, combining all forage categories, was equivalent in burned and unburned areas by the second year post-fire. The two non-native genera present – *Bromus* spp. (cheat grass and red brome) and *Erodium* sp. (filaree) showed no difference in abundance between burned and unburned sample sites ($P = 0.23$ for *Bromus* spp.; $P = 0.13$ for *Erodium* sp.). We applied predictive models to the specific landscapes of the Mt. Baxter and Sawmill Canyon winter ranges to determine the total peak green biomass of each herd (Table 2). After adjusting for size differences between winter ranges, we determined that the Sawmill Canyon winter range had more green biomass in the first year post-wildfire but by the second year the Mt. Baxter winter range provided more green biomass per square meter (Table 2).

The higher spatial resolution TM NDVI (30 m^2) was twice as strongly correlated with ground estimates of total green biomass

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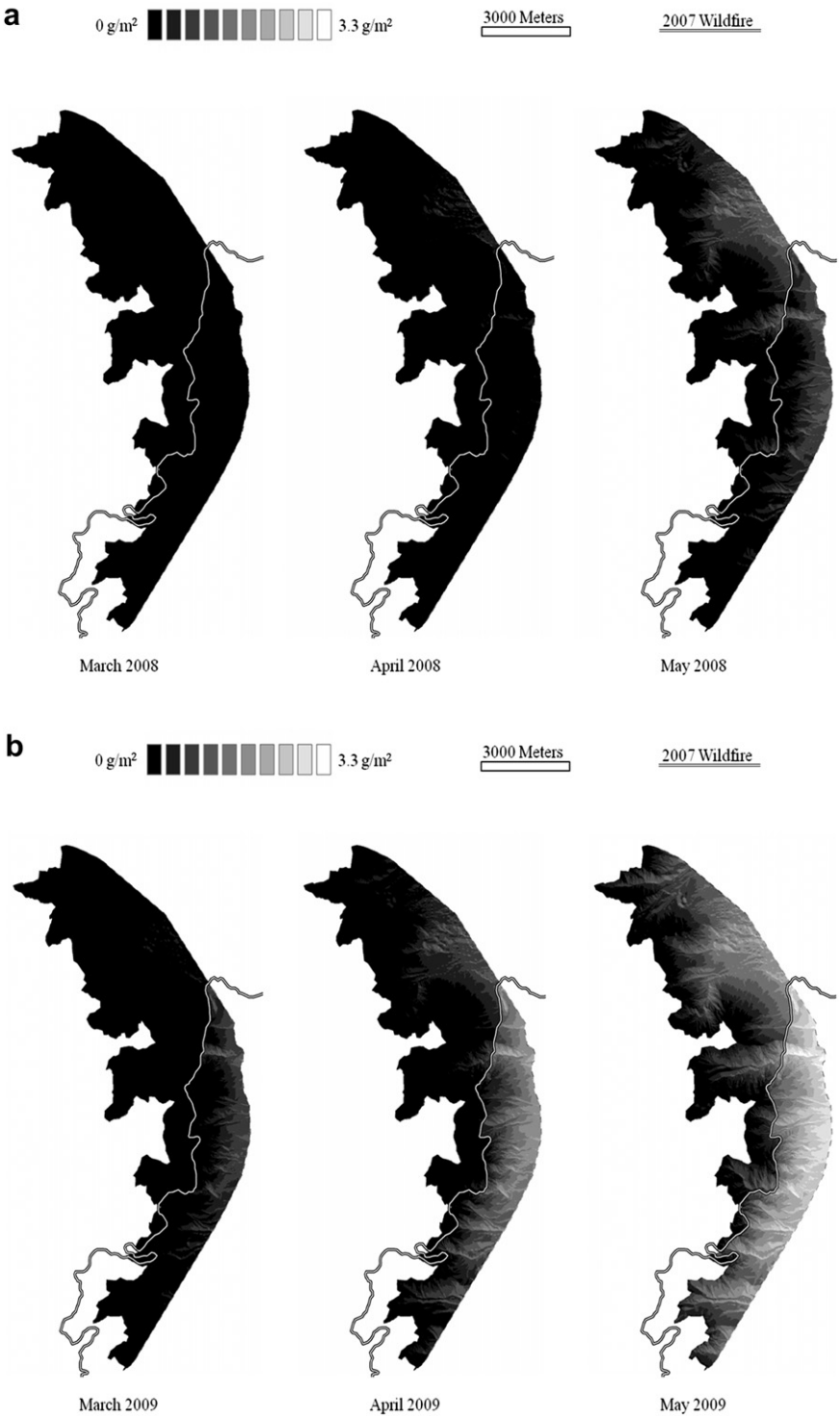

