SHORT-TERM EFFECTS OF WILDFIRE ON SIERRA NEVADA BIGHORN SHEEP HABITAT ECOLOGY

By

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ABSTRACT

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Short-term effects of wildfire on Sierra Nevada bighorn sheep habitat ecology

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We studied changes in vegetation and habitat selection by endangered Sierra Nevada bighorn sheep (*Ovis candensis sierrae;* hereafter Sierra bighorn) for 2 years following wildfire on winter ranges in eastern California. We hypothesized that wildfire would change both forage availability and predation risk. Green forage biomass on Sierra bighorn winter ranges rebounded quickly from wildfire. Within 2 years green forage biomass was equal in burned and unburned areas, although total forage biomass was greater in unburned areas. Plants in the burn had 3% greater crude protein but equivalent digestibility and phenology. Forage composition in burned areas was forb dominated compared with unburned areas that were shrub dominated. Visibility, a measure of predation risk, was 9% greater in burned areas at a 5 m radii compared with unburned areas. We found no change in fecal nitrogen between Sierra bighorn in burned and unburned areas but there was a shift to higher diet composition of forbs in the burn. We evaluated Sierra bighorn resource selection using seasonal resource selection functions that included spatiotemporal models of forage biomass and spatial models of predation risk by cougars (*Puma concolor*), the main predator of Sierra bighorn. In the first year post-wildfire, Sierra bighorn increased selection for new growth herbaceous biomass in response to the reduced biomass caused by wildfire. While wildfire initially reduced total forage biomass it also created pockets of the highest new forb biomass in areas of high cougar use. These pockets attracted Sierra bighorn causing an increase in overlap with cougars in winter 2008. Sierra bighorn showed consistent selection to be near escape terrain and remained closer to escape terrain in areas of high cougar use compared to areas with low cougar use. By spring 2008 and winter and spring of 2009 Sierra bighorn strongly selected total forage biomass where cougar use was low and in areas of high cougar use, Sierra bighorn avoided total forage biomass. As a result Sierra bighorn overlap with cougar use was reduced. We advise management to consider the effects of fire on both forage availability and predation when implementing prescribed burns to benefit ungulates.

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Table of Contents

List of Tables

List of Figures

CHAPTER 1: OVERVIEW

"The Sierra Nevada Mountain Sheep was a hardy animal, fitted to live in the narrow belt of alpine conditions found along the crest of the Sierras, and would be there in numbers today had it received any reasonable consideration from the white man."

- Joseph Grinnell and Tracy Irwin Storer, Animal Life in the Yosemite, 1924

This research was motivated to assist recovery of endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; hereafter Sierra bighorn). Concern for Sierra bighorn first prompted legislative action in 1878 when California legally protected bighorn from hunting (U. S. Fish and Wildlife Service 2007). While there was likely heavy hunting pressure from gold miners, hunting regulations failed to protect Sierra bighorn. Diseases spread from domestic livestock were another important factor causing further declines in Sierra bighorn (Wehausen et al. 1987). Despite livestock reductions that started in the 1930s that nearly eliminated grazing conflicts by the 1960s, Sierra bighorn failed to recover their population size and distribution (Wehausen et al. 1987). Their historic range spanned 250km of the Sierra Nevada, but by 1979 all remaining Sierra bighorn were clustered in a 50km stretch and the population was estimated at 300 (Wehausen 1980). The California Department of Fish and Game (CDFG) responded to the diminished Sierra bighorn distribution by implementing a translocation program in the 1979 (U. S. Fish and Wildlife Service 2007). Translocation was considered the only way to restore Sierra bighorn to previously occupied areas because bighorn are philopatric and slow colonizers of new habitat (Geist 1971, Valdez and Krausman 1999). Translocated populations initially increased, but by the mid-1990s the overall population estimate dropped to 100 (U. S. Fish and Wildlife Service 2007). Sierra bighorn qualified for emergency listing under the endangered species act in 1999 as a distinct population segment and permanent listing followed in 2000 (U. S. Fish and Wildlife Service 2007) and are currently recognized a distinct subspecies (Wehausen and Stephenson 2005).

The primary factors currently limiting Sierra bighorn recovery include disease, predation, low population size and limited distribution, loss of genetic diversity due to small population sizes and inadequate connectivity, and the availability of open habitat (U. S. Fish and Wildlife Service 2007). A joint federal-state recovery team is currently investigating management options within each of these categories. Recent research on the founding and translocated herds has concluded that predation by cougars (*Puma concolor*) is the proximate limiting factor for some herds (Johnson et al. 2010), although predation may interact with the availability of open habitat. For clarification, here we are using the 'structural' definition of habitat that represents the overall landcover or vegetation type that exists in space, within which resources are selected (Hutto 1985, Gaillard et al. 2010). Open habitat is thought to be important for all Sierra bighorn herds because it provides foraging opportunities in areas of high visibility. Visibility is important to bighorn sheep because they rely on vigilance behavior to avoid predation, preferring open areas near escape terrain that allows them to visually detect and flee from predators (Geist 1971, Berger 1978, Risenhoover and Bailey 1985). Therefore, our study focused on the loss of open habitat and its role in promoting Sierra bighorn recovery.

Unlike most endangered species, the historic range of Sierra bighorn is relatively intact and protected from human disturbance (U. S. Fish and Wildlife Service 2007). However, open habitats have been declining because of single-leaf piñon pine (*Pinus monophylla*) encroachment since Europeans arrived in the 1850s (Burwell 1999, Gruell 2001, Miller and Tausch 2001, Weisberg et al. 2007, Romme et al. 2009). The invasion of piñon includes expansion of overall area and increased canopy cover within existent forests (Romme et al. 2009). The cause of this invasion has not been clearly identified, but the common myth of fire suppression has been refuted (Baker and Shinneman 2004, Romme et al. 2009). It is more likely that climate, increased carbon dioxide CO_2 (Johnson et al. 1993), livestock grazing (Burwell 1999) and interactions between these factors have driven piñon invasion (Romme et al. 2009). Piñon invasion has occurred in lower elevation ranges (CDFG Bishop office, unpublished data) that Sierra bighorn use in winter and early spring (Wehausen 1980) causing decreases in forage (Arnold et al. 1964) and visibility.

The Sierra bighorn recovery plan identifies prescribed fires as a possible tool to combat piñon encroachment with prescribed fires (U. S. Fish and Wildlife Service 2007). Prescribed fires are the most cost-effective way to reduce piñon and juniper (*Juniperus* spp.) invasion (Aro 1971) However , others reported it is often difficult to use prescribed fire to combat piñon invasion, because piñon forests can be difficult to burn (Arnold et al. 1964, Bruner and Klebenow 1979). Successful prescribed fires tend to be performed when weather conditions encourage the spread of fire (e.g., high wind and high temperature) but prescribed fires under these conditions also have the greatest risk of escape (Aro 1971, Bruner and Klebenow 1979). When piñon and juniper are removed (regardless of the mechanism), there is a dramatic increase in herbaceous forage production (Arnold et al. 1964), which has translated into increased livestock production (Aro 1971). In contrast, Terrel and Spillet (1975) reported piñon and juniper removal had no effect on mule deer (*Odocoileus hemionus*) in Utah because mule deer are mid-succession specialists. However, Terrel and Spillett (1975) postulated that the effect of piñon and juniper removal may be different for grazers, such as bighorn sheep. Unfortunately, there is no direct information about the effect of piñon juniper removal on bighorn sheep.

In order to gain a better understanding of the effect of fire on Sierra bighorn, we took advantage the recent Seven Oaks wildfire near Independence, California. (The pronoun we is used in this document to represent the collaboration that occurred among Stephenson, Hebblewhite and me). In chapter 2 we quantified seasonal differences in forage quantity and quality between burned and unburned sites for 2 years after the Seven Oaks wildfire. We incorporated our ground sampling based models of forage into a series of seasonal resource selection functions in Chapter 3 to quantify how Sierra bighorn used resources and how the distribution of available resources affected the amount of overlap between Sierra bighorn and cougars. The pronoun we is used in this document to represent the strong collaboration that occurred between the three co-authors: myself, Tom Stephenson and Mark Hebblewhite.

We hope this thesis contributes to Sierra bighorn recovery. It is disheartening that despite a long history of protection, Sierra bighorn are still on the brink of extinction. History has clearly shown us how the limiting factors of Sierra bighorn can overlap and disguise each other. Sierra bighorn recovery is challenging because the limiting factors interact and change with time. As we continue to strive for Sierra bighorn recovery, it seems most wise to approach the problem from multiple angles and consider not only what the limiting factor is right now but also lay the groundwork to make it easier to identify limiting factors as they are uncovered, change, and interact with each other in the future. We tried to be comprehensive in our evaluation of the effect of wildfire on Sierra bighorn by incorporating multiple measures of forage and predation with the hope that we might contribute to maximize the effectiveness and minimize any untended consequences of future prescribed burns.

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CHAPTER 2: SHORT-TERM EFFECTS OF WILDFIRE ON THE WINTER RANGE OF SIERRA NEVADA BIGHORN SHEEP

Introduction

Fire has multiple indirect effects on ungulates through its direct effect on vegetation. Fire affects forage quantity, quality and species composition, and vegetation structure that affects behavior and predation risk (Cook et al. 1994, Fisher and Wilkinson 2005, Sachro et al. 2005). The variation in plant responses to fire and the varied relationships between forage quantity, quality and visibility makes it difficult to predict the effect of fire on ungulates. The Seven Oaks wildfire provided the opportunity to evaluate the effect of wildfire on endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierra;* hereafter Sierra bighorn). Due to the limited distribution of Sierra bighorn and fire on the eastern slopes of the Sierra Nevada, this is the first time a large natural fire has occurred within the winter range of Sierra bighorn. We were interested in evaluating and predicting the effect of fire on endangered Sierra bighorn because their recovery plan recommends prescribed burning to enhance winter ranges that are facing encroachment by piñon pine (*Pinus monophylla*; U.S. Fish and Wildlife Service 2007). Despite the potential importance of fire to Sierra bighorn, there are no specific studies on the effects of fire on Sierra bighorn to guide recovery actions. Therefore, before implementing a series of prescribed burns, we investigated the effects of a natural wildfire to determine the short-term effects of wildfire on forage quality, quantity and visibility.

In response to fire, forage quantity, or biomass, initially decreases but then quickly rebounds and often increases beyond the amount of forage in unburned areas. Shrubs followed this pattern after wildfire in the Upper Selway River in Idaho where shrub biomass in burned areas exceeded that of unburned areas by the third growing season post fire (Merrill et al. 1982). In Banff National Park, Sachro et al. (2005) quantified increases in herbaceous biomass within burned coniferous forests that persisted for 7 years after burning, while shrub dominated communities either had a decrease or no change in herbaceous biomass as a result of burning. In a study on the effects of fire in a semi-arid sagebrush steppe ecosystem, Cook et al. (1994) found total new growth biomass was greater in burned areas compared with control sites after three years. In general, burning increases biomass but the duration of this increase is variable and often dependent on the pre-burn conditions (Arnold et al. 1964).

Digestibility and crude protein are important components of forage quality that can also change following fires. Post-fire vegetation sometimes has higher protein than pre-fire vegetation as a result of increased soil nitrate concentrations (Christensen 1973, Boerner 1982), although the duration of nutrient bursts may vary (Boerner 1982, Seastedt et al. 1991). DeWitt and Derby (1955) documented an increase in crude protein in 3 of 4 browse species that persisted for 1 year after a low intensity fire and for 2 years after a high intensity fire in Maryland. Other studies failed to detect differences in forage quality between burned and unburned sites. Seip and Bunnell (1985a, 1985b) reported no difference in protein or digestibility in burned and unburned winter ranges of Stone's sheep (*Ovis dalli stonei*) in the northern Rocky Mountains although they considered "burned" to include areas burned within the last 9 years , whereas nutrient flushes tend to be shorter in duration (Boerner 1982). For example, Van Dyke and Darragh (2007) documented forage quality increased for 2 years after prescribed burning in sagebrush (*Artemesia* spp.) communities in Montana but when they re-visited sites 10 years after burning, there was no maintained increase in nitrogen. In general, plants that are older or have tannins are less digestible because lignin and plant defenses negatively affect digestibility (Van Soest 1994). Fires may also cause phenological differences in plants where burned areas tend to green-up earlier (Hobbs and Spowart 1984, Seip and Bunnell 1985b) resulting in earlier availability of high quality forage (DeWitt and Derby 1955, Seip and Bunnell 1985a).

In addition to forage quality, ungulate diet composition is important in determining diet quality which may also change following fire. Diet composition is determined by diet selection and the composition of available species. In a study on diet selection, Hobbs and Spowart (1984) found diet composition played a much larger role than forage quality in determining overall diet quality with tame bighorn (*O. canadensis*) and mule deer (*Odocoileus hemionus*) in the Front Range of the Rocky Mountains, Colorado. Diet quality in burns had higher crude protein and digestibility but only a small portion of this change was due to specific increases in crude protein and digestibility within species. Diet composition is determined by diet selection and the composition of available species. As with the effect of fire on biomass, changes in species composition depend on the pre-burn vegetation community. Cook et al. (1994) reported the community composition in burned areas had higher grass biomass while forbs remained similar to unburned conditions. Merrill et al. (1980) documented a shift in the balance of production toward increased forbs but also increased annual grasses, specifically non-native cheat grass (*Bromus tectorum*) in burns. In the semi-arid eastern Sierra Nevada, post-fire regeneration was examined with Jeffrey pine (*Pinus jeffreyi*) stands after the Donner fire in 1960 (Bock et al. 1978). After twenty years at this site, the burned Jeffrey pine community was still dominated by shrubs (Bock et al. 1978). In this way, burning-induced changed in species composition may in turn cause long-term increases in forage biomass.

Fire also affects forage and vegetation structure, which in turn affects visibility. Visibility is important for bighorn sheep 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 (Geist 1971, Berger 1978, Risenhoover and Bailey 1985). Fire generally results in increased visibility (Bentz and Woodard 1988, Smith et al. 1999) although this may vary with fire intensity (DeCesare and Pletscher 2004). Within historic and occupied bighorn ranges in Colorado, Wakelyn (1987) found vegetation classes that had higher visibility were more prevalent in occupied ranges compared with abandoned ranges and argued that shrub and forest encroachment were degrading bighorn habitat.

We evaluated the effects of fire on Sierra bighorn to test the overall hypothesis that fire will increase forage biomass, enhance nutrition, and increase visibility. We predicted that the 2007 wildfire in the eastern Sierra Nevada will initially decrease new growth (hereafter green) forage biomass, but that within the 2 years of this study, green biomass in burned areas will surpass that in unburned areas. We also predicted that forage quality will be greater in burned areas because of a nutrient flux, earlier greenup, and changes in forage class (grass, forb and shrub) composition. In addition, we predicted that visibility will be higher in burned areas. We tested these predictions by quantifying changes in forage quantity, forage quality, and visibility between burned and unburned areas. We used extensive ground sampling to build predictive models of short-term changes in forage biomass, forage class composition and visibility. Finally, we hypothesized that these changes in forage availability will lead to increased diet quality for Sierra bighorn. We tested this hypothesis by comparing 2 indicators of diet quality (fecal nitrogen and diet composition estimated from microhistological analyses) between 2 Sierra bighorn herds with contrasting amounts of burned available habitat.

Study Area

Our study area focused on the Sierra bighorn winter ranges of the Mt. Baxter and Sawmill Canyon herds located in the eastern Sierra Nevada, near Independence, California (Figure 2-1). In July 2007, the Seven Oaks wildfire burned 67% of the Mt. Baxter winter range, including all of the lowest elevation areas and 11% of the adjacent Sawmill Canyon winter range (Figure 2-1). These 2 herds played an important role in the recovery of Sierra bighorn because they are the largest of all relict populations and they were the main source for translocations used to restore Sierra bighorn to their historic range. Most Sierra bighorn in these herds migrate seasonally, spending summer high in the alpine (>3050m) and winter at lower elevations that provide snow free foraging areas with early exposure to spring greenup. The Mt. Baxter and Sawmill Canyon winter ranges are part of the Inyo National Forest and their pre-fire vegetation was dominated with 87% sagebrush scrub (Munz and Keck 1959) and also included 2% piñon woodlands (*Pinus monophyla*; Munz and Keck 1959) and 9% cliffs (slope >100%). Common grasses included: *Achnatherum* spp., *Bromus* spp. and *Poa* spp. Winter ranges had a large variety of forbs including: *Mentzelia* sp., *Phacelia* spp., *Dichelostemma* sp., *Galium* sp., *Eriogonum* spp., *Tauschia* sp., *Lupin* spp. and *Linanthus* spp. Shrub genera included *Eriogonum* spp., *Ephedra* spp., *Prunus* sp., *Ceanothus* spp., *Purshia* spp., *Chrysothamnus* spp., *Artemesia* spp., *Lupin* sp. and *Cercocarpus* sp. Total precipitation recorded from the nearest weather station in Independence, California for February through May was 20mm 2008 and 19mm 2009 and the long term average was 23mm (U.S. National Weather Service, Western Regional Climate Center http://wrcc.dri.edu/). 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 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 = 1.3).

We delineated each herd's winter range with a minimum convex polygon around GPS collar locations collected during the study period and buffered by 500m and elevation cutoffs at 1,400m and 2,600m (Figure 2-1). The Sawmill Canyon herd winter range was 1.2

times larger than the Mt. Baxter Herd winter range and the 2 herds overlapped by approximately 25%. The elevation distribution and mean were similar between the Mt. Baxter and Sawmill Canyon herds but the aspect distribution 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 dominated by east-facing terrain. The Mt. Baxter winter range aspect was 36% east, 23% southeast, 19% northeast, 9% north, 8% south, and <5% facing toward the west. Within the Sawmill Canyon winter range the distribution of aspect was 31% east, 29% northeast, 15% southeast, 14% north, 5% south and again roughly 5% toward the west.

