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Recent research suggested that habitat quality was likely limiting Jackson moose population growth. Thus, we evaluated seasonal browse condition and the quality of forage and diets, and monitored numerous demographic rates for this population. Winter range was more consistently and intensely browsed than summer range. Forage and diet quality was fairly homogeneous and of lower quality in winter than summer. Within summer, moose forages were of lower quality in burned compared with non-burned habitats. Despite selective foraging, the nutritional quality of diets resembled that of the habitat. Habitat-specific demographic rates were typically lower in burned compared with non-burned habitats. Overall the population is declining, however, habitat-specific population models suggest the portion of the population using burns is declining more rapidly than in non-burned habitats. Study findings suggest that wildfire on the summer ranges of these migratory moose is partially responsible for the observed population declines to present.

HABITAT CONDITION AND THE NUTRITIONAL QUALITY OF SEASONAL FORAGE AND DIETS: DEMOGRAPHIC IMPLICATIONS FOR A DECLINING MOOSE POPULATION IN NORTHWEST WYOMING, USA

By

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TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER ONE - GENERAL INTRODUCTION

Globally, landscape-scale disturbances are occurring at increasing rates (e.g., Barlow et al. 1998, Mann et al. 1999, Laporte et al. 2007), with unknown consequences for many wildlife populations. Rates of these changes can be relatively fast (i.e., logging) or gradual over time (i.e., climate) and their impact on wildlife habitats may vary in length and severity (Andersen et al. 1996, Foster et al. 1998, Parmesan and Yohe 2003). Fire, the most studied of natural disturbances, is an important force in many systems, creating mosaics of habitat patches that differ in composition and structure (Christensen et al. 1989, Keyser et al. 2008). Changes to natural fire regimes (i.e., fire suppression), however, can lead to less frequent, larger, more severe wildfires than has historically occurred (White 1979, Romme and Despain 1989, Debano et al. 1998). Such disturbances can influence movements and habitat use (Peek 1974, Pearson et al. 1995), with population-level consequences (Schaefer and Pruitt 1991, Courtois et al. 2007). The growing pace and extent of landscape disturbance, coupled with the varying responses of species to these changes, challenge our ability to conserve and manage wildlife populations.

Understanding the influence of habitat alteration on wildlife is particularly complicated for ungulates that migrate from higher elevation summer range to lower elevation winter range (Schoen and Kirchhoff 1985, Albon and Langvatn 1992) in response to gradients in forage quality (Langvatn and Albon 1986, Hjeljord and Histol 1999). During winter, ungulate densities in northern and mountainous areas are generally greater, because snow depths and forage availability constrain animals to lower elevation valleys and riparian areas (Albon and Langvatn 1992, Langley 1993, Hornocker and Ruth 1997). Because ungulates are nutritionally stressed during winter (Renecker and Hudson 1988, DelGiudice et al. 1991, Coughenour and Singer

1996, DelGiudice et al. 2001), winter range is generally considered more critical than summer range and is often the target of population and habitat surveys (Peterson and Page 1993, Anderson and Lindzey 1996). In contrast, summer forage is generally more available and of higher quality (Albon and Langvatn 1992, Hjeljord and Histol 1999). Because summer range is generally of higher quality it is typically not considered as limiting as winter range. Phenomena such as "carry-over" effects, whereby habitat quality on one seasonal range influences the fitness of individuals in the following seasons (Mech et al. 1987, Norris et al. 2004), further complicate our understanding of seasonal range importance. For example, previous winter snow accumulation is a good predictor of calf production and mortality during summer in Finland (Kumpula and Colpaert 2003). Thus, the differential importance of seasonal ranges hinders our ability to understand the influence of habitat alterations on ungulate physiology and demography.

Habitat selection by ungulates can provide information about how landscape disturbance influences habitat quality; however, study designs rarely connect preference of habitats to individual fitness (Focardi et al. 2002). For example, moose (*Alces alces*) have been shown to select for habitats with high shrub cover for foraging in winter (Poole and Stuart-Smith 2005), while reindeer (*Rangifer tarandus tarandus*) select for low areas with cool temperatures and high wind speed in summer to reduce exposure to insects (Skarin et al. 2004). Such studies generally assume that an animal's fitness is improved by occupying preferred habitats (Garshelis 2000). This assumption, however, is easily violated. For example, species with high fidelity to seasonal ranges may not alter their use patterns in an optimal manner after a disturbance (Andersen 1991a & b). Additionally, duration of time spent in different habitats may not accurately represent the relative importance or quality of those habitats to animals (Mysterud and Ostbye 1995, Garshelis 2000). Thus, studies should focus at examining the relationships between habitat use and

2

demography (Hobbs and Hanley 1990, Garshelis 2000). Some studies have successfully characterized the demographic value of preferred habitat but overall attempts have been few. For example, survival of roe deer fawns remained unchanged in high quality habitats and decreased >20% in medium to low quality habitats when density increased (Pettorelli et al. 2002). To evaluate the influence of habitat and understand the importance of alterations to seasonal habitat on ungulates, further investigation of habitat-demography relationships is warranted.

For many ungulate species, direct measures of habitat condition or quality have been important tools for monitoring habitat changes (Morellet et al. 2001, Keigley et al. 2002, Marshal et al. 2005). Habitat condition, the physical characteristics of vegetation structure and biomass, is typically an indicator of browsing pressure and growth rates (Keigley et al. 2002, Seaton et al. 2011). Forage quality, the digestibility and concentrations of nutrients in plant tissues, allows for assessments of the nutritional value of forage (Van Soest 1994, McDonald et al. 2002). Many studies infer the condition or quality of habitat through indirect measures by assessing fecal defecation rates (Andersen et al. 1992), or by quantifying morphological and physiological data obtained from live or dead animals (Swihart et al. 1998, Simard et al. 2008, Becker et al. 2010). In such cases, it is assumed that animals in poor condition are indicative of poor habitat. Such animals may produce skewed offspring sex ratios, exhibit higher reproductive rates, or increased survival compared with those in poorer condition (Swihart et al. 1998, Testa and Adams 1998, Sheldon and West 2004, Bardsen et al. 2008). Direct approaches of assessing habitat condition and quality include measuring vegetation biomass, diversity, utilization and the nutritional quality of key forage species, among other approaches (Johnstone et al. 2002, Keigley et al. 2002, Marshal et al. 2005). These direct measures can be affected by numerous factors including

ungulate density, precipitation, fire, and soils (Schaefer and Pruitt 1991, Turner et al. 1997, Seaton et al. 2011). Therefore, studies seeking to connect habitat variables to demography would benefit from directly measuring habitat quality and condition.

My research addresses these questions through the study of a declining population of Shiras moose (*Alces alces shirasi*) in northwest Wyoming that has experienced drastic, fire-induced habitat alterations to portions of their seasonal range. Using a multi-year data set, this study provides a unique opportunity to evaluate the effect of seasonal habitat use on moose demographic rates in an altered environment and will help inform the debate over seasonal limitations and their importance as drivers of ungulate population dynamics. I assessed landscape-level variation in the condition and quality of seasonal moose habitat and the relative influence of variation in habitat caused by wildfires on moose demographic rates and population growth. The overall goal of this study was to increase our current understanding of Shiras moose and determine the cause of the population decline observed in the Jackson Herd Unit. Specific objectives included:

1. Characterize moose habitat condition (i.e., browsing intensity and utilization) and the nutritional quality of forage in winter and summer and evaluate the factors that influence them (i.e., wildfires).

2. Evaluate the influence of wildfire-induced changes to summer range on adult female survival, pregnancy, parturition, neonate survival, and calf survival of collared moose from 2005-2010.

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4

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CHAPTER TWO - EVALUATING BROWSE CONDITION AND NUTRITIONAL QUALITY OF SEASONAL HABITAT FOR A DECLINING MOOSE POPULATION: IDENTIFYING POTENTIAL SEASONAL LIMITATIONS

ABSTRACT

In northern regions, food limitation during long, harsh winters can negatively influence ungulate condition and demography. A growing body of literature, however, suggests that summer-autumn nutrition may influence ungulate populations more strongly than winter. We evaluated spatial variation in browse condition and forage quality within and between seasons for a declining moose (*Alces alces shirasi*) population in northwest Wyoming. Browsing intensity was evaluated using the Keigley method. Based on microhistological analysis of fecal samples, important moose forages were analyzed for determination of acid detergent fiber, acid detergent lignin, acid detergent insoluble nitrogen, and total nitrogen; cellulose and available crude protein were then calculated. Winter browse was more consistently and intensely browsed than summer. Within winter, differences in browsing intensity were related to the proportion of radio-collared moose using different portions of winter range. Core winter areas received the most intense browsing pressure, while peripheral winter areas were lightly browsed. Fewer moose in peripheral areas, characterized by lower browsing intensity, may indicate that winter range has the potential to support higher moose densities than currently exist. Winter forage and diet quality was fairly homogeneous and of lower quality than during summer. Although the nutritional quality of summer forage was greater than in winter, wildfires created heterogeneity in summer forage and diet quality. Important moose forages in burned habitats were of lower quality than in non-burned habitats. Despite selective foraging, moose were not able to optimize their nutritional intake: the nutritional quality of diets resembled that of the habitat. The inability

of moose using burned summer areas to select diets equal in quality to those in non-burned summer areas has the potential to negatively influence moose condition and demography. These findings suggest that the decline of our study population may be partially due to habitat changes on summer range.

INTRODUCTION

Many ungulates migrate between distinct seasonal ranges, which complicates our understanding of the relationship between habitat quality and population performance (Gaillard et al. 2010). In temperate regions, ungulates often migrate from high elevation summer range to low elevation winter range (Albon and Langvatn 1992) in response to increasing winter snow depths at the former (Langley 1993). Because of these movements, densities are generally greater during winter when ungulates are aggregated at lower elevations (Skogland 1985, Monteith et al. 2011). Temperate ungulates typically experience a net energy deficit in winter because of lower availability and quality of forage (Anderson et al. 1972, Torbit et al. 1985), which results in depletion of fat reserves (DelGiudice et al. 1991); severe winters can cause decreased fecundity, survival, and recruitment (Skogland 1985, Portier et al. 1998). During summer, ungulates migrate to higher elevations following advancing plant phenology, thus gaining access to forage plants when their nutritional quality is highest (Mysterud et al. 2001). Elevated maternal condition achieved through increased nutrient availability allow females to meet the costs of lactation and replenish fat reserves, which increases the probability of conception, intrauterine survival, production of heavier calves, twinning, and survival of neonates (Cook et al. 2004, Parker et al. 2009). A growing body of literature has shown that if summer conditions are poor animals may not be able to offset winter fat losses, leading to lower juvenile body mass (Toigo et

al. 2006), reduced demographic performance (Post and Klein 1999) and lifetime reproductive success (Gaillard et al. 2000). Although changes to either seasonal habitat can influence the demography of migratory ungulates, making generalizations about the relative strength of summer vs. winter habitat limitation is challenging.

Browsing ungulates can have profound impacts on their seasonal habitats due to their forage selectivity and the high densities they often achieve (Augustine and McNaughton 1998, Danell et al. 2002). Because ungulates congregate on common winter range, browse use is typically greater in winter than summer (Palmer et al. 2004). Although it is common to infer the quality of habitat through measures of ungulate condition (Simard et al. 2008, Becker et al. 2010), few studies have sought to connect direct measures of habitat condition (i.e., browsing intensity) to measures of ungulate performance such as twinning rates and body condition (but see Hjeljord et al. 2000, Seaton et al. 2011). Despite a growing body of literature on ungulate-habitat relationships, we are unaware of any studies that directly evaluate the influence of summer browsing intensity on the demography of migratory ungulates.

Because nutrition is often limiting for ungulate populations (Cook et al 2004), the most important difference in habitat quality between seasonal ranges is arguably due to variation in forage quality (Van Soest 1994). Forage quality is generally lower in winter than summer, because winter plants are dormant, less digestible, and have lower protein and mineral content (Oldemeyer et al 1977, Van Soest 1994). During summer, nutrient levels of many forage plants peak early in the season and decline through the growing season (Klein 1990, Van Soest 1994). Access to plants at differing phenological stages can allow ungulates to optimally exploit temporal gradients in plant quality, as they do at the landscape scale through their seasonal migrations (Albon and Langvatn 1992). Although considerable variation exists in the seasonal

quality of forages, the fact that winter mortality is common (Young 1994) may have driven the notion that winter range is more limiting than summer. Carry-over effects may complicate this interpretation however, and overall the relative strength of forage limitations on each seasonal range has not been well characterized.

In northern regions, pronounced seasonal shifts in forage availability and quality are reflected in ungulate diets. Regardless of selection, ungulate diets are more restricted (i.e., less variable) in winter than summer, because newly emergent forage such as leaves, forbs, grasses, and aquatic plants are not available (Renecker and Hudson 1988, Larter and Gates 1991). Digestibility and protein content are also lower in winter than summer diets (Renecker and Hudson 1988, Larter and Gates 1991). Recently, researchers have argued that summer-autumn nutrition is critical for female ungulates because small differences can have substantial impacts on body condition and reproductive parameters (Cook et al. 2004, Tollefson et al. 2008). For example, captive elk (*Cervus elaphus*) fed lower quality diets were in poorer condition than those fed higher quality diets, which negatively influenced breeding success, calf growth rates, and over-winter survival, suggesting that summer-autumn nutrition may be more limiting than winter (Cook et al. 2004). Although ungulate diets are generally more diverse and of higher nutritional value in summer, much less is known about the ability of ungulates to optimize their diets when forage quality is diminished or altered.

The challenge of understanding how the quality of seasonal habitats influences ungulate population performance is made more difficult by the heterogeneous influence of disturbance. Natural disturbances like wildfires create mosaics of habitat patches, differing in composition and structure (Christensen et al. 1989, Keyser et al. 2008). For migratory ungulates in western North American landscapes, disturbances such as wildfires are likely to be more common on

high-elevation summer ranges compared to low-elevation winter ranges, where human development often occurs (eg., Vogel 1989, Knight et al. 1995). Increased production of summer forages used by ungulates following wildfire has been reported in several systems (Vogel and Beck 1970, Schaefer and Pruitt 1991); however, the response of habitat quality to fire severity is quite variable (DeWitt and Derby 1955, Wallace et al. 1995). The quality of selected diets also differs when habitats are burned. For example, Hobbs and Spowart (1984) reported that mountain sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) diets had higher crude protein and digestibility in burned compared with non-burned habitat in winter, but no differences were found in spring diets.