Fig. 2. Forb biomass predictions for Sierra bighorn winter ranges in 2008 (a) and 2009 (b).

($R^2 = 0.21$) compared to MODIS NDVI (250 m^2; $R^2 = 0.10$) despite having less temporal resolution than the MODIS data, when forested areas were excluded. MODIS and TM NDVI values were also correlated ($R^2 = 0.31$) to each other.

4.2. Forage quality

Crude protein was 3% higher in plants from burned than unburned sites ($N = 144$, $P = 0.008$), in contrast to IVDMD which did not differ between burned and unburned sites ($N = 144$, $P = 0.65$). Across forage classes, crude protein decreased with month and increased with elevation and year (Table 3). An interaction between elevation and burn was significant in a linear mixed model of crude protein with species as the random effect and predictor variables elevation, burn status, month and year (Fig. 4). Within the burn, crude protein levels increased with elevation while there was no effect of elevation outside the burn. In contrast, none of our predictor variables had significant relationships with

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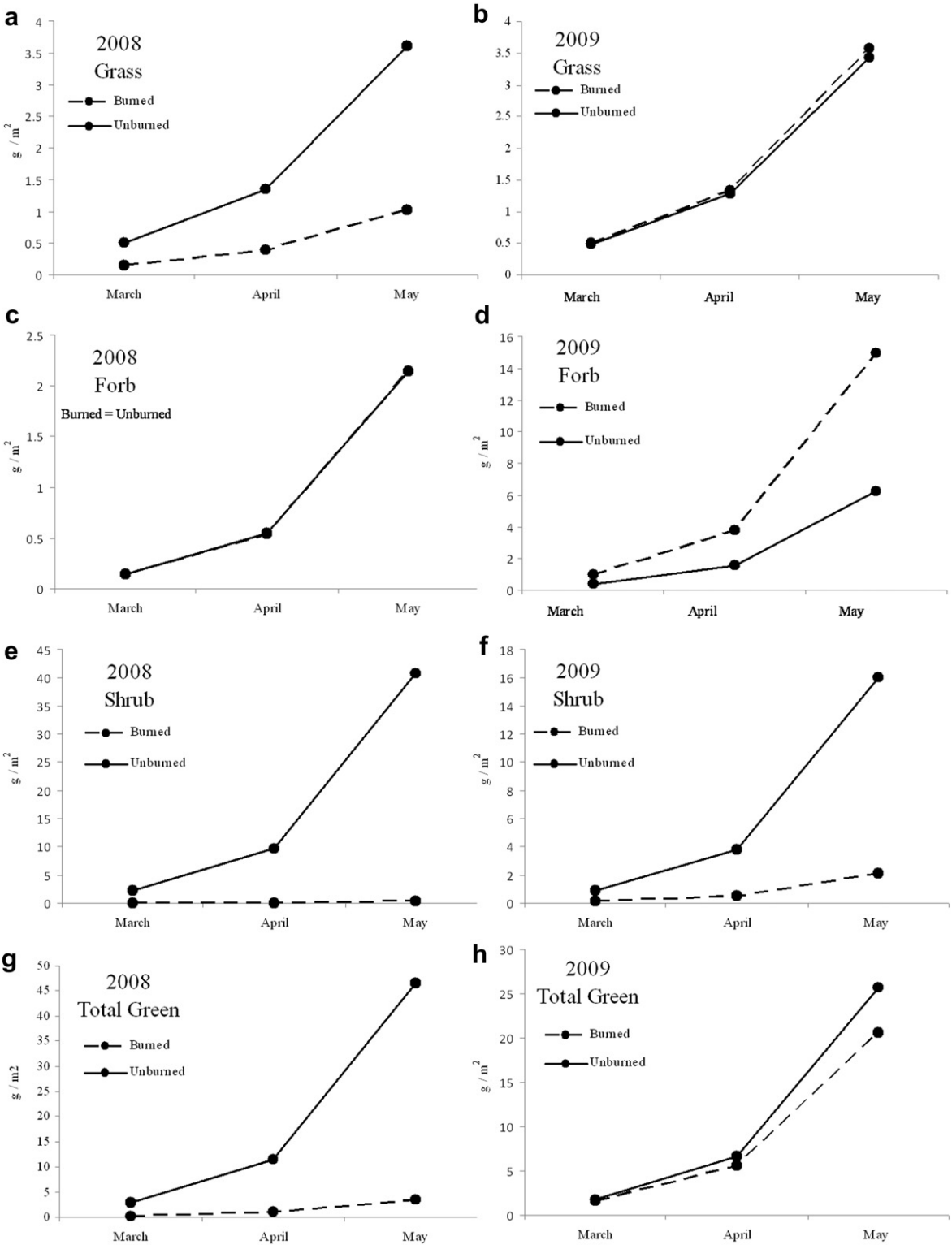