Methods

We combined field sampling of vegetation responses following fire into a suite of vegetation models to quantify the magnitude and duration of changes caused by wildfire on the landscape. We used a model based approach to account for differences in aspect between herds. We modeled changes in green growth biomass by vegetation class (i.e. grass, forb, shrub) as well as visibility. All models were built using data from extensive ground sampling. 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 used 2 fecal indices of diet quality: fecal nitrogen and diet composition via microhistological analysis.

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 and semi-random sampling design (Krebs 1989). Sites were stratified based on elevation, aspect, land cover type, slope, and burn status categories. For efficiency, sites were placed systematically along transects from 1,500m to 2,500m every 150m 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 3 times a year for 2 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. Sampling bouts roughly coincided with March, April and May. Sites were added as 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 5m or 10m 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, Elzinga et al. 1998). 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 implemented the comparative yield method (Haydock and Shaw 1975) to obtain a coarse estimate of total dry shrub biomass. Marshal et al. (2005) successfully estimated shrub forage biomass available to mule deer with this categorical double-sampling technique in an arid ecosystem. 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 lupin (*Lupinus* sp.) in which larger bush lupin actually had lower amounts of dry green biomass because of plant architecture. Therefore, we removed lupin from our statistical analysis because it is rare 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 2 years, by developing a set of linear mixed models from ground biomass estimates using Stata 10.0 (StataCorp 2007) and R 2.10.1 (R Development Core Team 2005). We used univariate analysis to identify significant predicator variables including land cover class (i.e., shrub, forest, and 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 had a value of 1 and northeast aspects had a value of -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. Variables were screened for collinearity and relevant interactions and non-linear relationships (through the use of quadratics, $X + X^2$) were investigated and top models were selected based on a combination of biological relevance and 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).

Forage Quality

We measured 2 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 2 different elevations 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 similar diameters as observed foraged species. We also included 3 samples of old growth *Achnatherum* spp., a dominant forage species (Wehausen 1980, Schroeder et al. In Press), to quantify the magnitude of difference between old and new growth. Samples were dried at 60°C for 24 hours and analyzed for IVDMD and crude protein at the Wildlife Habitat Nutrition Laboratory in 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 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.

Diet Quality and Composition

We tested our hypothesis that burns influenced diet quality and composition by comparing the fecal nitrogen and diet of the 'burned' Mt. Baxter herd (67% of winter range burned) with the 'unburned' Sawmill canyon herd (11% of winter range burned). We used fecal nitrogen as an index of diet quality from fecal samples collected opportunistically throughout winter range. Fecal nitrogen is a highly debated forage quality index (Hobbs 1987, Leslie and Starkey 1987, Robbins et al. 1987, Wehausen 1992, Brown et al. 1995, Blanchard et al. 2003, Leslie et al. 2008). However, for bighorn sheep, it sometimes depicts long term trends in nutrition over time within a population (Leslie et al. 2008). Fecal samples were air dried and analyzed for nitrogen on an organic content basis (Wehausen 1995) at the Wildlife Habitat

Nutrition Laboratory at Washington State University in Pullman, Washington. In addition, a subset of 38 samples received microhistological analysis (plant genus level with 25 views / slide and 4 slides / sample) to determine diet composition differences between burned and unburned areas. We tested for differences in fecal nitrogen and diet composition between the Mt. Baxter and Sawmill Canyon herds using ANOVA for fecal nitrogen and multiple linear regressions for diet composition. Our response variable for diet composition 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 found angular transformation did not improve residual distribution so we did not transform the data to make coefficients easier to interpret. We used univariate analysis to identify significant predictor variables and included all significant variables or interactions in top models. Model fit was evaluated with the coefficient of determination.

Visibility

Horizontal visibility was measured at all 69 vegetation sites using the staff-ball method (Collins and Becker 2001) at distances of 5 and 15m. An observer walked a complete circle around a tennis ball on a 1m tall stick held at the center of the site, systematically stopping and crouching down to 1m 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 2 year study period because all documented vegetation growth was < 1m. To test our hypothesis that visibility was lower in burned compared to unburned sites, we used a linear regression model with predictor variables elevation, land cover class, aspect and terrain ruggedness. Elevation, land cover class and aspect were measured in the field. Terrain ruggedness was calculated from USGS 10m digital elevation models with an extension developed by Sappington et al. (2005) for use in ArcGIS 9.3 (Environmental Systems Research Institute, California). It is recommended that percentage date be angular (arcsin square root) transformed but we found this to be unnecessary because it resulted in a negligible increase in the coefficient of determination, failed to improve residual distribution and made coefficients difficult to interpret.

Results

Forage Biomass

The biomass of green forage generally decreased with elevation and increased with month, year, and aspect, while the effects of burn were complicated by interactions between month and year (Table 2-1). The quadratic of elevation was significant in grass and shrub models indicating green biomass was greatest at intermediate elevations. Two interactions were significant: burn x year and elevation x month. The burn x year interaction represented an increase in biomass between years 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 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. Based on biomass model predictions several trends were detected in post-fire forage (Figure 2-2 and 2-3). In general, our models predicted that green biomass in burned areas caught up with unburned areas by the second year post-fire. Within unburned areas, shrubs dominated total green biomass and within burned areas, forbs dominated total green biomass. The 2 non-native genera present –*Bromus* spp. (cheat grass and red brome) and *Erodium* sp. (filaree) showed no change 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 and to determine the total peak green biomass of each herd (Table 2-2). 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 2-2).

Forage Quality

Crude protein was 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 2-3). An interaction between elevation and burn was significant in a linear mixed model with species as the random effect and predictor variables elevation, burn status, month and year (Figure 2-4). 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 IVDMD.

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. Our data did provide support for the general predictions of Van Soest (1982); forbs had the greatest crude protein and IVDMD followed by grasses and then shrubs (Table 2-4). With a small sub-sample we found old growth *Achnatherum* spp. had three times less crude protein than new growth and a ~20% reduction in IVDMD (Table 2-4).

Diet Quality and Composition

There was no effect of the wildfire on fecal nitrogen between the burned Mt. Baxter herd and unburned Sawmill canyon herds (P = 0.55, N =89 Figure 2-5). Based on microhistological analyses, average Sierra bighorn diets consisted mostly of grasses (50%), followed by shrubs (38%) and forbs (10%, N = 38; Appendix 2A), but this composition varied with time and by herd. Diet composition of forage classes changed with month and year and differed between the Mt. Baxter and Sawmill Canyon herds (N = 38, Table 2-5). The significant burn by month and burn by year interactions in the forb model meant that forb consumption increased with month and year within the Mt. Baxter herd but remained unchanged and at lower values in the Sawmill Canyon herd. The Mt. Baxter herd consumed 10% less grass, and more forbs, especially during the late spring than 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 2 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).

Visibility

Horizontal visibility was 9% greater in burned than unburned sites at 5m and 17% greater in burned than unburned sites at 15m based on linear model predictions (Table 2-6). 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).

Discussion

Biomass of green vegetation on Sierra bighorn winter ranges was resilient and rebounded quickly from fire. Within 2 years post fire there was no difference in green forage biomass between burned and unburned areas. Changes in forage class composition were longer lasting, however. After 2 years, forbs dominated burned areas and shrubs dominated unburned areas. This shift in forage class composition may translate into higher availability of high quality forage in burns because forbs tend to have a higher forage quality than shrubs (Table 2-4), which is further supported by the high level of forbs in the diet of Sierra bighorn with more access to burned areas. Within species, crude protein was 3% higher in burned areas at high elevations, although there was no difference in crude protein at low elevations and no difference in IVDMD. In addition to changes in the forage quality of individual forage species, 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. This may also have increased the quality of available forage in burns although it did not translate into any difference in fecal nitrogen (but see below for a discussion on our fecal nitrogen results). The greater visibility in burned areas may also have made them more appealing for Sierra bighorn because visibility is thought to decrease predation risk (Geist 1971).

Our data provide some support for the post-fire nutrient flush hypothesis (Christensen 1973, Boerner 1982, Knapp 1985, Tracy and McNaughton 1997). We documented an average 3% increase in crude protein within species at higher elevations that lasted for 2 years. In the semi-arid forests of the eastern Sierra Nevada specifically, fire is the dominant mechanism removing nitrogen from the soil (Johnson et al. 1997). Boerner (1982) found that plants in oligotrophic systems like ours, tend to have highly developed mechanisms for postfire nutrient conservation. This flow of soil nitrogen may have been picked up by plants and increased their protein levels immediately after fire with no parallel change in digestibility or phenology. This may have occurred only at higher elevations because nutrient rich ash was blown away from more exposed lower elevations. Alternatively, it is possible that our method of measuring phenology resulted in a type II error. We measured greenup based on the flowering date of several target species but it can also be measured in terms of sprouting or leafing out. In a study of post-fire vegetation changes, Peek et al.(1979) found *Agropyron* sp. initiated growth earlier, but flowered at the same time in burned and unburned sites. If phenology was advanced in burned sites, we would expect crude protein to be lower because crude protein decreases with plant age (Van Soest 1994). For this reason it is unlikely the increased crude protein in the burn was driven by phenology, and a nutrient flush is the more likely explanation for increased crude protein.

Despite increased forb composition, Mt. Baxter fecal pellets had indistinguishable fecal nitrogen values compared with the Sawmill Canyon herd. Fecal nitrogen has been alternatively praised (Leslie and Starkey 1987, Wehausen 1992, Blanchard et al. 2003, Leslie et al. 2008) and criticized (Hobbs 1987) as a measure of forage quality. Blanchard et al.(2003) provides the strongest evidence that fecal nitrogen can sometimes be a surrogate for nutritional quality in their long term study of bighorn sheep in Alberta, Canada. However, even Blanchard et al. (2003)caution about the inappropriate use of fecal nitrogen, supporting Hobbs' (1987) conclusion that it should not be used to compare between populations. Furthermore, Leslie et al. (1987) caution that fecal nitrogen should only be used as a measure of diet quality when the following assumptions are met: no dramatic changes in the consumption of secondary compounds and no dramatic changes in forage availability. Secondary plant compounds often increase fecal nitrogen because they make protein inaccessible for herbivores (Hobbs 1987, Robbins et al. 1987). The effect of secondary compounds is variable (Leslie et al. 2008) but in general make the link between fecal nitrogen and diet quality less direct. Clearly the differences in forage quantity and forage class composition that we quantified between burned and unburned sites violates important assumptions necessary for fecal nitrogen to be a viable indicator of forage quality. Even when we partitioned our data to test for difference just during the beginning of winter when we would expect overall forage crude protein to be low (because there was very little new growth available), we still found no significant difference in fecal nitrogen between the Mt. Baxter (67% burned) and Sawmill Canyon (11% burned) herds. For these reasons, we were unable to address potential consequences of burns to nutrition using fecal nitrogen, although the higher forb availability, higher forb diet composition, and higher crude protein are suggestive of potential bottom-up nutritional benefits of fire 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. In arid regions, plant growth and rainfall are closely tied (Beatley 1969) and the importance of a soaking rain in desert plant germination is further supported by an experimental study (Went 1949). The monthly precipitation and temperatures during this study were near long term averages based on records from the National Climate Data Center (http://www7.ncdc.noaa.gov/CDO/cdo). We would expect there to be more forage in burned areas following a wet year and less forage in burned areas following a dry year. In the arid Sonoran desert, Marshall et al. (2005)found rainfall was positively correlated with mule deer population trends, and this was likely caused by the positive relationship between rain and forage biomass. We expect fire-induced changes in forage could also have population level impacts.

While there are many studies that examined vegetation differences between burned and unburned areas, the effects of fire on ungulate demography are less established. Due to the nature of fires and the long lifespan of large ungulates, much of the evidence linking forage to demography is from artificial experimental systems, anecdotal, theoretical, or lacks replication. Cook et al.(2004) were able to link forage quality to vital rates in an experimental study on captive Rocky Mountain elk (*Cervus canadensis*) and provide a mechanistic understanding of how forage quality affects demography. Elk were maintained on a low, medium or high quality diets for summer and autumn that impacted calf and female survival as well as female and yearling conception rates. However, the application this research is limited because Cook et al. (2004) used experimental, captive fed elk and examined relatively large changes in forage quality that might not be observed following fire. Within a Rocky Mountain bighorn sheep herd in Colorado, Wakelyn (1987) provided anecdotal evidence linking shrub and forest encroachment with decreasing growth and vital rates. Based on theoretical understandings of forage dynamics, Illius (2006) developed mechanistic models for free ranging ungulates in Africa's savanna that illustrated a clear link between key resources and populations dynamics. In a demographic study on Rocky Mountain elk in Yellowstone National Park, Taper and Gogan (2002) uncovered evidence for a slight increase in elk populations in response to the 1988 fires for 3-4 years post-fire, however no clear mechanism was elucidated in this single population case study.

In addition to fire-induced forage changes, for a comprehensive understanding of the effect of fire on Sierra bighorn, two addition components - resource selection and predation, need to be considered. Within the Mt. Baxter herd winter range, 33% did not burn while 11% of the Sawmill Canyon herd winter range did burn. Strong habitat selection for either burned or unburned areas could have resulted in similar diets between the 2 herds despite the Seven Oaks Wildfire. In addition, without considering resource selection, we were unable to evaluate the relative importance of forage quantity, forage quality and visibility changes for Sierra bighorn. For example, Van Dyke and Darragh (2007) found elk in Montana selected for increased forage production and nutrition for 2 years after prescribed burning, but showed no selection after that time despite persistent changes in community composition and vegetation structure. We evaluate resource selection in Chapter 3, incorporating the effect wildfire on forage and visibility including several components of predation risk.

Management Implications

Further research should be directed at determining the duration of post-fire effects and the effect of burning in different seasons to provide management with recommendations for the timing and interval of prescribed fires. Prescribed fires are likely to be smaller in size, affect a reduced proportion of winter ranges and be lower intensity and severity because of the difference in timing of prescribed and natural fires. Therefore, we expect that many prescribed fires will have reduced effects on forage dynamics compared to wild fires. However, if a prescribed burn is implemented in a way that mimics a natural fire event, the results will likely be positive for Sierra bighorn from a nutritional perspective. Burned areas had greater green forb biomass and increased horizontal visibility. Within burned and unburned piñon pine 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 pine sites ($\overline{x}$ = 22g/m^2, N = 11) compared to unburned piñon pine sites ($\overline{x}$ = 4g/m^2, N = 10). Sierra bighorn with more burned area available consumed more forbs and although this did not translate into increases in fecal nitrogen, this may have be an inappropriate metric to compare between herds. We found no difference in non-native plant biomass between burned and unburned areas. We found no reasons not to move forward with a prescribed fire program from a nutritional perspective, but we do recommend managers take advantage of planned prescribed fires and implement a much stronger before, after, control, impact study design that includes vital rates to identify the effect of prescribed fire on Sierra bighorn demography.

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Table 2- 1. Coefficients for top predictive forage models of total new growth dry biomass (green) for the winter range of Sierra Nevada bighorn sheep (*Ovis canadensis sierra)* during 2008 and 2009, eastern California.

	Green grass		**Green forb**		**Green shrub**		**Total green biomass**	
Predictor Variable	**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 x 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 x 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	

Table 2-2. Biomass model estimates for peak new growth dry biomass of the Mt. Baxter (67% burned) and Sawmill Canyon (11% burned) winter ranges of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae),* eastern California. The Total category does not represent a separate model but was simply calculated by summing the forage classes.

	2008 Winter Range (kg)		**2009 Winter Range (kg)**		**Average g/m^2 2008**		**Average g/m^2 2009**	
	Baxter	**Sawmill**	**Baxter**	**Sawmill**	**Baxter**	**Sawmill**	**Baxter**	**Sawmill**
Grass	32,851	68,503	75,225	72,400	1.3	2.4	2.9	2.5
Forb	91,668	86,146	586, 916	332,691	3.5	3	22.7	11.7
Shrub	223,220	908,834	123,948	365,158	8.6	31.8	4.8	12.8
Total	347,739	1,063,483	786,090	770,249	13.4	37.3	30.3	27.0

Table 2-3. Mixed model results for crude protein and in vitro dry matter digestibility (IVDMD) of forage from Sierra Nevada bighorn sheep, *Ovis canadensis sierrae,* winter ranges in eastern California with genera as a random effect. Crude protein followed expected trends with burn status, elevation, year and month while no variables had statistically significant coefficients for IVDMD.

	Crude protein		**In vitro dry matter digestibility**	
Predictor variable	**β**	**p**	**β**	**p**
Burn	3.0 (1.05)	<0.01	2.7 (1.92)	0.165
Elevaton	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	

Table 2- 4. Forage quality characteristics on the winter range of Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*, in winter and spring of 2008 and 2009, eastern California.

	Crude protein			**IVDMD**		
Species	**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 2- 5. Multi-variate regression results for diet composition by forage class from microhistological analysis of Sierra Nevada bighorn sheep, *Ovis canadensis sierrae,* fecal pellets collected on winter ranges in 2008 and 2009, eastern California.

	Grass		**Forb**		**Shrub**	
Predictor Variables	**β**	**p**	**β**	**p**	**β**	**p**
Herd	-0.1	0.002	-0.2	0.05	0.6	0.006
Herd X Year			0.1	0.03		
Herd X 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	

Table 2- 6. Multi-variate regression results for horizontal visibility on the winter range of Sierra Nevada bighorn sheep, *Ovis canadensis sierrae,* after the Seven Oaks Wildfire, eastern California.

	5m		**15m**	
Predictor Variables	**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	82300	0.05	170700	<0.01
Aspect	-30	<0.01	-5	<0.01
Adjusted R^2	0.38		0.45	

Figure 2- 1. Sierra Nevada bighorn sheep, *Ovis canadensis sierrae,* winter ranges for the Mt. Baxter and Sawmill Canyon herds for the winters of 2007-8 and 2008-9, eastern California.