We evaluated the condition and quality of seasonal habitats used by a migratory population of Shiras moose (*Alces alces shirasi*) in northwest Wyoming, USA. Our study population, which has been declining since the early- to mid- 1990s (Brimeyer and Thomas 2004), provides an opportunity to study landscape-level variation of seasonal habitats, its potential influence on population performance, and the influence of large-scale disturbance on seasonal ranges. Recent research concluded that bottom-up processes are likely limiting this population (Becker 2008, Becker et al. 2010), however, direct measures of habitat quality were not conducted, and it is unknown which seasonal habitat would pose more limitations. The 1988 wildfires in and around Yellowstone National Park burned much of this population's summer range. Fire typically creates favorable moose habitat (Davis and Franzmann 1979), however, moose numbers have continued to decline despite these and more recent fires in the area. Our overall goal was to understand the variation occurring on each seasonal range by characterizing habitat condition via browsing intensity, evaluating forage quality, diet quality, and the influence of wildfire on summer habitat. We first predicted that browsing intensity would be heavier and

14

more homogeneous in winter than summer, because ungulates occur at higher densities on relatively smaller ranges in winter (Skogland 1985, Monteith et al. 2011). Second, we predicted that forage would be of higher quality and more heterogeneous in summer than winter, because most forage plants are in a dormant stage in winter (Van Soest 1994). Lastly, we predicted that diet quality would be greater in summer than winter. We also sought to assess the influence of past wildfires on moose forage and diet quality.

Study area

Our study area encompasses approximately 5,000 km^2 in the southern Greater Yellowstone Ecosystem, the majority of which are public lands. During winter, moose are restricted to low to mid elevations (2050-2150 m) dominated by lodgepole pine (*Pinus contorta*) intermixed with smaller stands of Douglas fir (*Psuedotsuga menziesii*) and aspen (*Populus tremuloides*) and they forage largely on willow communities along the Buffalo Fork and Snake Rivers. During summer, most moose migrate to higher elevation (mean=2470 m) habitats dominated by stands of Engelmann spruce (*Picea engalmanni*), subalpine fir (*Abies lasiocarpa*) and lodgepole pine, with smaller stands of whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*) and aspen throughout. Within areas recently burned, forbs and understory shrubs dominate the landscape, with minimal to moderate conifer and deciduous tree regeneration. Areas which experienced high severity burning during the 1988 wildfires incurred 80-100% tree mortality (Abendroth 2008).

MATERIALS AND METHODS

Capture and sampling areas

We sought to characterize primary moose seasonal ranges to evaluate between- and within-season variation in habitat condition and quality. Becker (2008) captured adult female moose in core winter range within our study area in February 2005 (n=20) and 2006 (n=6), and fitted them with TGW-3700 global positioning system (GPS) radio-collars (Telonics, Inc., Mesa, Arizona, USA). We captured additional adult female moose in February 2008 (n=19) and 2009 (n=5), across the entire winter range, in order to better delineate the majority of summer and winter range areas. Moose were captured via helicopter net-gunning, without immobilization agents, in 2008 and darted from the ground using either carfentanil (3 mg) or thiafentanil (A-3080; 10 mg) for immobilization, antagonized with 300 mg of naltrexone in 2009 (Kreeger and Arnemo 2007). Captured moose were fitted with the same GPS store on board radio-collars as in 2005 and 2006. Capture and handling procedures were approved by the University of Wyoming Institutional Animal Care and Use Committee.

Winter (January-April) and summer (June-September) sampling areas (n=6 in winter, n=5 in summer; Fig. 2.1) were delineated based on GPS collar data from 2005-2007, because these moose have high fidelity to their summer home ranges (Becker 2008). Summer sampling areas affected by the wildfires were 57-88% burned, of which 12-28% was severely burned. Because moose appeared more abundant in some areas than others, we sought to quantify variation in moose use across the winter range. If moose locations were clustered in a sampling area for greater than one week, indicative of foraging and not exploratory movements, the sampling area was considered "used" by that individual. We tested for differences in the proportion of the collared moose population using each sampling area among years (n=6) using ANOVA (PROC GLM, SAS v. 9.2, Cary, NC) with sampling area as the explanatory variable.

If area differences were significant, a means separation test was performed to characterize core versus peripheral winter range.

Landscape-level variation in browsing intensity

To determine if browsing intensity was different between seasons and to assess within-season variation we used a browse survey method developed by Keigley et al. (2002). This method provides an index of browsing intensity on key forage species, including determination of overbrowsing. Riparian willow communities were clipped to the edge of sampling areas and the proportion of willow within sampling areas was calculated using ArcGIS 9.2 (ESRI, Redlands, CA). We randomly located 5-15 transects within riparian communities in each sampling area in proportion to the amount of willow/riparian habitat available. Sixty three transects were monitored in 2008 (39 in winter, 24 in summer) and 83 in 2009 (49 in winter, 34 in summer) at the end of each season (April and September); not all transects were monitored in both years due to logistical constraints. Because species composition was highly variable among sampling areas, browse transects were not restricted to a single willow species. A focal willow was selected every 10 m along a transect and three measures were collected to assess browsing intensity: height to the tallest base of current year growth (H_{bcyg}), the length of its current year growth leader (L_{cyg}), and the height to the tip of the tallest completely dead annual increment (H_d). The live-dead (LD) index is the difference between the dead (H_d) and live (H_{bcyg}) increments: the greater the LD value the greater the likelihood that the plant will grow out of the browse zone (Keigley et al. 2002). Intensely browsed willows, with most to all of their current annual growth consumed each year, have LD values ≤ 0. We performed analysis of covariance (ANCOVA: PROC GLM) to assess within-season differences in the LD index. For summer,

17

sampling area, year, and a sampling area × year interaction were used as explanatory variables, with L_{cyg} as a covariate to account for growth differences among species. For winter, sampling area was used as the explanatory variable with L_{cyg} as a covariate. If among-area differences were detected, a means separation test was performed. To assess seasonal differences in browsing intensity, we corrected LD values for species-specific growth increments. For each transect we calculated adjusted LD values as: $LD_a = LD_u - \beta(L_{cyg} - \overline{X})$ where LD_u is the measured LD value, β is the slope coefficient of the LD to L_{cyg} regression for each season, and $\overline{X}$ is the L_{cyg} seasonal mean (Steel and Torrie 1980). Then, an ANOVA (PROC GLM) was performed with season and the area × year interaction nested within season as explanatory variables.

Landscape-level variation in forage quality

To assess landscape-level variation in seasonal forage quality we analyzed important forage species in winter (*Salix* spp*., Populus tremuloides, Abies lasiocarpa*) and summer (*Salix* spp*.*). Stem material of current year growth was used for between-season and within-winter comparisons. Salix leaf was used to assess within-summer differences. *Salix* species used in this analysis included booth (*S. boothii*), geyer (*S. geyeriana*), and drummond (*S. drummondiana*) willow. From each sampling area, vegetation samples ($\geq$ 30 g wet weight) were collected monthly, dried for 48 h at 55°C, and ground to pass through a 1mm screen (Wilmshurst et al. 1995). Samples were analyzed in duplicate for dry matter (DM) in an Isotemp oven (Fisher Scientific Co. L.L.C, Pittsburg, PA: AOAC 1990), total nitrogen (N) in a model FP-528 Leco Protein/Nitrogen Determinator (Leco Corporation, St. Joseph, MI), acid detergent fiber (ADF) in an ANKOM200 Fiber Analyzer (ANKOM Technology Corp., Fairport, NY), acid detergent lignin (ADL) in an ANKOM Daisy[ll] Incubator (ANKOM Technology Corp., Fairport, NY), and

acid detergent insoluble nitrogen (ADIN, bound N) in a model FP-528 Leco Protein/Nitrogen Determinator, at the University of Wyoming Ruminant Nutrition Laboratory. We estimated total crude protein by multiplying N by 6.25, calculated available crude protein by multiplying total crude protein by the proportion of total crude protein that was available [(100-ADIN)/100], and took the difference between ADF (cellulose and lignin) and ADL (lignin) to calculate cellulose. All forage metric data were placed on a dry matter basis before conducting statistical analyses.

Salix species composition was highly variable within and between seasons. Because moose are selective browsers (Renecker and Hudson 1988) and have shown preference for some Salix species (Houston 1967), we tested for species differences. First, we examined differences in forage measures between Salix leaf and stem material using a paired t-test (PROC TTEST) and among-species differences using 2-sample t-tests (Minitab Inc., State College, PA). Statistical tests of seasonal differences were conducted for each of the six forage metrics.

To evaluate the influence of wildfire on summer forage quality, a 2-factor ANOVA was performed with burn category (burned vs. non-burned), month, and a burn category × month interaction as explanatory variables. For winter, a 2-factor ANOVA was performed with sampling area and month as explanatory variables. Because two summer habitat types were evident, burned and non-burned, we sought to understand differences between both summer habitat types and winter, which we refer to as "seasonal habitat types" henceforth. To assess seasonal differences, two 1-factor ANOVAs were performed with either season or seasonal habitat type as the explanatory variable.

Nutritional quality of moose diets

19

Because moose may respond to variation in habitat by altering forage selection, we sought to determine diet composition across seasons and individual ranges. In winter and summer 2009, fecal samples (n=1-9; ≈ 10 pellets per group) were collected monthly from each sampling area. For each sampling area, composites were assembled using equal portions of individual fecals collected during the first and last two months of the sampling period (Jenks et al. 1989). The number of samples in each composite ranged from 5-16 in winter and 4-13 in summer. Composite samples were analyzed via microhistological analysis (100 microscopic views, Washington State University, Wildlife Habitat and Nutrition Laboratory) to determine the percentage of each forage consumed and to adjust forage measures for use in diet analyses.

To characterize the nutritional quality of diets within- and between-seasons, we analyzed forage species that represented at least 70% of moose diets for each sampling area in winter (79-91%) and summer (70-94%). For each diet, quality was estimated by weighting forage metrics based on the proportion that each forage type occurred in the diet. Forage and fecal composite samples were dried for 48 h at 55°C, and ground to pass through a 1mm screen. Samples were analyzed in duplicate, at the University of Wyoming Ruminant Nutrition Laboratory, for dry matter (DM), nitrogen (N), acid detergent fiber (ADF), acid detergent lignin (ADL), and acid detergent insoluble nitrogen (ADIN). Total crude protein, available crude protein and cellulose were determined, as for our analysis of forage plants. Acid detergent lignin was used as an indigestible marker to estimate the digestibility of each composite moose diet. We calculated dry matter digestibility (%DMD) of each diet using the equation: $\%DMD = 100 - 100 \left(\dfrac{\%ADL_f}{\%ADL_d} \right)$ where ADL_f is the % acid detergent lignin of the fecal composite, and ADL_d is the total % acid detergent lignin in the diet (Galyean 1997). Statistical analyses were conducted for each forage

metric and %DMD. One factor ANOVAs with sampling area, burn category, season, or seasonal habitat type as explanatory variables were performed to assess between- and within-season differences among sampling areas.

RESULTS

Core and peripheral winter range

For winter, differences were detected in the proportion of collared moose using each sampling area ($F_{5,30}$=19.06, P<0.0001), which allowed us to characterize sampling areas as core, intermediate or peripheral winter range. The most utilized winter range areas, Buffalo Valley East ($\bar{x}$=0.500 ± 0.050) and Buffalo Valley West ($\bar{x}$=0.414 ± 0.073), were different from all lesser used areas and classified as core winter range. Buffalo Valley South ($\bar{x}$=0.245 ± 0.032) was an intermediately used winter sampling area. Spread Creek ($\bar{x}$=0.054 ± 0.027), Pacific Creek ($\bar{x}$=0.069 ± 0.021) and West ($\bar{x}$=0.091 ± 0.022), were occupied far less frequently and thus were classified as peripheral winter range.

Landscape-level variation in browsing intensity

For winter, no differences in browsing intensity were detected between years so data were pooled for analysis. Browsing pressure differed among winter sampling areas ($F_{5,81}$=6.91, P<0.0001). Core winter range areas, Buffalo Valley East (LD=4.13 ± 2.76 cm) and Buffalo Valley West (LD=5.64 ± 1.54 cm) were more intensely browsed than peripheral areas, Spread Creek (LD=20.92 ± 5.38 cm), Pacific Creek (LD=22.78 ± 2.92 cm), and West (LD=30.32 ± 3.34 cm). Buffalo Valley South (LD=11.19 ± 4.09 cm), the intermediately used winter sampling area, was not different from core use areas or Spread Creek (Fig. 2.2a). Summer browsing pressure

was different among areas ($F_{4,48}$=9.58, P<0.0001); however, there was a significant area × year interaction ($F_{3,48}$=7.96, P=0.0002). Thus, browsing pressure was not consistent for summer use areas between years (Fig. 2.2b). Although there was considerable within-season variation among sampling areas, the seasonal comparison indicated that winter browsing pressure (LD=12.73 ± 1.47 cm) was more intense than summer (LD=23.26 ± 2.08 cm: $F_{1,125}$=9.04, P=0.0032: Fig. 2.2c).

Landscape-level variation in forage quality

Compared to leaves, salix stems had 17.3 ± 0.62% more acid detergent fiber (t_{56}=27.62, P<0.0001), 2.6 ± 0.51% more acid detergent lignin (t_{56}=5.08, P<0.0001), 14.7 ± 0.52% more cellulose (t_{56}=28.31, P<0.0001), and 18.8 ± 0.62% more acid detergent insoluble nitrogen (t_{56}=28.42, P<0.0001). Salix stems also had 10.0 ± 0.56% less total crude protein (t_{56}=17.76, P<0.0001) and 8.3 ± 0.40% less available crude protein (t_{56}=20.95, P<0.0001) than leaves. For leaves, ADF, ADL, and ADIN differed between at least two willow species (P<0.05). Comparisons of leaves to stems indicated that stems were of lower quality than leaves. For winter stems, ADF, cellulose, ADIN, total crude protein, and available crude protein differed between at least two species (P<0.05). For all stems (winter and summer), ADF, cellulose, ADIN, total crude protein, and available crude protein differences were detected between at least two willow species (P<0.05). Because such species differences were detected, we standardized forage quality metrics by species such that within- and between-season analyses were conducted on the residual differences from species means.