Fig. 3. Model predictions of green (new growth) biomass of each forage class in burned and unburned Sierra bighorn winter ranges for two years following a summer wildfire in 2007. To demonstrate the differences in vegetation, elevation and aspect are held constant at the mean values within the study area.

IVDMD. Our data did provide support for the general predictions of Van Soest (1994); forbs had the greatest crude protein and IVDMD followed by grasses and then shrubs (Table 4). With a small subsample we found old growth *Achnatherum* spp. had three times less crude protein than new growth and a ~20% reduction in IVDMD (Table 4) which supports our focus on green growth. Furthermore, we found no evidence to suggest the wildfire induced a change in phenology. Burn was an insignificant variable in generalized linear models of percent flowering in May across 4 target genera: *Purshia* spp., *Dichelostemma* spp., *Achnatherum* spp., and *Mentzeilia* spp. There was no difference in phenology between burned and unburned sites.

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Table 2
Biomass model estimates for peak new growth dry biomass of the Mt. Baxter (67% burned) and Sawmill Canyon (11% burned) winter ranges of Sierra bighorn.

	Average g/m^2 2008		Average g/m^2 2009	
	Baxter	Sawmill	Baxter	Sawmill
Grass	1.3	2.4	2.9	2.5
Forb	3.5	3	22.7	11.7
Shrub	8.6	31.8	4.8	12.8
Total	13.4	37.3	30.3	27.0

4.3. Diet composition

Based on microhistological analyses, average Sierra bighorn diets consisted mostly of grasses (50%), followed by shrubs (38%) and forbs (10%, $N = 38$). Over the duration of the study, the Mt. Baxter herd (67% burned) consumed 9% more forbs ($P = 0.03$), 13% less grass ($P = 0.002$) and equal amounts of shrubs ($P = 0.3$) as the Sawmill Canyon herd (11% burned) based on univariate regression analysis ($N = 38$). However, multivariate regression models show that forb and shrub consumption changed with month or year and differed between the Mt. Baxter and Sawmill Canyon herds (Table 5). The significant burn by month and burn by year interactions in the forb model meant that forb consumption increased with month in the second year within the Mt. Baxter herd but remained unchanged and at lower values in the Sawmill Canyon herd. Shrub consumption in the Mt. Baxter herd decreased with month while shrub consumption in the Sawmill Canyon herd was more consistent across months. At the genus level, we detected differences in diet composition between herds for only two genera that were statistically significant after Bonferroni's correction for multiple comparisons. The Mt. Baxter herd consumed 6% less *Agropyron* sp. ($P < 0.002$) and 6% more *Cercocarpus* sp. ($P < 0.002$) than the Sawmill Canyon herd. There was also no difference in the number of genera consumed between herds ($P = 0.31$). The only non-native genera in the microhistological analysis was *Bromus* spp. and there was no difference in the amount of *Bromus* spp. in fecal pellets from the Mt. Baxter and Sawmill Canyon herds ($P = 0.32$).