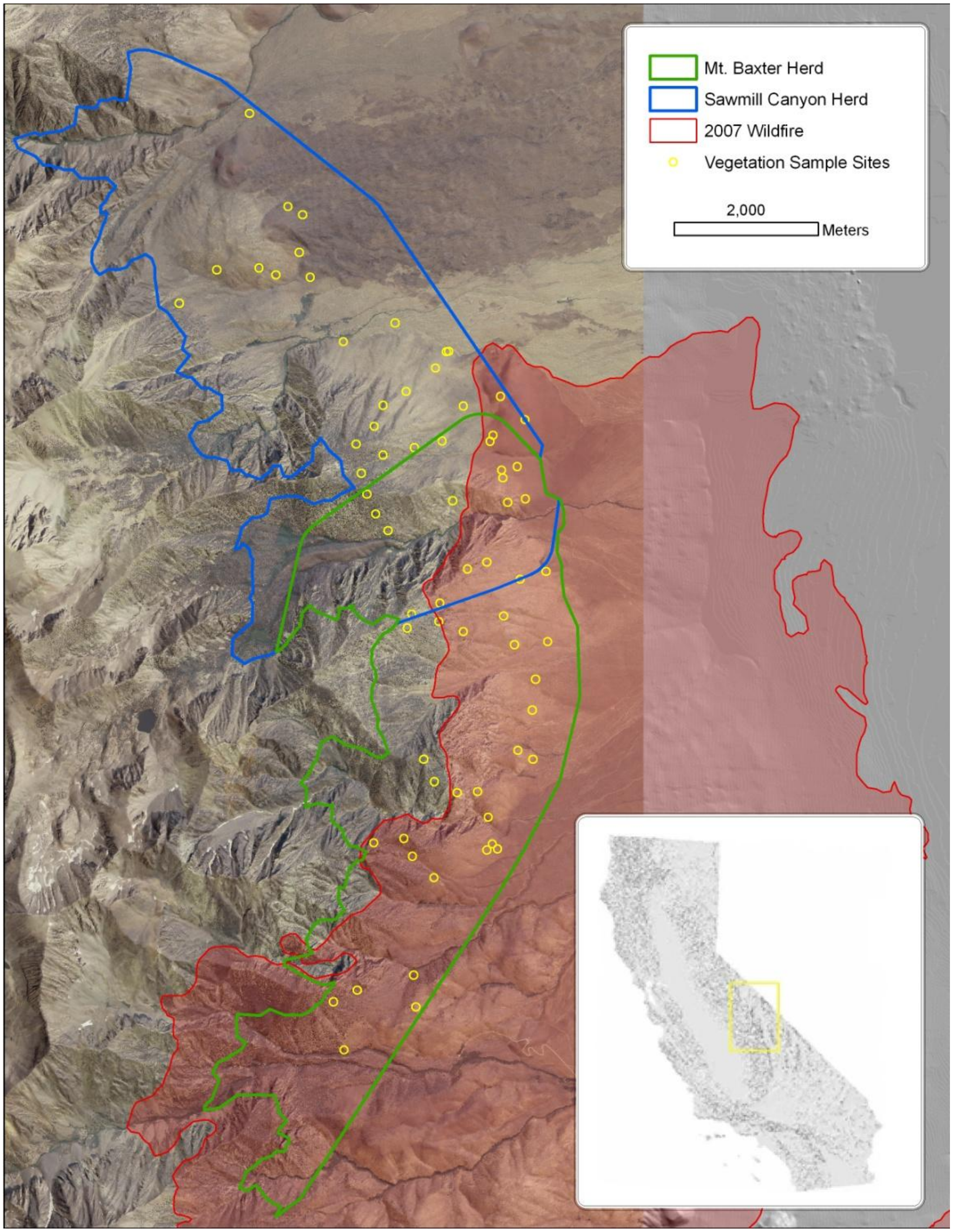
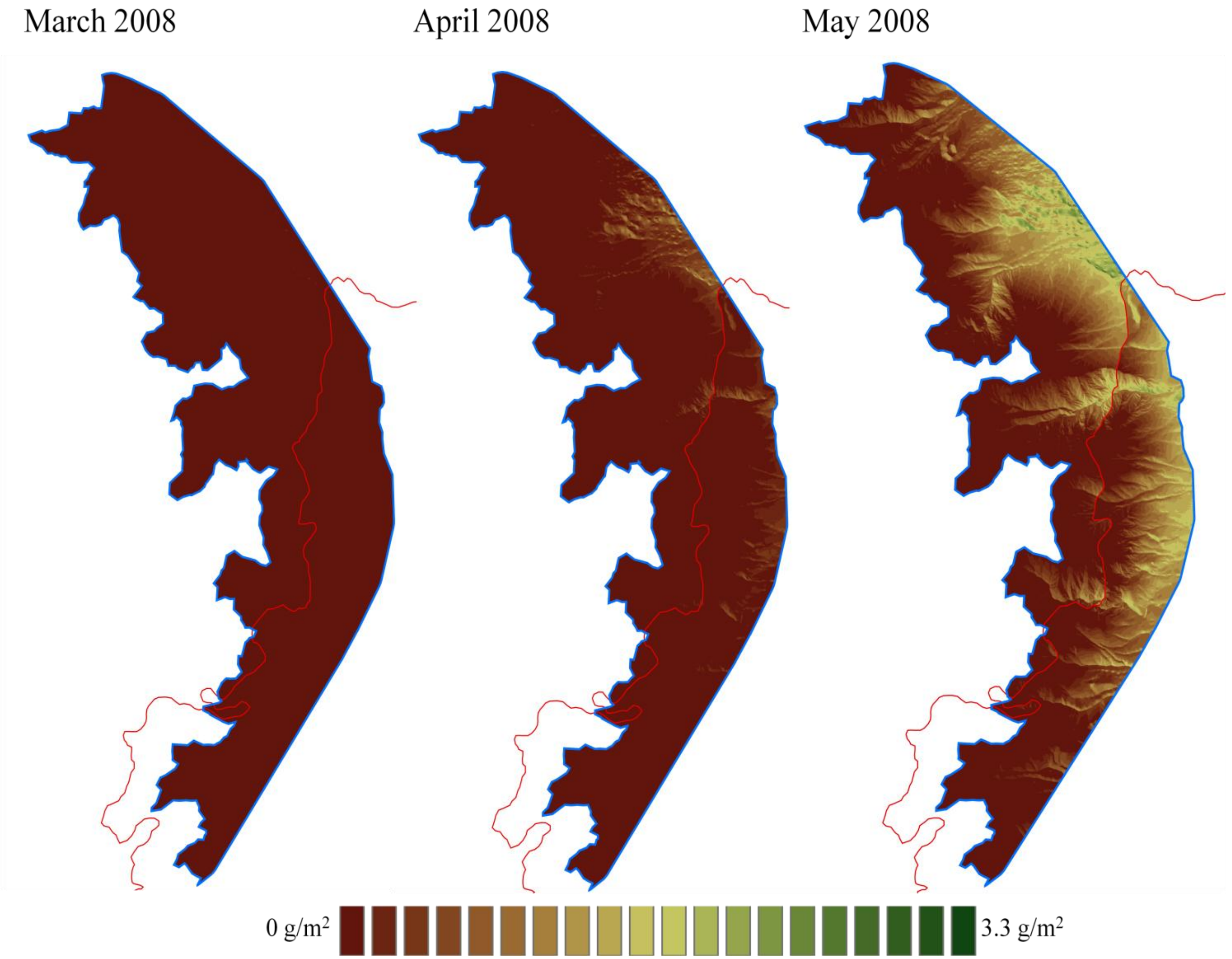


Figure 2- 2. Forb biomass predictions for Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) winter ranges in 2008 and 2009 in eastern California. The forb biomass model was developed from vegetation measurements using a generalized linear model based on predictor variables: elevation, aspect, land cover type, burn status and time.



March 2008

April 2008

May 2008

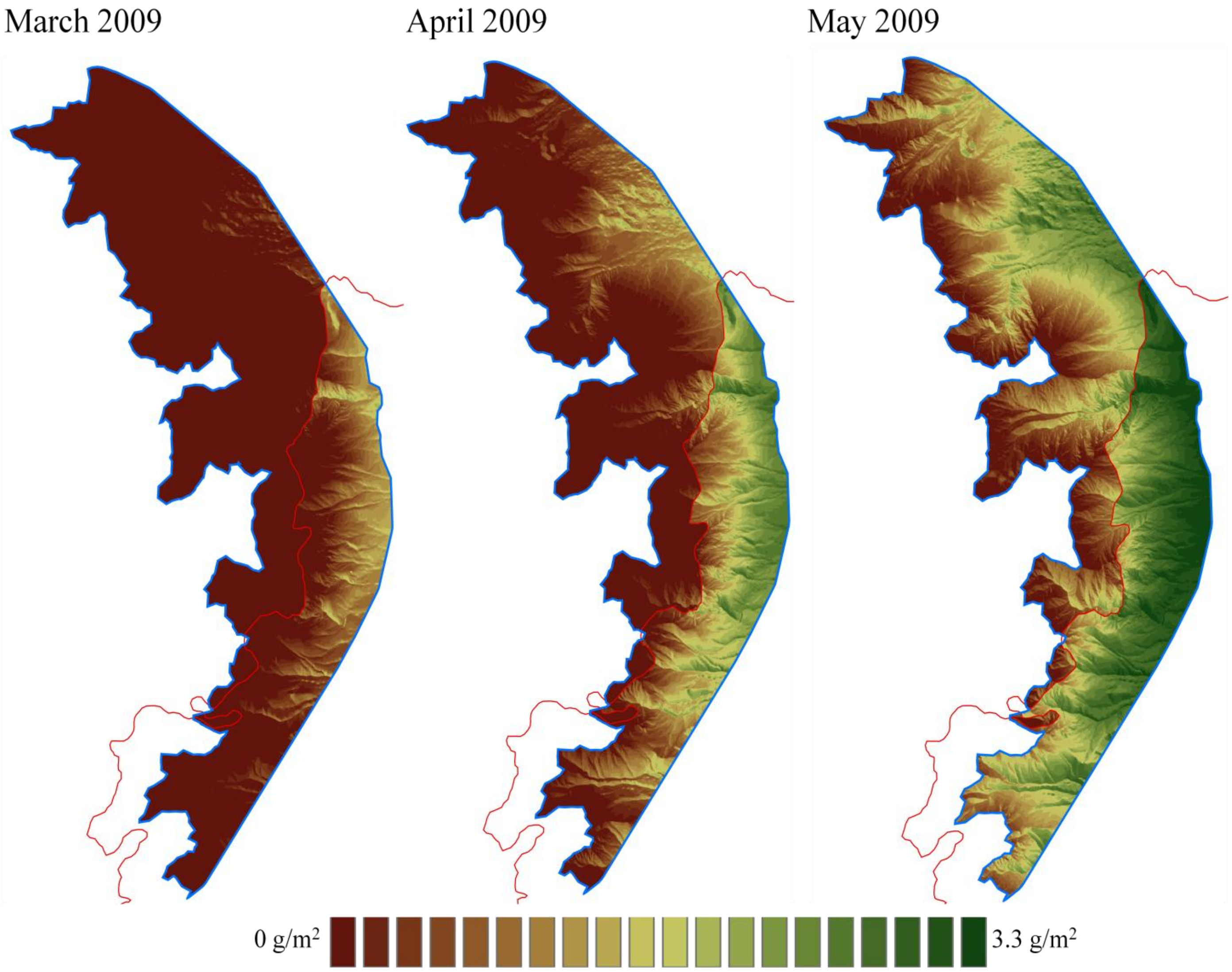

March 2009
April 2009
May 2009
0 g/m²
3.3 g/m²

Figure 2-3. Model predictions of green (new growth) biomass of each forage class in burned and unburned Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) winter ranges for 2 years following a wildfire in 2007 in the Eastern Sierra Nevada. Elevation and aspect are held constant at the mean values for the study area. Total green biomass rebounded within 2 years but forage class composition remained shrub dominated in unburned areas and forb dominated in burned areas.

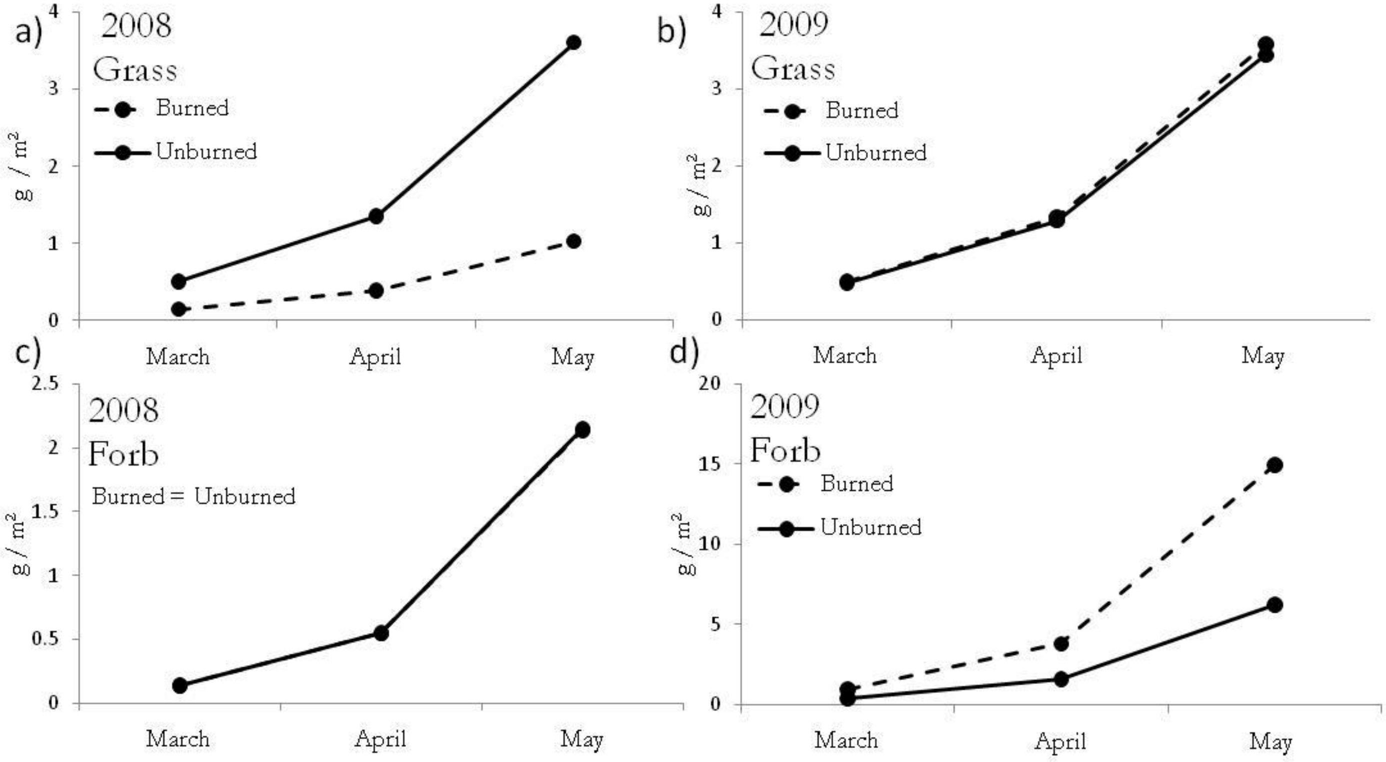


Figure 2-3. Continued

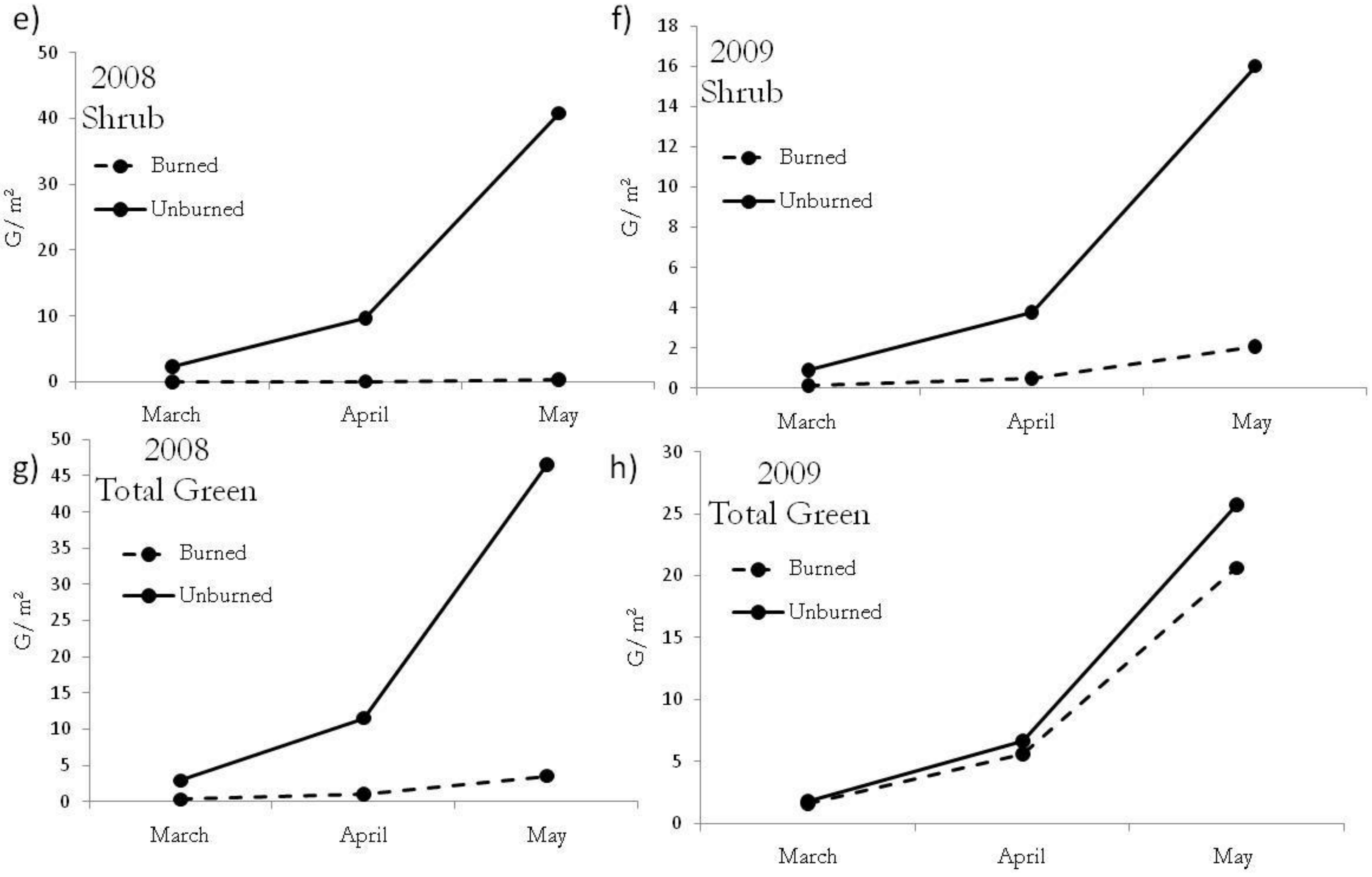


Figure 2- 4. Interaction between burn and elevation in forage species from Sierra Nevada bighorn sheep (*Ovis canadensis sierra*) eastern California. Data has been collapsed across months and years and display includes 95% confidence intervals. In a mixed model format with species as the random effect, this interaction is significant with P = 0.02