For winter, ADF, ADL, cellulose, ADIN, total crude protein, and available crude protein of willow stems were similar among sampling areas (Table 2.1), supporting our prediction that

winter forage is fairly homogenous among areas. A general declining trend across months in winter was detected for ADF ($F_{3,110}$=13.10, P<0.0001; Fig. 2.3a), ADL ($F_{3,110}$=51.63, P<0.0001), and ADIN ($F_{3,110}$=12.24, P<0.0001). A general increasing trend across months in winter was detected for total crude protein ($F_{3,110}$=5.58, P=0.001; Fig 2.3b) and available crude protein ($F_{3,110}$=10.03, P<0.0001: Fig. 2.3b). Differences were also detected by month for cellulose ($F_{3,110}$=3.03, P=0.033), however no directional trend was apparent.

Evaluating the influence of wildfires on summer forage quality we found that summer ADF was greater in burned than non-burned areas ($F_{1,49}$=51.56, P<0.0001; Table 2.1), with a significant month ($F_{3,49}$=14.45, P<0.0001) and a burn × month interaction ($F_{3,49}$=6.79, P=0.0006; Fig. 2.3c). Burned areas were also greater than non-burned areas for ADL ($F_{1,49}$=25.97, P<0.0001), cellulose ($F_{1,49}$=4.76, P=0.034), and ADIN ($F_{1,49}$=25.97, P<0.0001; Table 2.1). Total crude protein of forage was greater in burned than non-burned areas ($F_{1,49}$=9.37, P=0.004; Table 2.1); with a significant month ($F_{3,49}$=70.27, P<0.0001) and a burn × month interaction ($F_{3,49}$=4.65, P=0.006; Fig. 2.3d). There was no difference in available crude protein between burned and non-burned areas ($F_{1,49}$=0.02, P=0.88; Table 2.1), however, there was still a significant month ($F_{3,49}$=42.26, P<0.0001) and a burn × month interaction ($F_{3,49}$=43.35, P=0.026; Fig. 2.3d). Total- and available crude protein decreased over time in burned and non-burned summer areas.

Because only stem material is available in winter and willow is an important year-round forage, we used only willow stems to evaluate seasonal differences. Results indicated that ADF ($F_{1,124}$=77.22, P<0.0001), ADL ($F_{1,124}$=54.16, P<0.0001), cellulose ($F_{1,124}$=38.92, P<0.0001), and ADIN ($F_{1,124}$=51.52, P<0.0001; Table 2.1) were all significantly lower in winter than summer; which was likely attributable to differences in sampling of seasonal stem material. The

difference in total crude protein in winter and summer approached significance ($F_{1,124}$=3.72, P=0.056), as did the difference in available crude protein ($F_{1,124}$=3.08, P=0.082), although seasonal differences were slight (Table 2.1). The extent of the differences between seasons, however, was driven by summer areas that had burned. For ADF, all seasonal habitat types - burned summer, non-burned summer, and winter - were different ($F_{2,123}$=68.04, P<0.0001; Fig. 2.4a). The same differences were found for ADL ($F_{2,123}$=47.76, P<0.0001), cellulose ($F_{2,123}$=27.70, P<0.0001), and ADIN ($F_{2,123}$=35.38, P<0.0001; Table 2.1). Differences were also found among seasonal habitat types for total crude protein ($F_{2,123}$=35.38, P=0.045); burned summer habitat was different than winter, however non-burned summer was not different from either burned summer or winter habitat (Fig. 2.4b). When we accounted for protein that is unavailable (ADIN), the difference in total crude protein became equivalent. Surprisingly, the amount of available crude protein in burned summer habitats was as low as that of winter habitats (Fig. 2.4b).

Nutritional quality of moose diets

Winter moose diets did not differ in for ADF, ADL, cellulose, ADIN, and total crude protein among areas (Table 2.2). Differences were detected among winter areas in available crude protein ($F_{1,17}$=3.56, P=0.022; Table 2.2). Summer moose diets had higher ADF ($F_{1,17}$=18.55, P=0.0005; Fig. 2.5a), cellulose ($F_{1,17}$=25.98, P<0.0001) and ADIN ($F_{1,17}$=16.06, P=0.0009) in burned than non-burned areas; differences in ADL approached significance ($F_{1,17}$=3.79, P=0.068; Table 2.2). This suggests that moose could not overcome the poor quality of forage plants in burned habitats via diet selection. No differences were detected between diets in burned and non-burned areas for total crude protein or available crude protein (Fig. 2.5b). Seasonal

comparisons of moose diets indicated that winter diets were greater in ADF than summer diets ($F_{1,40}$=12.61, P=0.001;Table 2.2). Winter diets were also greater than summer diets in cellulose ($F_{1,40}$=10.78, P=0.002) and ADIN ($F_{1,40=15.39}$, P=0.0003); differences in ADL approached significance ($F_{1,40}$=3.93, P=0.055: Table 2.2). Winter diets were considerably lower than summer diets in total crude protein ($F_{1,40}$=99.34, P<0.0001; Table 2.2) and available crude protein ($F_{1,40}$=101.55, P<0.0001; Table 2.2). Seasonal diet comparisons, however, can be misleading when seasonal habitat types (burned summer, non-burned summer, and winter habitat) are not considered. For ADF, diet differences were detected among seasonal habitat types ($F_{2,39}$=20.84, P<0.0001): burned summer and winter diets were not different from one another, but both were greater than non-burned summer diets (Fig. 2.5a). The same differences were found for ADL ($F_{2,39}$=5.21, P=0.001, cellulose ($F_{2,39}$=19.99, P<0.0001), and ADIN ($F_{2,39}$=20.85, P<0.0001; Table 2.2). Differences were also detected for total crude protein ($F_{2,39}$=48.44, P<0.0001) and available crude protein ($F_{2,39}$=54.37, P<0.0001; Table 2): protein levels were similar in burned and non-burned summer diets, but both were greater than winter diets (Fig. 2.5b). Differences in digestibility were not detected among winter diets (Table 2.2) so data were pooled for seasonal analyses. Overall, winter diets were less digestible than summer diets ($F_{1,40}$=20.93, P<0.0001; Table 2.2). Digestibility, however, was greater in non-burned compared with burned summer diets, both of which were more digestible than winter diets ($F_{2,39}$=17.09, P<0.0001; Fig. 2.6).

DISCUSSION

For migratory ungulates, habitat condition and quality can strongly influence demography (Tollefson et al. 2008); however, a general understanding of how the condition and quality of

seasonal habitats varies across the landscape has yet to emerge. Overall, we documented that

winter habitat was more heavily and consistently browsed than summer habitat (Fig. 2.2c), which

was likely caused by relatively high winter moose densities. Forage plants were of higher

quality in summer than in winter, largely due to the availability of leaves (Table 2.1) and other

newly emergent forages. Consistent with other studies that have evaluated seasonal differences

in forage quality (Renecker and Hudson 1988, Klein 1990), our work supports the notion that for

migratory ungulates, summer habitat is of higher quality than winter habitat. Within winter, we

found that core winter habitat was more heavily browsed than peripheral areas (Fig. 2.2a), and

that there was little landscape-level variation in forage quality (Table 2.1). Within summer, we

found a considerable degree of heterogeneity in browsing intensity (Fig. 2.2b) and forage quality

(Fig 2.3c). In contrast to most studies that have shown positive effects of wildfire on moose

habitat, we found that forage in burned summer areas was high in fiber and fiber bound nitrogen

(ADIN), which negatively influences digestibility, and the amount of available crude protein,

respectively. Despite their selective foraging, moose were unable to compensate for differences

in forage quality, such that burned summer diets were of lower nutritional quality (Fig. 2.5a) and

digestibility (Fig. 2.6) than non-burned summer diets, a pattern that matches landscape-level

variation in forage quality. Our findings point to differences in landscape-level habitat quality

between seasonal ranges – including that caused by extensive wildfires – which may present a

challenge for ungulates seeking to optimize their summer foraging and fat accumulation.

In agreement with our prediction, winter habitat was more heavily and consistently

browsed than summer habitat (Fig. 2.2). It also exhibited consistently lower nutritional quality

across winter use areas in terms of forage (Table 2.1) and diets (Table 2.2), indicating that most

individuals that share this common winter range will experience net energy deficits (Anderson et

26

al. 1972, Torbit et al. 1985). Heavier browsing of winter habitat is probably due to the migratory

nature of our study population and the high densities of moose in lower elevation habitats on

their common winter range. Many migratory ungulates aggregate in high densities on their

winter ranges and occupy more expansive areas in summer, where they exist at lower densities

due to greater availability of forage across the landscape (Skogland 1985, Monteith et al. 2011).

Within winter, core and peripheral areas were distinct based on relative use by collared moose

and browsing intensity. General characteristics of core winter range included, higher prevalence

of preferred willow species and lower snow accumulation than peripheral winter range. Our

study population has been declining for 16-22 years (Brimeyer and Thomas 2004); Wyoming

Game and Fish Department population trend counts show declines from approximately 990

(1983-1989) to 386 (2003-2010). Thus, the low moose densities that exist currently suggest that

the moose population has contracted to its core habitat and that ample forage exists in peripheral

areas; suggesting that winter forage is abundant and not limiting for this population. If the

Jackson moose population recovers to greater numbers, however, peripheral areas are likely to

incur heavier browsing pressure. This suggests that winter range conditions are most likely to

regulate ungulates through a density-dependent mechanism that manifests at high population

densities. The identification of core and peripheral winter range during periods of low

abundance may aid our understanding of critical winter habitat for ungulates and provide insights

into the relationship between population density and habitat use.

In contrast to the consistent core and peripheral use on winter range, browsing pressure of

summer habitat was more heterogeneous, with some areas browsed as heavily as core winter

range and others showing minimal levels of browsing (Fig. 2.2b). The sheer size of summer

range when coupled with lower densities makes it unlikely that forage biomass alone is limiting

in summer. Furthermore, our study population has been declining for many years and, as is common for moose populations, has high fidelity to summer ranges (Becker 2008). It seems possible that the population decline has not been manifest uniformly across the landscape, creating variation in moose densities across summer range. Such heterogeneity in density, in combination with fidelity patterns, may make it unlikely that any one summer area will be overbrowsed enough to negatively influence individual fitness. However, because summer browsing pressure in some areas was as heavy as core winter ranges, summer habitat may at times be more limiting than is currently recognized.

Surprisingly, our comparisons suggested that winter stems were of higher quality than summer stems (Fig. 2.4). Research has shown that larger diameter *Salix* stems are of lower quality than smaller diameter stems. Stems collected at a diameter of 4 mm contained 7% more fiber content, 1.7% less crude protein and were 4.3% less digestible than stems collected at 2 mm (Hjeljord et al. 1982); suggesting our results are an artifact of our sampling strategy. We sampled winter stems based on monthly measurements of diameter at browse point, because we were interested in evaluating winter diets as precisely as possible. The average browse diameter over winter was 2.5 cm. Summer browsing was more difficult to detect so we collected stems in burned and non-burned habitats at a diameter of 4 mm, based on moose use of *Salix* (Shipley et al. 1999). Because of our sampling scheme, we likely underestimated the quality of summer stem material. The percentage unit differences in fiber (7%) and crude protein (1.7%) observed by Hjeljord et al. (1982) are enough to suggest that in our study, the quality of stem material was similar in winter and summer: seasonal differences in ADF and total crude protein values are within 10% and 1% respectively (Table 2.1).

Much of the heterogeneity in forage quality on summer range was related to past wildfire history, with plants in burned areas containing approximately 2-7% more fiber (ADF, cellulose, and ADL) than in non-burned areas. This finding was somewhat surprising, given that wildfire is often thought to increase forage quality for ungulates, including moose (Davis and Franzmann 1979). Plant biomass production is typically enhanced following fires, which can result in more structural tissue and thus higher fiber content (Skre et al. 1998). In grazing systems, studies have reported that high biomass forages have more fiber (Wilmshurst et al. 1995) and are less digestible (Bergman et al. 2001) than lower biomass forages. Many studies have reported no effect or increases in total nitrogen content of forages following fires (Hobbs and Spowart 1984, Long et al. 2008). In our study area, *Salix* spp. had more total crude protein in burned areas than non-burned areas, which is in agreement with total nitrogen content of browse species in burned areas of Norway (Skre et al. 1998). In burned areas, however, the increased amount of nitrogen bound to fiber (ADIN; Table 2.1) resulted in equal levels of available crude protein content, indicating that the bioavailability in burned areas was less than in non-burned areas. Although not statistically significant, this may be biologically important.   Because not all nitrogen is available for digestion, studies would benefit from assessing protein which is available for digestion.

Wildfires typically create mosaics of habitat patches on the landscape (Christensen et al. 1989, Keyser et al. 2008), among which, moose typically select for non-burned areas (Gasaway and Dubois 1985). Thus, moose with larger home ranges should be able to exploit high-quality areas and optimize their forage intake. Moose in our study area, however, have high fidelity to summer home ranges and are unlikely to abandon or modify the range to which they have fidelity (Andersen 1991, Becker 2008). Furthermore, for many moose in our study a large

29

percentage (61-99.5%) of their summer range was burned, making access to high quality forages limited. Our diet data indicate that moose using burned home ranges were not able to optimize nutrient intake, because diets were generally poor and similar to that of available forage. Our findings suggest that severe or large-scale wildfires, when coupled with high range fidelity, have the potential to negatively influence moose more than previously thought.

Summer diets of moose contained marginal amounts of stem material. Because our sampling strategy resulted in an overestimate of stem fiber content and an underestimate of protein content and digestibility, our results underestimate the quality of summer diets. Moose consumed twice as much stem material in non-burned habitat than in burned habitat; therefore, estimates of diet quality in non-burned habitats were more severely underestimated than in burned habitats. We do not however, expect these differences to alter our overall results because the contribution of stems to diet quality was relatively small.

Our findings that diet quality closely resembled that of available forages is in contrast to studies that have often found diets to be enhanced due to selection (Hobbs and Spowart 1984). We found that diets in burned habitat were of lower quality than diets in non-burned summer habitat, but still higher quality than diets in winter, as predicted. The high fiber content of diets in burned summer habitat was not different from diets in winter, and a corresponding decrease in digestibility was observed. Indeed, diets in burned summer habitat were only 6.7% more digestible than diets in winter. Although we did not find differences in available crude protein between burned and non-burned summer diets, the observed ~10% difference in digestibility between these habitats is likely to influence moose nutritional status, because small changes in digestibility greatly influence dry matter intake and energy retention (Blaxter 1962). For example, a 14% increase in digestibility and 27% increase in dry matter intake, resulted in a

268% projected increase in daily weight gain in reindeer (*Rangifer tarandus L.*; White 1983).