4.4. Visibility

Horizontal visibility was 9% greater in burned than unburned sites at 5 m and 17% greater in burned than unburned sites at 15 m based on linear model predictions (Table 6). Horizontal visibility was also driven by elevation and the quadratic of terrain ruggedness. The quadratic of terrain ruggedness indicates high visibility at areas with low ruggedness (e.g. flat areas) and also high ruggedness (e.g. cliffs).

Table 3
Mixed model results for crude protein and IVDMD of forage from Sierra bighorn winter ranges with genera as a random effect. Crude protein followed expected trends with burn status, elevation, year and month but none of these variables were significantly correlated with IVDMD.

Predictor variable	Crude protein		In vitro dry matter digestibility	
	β	p	β	p
Burn	3.0 (1.05)	<0.01	2.7 (1.92)	0.165
Elevation	3.2 (1.06)	<0.01	0.4 (1.92)	0.854
Year	−2.5 (1.09)	<0.01	−1.2 (1.96)	0.165
Month	−3.0 (0.75)	<0.01	−1.5 (1.35)	0.265
Within-sample R^2	0.21		0.0015	

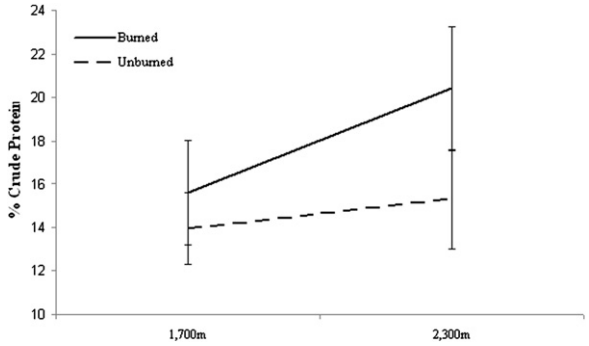

Fig. 4. Interaction between burn and elevation on crude protein within forage species of Sierra bighorn. Data has been collapsed across months and years and display includes 95% confidence intervals. In a mixed model format with species as the random effect, this interaction is significant with $P = 0.02$.

5. Discussion

The Seven Oaks wildfire shifted community composition from shrubs to forbs while total biomass of green forage was resilient and rebounded quickly. In accordance with other studies (Sachro et al., 2005), post-wildfire changes in forage composition were longer lasting than changes in overall green biomass. In Wyoming, post-wildfire biomass rebounded within 1 year at xeric sites (Merrill et al., 1980) but took three years in shrub dominated sites (Merrill et al., 1982). Thus, the two year rebound time-frame we documented fits with the literature as our study site is shrub dominated with limited xeric and forest cover.

NDVI is often used as a surrogate for above ground biomass (Pettorelli et al., 2005), however it can be problematic due to canopy interference (Huete et al., 2002) – specifically in desert areas where soil (Farrar et al., 1994) and shrub cover (Verlinden and Masogo, 1997) can interfere with the relationship between NDVI and biomass. This type of interference may have caused the weaker correlation for both MODIS ($R^2 = 0.1$) and TM ($R^2 = 0.21$) measures of NDVI to ground measures of total green biomass compared with ground based model approach ($R^2 = 0.50$). Another limitation of NDVI is that it fails to capture changes in specific forage categories, which may be important for Sierra bighorn. However, the significant and positive relationship between NDVI and green forage availability indicate that it may be a useful surrogate for green forage availability when used outside of forested areas when it is unrealistic to build ground-sampling based models. Ground-sampling based forage models demand a lot of resources and therefore are not a reasonable option for large study areas and also not an option for analyses of past resource selection. In addition, we expect that the relationship between NDVI and green forage availability will improve as higher resolution imagery becomes available.