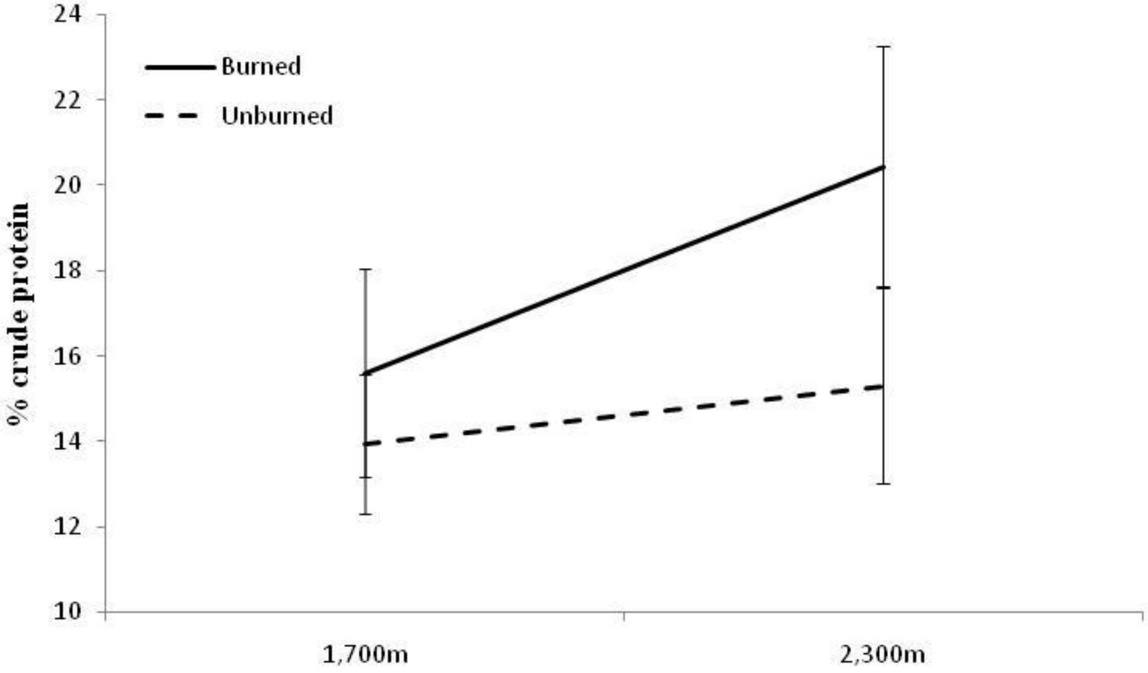
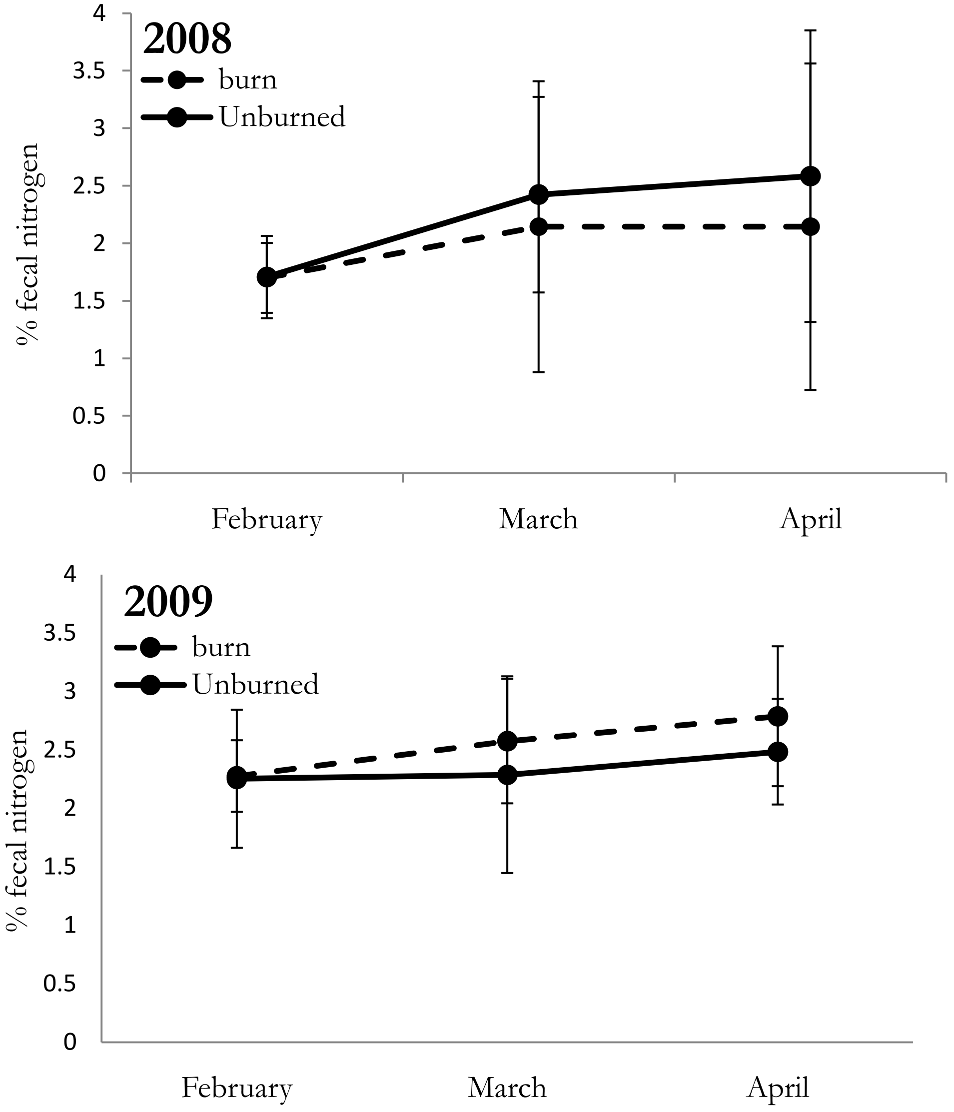


Figure 2- 5. Fecal nitrogen results from Sierra Nevada bighorn sheep (*Ovis canadensis sierra*) on winter ranges in the Easter Sierra Nevada, California. The overlap in 95% confidence intervals indicates there is no statistically significant difference between burned and unburned winter ranges.



Appendix 2A

Table 2A- 1.Microhistology results from Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*, in the Sawmill Canyon herd from fecal pellets collected on winter ranges in the eastern Sierra Nevada in 2008 and 2009.

Sawmill Canyon Herd	2008								2009										
Genera	February				March		April		February		March				April				Average
Achillea																		1	0
Convolvulus										1				1					0
Galium							2	1											0
Geranium									1				0						0
Lupinus							1	1		1									0
Mentzelia							7	6			4	4		1	3	2			1
Penstemon					1								1						0
Phacelia							8	2			1			1	3	1		2	1
Phlox/Leptodactylon	3	2	1	3				3	1	4	1				2		1		1
Polygonum							1												0
Solidago								1											0
Mustard							1		0	1			0		1		0	0	0
Unknown Forb		1		1				3	3	4		1	1	1	1	2	1		1
Total Forbs	3	3	1	5	1	0	21	17	4	10	5	5	3	4	8	6	2	3	6
Agropyron	10	19	12	17	9	20	17	16	18	9	9	7	20	9	16	16	13	20	14
Bromus tectorum		1					1					1							0

Bromus spp.	1		6	10		2	3	4	5	5	4	3	1	6	5	12	3	1	4
Elymus	1	2		1	2		4			3				1		1	2		1
Festuca	7	7	7	5	2	0	1	9	1	2	4	2			2	1			3
Oryzopsis		5	11	5	6	4	1	2	2	1			6	6		1		2	3
Phleum						1													0
Poa	10	8	13	21	19	6	7	4	23	15	8	17	22	14	15	11	11	10	13
Sitanion					2														0
Stipa	20	18	17	21	15	19	16	23	27	16	25	19	21	18	15	17	8	5	18
Trisetum						4													0
Unknown Grass	1	1	3	4	1	3	1	1	1	1	3	3	2	1	1		1		2
Total Grassses	49	59	69	83	57	59	49	59	77	52	52	52	72	54	55	60	38	39	57
Carex	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	4	0	0
Arctostaphylos patula stem						5													0
Artemisia tridentata leaf	8	17	6	4	6	13			7	15	4	10		1	6	6	35	39	10
Artemisia tridentata stem		1											1		1				0
Ceanothus cordulatus leaf					2														0
Cercocarpus leaf			2		10			1	2	2	5	1	1				2		1
Chrysothamnus leaf	0				3	1	4	1	1				0	1			4	2	1
Ephedra	5	1	7	2	1	17	8		1		11	15		2	1	1			4
Eriogonum leaf							7	12	6	18	4	9	12	17	12	13	1	3	6
Eriogonum stem												1					2		0
Prunus stem					2														0
Psorothamnus (Dalea)		1			1			1				1		1					0

Purshia tridenta leaf	32	17	14	6	16	4	7	8	1	2	17	3	11	13	4	6	11	10	10
Rosa stem	1																		0
Salix														1					0
Unknown Shrub leaf		1			1							1		1					0
Unknown Shrub stem	0			1	2	1	1			1	1			1	1		1	1	1
Total Shrubs	48	38	29	12	42	41	27	23	18	37	42	41	25	38	25	25	56	55	35
Misc			2	0			2	2	0	0	0	2	0	5	12	9	0	4	2
TOTAL	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

Table 2A- 2. Microhistology results from Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*, in the Mt. Baxter herd from fecal pellets collected on winter ranges in the eastern Sierra Nevada in 2008 and 2009.

Mt Baxter Herd	2008			2009						
Genera	February	March	April	February	March		April			Avg.
Achillea							1	1	1	0
Convolvulus					1					0
Equisetum	2									0
Erigeron						1			1	0

Eriogonum	1				1	1															0
Galium							1							1							0
Haplopappus	1																				0
Lupinus	1						2		23				2		10	39	11	46	33	30	10
Mentzelia													2	2	7	1	3	5			1
Monardella									2												0
Penstemon													2					2			0
Phacelia										1			1	3	1		1		3		0
Phlox/Leptodactylon		4	1	6	1				6				1	1				1			1
Polygonum									3					1							0
Rumex					1																0
Mustard									2		0	1		3	0	1	1	0		0	0
Unknown Forb		1			2		3		2		1		1	2	2	2	1	1	2	1	1
Total Forbs	2	5	2	6	6	1	5	0	37	1	1	1	10	12	20	42	17	55	38	33	15
Agropyron	14	12	9	4	8	2	9	3	14	5	10	4	25	4	4	2	14	11	15	2	8
Bromus spp.	1	1	6	7	1	2	1	1	8	5	2	1	1	5	2		6	3	8	2	3
Elymus		2	1	1	2	2	1	1		1				1			1				1
Festuca	5	4	2	4	7	2	1	5	5					1		2			3	3	2

Oryzopsis	6	1		3	4	4	3		3	8	2		2		3	1	5		3	3	2
Poa	13	10	8	12	17	11	10	16	9	13	2	8	16	9	16	7	13	12	10	9	11
Sitanion						1															0
Stipa	14	12	17	20	20	9	10	14	16	15	19	21	21	9	39	23	17	5	5	2	15
Unknown Grass	2	1			1	1	2		2	1	1		0		2	1	4	1	3	1	1
	55	42	42	51	60	31	38	40	54	47	34	33	64	29	66	35	60	32	47	23	44
Carex	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Arctostaphylos patula leaf																		2			0
Arctostaphylos patula stem	1			3	2									1			7	2			1
Artemisia tridentata leaf	9	12	14	10	6	39		1	7	4	1		0	1	1	3	5	4	3	32	8
Artemisia tridentata stem	1	3		4															2		0
Ceanothus cordulatus leaf	1				4	2	3	3													1
Ceanothus cordulatus stem	1																				0
Cercocarpus leaf	6	14	2	1	9	14	27	21		10	13	6	6	7		3			3	6	7
Cercocarpus stem										8		2									1
Chrysothamnus leaf		2		1		3	0	1	1	2						3	1		2		1
Ephedra	10	12	12	10	2	1	10	18	1	8	18	19	10	18	1		7	1			8

Eriogonum leaf										4	12	17	1	4	4	7					2
Eriogonum stem										5					2						0
Psorothamnus (Dalea)						1	3	2		1				1	1						0
Purshia tridenta leaf	9	8	25	12	8	3	10	10		8	19	22	3	21		5		3	1	7	9
Purshia tridenta stem				1		3															0
Ribes stem						2		2													0
Rosa stem	4	1	1		0		2	2					1		1						1
Salix										1											0
Unknown Shrub leaf											1	1	3	1				2	1		0
Unknown Shrub stem	1	1	2	1	0		2	1		1	1	1	1		2				3		1
	43	53	55	44	33	68	57	60	9	52	64	66	24	54	12	20	19	13	15	44	40
Miscellaneous			1	0					0	0	0	0	2	5	2	2	3	0	0	0	1
TOTAL	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	99	100	100	100	100

CHAPTER 3: FORAGE-PREDATION TRADE-OFFS FOR SIERRA NEVADA BIGHORN SHEEP FOLLOWING FIRE ON WINTER RANGES

Introduction

Animals select habitat based on the availability of resources and conditions including food abundance, food quality, competition, predation, and weather (Andrewartha and Birch 1954). These factors often conflict with each other forcing animals to choose between food and safety, perhaps the most common foraging decision animals face (Lima and Dill 1990, Lima 1998). For example, when food and predation are positively correlated, animals must make trade-offs between foraging and avoiding predation (Lima and Dill 1990, Lima 1998). Predation has been recognized as a strong evolutionary force that has resulted in habitat selection strategies to minimize predation risk (Lima and Dill 1990, Lima 1998). In support of the importance of predation-forage trade-offs, many studies document animals foraging on lower quality food to avoid areas of high predation (Kohlmann et al. 1996, Bleich et al. 1997, Cowlishaw 1997, Creel et al. 2005). Baboons (*Papio cynocephalus ursinus*) in Namibia selected areas with lower forage quality and low predation risk and avoided areas with higher forage quality and higher predation risk (Cowlishaw 1997). Similarly female desert bighorn sheep (*Ovis canadensis*) in the Mojave desert of California used areas of lower predator density and lower forage quality than males (Bleich et al. 1997). Despite similar energetic needs, Kohlmann et al.(1996) reported that lactating Nubian ibex (*Capra nubiana*) with following young avoided areas of high quality forage and higher predation risk compared to lactating Nubian ibex that did not have young with them. In addition, Creel et al. (2005) reported that elk (*Cervus canadensis*) temporally responded to changes in predation risk by wolves (*Canis lupus*) by selecting for cover and reducing their use of foraging habitat when wolves were present, and this reduced overall energy intake (Christianson and Creel 2010).

Habitat selection for risk and forage is also contingent upon what is available (Aebischer et al. 1993, Mysterud and Ims 1998, Heymann et al. 2010). The change in a consumer's intake rate with the availability of resources is described as their functional response (Holling 1959). Holling (1959) demonstrated that small mammal predation on pine sawfly (*Neodiprion sertifer*) followed an asymptotic (type II) functional response in relation to prey availability. Researchers have recently expanded the concept of functional response more broadly to encompass spatial habitat selection for resources (Mysterud and Ims 1998, Beyer et al. 2010). Mysterud and Ims (1998) documented a decreasing functional response in habitat selection by gray squirrels (*Sciurus carolinensis*) to the availability of open field habitat that had high forage quality. Gray squirrels strongly selected open fields when they were limiting (≤ 10 % of available) but this switched to avoidance as the availability of open fields increased and forage was no longer limiting (Mysterud and Ims 1998). Thus, availability determines which resources and conditions are limiting, and may have a dramatic effect on selection and therefore predation-forage trade-offs. For example, bighorn sheep often show strong selection for mineral licks (Holl and Bleich 1987, Ayotte et al. 2008, Mincher et al. 2008) and this selection is driven by limited mineral availability. Availability of resources affects selection not only when a particular resource is rare, but variation or temporal changes in availability can also drive changes in selection. Nielsen et al. (2009) documented seasonal changes in selection based on seasonal changes in food availability for grizzly bears (*Ursus arctos*). Similarly we might expect to see changes in resource selection after a disturbance event causes dramatic changes in resource availability.