Thus, we suspect that moose using burned summer habitats may experience decreased energy gain and reproductive performance as a result of poor diet quality (Post and Klein 1999, Cook et al. 2004).

Although burning of summer range appears to have reduced habitat quality, these moose also coexist with a full suite of native predators, some of which, wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), have been recovered or reintroduced during the period of decline. Researchers have shown that wolves predate on 2-10% of adult moose in areas of low to high moose density annually (Messier and Crete 1985) and grizzly bears predate on 0.6-3.9 adult moose annually, independent of moose densities (Boertje et al. 1987). Both studies, however, reported greater predation rates in spring/summer because predation was oriented toward calves. Our study has documented predation by grizzly bears, wolves and mountain lions, however, the majority of adult moose mortalities occurred in late winter, indicative of nutritional stress (Becker 2008). Although grizzly bears are known to predate on moose in Yellowstone, elk is consumed more than moose (53% vs. 18% of diets respectively; Mattson 1997). Our study population, like others in the GYE (Middleton et al., in review) is likely being influenced by decreased habitat quality and increased predation.

Past research suggests that summer nutrition may influence ungulate populations more than winter (Cook et al. 2004, Tollefson et al. 2008). Our findings suggest that disturbance from wildfire has the potential to create greater variability in summer range quality than existed pre-fire. In contrast to habitat studies reporting benefits of fire for summer forages (Skre et al. 1998, Long et al. 2008), severe large-scale wildfires in our study area resulted in summer forages that were as low in quality as winter forages. Moose appeared to be unable to compensate for low

quality summer forage, as diet quality in burned summer areas was only marginally better than diet quality on winter range. The availability of peripheral areas on winter range with low densities of moose suggests that more moose have been historically supported on winter range. For these reasons, we suspect that the decreased quality of burned summer areas may negatively influence moose condition and demography, and that the decline of the Jackson moose population may be partially due to habitat changes on summer range. Our results support the suggestion by Cook et al (2004) that under some circumstances, summer-autumn nutrition has the potential to be more limiting than during winter.

ACKNOWLEDGEMENTS

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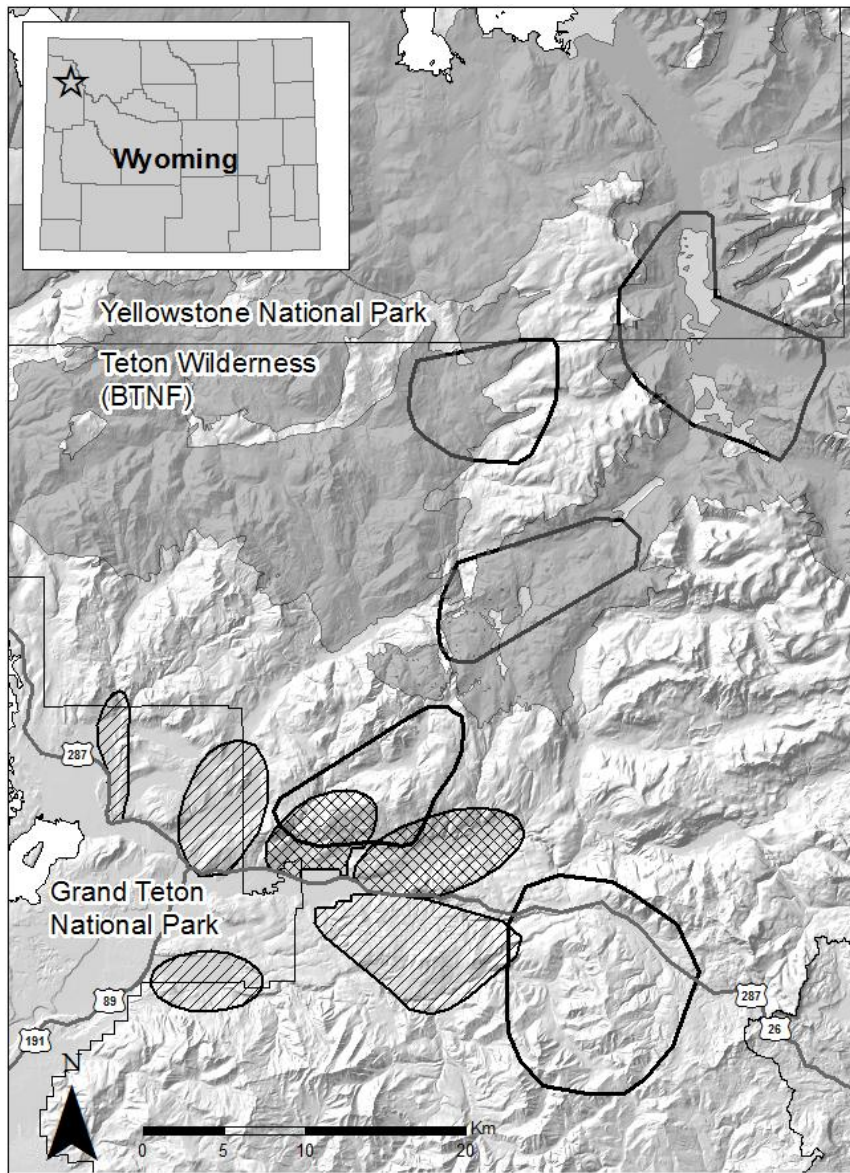
Figure 2.1. Project study area depicting core winter use areas (cross hatched), peripheral winter use areas (hatched), summer use areas (open polygons) and 1988 wildfires (dark grey area). Water bodies are shown as white areas.
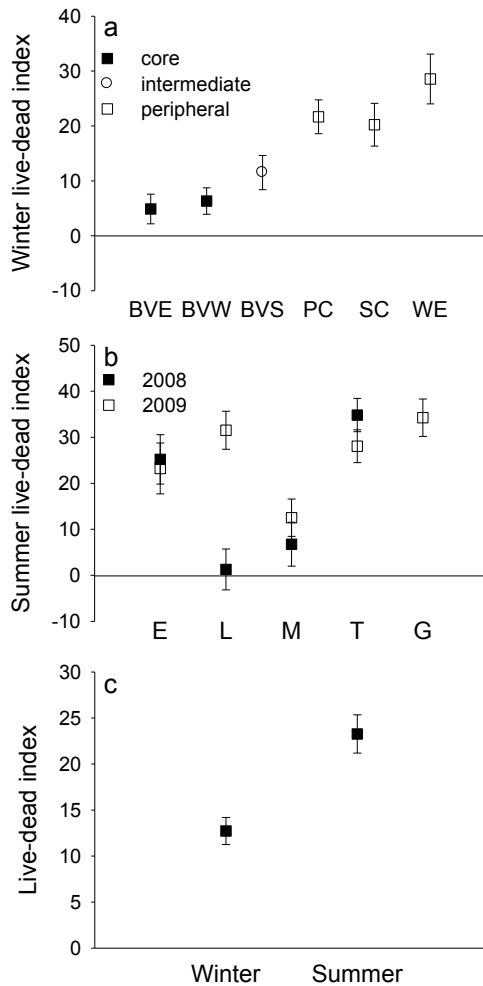
Figure 2.2. Browsing intensity across sites and seasons. In winter (a) peripheral winter range areas Pacific Creek (PC), Spread Creek (SC), and West (WE) were the least browsed areas and Buffalo Valley South (BVS) was not different from core areas or Spread Creek. Buffalo Valley East (BVE) and Buffalo Valley West (BVW) are core winter range areas. Summer sampling areas Enos (E), Mink (M), and Thorofare are burned areas; Lava (L) and Grizzly (G) are non-burned areas. Browsing intensity was not consistent for summer sampling areas (b) between

years. The significant area-by-year interaction was largely caused by the Lava area experiencing

less browsing in 2009 compared with 2008, resulting in inconsistent responses between years.

Regardless of within-season variation, winter was more heavily browsed than summer (c). Data

are means ± SE.
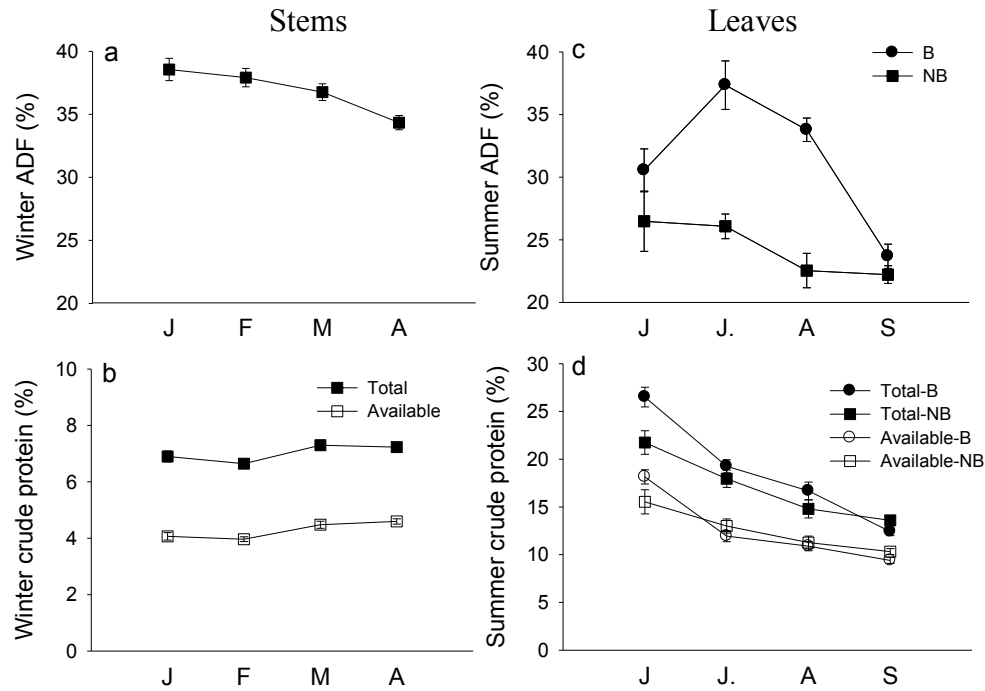
Figure 2.3. During winter (January-April), acid detergent fiber (ADF) decreased (a), while, total- and available-crude protein increased (b). During summer (June-September), burned habitats were greater in ADF than non-burned habitats (c). Total crude protein was greater in burned (B) than non-burned (NB) habitats, however, available crude protein was not different between burned and non-burned habitats (d). Data are means ± SE.
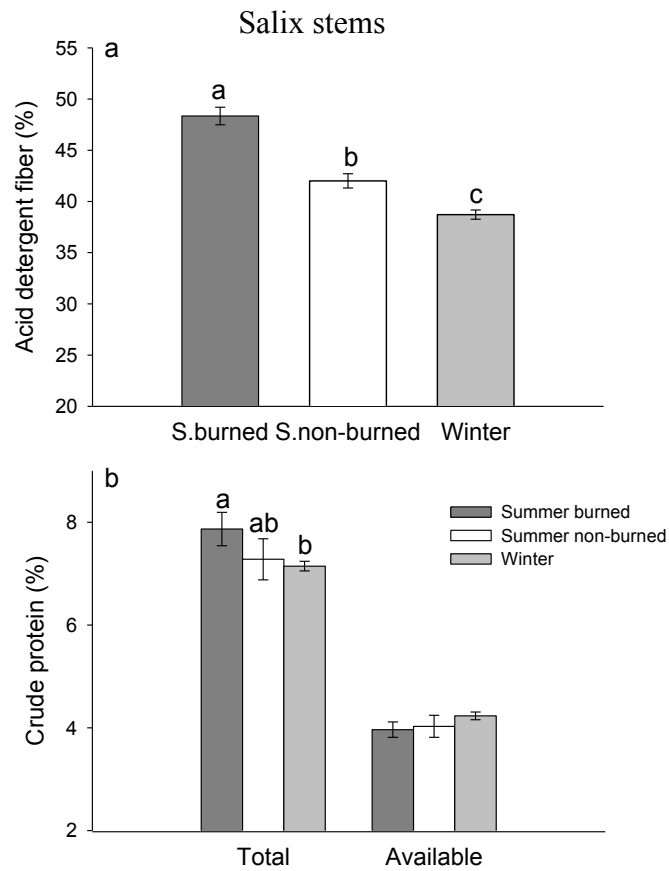
Figure 2.4. Acid detergent fiber (a) and total crude protein (b) of willow stems were compared among seasonal habitat types. Letters indicate significant differences detected by the LSD means separation test. No difference was detected in available crude protein among seasonal habitat types (b). Data are means ± SE.

Figure 2.5. In moose diets, acid detergent fiber (a), total-, and available-crude protein (b), were different among seasonal habitat types. Letters indicate significant differences detected by the LSD means separation test. Data are means ± SE.

Figure 2.6. Digestibility of moose diets were different among seasonal habitat types. Letters

indicate significant differences detected by the LSD means separation test. Data are means ± SE.

Table 2.1. Comparisons of acid detergent fiber, acid detergent lignin, cellulose, acid detergent insoluble nitrogen, total crude protein, and available crude protein of key seasonal moose forages to assess landscape-level variation in forage quality.