Our data on forage quality provide limited support for the post-fire nutrient flush hypothesis (Boerner, 1982). Similar to Hobbs and Spowart (1984), we documented a small (3%) increase in crude protein within species at higher elevations that persisted for two years. Nitrogen from ash was likely picked up by plants and increased their protein levels immediately after fire with no parallel change in phenology or digestibility. We had expected a greater response because oligotrophic systems like the eastern Sierra Nevada tend to have strongly developed mechanisms for post-fire nutrient conservation (Boerner, 1982). Instead we found increased crude protein occurred only at higher elevations which may be a result of nutrient rich ash being blown away from more exposed lower elevations or may be a result of the more arid conditions at lower elevations. In a study on controlled burns in semi-arid

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Table 4
Forage quality characteristics on the winter ranges of Sierra bighorn in 2008 and 2009.

Species	Crude protein			IVDMD		
	Mean	SE	*N*	Mean	SE	*N*
New *Achnatherum* spp.	16	1.3	3	53	2.3	3
Old *Achnatherum* spp.	5	1.1	20	43	11.7	20
Grass	15	7.2	33	55	12.3	33
Forb	20	7.2	36	75	10.6	36
Shrub	14	5.1	55	51	12.7	55

Table 6
Multi-variate regression results for horizontal visibility on the winter range of Sierra bighorn.

Predictor variables	5 m		15 m	
	β	p	β	p
Burn	8.6	0.03	17	<0.01
Elevation	−0.02	<0.01	−0.03	<0.01
Terrain ruggedness	−1700	0.1	−4840	<0.01
Terrain ruggedness^2	82,300	0.05	170,700	<0.01
Aspect	−30	<0.01	−5	<0.01
Adjusted R^2	0.38		0.45	

grasslands in Australia, Bennett et al. (2003) found N and P concentrations were greater in burned grasses compared to unburned grasses for four months post burning during wet conditions, but as the conditions got drier, N concentrations decreased to the level in unburned grasses and P concentrations decreased below the level of unburned grasses. The lower elevations in our study area were warmer and drier, which may explain the lack of difference in crude protein. Alternatively, it is possible that the difference in crude protein between burned and unburned sites was driven by phenology or digestibility. We documented no change in phenology but this could have been an artifact of our methodology because we measured greenup based on the flowering date instead of the date for sprouting or leafing out. For example, in Wyoming, *Agropyron* sp. initiated growth earlier, but flowered at the same time in burned and unburned sites (Peek et al., 1979). In general we would expect phenology to be earlier in burned sites due to increased solar radiation and therefore we would expect crude protein to be lower because crude protein decreases with plant age (Van Soest, 1994). In addition we would expect digestibility to decrease with plant age but we found no difference in digestibility (measured as IVDMD) between burned and unburned sites. For these reasons it appears the increase in crude protein was most likely driven by a post-fire nutrient flush.

In addition to direct changes in the forage quality of diet species, diet quality can be improved by shifting overall diet composition and through the removal of low quality forage. The longer term shift in forage class composition may translate into increased availability of high quality forage in burns because forbs tend to have a higher forage quality than shrubs (Table 4), which is further supported by the higher level of forbs in the diet of Sierra bighorn with more burned habitat. It is likely that Sierra bighorn will respond positively to changes in forage availability as other studies have found mountain sheep diet is correlated to forage availability (Wikeem and Pitt, 1992).

On a smaller scale, the forage quality within each bite can be affected by the forage growth pattern. A bite that consists of only new growth will have higher forage quality than a bite that has a combination of old and new growth (Willms and McLean, 1978). Although we were unable to quantify it, we did observe that burning may have increased access to new growth, especially in perennial bunchgrasses, which we would expect would further increase forage quality in burned areas.

Table 5
Multi-variate regression results for diet composition by forage class from micro-histological analysis of the Mt. Baxter (67% burned, Herd value = 1) and Sawmill Canyon (11% burned, Herd Value = 0) herds of Sierra bighorn fecal pellets collected on winter ranges in 2008 and 2009.