Wildfire is an important ecological disturbance that changes the availability of forage resources for many wildlife species (Fisher and Wilkinson 2005, Kennedy and Fontaine 2009), and especially for ungulates (Singer and Harter 1996, Sachro et al. 2005). Bighorn sheep generally select for burned areas (DeCesare and Pletscher 2006, Bleich et al. 2008), but the mechanisms that drive bighorn to select burned habitat are not completely understood. Seip and Bunnell (1985) documented higher lamb/ewe ratios, lower lungworm counts, greater horn growth in rams and higher fecal nitrogen in Stone's sheep (*O. dalli stonei*) that used burned ranges. They attributed these advantages to increased winter forage biomass (Seip and Bunnell 1985). Increased fecal nitrogen in bighorn sheep that foraged within burns has also been attributed to higher forage quality attained through a change in diet selection for different species within burned sites (Hobbs and Spowart 1984). Despite increases in forage quantity or quality in burned areas, the net impact on herbivores may be negative due to increased predation if predators also select burns (Hebblewhite et al. 2006). Alternatively, burns may have a positive effect on ungulates by reducing cover and improving predator avoidance. Visibility is important for bighorn sheep because they rely on anti-predator vigilance behavior and select open areas near escape terrain, which allows them to detect and flee from predators (Geist 1971, Berger 1978, Risenhoover and Bailey 1985). Despite finding no difference in forage between burned and unburned sites, Bentz and Woodard (1988) found Rocky Mountain bighorn sheep (*O. canadensis*) preferred burned areas and speculated that it was because of higher visibility. In contrast, Lawrence (1966) found an increased number of predators in newly burned areas in the Sierra Nevada foothills and hypothesized that predators were more successful in burned areas because cover was reduced. Because burning affects forage quantity, forage quality, predator resource selection, and predator avoidance, all of these factors should be considered to determine the impact of fire.

In 2007, the seven oaks wildfire burned portions of the winter ranges of the Mount Baxter and Sawmill Canyon herds of endangered Sierra Nevada bighorn sheep (*O. c. sierra;* hereafter Sierra bighorn) with potential positive and negative effects. In 2007, the entire population of Sierra bighorn was estimated at 185 females (based on summer mark-resight estimates; Wehausen et al. 2008) with a minimum count of 35 ewes in the Mt. Baxter and Sawmill Canyon herd winter ranges. The Mt. Baxter and Sawmill Canyon herds have played a critical role in restoring Sierra bighorn to their historic range because they have been the main source of animals for translocation throughout the Sierra Nevada. Concern about the possible negative consequences of fire motivated this study and our goal was to identify the effect of fire on resource selection for endangered Sierra bighorn within winter ranges. We considered the effects of fire on measures of forage quantity, forage quality and predation risk. We accounted for predation risk by cougars (*Puma concolor*), the main predator of Sierra bighorn (U. S. Fish and Wildlife Service 2007), by including spatial measures of distance to escape terrain, visibility and a relative measure of cougar use. Depending on the spatial distribution of forage and predation risk on the landscape, we hypothesized that the post-fire short-term reduction in forage (Chapter 2) could exacerbate forage–predation trade-offs. In areas where forage and predation risk were correlated, we predicted Sierra bighorn would minimize predation risk by reducing selection for forage. To test these hypotheses, we developed seasonal resource selection functions (Manly et al. 2002; RSFs) that included spatiotemporal vegetation models (Chapter 2) and spatial models of predation risk for Sierra bighorn for 2 years following a wildfire. We predicted there may be some threshold of forage availability below which forage limitation results in strong positive selection for forage and above which there would be no consistent selection. The effects of fire are particularly relevant because prescribed burning has been identified as a possible management action to aid in Sierra Nevada bighorn sheep recovery (U. S. Fish and Wildlife Service 2007). The goal of prescribed burns is to increase open habitat and minimize piñon pine (*Pinus monophylla*) encroachment on winter ranges (U. S. Fish and Wildlife Service 2007). A natural wildfire created the opportunity to investigate the effect of fire on Sierra bighorn resource selection that also provides insight into the possible effects of future prescribed fires.

Study Area

We focused on the winter ranges of the Mt. Baxter and Sawmill Canyon Sierra bighorn herds located in the eastern Sierra Nevada, California from 1,400 – 2,600m (Figure 2-1). Due to the overlap in ranges between these herds and similar population trajectories, we consider the Mt. Baxter and Sawmill Canyon herds identified in the recovery plan (U. S. Fish and Wildlife Service 2007) as the Baxter Sawmill herd hereafter. Winter range consisted of 2 general vegetation communities: piñon woodlands (*Pinus monophyla*; a subset of the piñon-juniper vegetation type) and sagebrush scrub (*Artemesia* spp.) and open talus fields (Munz and Keck 1959, Wehausen 1980, Thorne et al. 2007). Our study area classifies as a high desert; the nearest weather station in Independence, California recorded 139mm of rain equivalent precipitation from November through May of 2007-8 with average temperatures of 10.7°C and 60mm or rain equivalent precipitation from November through May 2008-9 with average temperatures of 11.7°C (U.S. National Weather Service, Western Regional Climate Center http://wrcc.dri.edu/). The average values from 2003-2010 for November through May (based on available data) was 90mm rain equivalent precipitation (min = 28mm, max = 139mm) and the average temperature 11.3°C (min = 10.7°C, max = 12.0°C).

In July 2007, the Seven Oaks wildfire burned ≤ 83% of individual Sierra bighorn winter home ranges (range 0-83%, Table 3-1). Based on extensive ground sampling, we determined that over the study period, there were large wildfire induced changes in forage availability (Chapter 2). Within burned areas, total green forage biomass was initially very low, but rebounded to levels within unburned areas within 2 years, although forage class (grass, forb, and shrub) composition remained forb dominated in burned areas and shrub dominated in unburned areas. Mule deer (*Odocoileus hemionus*) were the dominant ungulate in the study area and the main predator of both mule deer (Pierce et al. 2004) and Sierra bighorn (Wehausen 1996) was cougars. The minimum count of Sierra bighorn on the Baxter

Sawmill winter range was 35 females in 2008 (Wehausen et al. 2008) and 46 females in 2009 (Wehausen et al. 2009).

Methods

We quantified Sierra bighorn resource selection within winter ranges (e.g., third order, Johnson 1980) for the Mt. Baxter and Sawmill Canyon herds during 2 years following the Seven Oaks fire. Johnson (1980) identifies four levels of habitat selection; first order is the distribution of an animal, second order is the location of the home range, third order is within home range use and fourth order is selection of individual food items, e.g., plants for ungulates. We were interested in third order selection because our goal was to determine the impact of the burn on individuals in the vicinity of the burn. We assessed Sierra bighorn resource selection using seasonal mixed-model resource selection functions (RSF's, Manly et al. 2002, Gillies et al. 2006) that incorporated spatiotemporally dynamic measures of forage and spatial measures of predation. We created seasonal RSF models for winter and spring for the first 2 years after the Seven Oaks Wildfire. We defined "winter" as November 1 - March 14 during which there was little new growth and "spring" as March 15 – May 16, during which most of the new growth occurred. We ended our study period on May 16 because at this time most Sierra bighorn had left the winter range or were moving toward lambing habitat.

RSF's were developed using global positioning system (GPS) collar data (14 Televilt Tellus Basic and 2 ATS G2110) from 15 females (one animal was re-collared) that recorded locations every 4 hours (Table 3-2). Collar fix rates averaged 89% and ranged from 74 - 99%. These rates are high enough to avoid bias (D'Eon 2003), although there was still a possibility of type II errors (Frair et al. 2004). Females were caught in October 2007 and 2008 using a net-gun fired from a helicopter (Krausman et al. 1985), following a protocol approved by the Institutional Animal Care and Use Committee (University of Montana IACUC AUP 024-07) with oversight from the California Department of Fish and Game (CDFG). Variable capture success and individual survival rates resulted in an uneven distribution of data over time (Table 3-2). In winter 2008 there were 4 GPS collared females on the winter range, and 3 GPS collared females in spring 2008 (Table 3-2). Despite this limited sample size in 2008, we interpret these collars as representative of the female winter range population because the average female group size observed in winter 2008 was 3.7 (N = 23 based on systematic population surveys) and the average number of collars per group was 0.9. This indicates that each collar represented approximately 4 individuals. Our lowest sample size of 3 individuals occurred in spring 2008, but after accounting for group size, these three individuals represented 34% of the minimum count of 35 females. By 2009 the sample size was increased to 14 females in winter and 10 females in spring. After accounting for group size ($\overline{x}$ = 5.9, N = 24), our collared females in 2009 represented the entire winter range population. Within each season, the contribution of points/individual varied from 24 to 495 due to collar failure and mortality. Despite the challenges of achieving large sample sizes, over the 2 years of the study we sampled an average of 22% of individuals.

We used a mixed model design with individual as the random intercept to account for individual animals as the sample unit (Gillies et al. 2006). RSF's use binary logistic regression to approximate the exponential RSF model (Johnson et al. 2006) based on the ratio of used to available resources to predict the relative probability of use as a function of resources (Manly et al. 2002, Sappington et al. 2005). We quantified available resources by generating 500 random points for each individual within their 95% fixed kernel home range, using the reference smoothing factor in HRT (Rodgers et al. 2007; http://blue.lakeheadu.ca/hre/) and all GPS use points < 2,600m (also the elevation limit for our forage models see Chapter 2). Individual winter home ranges averaged 10km^2 and ranged from 2km^2 to 26km^2 (Table 3-1). The average percent of each winter home range that burned was 54% and ranged from 0 to 83% (Table 3-1).

We developed families of resource selection function models to test our hypotheses with the following *a-priori* framework:

1) Base $w(x) = \exp(\mathbf{BX})$
2) Burn $w(x) = \exp(\beta_1 B_1 + \mathbf{BX})$
3) Forage $w(x) = \exp(\beta_2 F_2 + \mathbf{BX}))$
4) Predation $w(x) = \exp(\beta_5 P_3 P_4 + \beta_3 P_3 + \beta_4 P_4 + \mathbf{BX})$
5) Interaction $w(x) = \exp(\beta_6 F_2 P_3 + \beta_5 P_3 P_4 + \beta_2 F_2 + \beta_3 P_3 + \beta_4 P_4 + \mathbf{BX})$

Where β = the selection coefficients for: F (forage availability), P(predation risk), and the vector **BX** represents important covariates (elevation, aspect and land cover) that were important to control for, but did not relate to our specific hypotheses. The base model assumes Sierra bighorn are unaffected by forage or predation. We added a categorical burn covariate to the base model to understand selection for burns and also more detailed forage and predation models to represent more mechanistic models of Sierra bighorn resource selection. The forage model family included selection for quality that we represented as the dry weights of new growth (hereafter green) for grasses and forbs and forage quantity which we represented as the dry weight total biomass, including old and new growth of all forage classes (hereafter total: see below for description of forage models). We considered new growth of grasses and forbs to be high quality because they tend to be high in protein content and digestibility (Table 2-4;Van Soest 1994). The predation family of models included cougar use as a correlate for the rate of encounter (see predation risk section below for a description) and selection for proximity to escape terrain and visibility as correlates for attack success (see predation risk modeling below). We tested for the forage-predation trade-off with the interaction model set (Hebblewhite and Merrill 2009). Within each season and year we compared each family of models (e.g. base, burn, forage, predation, interaction) models using Akaike's information criterion for small sample sizes (ΔAICc; Anderson and Burnham 2002) to select the top models (Manly et al. 2002). We retained only significant ($P \leq 0.05$) and non-collinear ($|r| \leq 0.70$) variables of interest in our top models. Considering our a priori model selection framework, we felt that top models would identify the most important variables in resource selection that should be correlated with relative fitness (Gaillard et al. 2010). We compared β coefficients of forage models between seasons and years to test for a functional response in resource selection for forage. To validate the top RSF model predictions, we used k-fold cross validation (Boyce et al. 2002). We developed models with 80% of the data, and withheld 20% of use locations from each individual (Koper and Manseau 2009) for model testing. We performed Spearman's rank correlation analysis on the frequency of use across ten RSF bins of equal area to test the predictive capacity of top RSF models.

Forage Biomass Model

We used previously developed seasonally predictive forage biomass models for the study area based on double-sampling (Bonham 1989) of 69 sites that we re-visited three times a year for 2 years (Chapter 2). We developed spatiotemporal forage biomass models using a negative binomial mixed-model (StataCorp 2007) with site location as a random effect. We predicted forage biomass (g/m^2) with regression models of the following forage components: green grass, green forbs, green shrubs and total biomass (Chapter 2). Top models were determined based on a combination of biological relevance and AIC$_c$ as recommended by Hosmer and Lemmeshow (2000).

We improved the predictive power of these previously developed vegetation models by including the normalized difference vegetation index (NDVI), a remotely sensed measure of vegetation productivity (e.g., greenness) available from the Moderate Resolution Imaging Spectroradiometer (MODIS; Huete et al. 2002) that has been a useful spatial predictor of forage dynamics for other ungulates (Pettorelli et al. 2005; Appendix 3A). Forage quality for ungulates can be challenging to measure because it is a function of protein content, digestibility and biomass (Van Soest 1994, Barboza et al. 2009). However there are some general trends: forage quality tends to be greater in new growth because it has both higher digestibility and higher protein and within new growth forage quality tends to be greatest in forbs followed by grasses (Table 2-1; Van Soest 1994, Barboza et al. 2009). Evaluating selection for green forbs and grasses tested the importance of forage quality, compared to selection for total biomass which tested Sierra bighorn selection for forage quantity. In addition to univariate forage models, we also considered non-linear functions of grass and forb biomass in RSF models using quadratics ($X+X^2$)and multiple forage effects (e.g., grass and forb models) when the two were not highly correlated or confounding.

Predation Risk Modeling

To evaluate the role of predation risk in Sierra bighorn resource selection, we included variables that were hypothesized to be related to the encounter rate or attack success of cougars. Because cougars are elusive animals, there is very little information on cougar attack success. We assumed that both selection for escape terrain and visibility would reduce attack success. We included Johnson et al.'s (2010a) cougar kernel density estimator (KDE) as a spatially explicit relative probability of cougar use. Johnson et al. (2010a) developed the KDE (Worton 1989) with cougar GPS collar data from December to April of 2002 to 2009 (5,673 locations collected on 4 and 8 hour cycles). Data were restricted to represent prime hunting hours from 1 hour pre-sunset to 1 hour post-sunrise (Pierce et al. 1998) and included only the first location from "clusters" of nighttime locations indicative of kill/feeding sites. Johnson et al. (Johnson et al. 2010a) validated the KDE using the locations of 52 out-of-sample cougar killed Sierra bighorn (e.g., Hebblewhite and Merrill 2007). The Spearman's rank correlation between 5 equal area bins of KDE values and the number of cougar-killed sheep within the same frequency bins was 0.872 ($p = 0.054$; Boyce et al. 2002), indicating the KDE was a strong predictor of cougar predation risk. We assumed the cougar KDE represented the relative probability of being encountered by a hunting cougar, which we call cougar use hereafter (Kristan and Boarman 2003, Hebblewhite et al. 2005). We included ground-based, spatial visibility models (previously developed in Chapter 2; Table 2-4) and distance to escape terrain as a measure of attack success. Our visibility models were developed from ground estimates of visibility using the staff ball method (Collins and Becker 2001) at 5m from a central point at 69 different locations. Spatially explicit models of visibility were developed using linear regression and topographic and landcover predictor variables (Chapter 2; Table 2-4). Researchers reported differing results when correlating bighorn resource selection with visibility (DeCesare and Pletscher 2006, Schroeder et al. In Press), but in general bighorn are expected to select areas of high visibility so that they may detect predators (Geist 1971, Risenhoover and Bailey 1985). We included selection for proximity to escape terrain as an additional component of attack success. Selection for escape terrain is assumed to be a form of anti-predator behavior because surefooted bighorn are able to escape from predators in steep and rocky terrain(Geist 1971, Valdez and Krausman 1999). We used a geographic information system (ESRI 2008) to calculate distance to escape terrain from 10m resolution digital elevation models from the United States Geological Survey National Elevation Dataset (http://ned.usgs.gov). We defined escape terrain as areas greater than 0.7 hectares (e.g., DeCesare and Pletscher 2006) with a slope >60% (e.g.,Smith et al. 1991, McKinney et al. 2003). In addition to univariate and additive effects of these 3 measures of predation risk, we considered an interaction of predator avoidance strategies and cougar use, expecting that in areas of high cougar use, Sierra bighorn would stay closer to escape terrain and in areas of higher visibility. For each year and season we compared models using AIC_c to determine the top predation-based model.

Forage-Predation Trade-offs

We considered additive models of forage and predation and all possible combinations of significant forage and predation models. We tested for forage predation trade-offs by including interactions between cougar use and 3 forage measurements (grass, forb and total biomass) for each year and season to the base model. The existence of a trade-off was determined by the significance ($P < 0.05$) of the interactions and all significant interactions were compared using AIC_c to determine the most important forage-predation interactions. Finally, we compared the families of models representing forage, predation, forage-predation interactions for each season and year using AIC_c to select the best overall model of Sierra bighorn resource selection.

Functional Response

To assess the importance of changes in forage availability on selection (e.g., functional response), we evaluated the magnitude of selection for forage across a gradient of forage availability. Because we were interested in the functional response of available forage, a continuous variable, we had to modify the approach Mysterud and Ims (1998) developed for categorical variables. We used coefficients for selection from RSFs of each forage component added to the base model and measured forage availability as the average g/m^2 across each individual's home range based on forage models (Chapter 2). We used a student's t-test to test observed thresholds and regression to determine the significance of observed patterns.

Resource Covariates

The burned and unburned designation was determined using a polygon GIS coverage developed by the US Forest Service (www.fs.fed.us/r5/rsl/clearinghouse/). We reclassified the CALVEG regional dominance (www.fs.fed.us/r5/rsl/clearinghouse) landcover classification into open and closed cover types because we noted differences in selection based on these categories in preliminary analyses. In addition to the explanatory variables of highest interest (burned, forage availability, and predation risk) we included a basic set of factors that have been shown in the literature to be important for bighorn sheep resource selection. These covariates included landcover type and 2 topographic features, elevation and aspect, which we calculated from 10m resolution digital elevation models (http://ned.usgs.gov). The quadratic of elevation was included to represent selection for intermediate elevations (Anderson and Burnham 2002). McCullough and Schneegas (1966) documented Sierra bighorn selection for southern aspects in the winter. Following the method outlined by Cushman and Wallin (2002) we transformed aspect to a more useful continuous variable but modified it slightly by taking the –cos (aspect +35) so that SSE had a value of 1 and NNW had a value of -1 because in our study region slightly southeast is the sunniest and warmest aspect. We included only variables that were not collinear or confounding (Hosmer and Lemeshow 2000). Our base model included only variables that maintained significance across seasons and years.