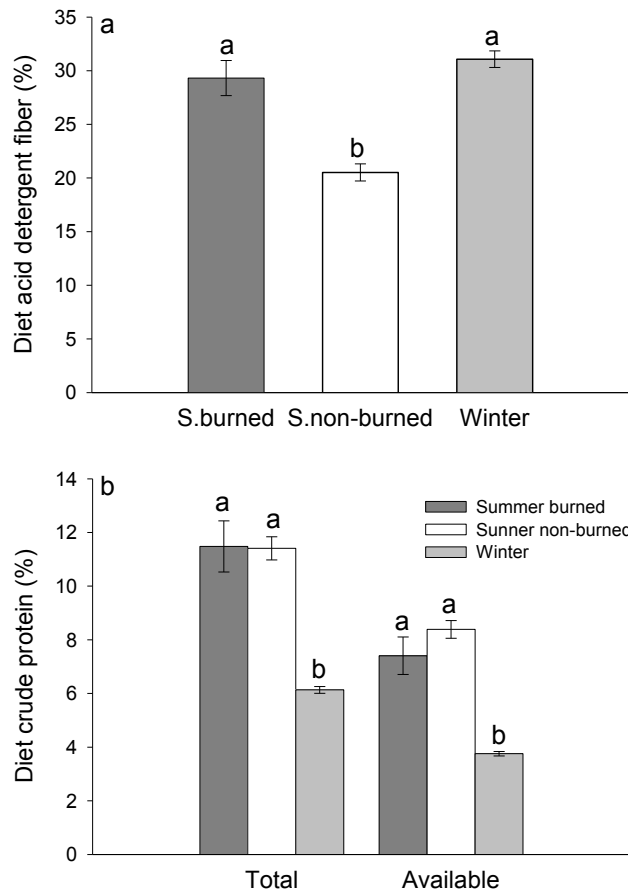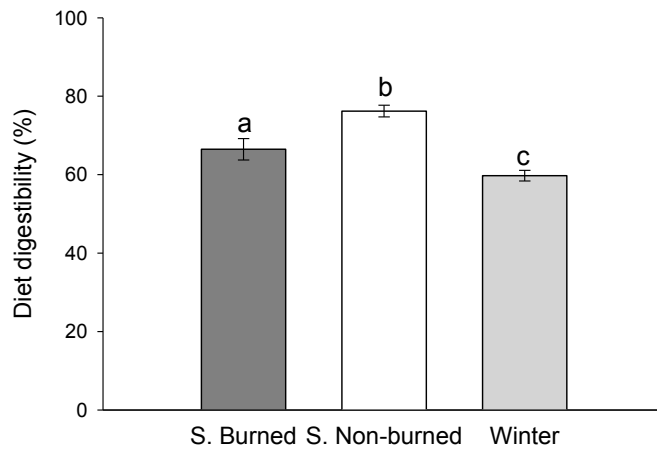| Comparison	Acid detergent fiber		Acid detergent lignin		Cellulose		Acid detergent insoluble N		Total crude protein		Available crude protein	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Winter sampling area (stems)												
BVE	36.88[a]	0.80	14.52[a]	0.49	22.36[a]	0.76	39.10[a]	0.94	6.83[a]	0.15	4.16[a]	0.12
BVS	36.55[a]	1.01	14.91[a]	0.49	21.64[a]	0.94	38.54[a]	1.13	7.01[a]	0.11	4.31[a]	0.11
BVW	37.13[a]	0.95	14.53[a]	0.50	22.60[a]	0.94	39.58[a]	0.96	7.16[a]	0.29	4.34[a]	0.21
PC	36.49[a]	0.73	14.77[a]	0.49	21.72[a]	0.68	38.31[a]	0.80	7.27[a]	0.16	4.48[a]	0.12
SC	37.17[a]	1.04	15.96[a]	0.55	22.21[a]	0.78	39.66[a]	1..03	7.10[a]	0.21	4.28[a]	0.15
WE	36.67[a]	1.21	13.87[a]	0.44	22.80[a]	1.12	39.23[a]	1.29	6.70[a]	0.15	4.07[a]	0.14
Summer habitat type (leaves)												
Burned	31.41[a]	1.15	17.98[a]	0.85	13.43[a]	0.56	32.02[a]	1.20	18.00[a]	0.92	12.09[a]	0.59
Non-burned	24.33[b]	0.81	12.57[b]	0.70	11.75[b]	0.52	26.06[b]	1.00	17.02[b]	0.79	12.53[a]	0.56
Season (stems)												
Winter	38.72[a]	0.45	14.66[a]	0.21	24.06[a]	0.35	40.95[a]	0.49	7.14[a]	0.09	4.23[a]	0.08
Summer	45.68[b]	0.71	18.29[b]	0.48	27.39[b]	0.45	47.09[b]	0.76	7.60[a]	0.25	3.99[a]	0.12
Seasonal habitat type (stems)												
Burned summer	48.34[a]	0.86	19.81[a]	0.61	28.54[a]	0.56	49.01[a]	1.06	7.87[a]	0.33	3.96[a]	0.15
Non-burned summer	42.01[b]	0.70	16.20[b]	0.53	25.81[b]	0.60	44.46[b]	0.81	7.28[ab]	0.40	4.02[a]	0.21
Winter	38.72[c]	0.45	14.66[c]	0.21	24.06[c]	0.35	40.95[c]	0.49	7.14[b]	0.09	4.23[a]	0.08

Notes: All nutritional values are on a % dry matter basis; reported data are raw values; within a group, rows distinguished by different letters are significantly different from one another (p<0.05) means separation LSD and are based on statistical analysis of the nutritional value standardized for species type (i.e., residual difference from species means).
A significant month effect was found for summer acid detergent fiber, acid detergent lignin, acid insoluble nitrogen, total- and

available- crude protein.

A significant burn x month interaction was found for summer cellulose.

Differences in total crude protein (p=0.056) and available crude protein (p=0.082) approached significance between seasons.

Table 2.2. Comparisons of total dietary, acid detergent fiber, acid detergent lignin, cellulose, acid detergent insoluble nitrogen, total crude protein, available crude protein, and dry matter digestibility in moose diets within- and between-seasons.

Comparison x Diet	Acid detergent fiber		Acid detergent lignin		Cellulose		Acid detergent insoluble N		Total crude protein		Available crude protein		Dry matter digestibility	
	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE	$\overline{x}$	SE
Winter sampling area														
BVE	32.62^a	0.80	13.02^a	0.55	19.44^a	0.57	34.53^a	0.84	6.67^a	0.21	4.12^a	0.10	57.98^a	2.23
BVS	28.66^a	0.61	12.95^a	0.53	15.90^a	0.42	30.14^a	0.67	6.30^a	0.23	4.01^a	0.16	57.28^a	1.75
BVW	33.02^a	1.17	12.36^a	0.43	19.80^a	1.60	35.04^a	1.07	6.10^a	0.35	3.64^{abc}	0.24	61.61^a	1.28
PC	31.19^a	0.55	12.36^a	0.77	18.95^a	0.34	32.69^a	0.79	6.29^a	0.20	3.88^{ab}	0.17	60.48^a	3.29
SC	30.76^a	3.98	12.10^a	1.84	18.48^a	2.53	32.59^a	4.16	5.83^a	0.39	3.45^{bc}	0.14	59.85^a	7.00
WE	29.88^a	1.93	11.68^a	0.68	17.77^a	1.67	32.03^a	2.01	5.43^a	0.09	3.31^c	0.13	61.83^a	2.70
Summer habitat type														
Burned	29.32^a	1.63	12.05^a	1.06	17.54^a	0.97	30.31^a	1.68	11.48^a	0.95	7.41^a	0.70	66.48^a	2.74
Non-burned	20.52^b	0.80	9.42^b	0.61	11.53^b	0.30	21.73^b	0.94	11.41^a	0.43	8.39^a	0.33	76.21^b	1.48
Season														
Winter	31.07^a	0.77	12.44^a	0.36	18.42^a	0.58	32.87^a	0.81	6.13^a	0.13	3.75^a	0.08	59.75^a	1.37
Summer	25.61^b	0.71	10.94^a	0.72	15.01^b	0.90	26.70^b	1.43	11.45^b	0.57	7.82^b	0.43	70.58^b	2.01
Seasonal habitat type														
Burned summer	29.32^a	1.63	12.05^a	1.06	17.54^a	0.97	30.31^a	1.68	11.48^a	0.95	7.41^a	0.70	66.48^a	2.74
Non-burned summer	20.52^b	0.80	9.42^b	0.61	11.53^b	0.30	21.73^b	0.94	11.41^a	0.43	8.39^a	0.33	76.21^b	1.48
Winter	31.07^a	0.77	12.44^a	0.36	18.42^a	0.58	32.87^a	0.81	6.13^b	0.13	3.75^b	0.08	59.75^c	1.37

Notes: All nutritional values are on a % dry matter basis; within a group, rows distinguished by different letters are significantly different form one another (p<0.05) means separation LSD.
The difference in acid detergent lignin between burned and non-burned summer habitat approached significance p=0.055.

48

The difference in acid detergent lignin between winter and summer approached significance p=0.068.

CHAPTER THREE - EFFECT OF WILDFIRES ON POPULATION GROWTH OF A MIGRATORY MOOSE HERD IN THE SOUTHERN GREATER YELLOWSTONE ECOSYSTEM

ABSTRACT

Throughout Alaska and Canada, moose populations often respond positively to increased habitat heterogeneity created by fires. Challenging this general rule, moose in the southern Greater Yellowstone Ecosystem (GYE) began declining shortly after the Yellowstone wildfires of 1988. Our previous research in the southern GYE revealed that the quality of summer moose forage and diets were lower in areas that burned compared with non-burned areas. Here we evaluated whether differential use of summer habitat (i.e., burned or non-burned) by moose influenced their demography and population growth. We radio-collared 102 moose to characterize summer habitat use and demographic rates, determined if demographic variables differed between the two habitat types, and modeled population response as a function of habitat use. Moose inhabiting burned summer habitat had significantly lower rates of pregnancy, birth, and neonate and calf survival. Although adult female survival was not different between the two habitats, this rate ranged from 64-94%. As is common for long-lived species with low fecundity, sensitivity analysis revealed that population growth rate (λ) was most sensitive to adult female survival. A Life Table Response Experiment (LTRE), however, indicated that considerable differences in λ between burned and non-burned habitats were attributable to differences in calf survival. Furthermore, although λ was less than 1 for both portions of the population, it was $\approx$8% lower in burned habitats. Our results suggest that in northwest Wyoming, the negative influence of wildfires on moose recruitment is at least partially responsible for recent population declines.

INTRODUCTION

Understanding the influence of landscape-level disturbances on ungulate populations is complicated by the fact that disturbances occur at various scales and intensities, and their impacts vary in length and severity (Andersen et al. 1996, Foster et al. 1998, Parmesan and Yohe 2003). Disturbances like wildfires are often considered agents of renewal, creating mosaics of habitat patches, differing in composition and structure (Christensen et al. 1989, Keyser et al. 2008). Fires typically enhance the quality of ungulate habitat by creating edge habitat, and abundant early successional vegetation (Davis and Franzmann 1979, Schwarts and Franzzman 1989), and by promoting the growth and regeneration of important forages such as endemic herbaceous plants and aspen (*Populus tremuloides*) (Carlson et al. 1993, Bailey and Whitham 2002). Ungulates tend to select such disturbed habitats (Pearson et al. 1995), and their use often yields increased reproductive success, and abundance (Schwarts and Franzzman 1989). Fire suppression can lead to less frequent wildfires that are larger and more severe (Romme and Despain 1989, Debano et al. 1998), and the intensity of such fires may modify habitat in ways that challenge our understanding of the influence of fire on ungulate populations.

The influence of wildfires on ungulates can be further complicated by migration and fidelity patterns, which may constrain the ability of individuals to respond to large-scale disturbances. In temperate regions, ungulates typically migrate from lower elevation winter ranges to higher elevation summer ranges in response to forage phenology and production (Schoen and Kirchhoff 1985, Langvatn and Albon 1986, Albon and Langvatn 1992, Hjeljord and Histol 1999). Many ungulates exhibit high site fidelity, returning to seasonal home ranges annually (Tierson et al. 1985, Sweanor and Sandegren 1989) and using traditional migration

routes transmitted from mother to young (McCullough 1985, Sweanor and Sandegren 1988). In Norway, high fidelity of moose (*Alces alces*) to one traditional range that had deteriorated in quality resulted in reduced reproductive success (Andersen 1991). By contrast, some ungulates can flexibly alter their migratory strategies (Nelson 1998, White et al. 2007) or patterns of habitat selection (Loft et al. 1991, Pearson et al. 1995), which may allow them to benefit from habitat changes. The extent to which migration fidelity constrains the ability of ungulates to avoid deteriorated habitat is largely unexplored.

Numerous studies have evaluated how ungulate habitat selection is influenced by fire or other disturbances (Schaefer and Pruitt 1991, Pearson et al. 1995, Sawyer et al. 2009). Such studies provide important information about how landscape disturbance influences habitat quality; however, habitat use is rarely understood in the context of an animal's fitness (Focardi et al. 2002). It has proved difficult to evaluate the demographic consequences of differential habitat use, in part because the time spent in different habitats may not accurately represent relative habitat quality (Mysterud and Ostbye 1995, Garshelis 2000). A number of studies have successfully characterized the demographic value of preferred habitat, but overall there have been few attempts (see Pettorelli et al. 2002, Helle and Kojola 2008, Simard et al. 2008). Thus, evaluating the influence of fire on ungulates represents a challenge that is common among efforts to connect habitat change to ungulate demographic performance.

Research on the benefits of fire for moose began in the mid-1940s and has remained a topic of interest in moose conservation and management. Most research has been conducted at the northern extent of moose ranges across Alaska and Canada (Davis and Franzmann 1979). Because such research has found that fire positively influences moose populations in Alaska (Schwatrz and Franzmann 1989, Maier et al. 2005), Canada (Davis and Franzmann 1979), and

Maine (Lautenschalager et al. 1997), it is generally accepted that fires benefit moose by creating

forest mosaics, and edge habitat with abundant high-quality forage (Davis and Franzmann 1979).

Other studies, however, have reported no benefits of fire to moose (Peek 1974, Gasaway et al.

1989), or that response of moose to environmental variation (Maier et al. 2005) may have

reduced their ability to optimize use of the high-quality habitat that fire creates (Gasaway et al.

1989). Weixelman et al. (1998) cautioned against extrapolating the benefits of fire to moose

populations living at low density or under different ecological conditions. For example, forests

in the southern part of the range share some common species to the northern boreal forests, but

they may differ in species composition, nutrient cycling, and climate (Perry et al. 2008). Such

differences may influence the quality of moose habitat following fire due to species-specific

tolerances and differences in forest succession. Thus, an evaluation of the effect of fire

(including intensity) on moose in the southern periphery is warranted.

During the summer of 1988, wildfires were abundant throughout the Greater Yellowstone

Ecosystem (GYE), burning 570,000 ha of habitat (Christensen et al. 1989). On the northern

range of Yellowstone, moose populations declined following the 1988 fires, starting in winter

1990-1991 and continuing to decline by at least 75% as of 2001; reductions in moose numbers

were greatest in severely burned areas (Tyers 2006). These findings were surprising and in

contrast to the positive responses of moose populations to wildfires in Alaska (Schwartz and

Franzmann 1989). We have been studying a migratory population of Shiras moose (*Alces alces

shirasi*) in the southern GYE that has been declining since the early- to mid-1990s (Fig. 3.1).