Predictor variables	Grass		Forb		Shrub	
	β	p	β	p	β	p
Herd	−0.1	0.002	−0.2	0.05	0.6	0.006
Herd × Year			0.1	0.03		
Herd × Month			0.09	0.04	−0.2	0.009
Year			−0.03	0.6		
Month			0.03	0.3	0.02	0.6
Adjusted R^2	0.22		0.5		0.21	

The greater forb availability, increased crude protein, higher forb diet composition, and increased access to new growth suggest bottom-up nutritional benefits of fire for Sierra bighorn such that after two years, the Seven Oaks wildfire seems to have enhanced the winter range for Sierra bighorn. Although IVDMD and fecal microhistological analyses have been critiqued as potentially biased methods, the strength in our argument comes from using multiple lines of evidence. In addition, we minimized the potential for bias with careful analyses. Estimates from in vitro dry matter digestibility (IVDMD) are sensitive to both inoculum source and secondary compounds (Van Soest, 1994). In general in vitro methods have been recognized to identify the relative rank of digestibility, but not the true level of digestibility (McDonald et al., 2005). By using a regression model of digestibility, we assumed IVDMD represented the relative changes in digestibility. In addition, secondary compounds which tend to be present in both forbs and shrubs can influence IVDMD (Van Soest, 1994). This is particularly problematic when mixed diets are analyzed. However in this case we used a mixed model approach with species as a random effect so we were investigating changes in digestibility within species. However our results could still be influenced by differences in secondary compounds within a species between plants that grow on burned vs. unburned plots. Diet composition from fecal microhistological analyses tends to overestimate shrubs in the diet and underestimate forbs (McDonald et al., 2005) because woody structure and secondary compounds influence digestibility. Although fecal micro-histological data my not represent the true abundance of a diet item, if the bias is consistent (but see Gill et al., 1983 for a contrary view), this method will still appropriately identify differences in diet composition. We attempted to collect bite count data to corroborate our fecal based diet estimates but found it unfeasible because of the cautious nature of Sierra bighorn and the rocky terrain they inhabit. In particular, in burned areas it was impossible to consistently differentiate foraging on new shrubs from forbs as they were similar in stature and therefore we relied on fecal microhistological data to quantify Sierra bighorn diet.

The greater visibility in burned areas may also have made them more appealing for Sierra bighorn because visibility is thought to decrease predation risk (Risenhoover and Bailey, 1985). In general, lion (*Panthera leo*) predation success has been negatively correlated with visibility. For example, in South Africa, sites of African buffalo (*Syncerus caffer*) mortality from lion predation had lower visibility compared with other sites of observed buffalo use (Hay et al., 2008). Unfortunately we were unable to find any similar studies on mountain lions (*Puma concolor*), but it seems reasonable to assume that because lions and mountain lions employ a similar sit and wait predation style, they would also have a similar relationship between attack success and

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visibility. Increased visibility could ultimately increase the available foraging habitat for Sierra bighorn.

The long life span of ungulates, the endangered status and low population size of Sierra bighorn, and the difficulty and expense of getting demographic data in addition to the erratic nature of wildfires makes it difficult to identify the demographic consequences of a wildfire. However, we think the fire-induced changes in vegetation that we documented could have a positive impact on Sierra bighorn populations. While several studies have shown that mountain sheep use burned areas (Bentz and Woodard, 1988; Riggs and Peek, 1980), the effects of fire on ungulate demography are less established. One exception is from Yellowstone National Park, where Rocky Mountain elk (*Cervus elephus*) populations increased slightly for 3–4 years after the 1988 fires (Taper and Gogan, 2002), but the mechanism of the population increase is unclear. In our study area, we found wildfire increased forage quality by increasing crude protein at higher elevations and also by increasing the relative amount of forbs available. The strongest evidence of forage quality affecting ungulate vital rates comes from Cook et al.'s (2004) study on captive elk. Elk given diets of low quality suffered decreased calf and female survival as well as decreased female and yearling conception rates compared to elk given high quality diets. Similarly, increased forage availability had a positive impact on fawn and adult survival in an experimental study on mule deer (*Odocoileus hemionus*; Bishop et al., 2009). Based on these studies that link forage with increased vital rates, the increase in forage quality we observed may translate into a positive demographic effect for Sierra bighorn.