Results

Sierra bighorn showed consistent selection for mid level elevations (represented in our models by the quadratic of elevation), southeast aspects, and selection for open landcover types across seasons and years (Table 3-3). These variables were included in all subsequent models and with a few exceptions, selection for them remained consistent and significant (Table 3-3). In the first winter after the Seven Oaks wildfire, Sierra bighorn avoided burned areas but by spring they showed no selection for burned areas and positive selection throughout 2009 (Figure 3-1). To determine the underlying mechanisms driving this avoidance and selection of burned areas, we sequentially considered the roles of forage and predation, and finally assessed predation-forage trade-offs by Sierra bighorn.

Forage Biomass Models

When we incorporated forage models into our base model, we found positive selection by Sierra bighorn for total forage biomass in the winter of 2008 (Figure 3-2 d). After winter of 2008, selection for total forage biomass was insignificant or negative, indicating Sierra bighorn did not select for total forage biomass, and in spring of 2009, they slightly avoided total biomass. Selection coefficients for grasses and forbs were positive in winters of 2008 and 2009 and much smaller or not significant in spring of 2008 and 2009 (Figure 3-2 a, b). The strongest selection occurred in winter 2008 and the magnitude of selection was strongest for forbs, followed by grasses, then total biomass (Figure 3-2). For winter 2008, the top forage model was positive selection for both forbs and shrubs. For spring 2008, the top forage model was avoidance of shrubs. In both winter and spring of 2009 the top forage model included positive selection for grasses and avoidance of total biomass.

Predation Risk Models

We had mixed results in terms of resource selection by Sierra bighorn as a strategy to avoid predation. When we added visibility alone to our base model, we found either no preference or avoidance of visibility (Figure 3-3). For distance to escape terrain we found consistent avoidance of areas far from escape terrain (which translated into positive selection to be near escape terrain). The magnitude of selection for escape terrain was stronger in winter compared to spring and strongest in the first winter after the Seven Oaks wildfire. Unexpectedly, in univariate analysis, Sierra bighorn showed positive selection for cougar use for the duration of the study with the exception of spring 2008 when there was weak avoidance (Figure 3-3).The interaction between cougar use and visibility was significant throughout study period, however, and followed an interesting pattern that partially explains the unexpected pattern of Sierra bighorn selection for cougar use (Figure 3-3). Sierra bighorn selection for visibility changed from negative (avoidance) to positive (selection) with increasing cougar use. This shift from avoidance to selection for visibility varied across seasons, generally occurring at lower cougar use in spring, and at the highest level of cougar use in the winter of 2008 (Figure 3-3). Interactions between selection for escape terrain and cougar use were also significant in winter 2008 and winter and spring of 2009. In areas with low cougar use, Sierra bighorn were located farther from escape terrain than in areas of high cougar use. (Figure 3-5).

Forage-Predation Trade-off

Interactions between forage and predation were often significant (Figure 3-6). In the top model for winter 2008, Sierra bighorn selection for cougar use interacted positively with selection for forb biomass (Figure 3-6a), indicating a predation-forage trade-off where Sierra bighorn selected for forb biomass at the cost of being exposed to cougar use. To visualize this interaction, we dichotomized cougar use into high (> average available cougar use for each season) and low (< average available cougar use for each season) categories (Figure 3-6). In areas of high cougar use in winter 2008, Sierra bighorn use was positively correlated with green forb biomass while in areas of low cougar use, Sierra bighorn use had a slightly negative relationship with green forb biomass (Figure 3-6a). The result of this selection was that 89% of Sierra bighorn use occurred in high cougar use areas. During winter 2008, all available points with estimated forb biomass > 1g/m^2 occurred in burned areas that also had high cougar use. The top model for spring 2008, however, included a negative interaction between cougar use and total biomass (Figure 3-6b). Thus, in spring 2008, Sierra bighorn was use was positively related to total biomass in areas of low cougar use and Sierra bighorn use was negatively related to total biomass in areas of high cougar use. As a result, 48% of Sierra bighorn use occurring in areas of high cougar use in spring 2008. The forage predation interaction in winter and spring 2009 was similar to spring 2008; Sierra bighorn tended to use areas with high total biomass only where cougar use was low (Figure 3-5, c-d). The positive forage-predation interaction in spring 2008 and winter and spring 2009 indicates that Sierra bighorn did not have to trade-off forage and predation because Sierra bighorn there were areas on the landscape that had both high total biomass and low cougar use. As a result of Sierra bighorn selection mediated by a forage-predation interaction, 64% of Sierra bighorn use occurred in areas of high cougar use for both winter and spring in 2009.

From a model selection perspective, there was a consistent trend of forage models outperforming the base model and predation models outperforming forage models (Table 3-2). Top models were always interaction models that included forage-predation interactions and selection to be near escape terrain that was modified by cougar use. The top model for winter 2008 included positive selection for forbs, grasses and an interaction between forbs and cougar use. This top model for winter 2008 validated well against random subsets of withheld GPS locations, with a mean Spearman's rank from k-folds cross validation of 0.96 (SD = 0.055). The top model for spring 2008 included positive selection for grass and selection for total biomass that was modified by cougar use and validated with a mean Spearman's rank of 0.94 (SD = 0.027). The top winter and spring models in 2009 had the same variables as spring 2008 and validated well with mean Spearman's rank of 0.99 (SD = 0.01) and 0.98 (SD = 0.01) respectively (Table 3-3).

Functional Response

There was no evidence for Sierra bighorn selection for grasses or forbs when average new growth biomass was greater than 1 g/m^2 (Figure 3-7a-b). When grass and forb biomass was less than 1 g/m^2 there tended to be positive selection for grasses (Figure 3-7a), although due to high variance, regression analyses of individual selection coefficients and forage biomass availability were not significant for grass ($P = 0.39$) and forbs ($P = 0.62$). However, where grass biomass was < 1 g/m^2, 13 individuals selected positively for grass, 8 individuals avoided grass, and 2 were indifferent (Figure 3-7a). The seasonal population averaged values of selection for grass using a mixed model with the individual as the random effect were $\beta_{grass} = 1.03$, $\overline{x}$ available grass g/m^2 = 0.25 in winter 2008, $\beta_{grass} = 0.17$, $\overline{x}$ available grass g/m^2 = 0.27 in spring 2008, $\beta_{grass} = -0.01$, $\overline{x}$ available grass g/m^2 = 0.63 in winter 2009, and $\beta_{grass} = 0.03$, $\overline{x}$ available grass g/m^2 = 1.50 in spring 2009. Where forb biomass was < 1 g/m^2 16 individuals had positive selection for forb biomass and 7 avoided forb biomass and 2 individuals showed no selection (Figure 3-7b). The population averaged values of selection for forbs was positive when average forb biomass was < 1g/m^2: $\beta_{forb} = 2.7$, $\overline{x}$ available forb g/m^2 = 0.21 in winter 2008, $\beta_{forb} = 0.01$, $\overline{x}$ available forb g/m^2 = 0.69 in spring 2008, $\beta_{forb} = 0.81$, $\overline{x}$ available forb g/m^2 = 0.19 in winter 2009, and $\beta_{forb} = 0.003$, $\overline{x}$ available forb g/m^2 = 4.36 in spring 2009. Within shrubs, a regression model was significant and positive between selection for shrub biomass and the availability of shrub biomass ($\beta = 0.65$, $P = 0.02$) after removing one outlier (Figure 3-7c). The avoidance of shrubs decreased with increasing shrub biomass. However this pattern was not consistent across the seasonal population averaged models of Sierra bighorn selection for shrub biomass: $\beta_{shrub} = 0.05$, $\overline{x}$ available shrub g/m^2 = 0.49 in winter 2008, $\beta_{shrub} = -0.5$, $\overline{x}$ available shrub g/m^2 = 2.91 in spring 2008, $\beta_{shrub} = -0.02$, $\overline{x}$ available shrub g/m^2 = 0.96 in winter 2009, and $\beta_{shrub} = -0.2$, $\overline{x}$ available shrub g/m^2 = 1.8 in spring 2009. There was no obvious threshold apparent between Sierra bighorn selection for total biomass and availability and the regression was also insignificant (Figure 3-7d, $P = 0.74$).

Discussion

Our results suggest that Sierra bighorn selection for green forb biomass in burned areas in the first winter post wildfire may have increased Sierra bighorn exposure to predation risk by cougars. Sierra bighorn avoided burned areas in winter 2008 and then shifted to selecting for burned areas by winter 2009 when forage conditions had rebounded (Figure 3-1). However the impact of Sierra bighorn avoidance and selection for burned areas was not clear until we considered the wildfire-induced changes in forage. During winter 2008, the only areas with forb biomass > 1 g/m^2 also occurred in areas with high cougar use forcing Sierra bighorn to choose between accessing high quality forage and minimizing overlap with cougars. Contrary to our expectations, Sierra bighorn selected strongly for forb biomass and increased use of areas with higher cougar use. For the rest of the study period, total biomass was distributed across areas of low and high cougars use so Sierra bighorn were not forced to choose between forage and predation resulting in less overlap between Sierra bighorn and cougars.

Sierra bighorn showed the strongest selection for grasses and forbs in winter 2008, which may be a result of a functional response in resource selection to the reduced forage conditions caused by the wildfire. In the first year post-fire individual based forage availability was 4.8 g/m^2 in 2008 and 7.3 g/m^2 in 2009 (Table 3-1), nearly doubling between the first and second years post-fire. When grass and forb biomass was limiting, Sierra bighorn showed strong selection for it, compared to when forbs and grasses were abundant and Sierra bighorn tended to use forbs and grasses in proportion to availability (Figure 3-7). The functional response of Sierra bighorn to forage availability provides a potential mechanism to explain why Sierra bighorn risked higher exposure to cougars to gain access to forb biomass during that first season post-fire when available biomass was at its lowest.

While our forage models clearly captured general trends, which should transfer into reliable estimates of forage availability, our forage models may not have picked up on small-scale anomalies such as an ephemeral spring source or late snow patches that created unexpected pockets of forage biomass. Sierra bighorn with access to these undetected forage pockets would appear to be avoiding predicted forage biomass, which may explain some of the variance in selection for forb and grass biomass. The significant positive relationship between shrub biomass and selection for shrubs was unexpected, especially considering how significant shrubs were in the diet (Chapter 2). When shrubs were less abundant or rare, Sierra bighorn avoided shrubs, but when shrubs were abundant, Sierra bighorn did not go out of their way to avoid them resulting in use that was equal to availability or selection near zero. This functional response may have been driven by phenology. Shrubs may be avoided early in the growing season when there is very little new shrub growth, but as the green shrub biomass increases, Sierra bighorn start using shrubs in proportion to availability. These results suggest shrubs are not a preferred forage species but they make up a significant part of the diet simply because they are so abundant. The lack of pattern between selection for total biomass and its availability suggests total biomass was never a limiting factor.

We provide evidence that Sierra bighorn altered their selection for escape terrain and visibility based on cougar use. In areas with high cougar use, Sierra bighorn stayed closer to escape terrain (Figure 3-4) and in areas with higher visibility (Figure 3-3). We found Sierra bighorn selection for visibility was significant only after including the interaction between visibility and cougar use which may explain why previous studies have found variable results for bighorn selection of visibility (DeCesare and Pletscher 2006). In winter, Sierra bighorn shifted selection for visibility at higher cougar use levels than in spring, and this occurred at the greatest cougar use levels in winter 2008 (Figure 3-6). This indicated that with increased exposure to cougars, Sierra bighorn may have compromised their selection for visibility when there was less available forage following wildfire. In addition to selection for visibility, Sierra bighorn may also be more vigilant in areas of high cougar use to compensate for increased predation risk. Hochman and Kotler (2007) documented increased vigilance with distance to escape terrain in Nubian ibex and we expect this pattern would also be found in Sierra bighorn. However, we were unable to consider the extent to which Sierra bighorn can behaviorally control their risk of predation (Lima and Dill 1990). Depending on the effectiveness of different anti-predatory behaviors, limited forage conditions in winter may have exposed Sierra bighorn to increased predation. Despite the potential population implications of these predation-forage interactions, we were unable to detect a change in mortality rates within our small sample of the population. In addition Wehausen (1996) hypothesized that there could be negative population consequences if Sierra bighorn abandon winter ranges in response to predation. We did not find any evidence supporting abandonment of winter ranges (Wehausen 1996) in response to increased overlap with cougars in winter 2008. All collared females that survived in 2008 returned to winter ranges in 2009.

One limitation of our predation risk metrics was the ability to consider temporal variation in cougar use because cougars were not collared consistently over the study period. According to the risk allocation hypothesis, we would expect temporal variation in predation risk to effect behavior (Lima and Bednekoff 1999). However, because we focused on only 2 seasons and a restricted area, it is likely that the simple spatial distribution cougar use was correlated with perceived predation risk. With wolves and elk in Yellowstone National Park, Kauffman et al. (2007) found that despite changes in predator density, specific areas on the landscape were consistently used as hunting grounds while other areas consistently provided refuge. In our study area the assumption of consistent relative risk is supported by the strongly significant interactions we saw between cougar use and selection for escape terrain and visibility. Furthermore, Johnson et al. (2010a) and others (Kauffman et al. 2007, Hebblewhite and Merrill 2009) found strong correlations between predator density and the frequency of predator-caused mortalities, confirming that spatial patterns of predator density can consistently reflect risk as perceived and realized by prey species.

Despite these potential limitations of our measures of predation risk, the strongest single factor driving Sierra bighorn resource selection was distance to escape terrain. In univariate analysis it has the highest R^2, and it alone accounts for 4 to 14 percent of the variation in selection across seasons. Across all of our used locations, the average distance to escape terrain was 4m (max = 1,099m) and the average distance to escape terrain available was 39m (max = 911m). Within RSF models, selection for escape terrain remained consistent regardless of other variables and models and with escape terrain always out-performed models based on forage or visibility. This strong selection for escape terrain is consistent across nearly all studies of bighorn sheep and further supported by a physiological study by Stemp (1982) on bighorn sheep in Alberta, where he documented an exponential increase in heart rates with distance to escape terrain.

All resource selection studies should be interpreted cautiously because of the difficulties in defining available resources, behavioral mechanisms of selection, and the assumption that fitness equates to selection (Aebischer et al. 1993, Garshelis 2000, Beyer et al. 2010). We defined availability to address the question of selection within the burn, but this does not address the question of sheep that may have avoided returning to winter range at the larger seasonal home range scale because of the burn. However, because we were interested in providing management with information regarding the use of prescribed burns, we felt this was the appropriate scale. From a behavioral perspective, Sierra bighorn appeared to divide their time between three simple states: foraging, bedding, and moving. If predation risk varies with behavioral state, this could be important to consider in future research. Perhaps the most problematic aspect of resource selection studies is the challenge of linking selection to fitness (Garshelis 2000). While it is likely that resource selection evolved to maximize fitness (MacArthur and Pianka 1966, Boyce and McDonald 1999), the existence of attractive sinks draws this assumption into question (Robinson et al. 2008). To understand why a resource is selected requires knowledge of the fitness cost of this decision (Gaillard et al. 2010). Unfortunately, it is very difficult to estimate demographic fitness, often measured as the lifetime reproductive success of the individual, because it requires extensive data (e.g. McLoughlin et al. 2006, McLoughlin et al. 2007). However declining Sierra bighorn populations are being driven by variable female survival (Johnson et al. 2010b) and one of the main factors effecting female survival in the last 2 years in the Mt. Baxter and Sawmill Canyon herds is predation, that may be exacerbated based on our results, by the Seven Oaks wildfire.

Management Implications

The Sierra bighorn recovery plan (U. S. Fish and Wildlife Service 2007) identifies prescribed fire as a potential management option to improve winter ranges. Future prescribed burns are planned to be much smaller and likely to burn at lower intensities in cooler seasons compared to the large and natural Seven Oaks wildfire we studied. However our study does highlight the need to consider the potential for fire to affect both forage and predation. We documented that wildfire may initially have negative consequences for Sierra bighorn by increasing attractive new forb growth in burned areas that may, depending on the location of the burn, increase the encounter rate of Sierra bighorn and cougars. The indication of a 1 g/m^2 threshold in the functional response of Sierra bighorn to grasses and forbs suggests future wildfires or burns may expose bighorn to areas of higher cougar use in the first winter post-fire when available forage is most reduced. To avoid the potential for a prescribed burn to increase predation risk, we recommend having small prescribed burns that are unlikely to have large effects on total biomass availability and to target burns in areas with low cougar use that are also near escape terrain.

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Table 3- 1. Characteristics of Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, individual winter home ranges from 2008 to 2009 in the Mt. Baxter and Sawmill Canyon herds, eastern Sierra Nevada, California. This table includes model estimates of total biomass (old and new growth for all forage classes) and green forb biomass for winter and spring from forage biomass models developed in Chapter 2.