Our previous research indicated that habitat quality is fairly homogeneous across winter range,

while recent fire events have created strong heterogeneity in summer forage quality by reducing

the nutritional quality of moose forages and diets in burned areas (Vartanian, Chapter 2). For

example, average digestibility of winter diets (59.8%) was lowest, followed by digestibility of burned summer range diets (66.5%) and non-burned summer diets (76.2%). All these moose are subject to similar conditions on a shared winter range, but because they exhibit high fidelity to summer ranges (Becker 2008), the ≈10% difference in digestibility between burned and non-burned summer ranges may lead to differences in summer fat gain and annual demography. Using a multi-year data set, we evaluated the influence of summer range wildfires on numerous moose vital rates. Because previous research has shown that summer-autumn nutrition strongly influences ungulate physiology and demography (Cook et al. 2004), we predicted that moose vital rates would be negatively influenced by burning of their summer ranges. We then evaluated the potential influence of the 1988 fires on the decline of this population by incorporating vital rates of moose using burned and nonburned areas into matrix models to assess population-level consequences of this large-scale disturbance.

MATERIALS AND METHODS

Study area

Our study area was largely comprised of the Bridger-Teton National Forest (~5,000 km^2), and extended north into the mountains of southern Yellowstone National Park and the Teton Wilderness, west into Grand Teton National Park, and south into the Jackson Hole valley (Fig. 3.2). Over a 20 year period (1990-2010), mean annual precipitation at Moose, Wyoming averaged 54.7 cm, most of which deposits as snow (Boyce 1989). Mean annual snow depths averaged 383.8 ± 23.9 cm and mean annual temperatures averaged 3.0°C (National Oceanic and Atmospheric Administration *accessed June 2011*).

During winter, moose use low to mid elevations (2050-2150 m) where plant communities are dominated by lodgepole pine (*Pinus contorta*) stands intermixed with smaller stands of Douglas fir (*Psuedotsuga menziesii*) and aspen. As snow depth increases in winter, forage becomes restricted to vast willow communities along the Buffalo Fork and Snake Rivers. Individual moose exhibit fidelity to their seasonal home ranges, and often use the same migration routes between years (Becker 2008). During summer, most moose migrate to higher elevations (mean 2470 m) dominated by stands of Engelmann spruce (*Picea engalmanni*), subalpine fir (*Abies lasiocarpa*) and lodgepole pine; smaller stands of whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*) and aspen are found throughout. At all elevations, grasses and forbs dominate subalpine meadows, and willow (*Salix* spp.) dominate riparian areas. Within areas recently burned, forbs and understory shrubs are common, with minimal to moderate conifer and deciduous tree regeneration. The Yellowstone fires of 1988 burned approximately 1800 km^2 in southern Yellowstone and the Teton Wilderness, of which ~30% was severely burned. Abendroth (2008) reported 80-100% tree mortality in these severely burned areas.

Numerous other ungulate and carnivore species were seasonally present. During winter, co-occurring ungulate species included mule deer (*Odocoileus hemionus*), bison (*Bison bison*) and elk (*Cervus elaphus*). During summer, pronghorn antelope (*Antilocapra americana*), domestic cattle and horses were also present. During winter, potential predators of moose included mountain lion (*Puma concolor*) and gray wolves (*Canis lupus*); in summer, black bear (*Ursus americanus*) and grizzly bear (*U. arctos*) were also present. In addition to natural predation, limited moose harvest was permitted in the study area.

Capture and home range characterization

To evaluate the demographic influence of wildfires on summer ranges of migratory moose, we sought to identify the presence and degree of burning in home ranges used by marked moose. Radio-collared moose from multiple capture efforts were monitored during our study. Adult female moose captured by Berger (1999) in 1996-1998 (n=10) and Wyoming Game and Fish Department in 2004 (n=8) were fitted with VHF collars (ATS, Isanti, Minnesota, USA) and were included in our monitoring as of 2005. We captured adult female moose within our study area in February 2005-2007, and fitted them with global positioning system (GPS) radio-collars (Telonics, Inc., Mesa, Arizona, USA; n=27) or VHF radio-collars (ATS, Isanti, Minnesota, USA; n=21; Becker 2008). Additional adult female moose were captured in February 2008 (n=19 GPS, n=13 VHF) and 2009 (n=5 GPS). Captures were conducted via helicopter net-gunning, without immobilization agents, in 2008 and darted from the ground using either carfentanil (3 mg) or thiafentanil (A-3080; 10 mg) for immobilization, antagonized with 300 mg of naltrexone in 2009 (Kreeger and Arnemo 2007). Captured moose were fitted with the same GPS store on board and VHF radio-collars as in 2005-2007. The total sample of radio-collared moose available for use in our analysis was 102 (n=50 GPS, n=52 VHF). Capture and handling procedures were approved by the University of Wyoming Institutional Animal Care and Use Committee.

In earlier work, we sampled forage and diet quality across all seasonal ranges and found that burned summer ranges were of lower quality than non-burned summer ranges. Therefore, to simplify demographic analyses, we sought to characterize moose as occupying either burned or non-burned summer ranges. For GPS collared moose, we estimated 95% kernel home ranges with a 0.80 bandwidth (Kie et al. 2010) using the Home Range Tools extension in ArcGIS 9.3 (ESRI, Redlands, CA) and then calculated the percent of the home range that burned. To assess

the accuracy of our kernel home range estimate we regressed the percentage of GPS collar

locations that occurred within the burn by the estimated percentage home range burned. This

regression allowed us to characterize moose as using non-burned (<25% of their home range

burned n=17) and burned habitat (>25% of their home range burned n=23). Home ranges for

VHF-collared moose were estimated, because actual locations were obtained only during survey

flights and at mortality sites. Survey locations for neonates of GPS collared moose (see below)

always occurred within their 60% core home range, thus, for VHF-collared moose, home ranges

were estimated by buffering these locations to the average home range size of all GPS collared

moose (34 km^2). The percent of the estimated home range that burned was then calculated to

determine habitat use and assign individuals into the appropriate group (burned and non-burned).

A total sample of 79 moose were classified as using burned (n=44) and non-burned (n=35)

summer ranges by combining GPS (n=40) and VHF (n=39) collared moose. Remaining moose

could not be classified into these groups because they died in late winter before summer home

range use could be determined; three were captured related mortalities.

Vital rate estimates

We used a multi-year set of demographic data from marked individuals to assess the influence of

burning on pregnancy, births, twinning, and survival of neonates, calves, and adults. During

captures (2005-2009), blood was collected to assess pregnancy using pregnancy-specific protein

B (Huang et al. 2000). Pregnancy was not estimated in 2009 due to a low number of sampled

moose. Because pregnancy was not estimated in all years, we were not able to estimate true

parturition rates. We instead calculated the proportion of radio-collared females that gave birth

annually. Because peak parturition typically occurs around 25 May (Bowyer et al. 1998, Testa et

al. 2000), we conducted helicopter surveys to determine if radio-collared moose had a calf at side during the first week of June, and the third week of July to assess births and neonate survival, respectively. Twinning rates were calculated as the number of twinning events recorded divided by the total number of females that gave birth. Each collared female that gave birth was subsequently relocated on winter range to determine annual calf survival. To determine whether reproductive and recruitment parameters were influenced by burning we used general linear models (PROC GENMOD, SAS v. 9.2, Cary, NC) with binary response variables of each vital rate and categorical explanatory variables for burning and year effects. All annual vital rates were estimated based on a biological year starting 1 June and ending 31 May. Variances for the vital rates were estimated based on the variance of the binomial distribution (Akcakaya 2002).

Attempts were made to locate all radio-collared moose monthly via ground or aerial telemetry to monitor adult female survival. Using the Kaplan-Meier approach, which accounts for staggered entry into the study (Pollock et al. 1989), we calculated annual estimates of female survival using the R statistical package version 2.13 (http://cran.r-project.org/). From 2005-2010, 20 of 47 mortalities occurred in the first spring after initial capture, prior to spring migration, which precluded identification of summer habitat use for those individuals. Therefore, data were pooled and adult female survival rates were estimated using all individuals regardless of known summer habitat use, which allowed for a more robust estimate of overall survival. Because we did not radio-collar yearlings, we estimated yearling survival using values from studies that reported both annual adult female and yearling moose survival under various conditions (e.g., Kunkel and Pletscher 1999, McLaren et al. 2000). We calculated the average percent difference between the two rates and subtracted that difference from our empirical

estimate of adult survival, maintaining yearling survival as a consistent proportion of adult survival.

Population modeling and life table response experiment

To test for the influence of wildfires on moose population growth rate (λ), we created two demographic matrix models for animals using burned (H_b) and non-burned (H_{nb}) summer ranges and parameterized them with habitat-specific demographic rates, where applicable. Each matrix was a 3 x 3 stage-structured post-birth matrix model (Caswell 2001). The basic form or the population projection matrix, H_{hab}, was:

$$H_{hab} = \begin{bmatrix} 0 & 0 & S_a F_{hab} T \\ S_{c,hab} & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix}$$

where the matrix elements were composed of vital rate estimates including calf survival [$S_{c,hab}$; where the hab subscript denotes populations using burned (b) or non-burned (nb) summer habitat], yearling survival (S_y), adult female survival (S_a), proportion of females that gave birth to a female calf (F_{hab}), and probability of being born a twin (T). We assumed a 50:50 sex ratio at birth. Because only adult females were captured during this study, we could not estimate yearling fecundity from our own data. Houston (1967) reported yearling pregnancy rates of 5-6% when this moose population was exhibiting exponential growth. Because this population has been declining for ~20 years and overall adult pregnancy rates are relatively low, we assumed no breeding of yearlings in our model. To assess the accuracy of the population growth rate generated from the demographic matrix model, we estimated the population growth rate from trend counts data as e^x where x is the arithmetic mean of $\ln(N_{t+1}/N_t)$ from 1988 to present.

From burned and unburned matrices we calculated the difference in λ attributed to habitat variation as $\Delta\lambda = \lambda_{nb} - \lambda_b$, where λ_{nb} is from the non-burned matrix and λ_b from the burned matrix. We used a Life Table Response Experiment (LTRE; Caswell 2001) to evaluate the vital-rate differences driving our estimate of $\Delta\lambda$ between the two matrices. Sensitivities for the LTRE were calculated from a matrix using vital rate averages between H_b and H_{nb} in Matlab (2010a; MathWorks, Natick, Massachusetts, USA). We then modified the program limitsens.m (Morris and Doak 2002; www.sinauer.com/PVA) for our study, using vital rate means and their associated variance estimates. We conducted a parametric bootstrap (n=1000 model runs) to generate 95% confidence intervals for the mean λ for each matrix type. For all matrix simulations, we based T (the probability of twinning) off the actual twinning probability (t) using the equation $T = ((1-t)+(2t))$ which constrains T to be ≥ 1.

RESULTS

Vital rate estimates

Vital rates of moose differed consistently between burned and non-burned summer ranges. Pregnancy rates of captured moose were greater in non-burned (97.06 ± 2.9%) compared with burned habitat (83.72 ± 5.7%; χ^2_1=5.15, *P*=0.023; Fig. 3.3a). Rates of pregnancy were similar among years, but within a given year pregnancy was consistently lower in burned relative to non-burned habitat. More females gave birth to calves in non-burned (82.35 ± 6.6%) than in burned habitat (59.26 ± 6.7%; χ^2_1=4.51, *P* =0.034; Fig. 3.3b), and birth rates in 2009 (mean=44.4%) were lower following the harsh winter of 2008 than in all other years (*P*=0.02). Interestingly, we documented an effect of capture on the probability of giving birth. Moose handled in a given

year (Feb) were less likely to give birth (early June) than moose that were not handled. In the spring following capture, handled moose were more likely to give birth in non-burned (40.63 ± 8.8%) than burned habitat (16.67 ± 5.8%; χ^2_1=4.85, P =0.028; Fig. 3.3b); no difference was detected among years. This result supports a negative effect of wildfires on individual nutrition and productivity. There was no difference in twinning rates (P=0.133) between non-burned (10.81 ± 5.2%) and burned habitat (2.63 ± 2.6%), thus data were pooled to estimate this vital rate. The overall twinning rate was estimated as 6.67 ± 2.9%. Neonates were also more likely to survive if born to moose using non-burned (68.29 ± 7.4%) compared with burned habitat (46.15 ± 8.1%, χ^2_1=5.68, P =0.017; Fig. 3.3c); annual variation was also evident, with neonate survival in 2007 (mean=74.5%) being higher than in all other years (P=0.03). Neonate survival was consistently lower among years in burned relative to non-burned habitat. Annual calf survival (which includes the neonate period) was greater for calves born to moose using non-burned (51.35 ± 8.3%) compared with burned habitat (28.95 ± 7.5%; χ^2_1=4.98, P=0.026; Fig. 3.3d); no difference was detected among years. Calf survival was consistently lower in burned than non-burned habitat for all years of study.

Adult female survival, typically a stable vital rate in ungulate populations (Gaillard et al. 2000), was highly variable among years, ranging from a high of 94.1% in 2006 to a low of 64.7% during a long and severe winter in 2008 (Fig. 3.4). Mean adult survival was 80.55 ± 3.6%. Past studies (e.g., Kunkel and Pletscher 1999, McLaren et al. 2000) reported that mean yearling survival was on average 6.43% lower than adult survival; thus we estimated yearling survival as $S_y = S_a$ - 6.43% or 74.12 ± 3.6%.

Population modeling and life table response experiment

Population growth rate for the entire population ($\lambda=0.914$) using the mean vital rates from both habitats was considerably below the stable population growth rate ($\lambda=1$). Population growth rates calculated with vital rates from the burned and non-burned matrices were also below the stable population growth rate irrespective of habitat, with a higher λ estimated in non-burned ($\lambda=0.954$; 95% CIs = 0.891, 1.012) compared with burned habitats ($\lambda=0.877$; 95% CIs = 0.8112, 0.936; Fig. 3.5). In non-burned habitats, sensitivity of λ was greatest for adult female survival, followed by fecundity, calf survival, and yearling survival. In burned habitats sensitivity of λ was also greatest for adult female survival; however, the next strongest influence was calf survival, followed by fecundity and yearling survival. The population growth rate from trend count data was estimated as $\lambda=0.957$, which was only slightly higher than the overall λ estimate of 0.914 from the matrix.

Results from the LTRE revealed that calf survival explained 1.7 times more variation in λ than did fecundity between burned and non-burned (Fig. 3.6). Although the sensitivity of λ to fecundity was greater than to calf survival, the difference in sensitivity between these vital rates was marginal. The change in calf survival between the two habitat types was approximately twice the change in fecundity. The contribution of adult and yearling survival to the LTRE, however, was zero because these vital rates could not be estimated separately for each habitat.