Our inferences are limited to the short-term effects of fire on vegetation with the weather conditions of 2008 and 2009. Wehausen (1992) documented that temperature and precipitation, particularly the date of the first soaking storm, were major drivers of Sierra bighorn winter forage quality, as indexed by fecal crude protein. In arid regions, plant growth and rainfall are closely tied (Bennett et al., 2003) and soaking rain is important for desert plant germination (Went, 1949). We were unable to ascertain the date of the first soaking storm as the weather station data from Independence (U.S. National Weather Service, Western Regional Climate Center http://wrcc.dri.edu/) is compiled monthly but expect that this factor, like overall precipitation and temperature was about average for the region. In desert regions especially, weather conditions can have a strong affect on vegetation (Bennett et al., 2003) and also herbivore populations (Marshal et al., 2005). In the arid Sonoran desert, rainfall was positively correlated with mule deer population trends, and this was likely caused by the positive relationship between rain and forage biomass (Marshal et al., 2005). The results of our study were strongly affected by the near average weather conditions of 2008 and 2009.

5.1. Management implications

Our results suggest that within two years, large natural fires can improve Sierra bighorn sheep winter range condition by increasing green forage availability, shifting forage and diet composition to include more forbs, and may decrease predation risk by increasing visibility. However, further research should be directed at understanding prescribed fires, the duration of post-fire community composition changes, and effects of fire timing on forage enhancement for Sierra bighorn. Prescribed fires are likely to be smaller in size, affect a reduced proportion of winter ranges and be lower intensity and severity because prescribed fires often occur during the cool season while natural wildfires tend to be in the warm season. Therefore, we expect that prescribed fires may have a reduced effect on forage dynamics compared to wildfires. However, if a prescribed burn is implemented in a way that mimics a natural fire event, it will likely improve winter range conditions within two years, as we quantified with the Seven Oaks wildfire. Within burned and unburned piñon sites which are likely to be targeted with prescribed burning, we found no change in green biomass in the first year following fire ($N = 19$, $P = 0.37$) but by the second year post-wildfire there was 5 times more new growth in burned piñon sites ($\bar{x} = 22$ g/m^2, $N = 11$) compared to unburned piñon sites ($\bar{x} = 4$ g/m^2, $N = 10$). However, we caution against too much enthusiasm toward burning piñon, and do not consider it habitat restoration, but more specifically habitat enhancement. While there may be some pockets of piñon encroachment, there is little evidence that this process is ubiquitous throughout the Sierra Nevada (Latham, 2010).

In addition, the benefit of improving winter ranges should be compared to the relative benefit of other management actions including disease prevention, predator control and augmentation (Johnson et al., 2010). Although we found no difference in non-native plant biomass between burned and unburned sites, this may be a result of the limited timeframe and area sampled. We recommend continued and more targeted monitoring of *Bromus* spp. because through the Great Basin, *Bromus* spp. have degraded forage conditions (Knapp, 1996) and it has recently been observed that *Bromus* spp. are now abundant in some burned sections of the study area (L. Greene, pers. obs.). In conclusion, we found no reason not to move forward with a prescribed fire program from a nutritional ecology perspective, but we do recommend managers take advantage of planned prescribed fires and implement a before, after, control, impact study design that includes bighorn vital rates to identify the direct effects of prescribed fire on Sierra bighorn.

Contributions

Lacey Greene planned and implemented data collection, managed and analyzed data and was the lead on interpreting the results and writing the manuscript.

Mark Hebblewhite guided the study design, assisted in the field with data collection, provided expert advice on data analysis and interpretation, and contributed to writing the manuscript.

Thomas R. Stephenson contributed intellectually to the main ideas and provided the applied framework. In addition he provided methodological advice, assisted in the field with data collection, and contributed to writing the manuscript.

All authors have approved this final article.

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