			2008 g/m^2 total		**2009 g/m^2 total**		**2008 g/m^2 forb**		**2009 g/m^2 forb**	
Individual	**Size km^2**	**% Burned**	**Winter**	**Spring**	**Winter**	**Spring**	**Winter**	**Spring**	**Winter**	**Spring**
128	2	0	--	--	12.2	24.3	--	--	0.0	0.5
129	6	0	--	--	9.2	17.9	--	--	0.0	0.5
127	20	18	--	--	19.5	--	--	--	0.2	--
110	7	28	--	18.1	13.2	24.5	--	0.7	0.2	5.0
126	4	42	--	--	17.3	31.9	--	--	0.3	7.5
50	14	56	--	--	5.9	16.7	--	--	0.2	5.0
123	6	61	--	--	3.5	13.4	--	--	0.2	4.0
109	17	62	6.2	--	--	--	0.2	--	--	--
30	11	67	5.2	8.6	5.3	--	0.2	0.8	0.3	--
108	26	68	5.3	--	5.5	17.9	0.2	--	0.3	7.0
31	7	79	--	--	2.1	--	--	--	0.1	--
107	11	79	2.6	5.1	2.5	12.8	0.2	0.6	0.2	4.7
132	8	81	--	--	2.7	13.5	--	--	0.2	4.7
139	10	82	--	--	2.2	12.7	--	--	0.2	4.8
131	3	83	--	--	1.5	--	--	--	0.2	--
Average	10	54	4.8	10.6	7.3	18.6	0.2	0.7	0.2	4.4

Table 3- 2. Comparison of resource selection function models of Sierra Nevada bighorn sheep, *Ovis canadensis sierra,* based on forage and predation for winter and spring 2008 and 2009. Cougar use , which we considered surrogate or the encounter rate with a kernel density estimator by Johnson et al. (2010b). All variables included in interactions were also individually.

Winter 2008	**Variables**	**# collars**	**df**	**Used**	**Avail**	**AICc**	**Δ AIC**
Base	Elev + Elev^2 + Aspect + open	4	6	1374	2000	4165	814
Burn	Burn + Base	4	7	1374	2000	4156	805
Forage	Grass + Forb + Base	4	8	1374	2000	3994	643
Predation	Escape x Cougar + Base	4	9	1374	2000	3471	120
Forage x Predation	Forb x Cougar + Base	4	9	1374	2000	3872	521
Additive	Grass + Forb x Cougar + Escape x Cougar + Base	4	10	1374	2000	3351	0
Spring 2008	**Variables**		**df**	**Used**	**Avail**	**AICc**	**Δ AIC**
Base	Elev + Elev^2 + Aspect + open	3	6	482	1500	1906	128
Burn	Burn + Base	3	7	482	1500	1910	132
Forage	Shrub + Base	3	7	482	1500	1904	126
Predation	Esc + Base	3	7	482	1500	1865	87
Forage x Predation	Total x Cougar + Esc + Base	3	10	482	1500	1788	10
Additive	Grass + Total x Cougar + Escape x Cougar + Base	3	12	482	1500	1778	0
Winter 2009	**Variables**		**df**	**Used**	**Avail**	**AICc**	**Δ AIC**
Base	Elev + Elev^2 + Aspect + open	14	6	2818	7000	10007	935
Burn	Burn + Base	14	7	2818	7000	9814	742
Forage	Grass + Total + Base	14	8	2818	7000	9911	839

Predation	Escape x Cougar + Base	14	9	2818	7000	9148	76
Forage x Predation	Forb x Cougar + Base	14	9	2818	7000	9699	627
Additive	Grass + Total x Cougar + Cougar x Esc + Base	14	11	2818	7000	9072	0

Spring 2009	**Variables**		**df**	**Used**	**Avail**	**AICc**	**Δ AIC**
Base	Elev + Elev^2 + Aspect + open	10	6	2085	5000	7373	347
Burn	Burn + Base	10	7	2085	5000	7246	220
Forage	Grass + Total + Base	10	8	2085	5000	7241	215
Predation	Cougar x Esc + Cougar + Esc + Base	10	9	2085	5000	7157	131
Forage x Predation	Total x Cougar + Total + Cougar + Base	10	9	2085	5000	7217	191
Additive	Grass + Total x Cougar + Escape x Cougar + Base	10	12	2085	5000	7026	0

[a] New growth only [b] Total biomass including old and new growth of all forage classes [c] Distance to escape terrain.

Table 3- 3. Top resource selection models of Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, resource selection for winter and spring 2008 and 2009. Cougar use which we considered a surrogate for encounter rate, was calculated with a kernel density estimator by Johnson et al.(2010b).

	Winter 2008		**Spring 2008**		**Winter 2009**		**Spring 2009**	
Variable	**β**	**SE**	**β**	**SE**	**β**	**SE**	**β**	**SE**
Grass	0.5	0.12	0.3	0.11	0.5	0.07	0.17	0.03
Forb	2.6	0.75	---	---	---	---	---	---
Total	---	---	0.06	0.013	-0.007	0.0048	-0.03	0.005
Forb x Cougar	-0.5	0.025	---	---	---	---	---	---
Total x Cougar	---	---	-0.007	0.0012	-0.001	0.0003	---	---
Escape	-0.04	0.004	-0.002	0.0049	-0.01	0.002	-0.006	0.003
Cougar Use	0.04	0.01	0.02	0.011	0.03	0.004	0.03	0.007
Cougar x Esc	-0.002	0.0009	-0.002	0.0007	-0.003	0.0004	-0.001	0.0003
Elevation	0.006	0.0023	0.02	0.004	-0.005	0.0016	0.04	0.002
Elevation^2	-2E-06	-6E-07	-4E-06	9E-07	1.1E-06	3.7E-07	-8E-06	5E-07
Aspect	0.3	0.08	0.9	0.13	1.4	0.06	1.2	0.07
Open	0.8	0.16	1.4	0.27	0.7	0.09	0.9	0.12

[a] New growth only. [b] Total biomass including old and new growth of all forage classes [c] Distance to escape terrain.

Figure 3- 1. Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, selection (β coefficient) for burns for 2008 and 2009 after the Seven Oaks Wildfire on winter ranges in the eastern Sierra Nevada, California. Within one year, selection for burned areas switched from being negative to positive.

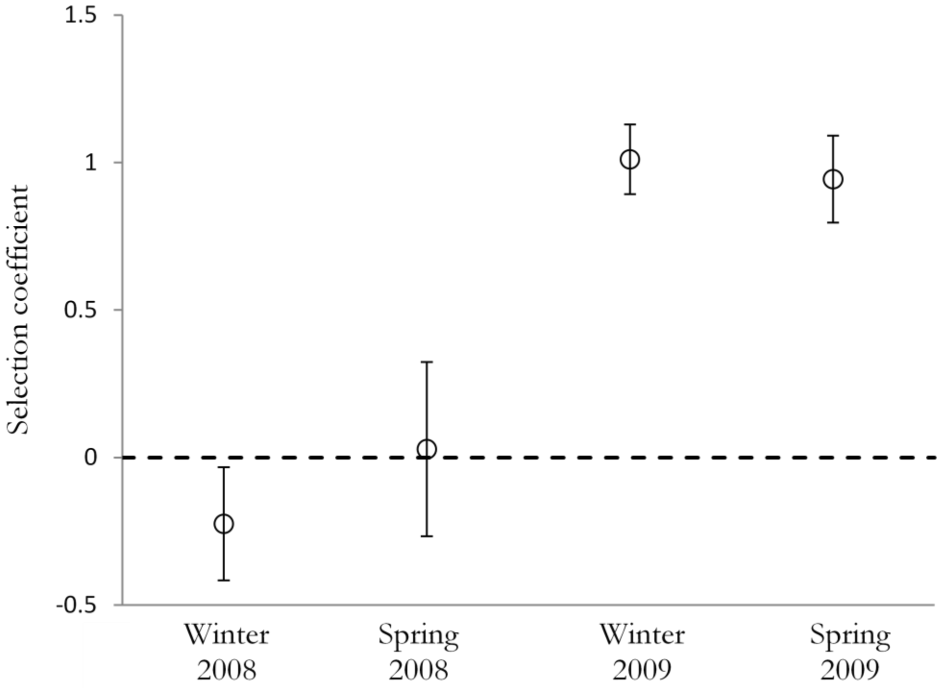


Figure 3- 2. Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, selection (β coefficient) with 95% confidence intervals for forage on winter ranges. Selection coefficients were calculated using seasonal resource selection functions that included elevation, aspect and landcover type. Grass, Forb and Shrub refer to new growth only and Total biomass includes both new and old growth of both forage classes.

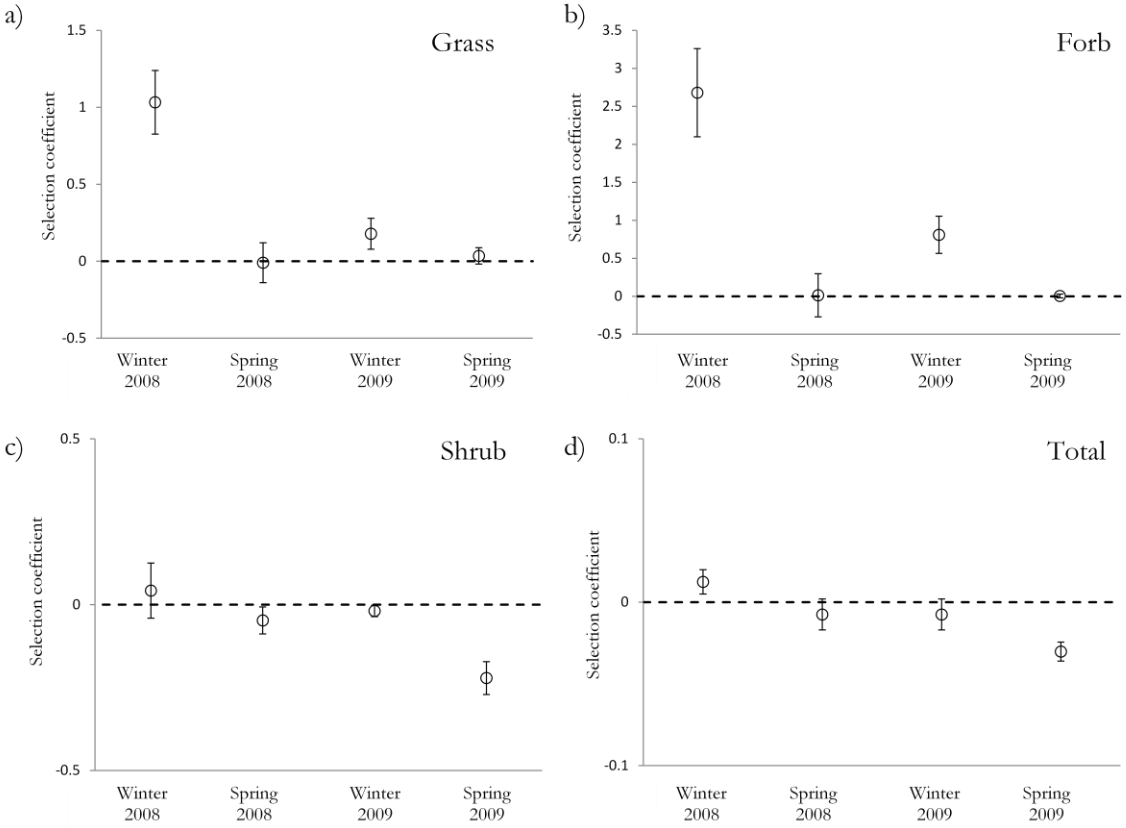


Figure 3- 3. Selection for anti-predatory landscape features and cougar use in Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, winter ranges. Selection coefficients were calculated using seasonal resource selection functions that included elevation, aspect and open landcover.

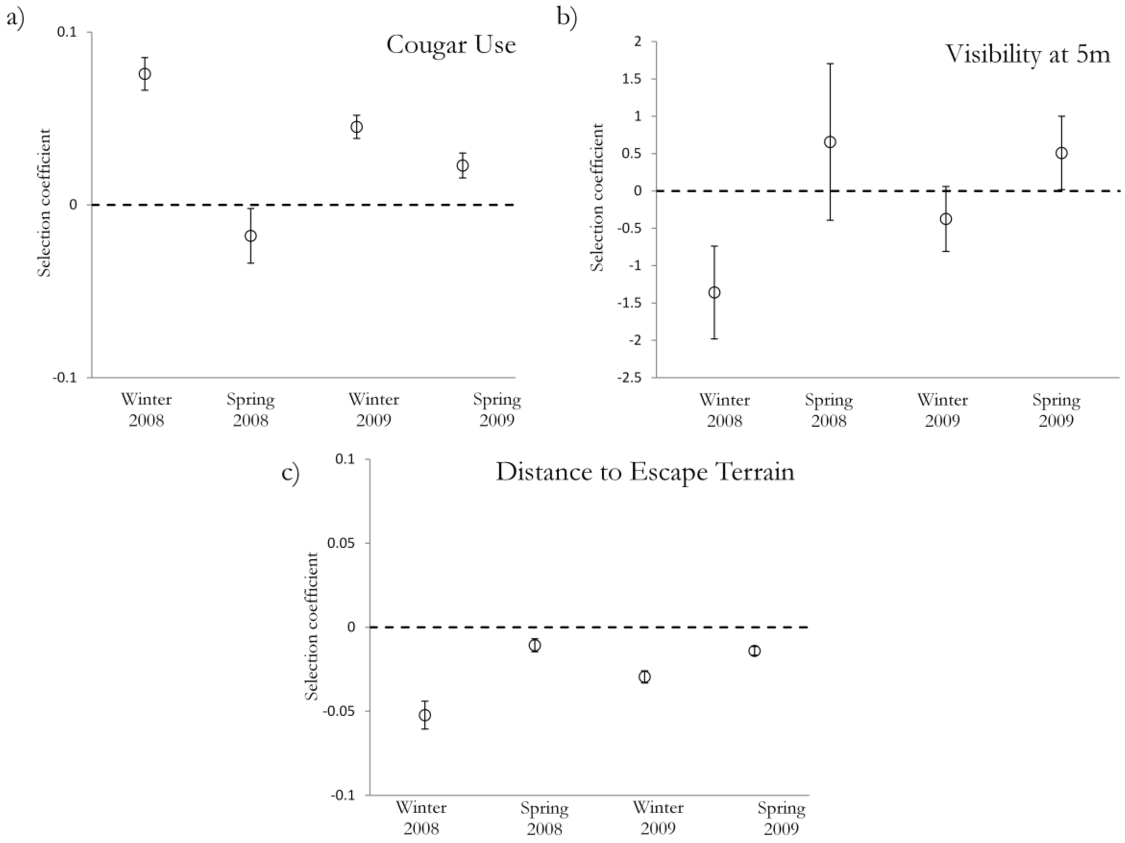


Figure 3- 4. Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, selection coefficients for visibility across a gradient of cougar use on winter ranges in eastern California in 2008 and 2009. This indicates the threshold cougar use level that shifted to positive selection for visibility varied seasonally.

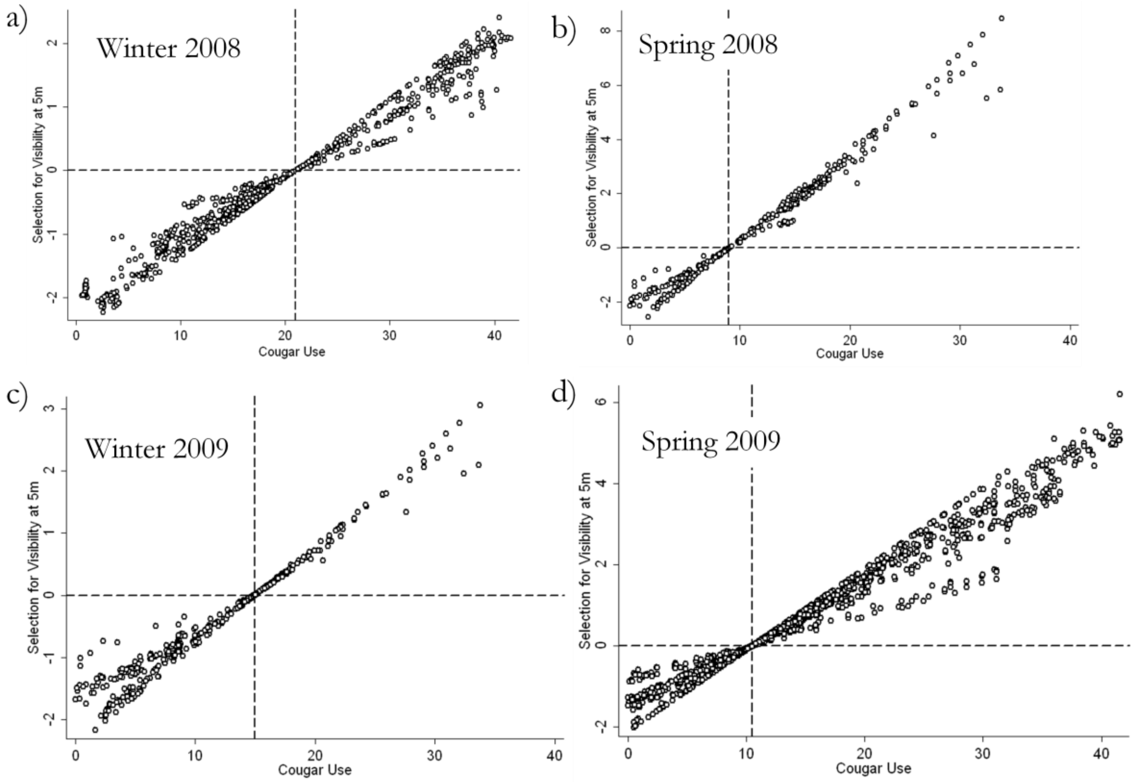


Figure 3- 5. Relative probability of use by Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, for distance to escape terrain interacting with cougar use in the eastern Sierra Nevada, California, from 2006 – 2009. Sierra bighorn are more likely to use areas close to escape terrain when there is high cougar use.