DISCUSSION

Habitat quality can strongly influence ungulate demography (Testa and Adams 1998, Tollefson et al. 2008), and disturbance can alter the distribution of high-quality habitats on the landscape. Despite its importance, a general understanding of how disturbance-induced habitat changes influence ungulate population performance has yet to emerge. Our study successfully connected

habitat use to the demographic performance of moose, a task that has been rarely achieved in studies of large ungulates. Roughly two decades after the severe Yellowstone wildfires, we documented ongoing impacts of this disturbance on the demography of a large herbivore. Use of poor quality (i.e., burned) habitat depressed reproduction and recruitment (Fig. 3.3), resulting in lower population growth compared with moose using higher quality non-burned habitat (Fig. 3.5). Differences in calf survival coupled with those in fecundity produced a $\approx 8\%$ change in λ, illustrating the importance of ungulate recruitment dynamics to population growth. Overall, our results suggest that decreased forage quality following the 1988 wildfires (Vartanian, Chapter 2), coupled with high site fidelity, are negatively influencing moose demography more than 20 years post-fire, which is at odds with the generally positive influence of fire on Alaskan moose (Davis and Franzmann 1979). Our work suggests that wildfire on the summer ranges of these migratory moose is partially responsible for the continued population declines observed in this population, and our findings are consistent with those of Tyers (2006) who reported negative effects of the 1988 fires on moose in northern Yellowstone.

Life-history theory, as related to large ungulates, has identified consistent relationships between numerous vital rates (i.e., neonate and calf survival, and fecundity of young females), and environmental variation and density (Gaillard et al. 2000). In agreement with these generalizations, neonate and calf survival in our study were strongly influenced by wildfires on summer ranges and were highly variable from year to year in both types of habitats; rates in burned habitat were 22% and 23% lower than in non-burned habitat, for neonate and calf survival, respectively. Decreased neonate survival in burned habitat may be the result of decreased maternal investment in young, a strategy to minimize deterioration of female condition in areas of poor nutrition (Heard et al. 1997, Festa-Bianchet and Jorgenson 1998). During

63

drought years in north-central New Mexico, mule deer fawn survival was nearly zero, but survival and litter size increased significantly with above average precipitation, likely due to increased maternal condition (Lomas and Bender 2007). Results of the LTRE suggest that calf survival explains the greatest proportional change (0.63) in λ (Fig. 3.6), which is in agreement with a growing number of studies suggesting that juvenile survival is the primary driver of population dynamics for temperate ungulates (Unsworth et al. 1999, Gaillard et al. 2000, Raithel et al. 2007). Overall, these demographic patterns support the general notion (Gaillard et al. 2000) of a strong influence of environmental and habitat variation on temperate ungulates in their first year of life.

Typically, adult female survival and adult fecundity are high, fairly stable, and not often influenced by environmental variation; however, some annual variability in adult fecundity has been documented (Gaillard et al. 2000). Our findings stand in contrast to these general expectations. Although we did not document differences in adult female survival between habitat types , possibly due to winter mortality rates, it was highly variable from year to year, greater than has typically been reported elsewhere (e.g., Bangs et al. 1989, Ballard et al. 1991). Birth rates were also influenced by wildfire modification of summer ranges, with birth rates 23% and 24% lower in burned compared with non-burned habitat for non-handled and handled moose, respectively. Pregnancy rates of adults were fairly stable, remaining relatively constant from 2004-2006 but declining in 2007 during a long and severe winter. Although relatively stable, pregnancy was greater for moose that used non-burned compared with burned summer habitat, likely a function of decreased maternal condition of moose using burns. Our identification of habitat-specific differences in birth rates and pregnancy rates, and high annual

variability in birth rates and adult female survival fits well with the life-history expectations of a nutritionally stressed population.

It is well documented that forage constraints in winter can result in decreased survival and recruitment in temperate ungulates (Skogland 1985). Our evaluation of forage quality for this population (Vartanian, Chapter 2) suggests that winter forage quality was lower than that of summer and relatively homogeneous across the entire shared winter range. Thus, because these moose are subject to similar nutritional constraints during winter, winter forage quality cannot explain the variation in vital rates we observed. After spring migration, however, moose return faithfully to their respective summer ranges. These patterns of fidelity create two distinct population segments: those summering in burned areas and those summering in non-burned areas. In agreement with our predictions, summer habitat quality influenced multiple vital rates (Fig. 3.3). Moose using burned habitats performed less well in terms of pregnancy, probability of birth, and neonate and calf survival compared with moose using non-burned habitats. This is in agreement with previous research on elk and mule deer, which reported decreased probability of pregnancy and twinning, growth and fat accumulation, and overwinter survival of calves that received poor summer-autumn nutrition (Cook et al. 2004, Tollefson et al. 2008). In contrast to research by Tollefson et al. (2008), we did not observe reduced twinning rates in low quality (i.e., burned) habitat, however, this may be an artifact of small sample size. A total of five twinning events were observed over six years, of which, only one was associated with burned habitats. The high degree of annual variability in adult female survival observed in our population is likely related to decreased condition entering winter (Cook et al. 2004), making moose more sensitive to winter severity. Indeed, the lowest survival rate we estimated (64%) followed a long, severe winter when starvation was prominent. The high variability and lower

than average vital rates observed in our study support the notion that changes to summer forage quality and nutrition brought about by disturbance can be important drivers of ungulate demography and population performance.

Disturbance can be beneficial for large herbivores when they are able to exploit the heterogeneity in forage resources that it produces (Hobbs and Spowart 1984, Long et al. 2008). For this population, patterns of site fidelity may constrain the ability to optimally forage amid summer ranges transformed by wildfire. Such patterns of fidelity are not uncommon for moose populations, even in the face of disturbance (Andersen 1991, Sweanor and Sandegren 1989). The strength of fidelity is such that, Bailey and Franzmann (1983) suggested that moose using unfamiliar areas following disturbances, including wildfires, may exhibit lower survival than moose occupying familiar habitat. These inferences, however, come from a study of captive moose and may not apply to wild populations. Other studies in which moose exhibit high seasonal range fidelity, reported that annual home range overlap varied from year to year in disturbed (Tyers and Irby 1995) and undisturbed habitats (Cederlund et al. 1987). Although we do not know whether changes in home range overlap occurred following wildfire in our study area, individuals typically use the same migration routes and return to the same summer home ranges regardless of whether or not those habitats are burned (Becker 2008). Thus, it is likely that moose did not abandon their summer home ranges post-fire and that high fidelity to these low quality ranges is partially responsible for the observed decrease in demographic rates.

Moose throughout the southern GYE coexist with a suite of native predators and they represent alternative prey for grizzly bears, wolves and mountain lions. In Alaska, where moose are the primary prey species, predation can maintain moose populations at low densities (Gasaway et al. 1992). Predation of moose by wolves and grizzly bears has been documented in

this system (Mattson 1997, Smith et al. 2003); however, elk are the primary prey of these predators in the GYE (Smith et al. 2003, Barber-Meyer et al. 2008). Although predation by wolves and grizzly bears may have contributed to the observed population declines, our research suggests that poor nutrition, brought about by changes to summer habitat (Vartanian, Chapter 2), is a contributing factor to the decline of this moose population.

The population growth rate from the trend counts (λ=0.957) was a good fit to the estimate from the demographic data. The stochastic lambda (i.e., population growth rate estimated from trend count data) suggests that the population is declining 4-5% per year, which is in agreement with the demographic growth rate from the non-burned portion of the population (i.e., higher estimated growth rate). This result may be explained by a diminishing influence of moose using burns to the overall population decline as their numbers are declining more rapidly than moose using non-burned habitats.

Taken together, demographic evaluation and population modeling of this moose population confirms that the population is in a declining phase and that declines are most severe for the portion of the population that summer in burned areas. Rates of birth and calf survival, between burned and non-burned habitat created considerable differences in population growth rate. Although population trajectory for both groups of moose is negative, population growth was $\approx$ 8% lower for the portion of the population using burns. For moose summering in non-burned habitat, the upper 95% confidence interval (λ=1.012) overlaps with λ=1 (Fig. 3.5), indicating that during good years this portion of the population may remain stable. The upper 95% confidence interval (λ=0.936) for the portion of the population using burned habitat is of particular concern and suggests that lower recruitment among animals using burned areas may have contributed most to recent declines. The trend of lower vital rates and λ for moose

summering in burned areas suggests that these fires have also been a force influencing the relative abundance and distribution of moose: there are likely fewer moose now that have cultural knowledge of the migration routes and behaviors necessary to access these habitats. Thus, unlike the benefits of wildfire reported for Alaskan moose, wildfires in northwest Wyoming have contributed to population-level declines in Shiras moose for 22 years post fire, and it is unknown how long these impacts will remain. Romme et al. (2011) reported both short- and long-term impacts of the 1998 Yellowstone wildfires on tree densities, stand structure, soil nitrogen, stream sediment load, and insect biomass, among other ecological processes. Our work suggests that the ecological legacy of these fires also includes reduced moose demographic performance due to the influence of this disturbance on their summer habitats.

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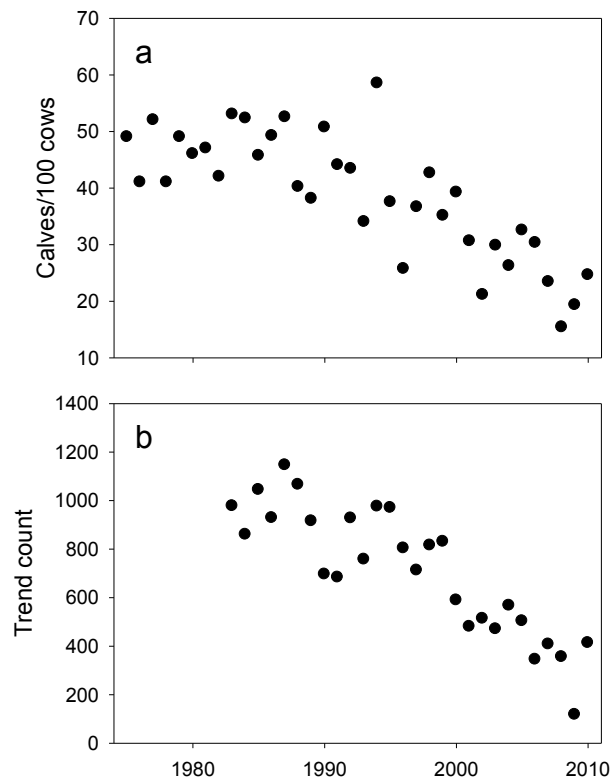
Figure 3.1. Winter calf:cow ratios (a) and population trend counts (b) obtained by Wyoming
Game and Fish Department depict moose population declines in the study population beginning
in the early- to mid- 1990s.
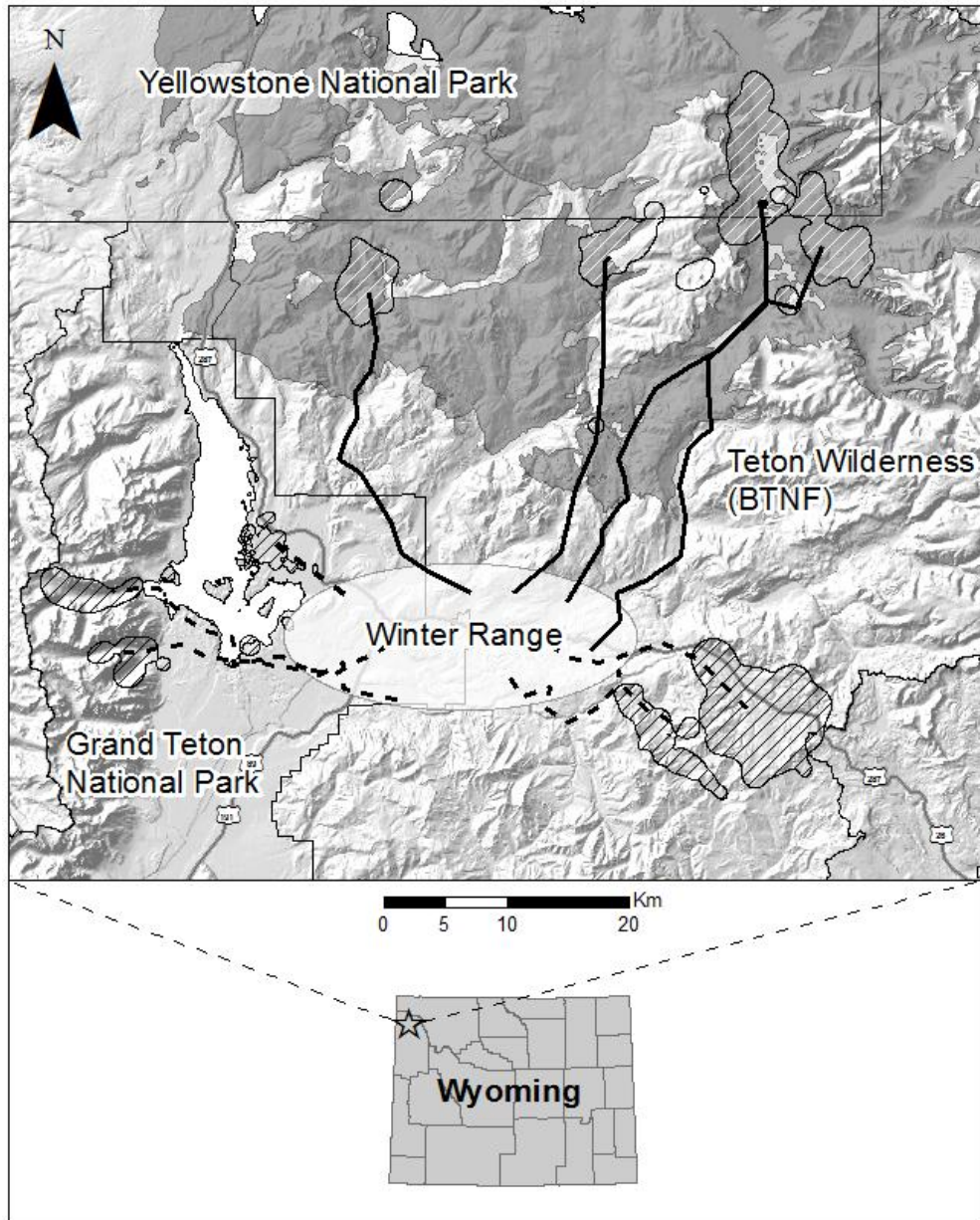
Figure 3.2. Project study area with public land ownership, depicting seasonal migrations of moose from a common winter range to individual summer home ranges. Migrations to burned home ranges (white hatched polygons) are shown as a solid line and to non-burned home ranges (black hatched polygons) are shown as a dashed line. The 1988 Yellowstone wildfires are depicted by the dark gray area, and water bodies are depicted by white shapes.
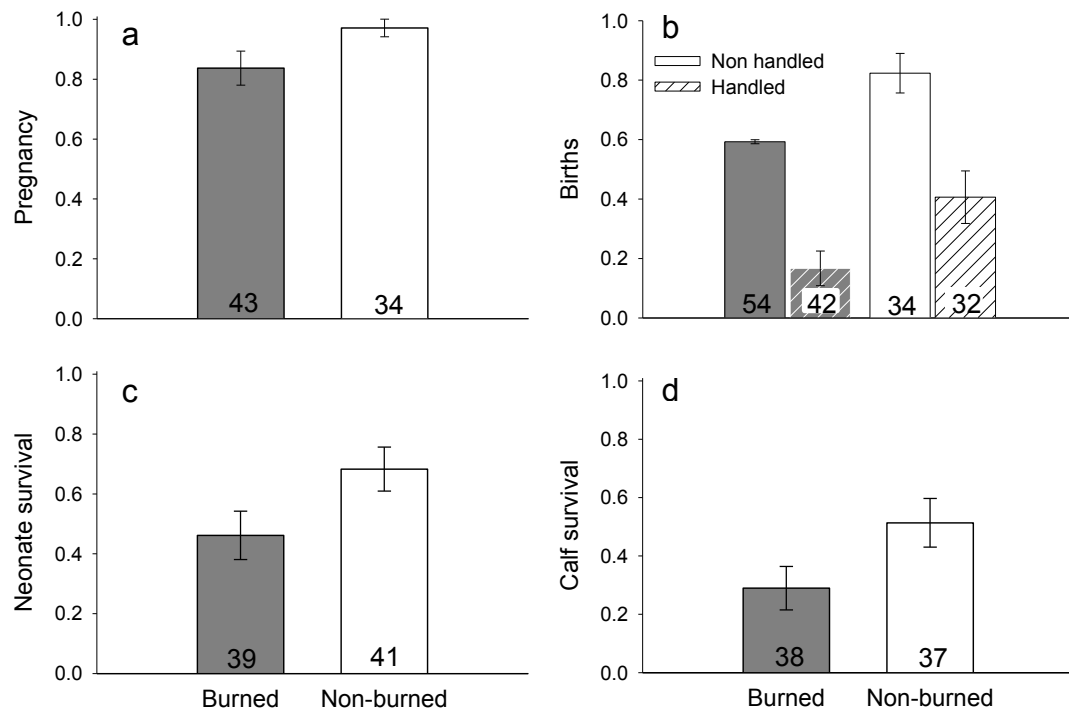
Figure 3.3. Demographic rates of migratory moose in the southern GYE for individuals summering in burned and non-burned habitat. The proportion of a) adult females pregnant at capture (mid Feb), b) adult females that gave birth (handled moose are depicted by hatching), c) neonates that survived, and d) calves that survived to winter (mean $\pm$ SE), were lower for moose using burned compared with non-burned habitats ($P<0.05$). Sample sizes are shown inside bars.
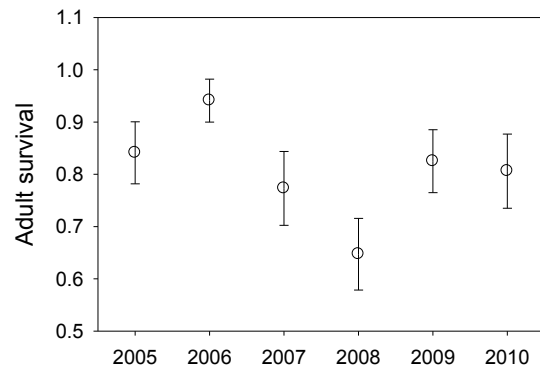
Figure 3.4. Adult female survival estimates (mean ± SE) for moose in the southern GYE showed

considerable annual variability. The low rate of survival observed in 2008 was the result of high

winter mortality incurred over a long, severe winter.
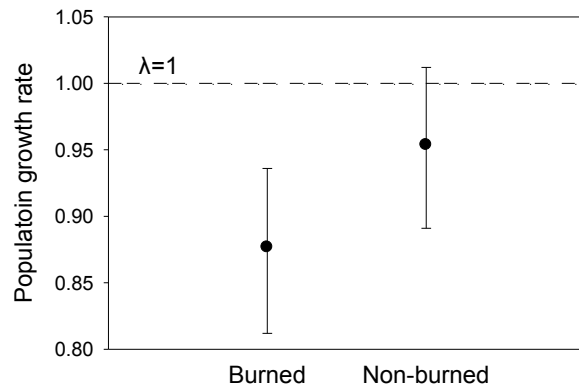
Figure 3.5. Modeled population growth rates (λ) for migratory moose summering in burned vs.

non-burned habitat. Error bars are 95% bootstrapped confidence intervals.
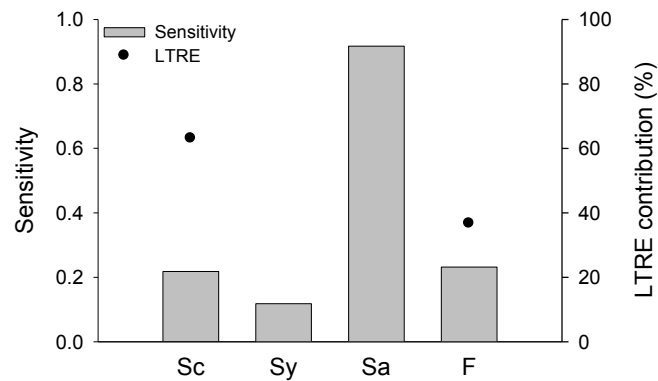
Figure 3.6. Sensitivity of λ (bars) and percent contribution of the LTRE (closed circles) for moose vital rates used in modeling population growth. Vital rates are calf survival (S_c), yearling survival (S_y), adult female survival (S_a), and fecundity (F). No contribution to the LTRE is shown for adult and yearling survival, because we could not evaluate differences in these vital rates between burned and non-burned summer habitats.

CHAPTER FOUR - GENERAL DISCUSSION

By evaluating variation in habitat quality between- and within-seasons we found a disparity in the nutritional quality of summer habitat, related to the 1988 Yellowstone wildfires. We then determined that the disparity in summer nutrition explained variation in all but two of the demographic variables we monitored, resulting in differences in population growth between moose using non-burned compared with burned habitats. Thus, we were able to successfully connect use of high quality habitat (i.e., non-burned areas) to higher demographic performance for a migratory moose population.

For many migratory species, seasonal habitats have the potential to limit populations. Researchers have shown that attributes of both winter and summer can negatively influence ungulate performance (Portier et al. 1998, Cook et al. 2004). For example, density dependent food limitation decreases ungulate survival and reproductive performance (Skogland 1985, Stewart et al. 2005). Our study population, however, is at a post-colonization low, and our results indicate that winter and summer range forage is sufficient to support a larger population of moose. Thus, browse condition and forage availability do not appear limiting for this population.

Nutrition also influences ungulate demography. Recent studies have reported that poor summer nutrition can negatively influence demographic performance (Post and Klein 1999, Kumpula and Colpaert 2003) and lifetime reproductive success (Gaillard et al. 2000a). Because most ungulate forage is dormant during winter, the nutritional quality of forage is lower in winter than summer (Renecker and Hudson 1988, Larter and Gates 1991). The quality of forages and diets in our study were homogenous and of lower quality in winter than in summer, indicating

that all moose are subjected to the same nutritional conditions in winter regardless of their distribution. In summer, however, wildfires created heterogeneity in the quality of forage and diets; burned habitat was of lower quality than non-burned habitat. Although both summer habitats were of higher quality than winter, diets in burned habitats were only marginally (i.e., 6.7 percentage units) more digestible than diets in winter, whereas diets in non-burned habitats were substantially more digestible (i.e., >16 percentage units) than diets in winter. Thus, the results of our research support the suggestion by Cook et al. (2004) that, in some ecosystems, the effects of summer-autumn nutrition may be more limiting than winter.

Because habitat can strongly influence ungulate demography (Testa and Adams 1998, Tollefson et al. 2008), the potential exists for variation in summer nutrition, due to wildfires, to influence demography and population growth of our study population. Thus, we monitored a suite of demographic rates including pregnancy, births, twinning, and neonate, calf and adult female survival. We found that pregnancy, probability of giving birth, and neonate and calf survival, were negatively influenced by use of low-quality (i.e., burned) summer habitats. Twinning rates were not different between the two habitats; however, our sample size was low. Research has reported that poor summer nutrition can negatively influence reproductive success, juvenile body mass, calf growth rates, and over-winter survival in other ungulate taxa (Cook et al. 2004, Monteith et al. 2009). Although we did not assess growth rates, our study supports research which suggests that poor summer nutrition negatively influences ungulate demography (Cook et al. 2004, Tollefeson et al. 2008).

Unfortunately, we were unable to assess differences in adult female survival between the two subsets of the population using our full data set. Twenty of the 47 documented mortalities occurred before characterization of summer habitat use was possible. Although using the

remainder of our sample, adult female survival was similar between habitats; we documented

large annual fluctuations from 64-94% in adult female survival, which is atypical of large

ungulate populations (Gaillard et al. 1998, Gaillard et al. 2000b) and indicative of a nutritionally

stressed population. Annual environmental variation such as temperature or precipitation may

also contribute to such fluctuations. Moose are sensitive to thermal stress (Renecker and Hudson

1986), and Coughenour and Singer (1996) reported that mortality of adult elk (*Cervus elaphus*)

in Yellowstone was influenced by precipitation. For declining populations, understanding the

influence of such environmental variation on adult survival is complicated because their effects

can interact with predation (Owen-Smith et al. 2005). Although we did not evaluate temperature

and precipitation, the potential exists for them to influence this population.

Using the results from two deterministic post-birth population models, we successfully

connected the use of poor quality habitats to reduced population growth. Although the entire

moose population is declining with $\lambda < 1$, the estimated λ for moose using high-quality summer

habitat was $\approx 8\%$ greater than the estimated λ for moose using low-quality summer habitat. Thus,

although summer nutrition appears to be limiting for the portion of this population using low-

quality summer habitat, other factors such as warming temperatures due to climatic shifts and

predation may also be contributing to the observed decline.

MANAGEMENT IMPLICATIONS AND RESEARCH NEEDS

The Shiras moose population inhabiting habitats northeast of Jackson, Wyoming has been

declining since the early- to mid-1990s. Our research suggests that at least a portion of the

observed decline is related to changes in the quality of summer habitat, attributable to the 1988

Yellowstone wildfires. This complex of wildfires burned fast and hot, resulting in 80-100% tree

mortality in severely burned areas (Abendroth 2008) and decreased nutritional quality of moose

forage within the burns (Chapter 2). These moose have high fidelity to their summer home

ranges (Becker 2008) regardless of the extent to which their home range burned; many individual

summer home ranges were entirely within burned areas. The quality of diets within burns

resembled that of available forages, suggesting that fidelity patterns inhibited moose from

exploiting high quality habitats following these landscape-scale disturbances.

Furthermore, because moose are easily heat stressed, decreased cover associated with

these burns has the potential to influence metabolism, heart rates, respiration rates, and foraging,

which can result in summer weight loss (Renecker and Hudson 1986). Habitat use patterns may

also be altered (Flook 1959, Knorre 1959), further reducing moose condition by increasing the

time necessary to meet thermoregulatory needs instead of foraging. To address the potential for

loss of cover to influence autumn moose condition or performance, research to assess behavioral

changes or habitat selection in response to thermoregulatory needs in altered habitats is

warranted.

Our ability to manage the portion of the moose population using burns is limited because

the burned areas reside within federally designated wilderness and Yellowstone National Park.

Thus, the potential to implement habitat enhancements such as low intensity prescribed burns

and mechanical treatments on burned summer range is unlikely. Although conducting habitat

enhancements on winter may increase the quality of winter forage via increased nutrition (Hobbs

and Spowart 1984), moose share winter range with a large elk herd and increased competition by

elk for high quality browse may mitigate the benefits of such efforts. Currently, habitat

enhancements aimed at increasing winter browse abundance do not appear necessary because

peripheral winter range areas, characterized by low browsing intensity and equivalent nutrition to

core winter areas, are abundant. Thus, if habitat enhancements to increase forage quality are implemented on winter range they should be conducted with careful planning to minimize the potential for any negative impacts.

Fortunately, a portion of this moose population does not use areas influenced by the 1988 wildfires or under "natural regulation" policy (i.e., wilderness areas), and has access to higher quality forage and the resulting increased nutrition obtained via diet selection. Modeling results indicate that the population growth rate for moose using high quality habitat has confidence intervals overlapping with 1; indicating that in good years this portion of the population can replace itself, although it is declining on average. The majority of this portion of the population resides on national forest and portions of Grand Teton National Park in summer. Thus, through interagency cooperation and planning, successful implementation of summer range habitat enhancements are possible and suggested. If successful in improving the quality of summer forage, these enhancements may contribute to increased demographic performance and population growth for this segment of the population. To assess if habitat enhancements are benefiting moose via increased forage quality and to determine the onset and duration of the benefit, we encourage post-enhancement monitoring of forage quality.

Further investigation of other causes with the potential to influence the demography of this population, such as predation and climate appears warranted. During the course of this study, we monitored moose survival, and when possible, assessed cause of death (O'Gara 1978) and condition at time of death via determination of percent bone marrow fat (Neiland 1970). Although the majority of winter moose mortality was attributed to starvation and other natural causes such as disease, we did document predation of adult female moose in late-winter and early-spring by grizzly bears, wolves and mountain lions. Examination of percent bone marrow

fat indicated that the majority of moose were in poor (moderate-starvation) condition at time of death, with bone marrow fat as low as 7.67%. These observations suggest that predation is not a major contributor to the observed declines, but they are inconclusive because we did not assess the role of predation directly and we did not evaluate predation of moose neonates.

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