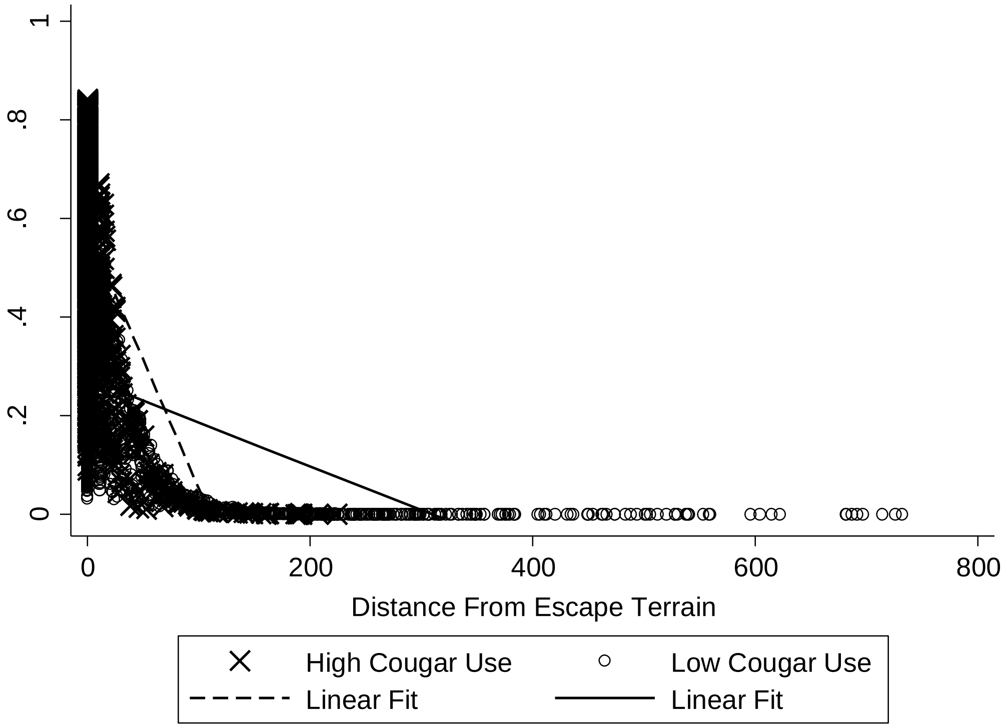
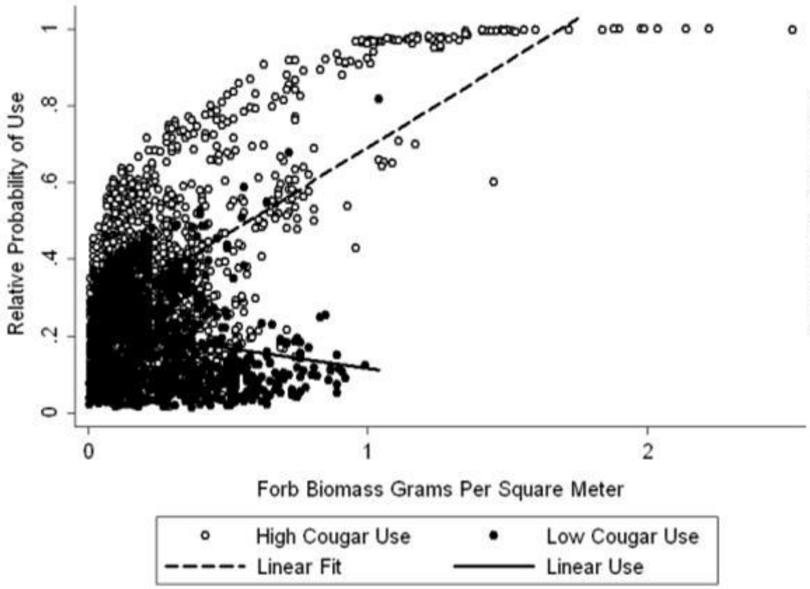
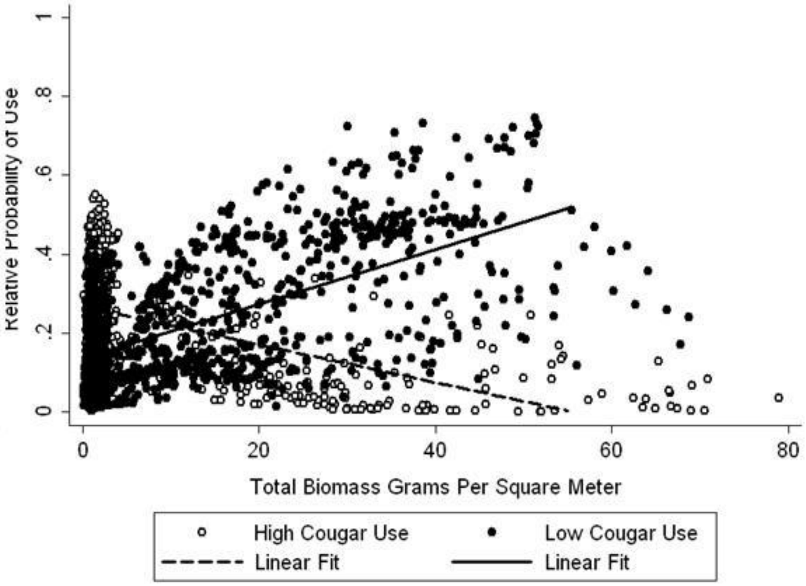
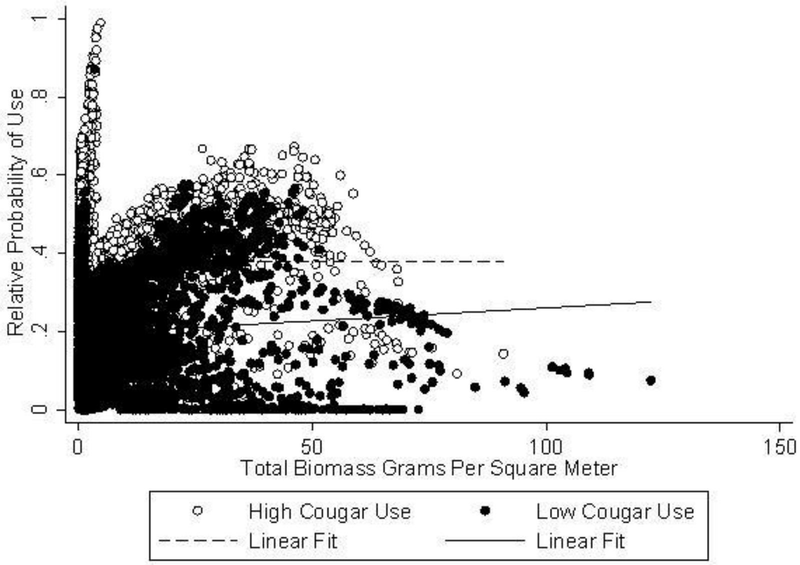


Figure 3- 6. Predictions from forage predation interactions in top forage based resource selection functions of Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, on winter ranges in eastern California. We used the mean value of cougar use in available habitat per season to separate high and low cougar use. The linear fit is added to help visualize the interaction.


Relative Probability of Use
0
.2
.4
.6
.8
1
0
1
2
Forb Biomass Grams Per Square Meter
High Cougar Use
Low Cougar Use
Linear Fit
Linear Use


Relative Probability of Use
0
.2
.4
.6
.8
1
0
20
40
60
80
Total Biomass Grams Per Square Meter
High Cougar Use
Low Cougar Use
Linear Fit
Linear Fit


Relative Probability of Use
0
.2
.4
.6
.8
1
0
50
100
150
Total Biomass Grams Per Square Meter
High Cougar Use
Low Cougar Use
Linear Fit
Linear Fit

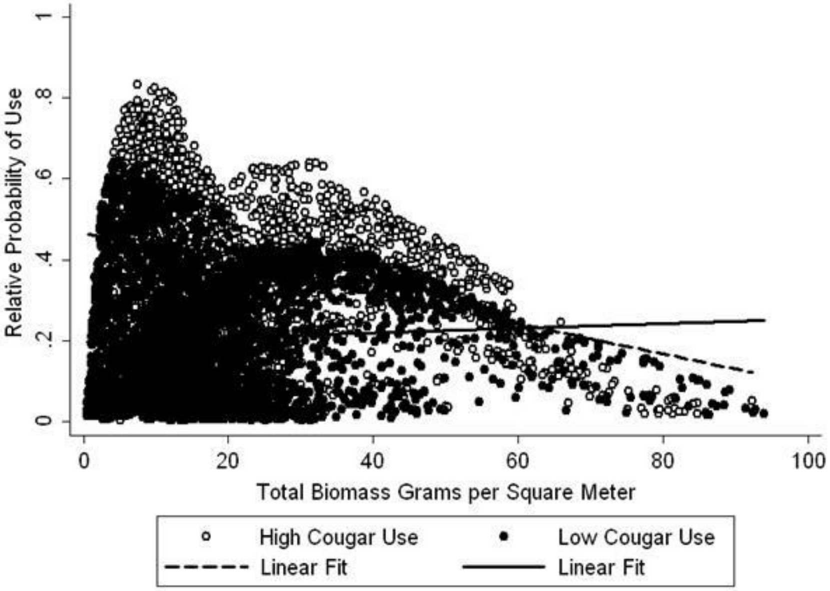
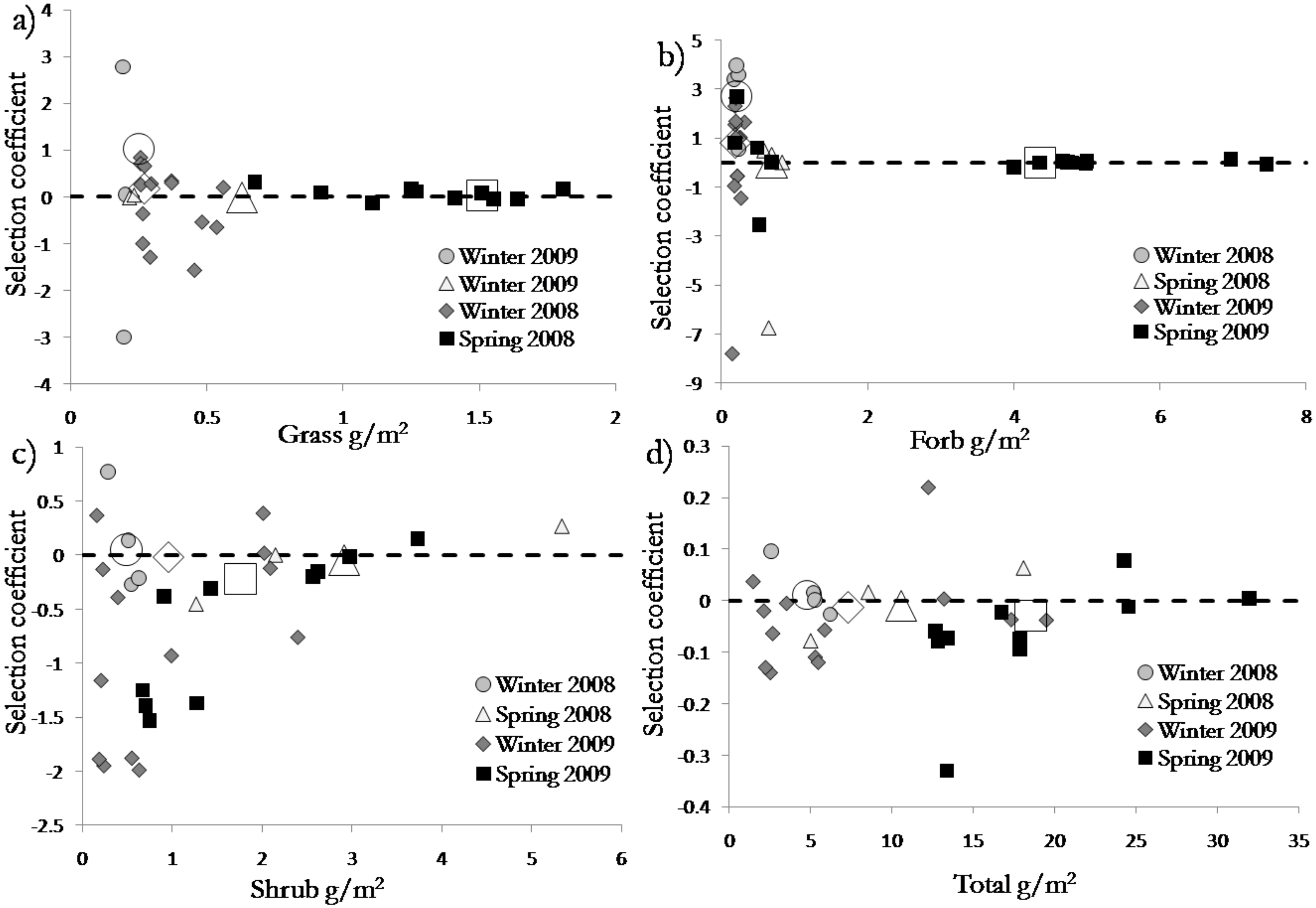

Relative Probability of Use
0
.2
.4
.6
.8
1
0
20
40
60
80
100
Total Biomass Grams per Square Meter
High Cougar Use
Low Cougar Use
Linear Fit
Linear Fit

Figure 3- 7. Sierra Nevada bighorn sheep, *Ovis candensis sierrae*, selection for forage in relation to availability on winter ranges in eastern California. Each filled symbol represents an individual selection and the larger open symbols are the population averaged coefficients for each time period. The same individuals are included multiple times when there was data available for multiple seasons. Available forage was averaged across individual winter home ranges based on predictive models. The 2 most extreme points were removed, but the data was maintained in the population averaged value. Grass, forb and shrub refer to new growth and total refers to both new and old growth of all forage classes combined. These selection coefficients were derived from models that included the base model (elevation, aspect and open landcover). Selection is more variable at lower biomass levels, which may indicate a threshold.


a)
Selection coefficient
4
3
2
1
0
-1
-2
-3
-4
0
0.5
1
1.5
2
Grass g/m²
● Winter 2009
△ Winter 2009
◆ Winter 2008
■ Spring 2008
b)
Selection coefficient
5
3
1
-1
-3
-5
-7
-9
0
2
4
6
8
Forb g/m²
● Winter 2008
△ Spring 2008
◆ Winter 2009
■ Spring 2009
c)
Selection coefficient
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
0
1
2
3
4
5
6
Shrub g/m²
● Winter 2008
△ Spring 2008
◆ Winter 2009
■ Spring 2009
d)
Selection coefficient
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
0
5
10
15
20
25
30
35
Total g/m²
● Winter 2008
△ Spring 2008
◆ Winter 2009
■ Spring 2009

Appendix 3A

Adding NDVI to our forage models changed model coefficients and improved the within sample coefficient of determination (Table 3A-1). We did not initially include NDVI in our vegetation models (see Chapter 2) because they were created to quantify differences caused by wildfire and NDVI was influenced wildfire. Our interest in this chapter is the predictive capacity of forage models, which improved when we integerated NDVI and the interaction of burn and NDVI into our models. We also included the interaction between NDVI and burn because this interaction was highly significant in all forage models except the new growth shrub model (Table 3A-1). We interpret the significance of this interaction to mean that within the burn, NDVI was correlated with new growth of grass and forbs, but outside of the burn it was not (Figure 3A-1). In addition, following the same methodology outlined in Chapter 2, we generated a new forage model for total forage biomass (new and old growth) that represents selection for forage quantity (Table 3A-1).

Figure 3A- 1. Interaction of Burn and NDVI within forage sample sites on the winter range of Sierra bighorn in the eastern Sierra Nevada.

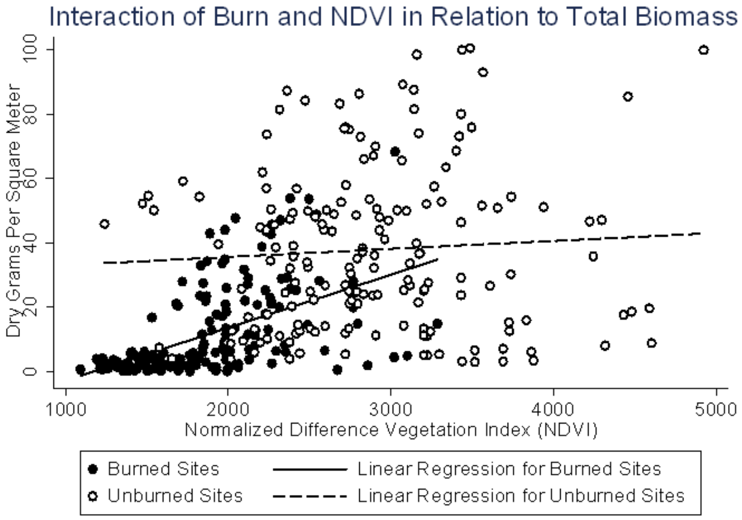


Table 3A- 1. Coefficients for top predictive models of dry biomass for the winter range of Sierra Nevada bighorn sheep, *Ovis canadensis sierrae* during 2008 and 2009.

	Green Grass		**Green Forb**		**Green Shrub**		**Total Biomass**	
Predictor Variable	**β**	**p**	**β**	**p**	**β**	**p**	**β**	**p**
Burn	-4.9	< 0.01	-2.7	< 0.01	-4	< 0.01	-5.9	< 0.01
Burn x Year	0.9	0.008	0.2	0.5	2.5	< 0.01	1.6	< 0.01
Burn x Month	---	---	---	---	---	---	0.7	< 0.01
Year	-0.09	0.7	1.4	< 0.01	-0.9	< 0.01	0.09	0.5
Month	-0.09	0.9	1.2	< 0.01	1.4	< 0.01	-1.5	0.003
NDVI	-0.0004	0.06	-0.0004	0.03	0.0006	0.001	0.0001	0.3
Burn x NDVI	0.002	< 0.01	0.002	< 0.01	---	---	0.0008	0.002
Elevation	0.029	< 0.01	-0.003	< 0.01	0.009	0.04	0.006	0.02
Elevation^2	-8E-06	< 0.01	---	---	-3E-06	0.01	-2E-06	< 0.01
Elevation x Month	0.0005	0.3	---	---	---	---	0.0009	< 0.01
SE Aspect	1	< 0.01	0.6	< 0.01	---	---	0.6	< 0.01
Pseudo R^2	0.2		0.24		0.17		0.11	
Within sample R^2	0.26		0.49		0.43		0.47	
N	336		336		336		336	