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Seasonal movements, habitat selection, physiological health, and demography of Shiras moose (*Alces alces shirasi*) were studied in the Jackson Valley of northwest Wyoming. Moose congregated on low-elevation ranges during winter and migrated to more dispersed, mid-elevation ranges during summer. Moose selected winter habitat dominated by deciduous shrubs, whereas they selected summer habitat that was more variable. Blood parameters indicated that moose were in moderate physical condition. Ultrasonic rump fat measurements were relatively high, but there were indications of nutritional deficiencies. Diseases and parasites appeared to have minimal population-level effects. Population modeling suggested that the moose population was more likely to be declining than stable or increasing and the population growth rate was influenced primarily by late-winter and early-spring adult female mortality. Pregnancy rates were high, but calf production was relatively low. Neonate and annual calf survival were relatively high. Habitat quality appeared to be the primary factor limiting population growth while the effects of predation appeared to be less important.

HABITAT SELECTION, CONDITION, AND SURVIVAL OF SHIRAS MOOSE IN NORTHWEST WYOMING

by
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DEDICATION

Dedicated to the memory of:

Stanley H. Anderson

1939 – 2005

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1

GENERAL INTRODUCTION

It is generally believed the first modern moose (*Alces alces*) arrived in North America from Siberia via the Bering land bridge during the last ice age 10,000–14,000 years ago (Peterson 1955, Bubenik 1997, Bowyer et al. 2003, Hundertmark et al. 2003). With the retreat of the continental glaciers, moose began to inhabit portions of North America once covered with ice, although the exact patterns of dispersal and speciation are debated (Peterson 1955, Bubenik 1997, Bowyer et al. 2003, Hundertmark et al. 2003). Nevertheless, 4 distinct subspecies of moose evolved in North America, each strongly associated with the distribution of coniferous forests. The Eastern or Taiga moose (*A.a. Americana*) occur from Ontario, Canada eastward to the Atlantic Ocean; the Northwestern moose (*A.a. andersoni*) inhabit the region from western Ontario, Canada and northern Michigan, USA to British Columbia and the Yukon Territory, Canada; Alaskan moose (*A.a. gigas*) primarily inhabit Alaska, USA, but also occur in western Yukon Territory, Canada; and Shiras moose (*A.a. shirasi*) inhabit the Intermountain West along the Rocky Mountains from Colorado, USA to southern Alberta and southeastern British Columbia, Canada (Bubenik 1997).

Few, if any, moose existed in Wyoming prior to 1850 (Houston 1968, Brimeyer and Thomas 2004). Between 1834 and 1843, Osborne Russell traveled extensively throughout western Wyoming and kept a detailed journal of his travels yet never mentioned observing a moose although descriptions of other wildlife species were noted (Haines 1955). Sporadic observations of moose occurred in northwest Wyoming after

1850 (Houston 1968), but it is believed the population did not begin to increase and expand until after the establishment of Yellowstone National Park (YNP) in 1872 (Peterson 1955, Denniston 1956). By the late 1890s and early 1900s, observations of moose in the Jackson Valley were on the rise (Peterson 1955). Houston (1968) believed that a self-sustaining moose population in the Jackson Valley occurred shortly before 1912 via emigrations from YNP.

Moose management in Wyoming began shortly after moose appeared in the state (Blair 1987). In 1882, the first hunting seasons for moose were set from 1 August through 15 November in an attempt to protect the species from overexploitation. However, by 1899, moose numbers were in decline so the Wyoming legislature granted moose full protection from harvest for at least 10 years (Brimeyer and Thomas 2004). By 1912, there were an estimated 500 moose in Wyoming, predominately in the northwest region, and populations were deemed large enough to sustain limited harvest (Brimeyer and Thomas 2004). From that time, moose populations have continued to increase in Wyoming and, through natural emigration or translocation, currently occupy almost all available habitats in the state.

Concurrent with moose population expansion in northwest Wyoming was a large-scale predator reduction program to protect livestock and game animals (Blair 1987). During the late 1800s and early 1900s, state and federal predator removal programs greatly reduced large carnivore populations in the state. Gray wolves (*Canis lupus*) were extirpated by the 1930s (Weaver 1978, Wyoming Game and Fish Department [WGFD] 2007*a*) while cougar (*Puma concolor*) and grizzly bear (*Ursus arctos*) numbers were reduced. By 1940, most grizzly bears were restricted to YNP (Blair 1987). Grizzly bears were listed as “threatened” under the Endangered Species Act in 1975 (Fed. Reg. 40:145, 31734-31736) and since the early 1990s, have steadily expanded their range in the Greater Yellowstone Ecosystem (Schwartz et al. 2006). Gray wolves were reintroduced into YNP in 1995 and 1996 (Bangs and Fritts 1996) and were first observed in the Jackson Valley during the winter of 1997-1998 (Smith et al. 1999). At present, cougar populations are suspected to be increasing statewide (WGFD 2006). Although historical data are lacking for black bears (*U. americanus*), harvest data suggest a stable population trend (WGFD 2007*b*).

Early moose research in northwest Wyoming occurred during the period when large predators were less common. Most studies examined the winter food habits and social dynamics of moose in the Jackson Valley (Rudersdorf 1952, Denniston 1956, Harry 1957, Altmann 1959). Humans were presumed to be the primary predator of moose (Denniston 1956) and, due to the lack of large predators, several studies reported overutilization of winter ranges and a need to reduce wintering moose numbers (Rudersdorf 1952, Harry 1957). Houston (1968) provided extensive data on the habitat relationships, life habits, and population dynamics of moose in the Jackson Valley during the mid-1960s. He suggested that moose populations fluctuated between 1950 and 1966 in response to the condition of willows on winter range and periodic die-offs that occurred during severe winters. He also indicated that disease and parasites had little influence on the dynamics of the Jackson moose herd.

During the late 1970s, the north Jackson moose herd was in decline, possibly exacerbated by liberal harvest of antlerless moose (Figure 1.1; WGFD 1982). Therefore, antlerless moose licenses were reduced and moose responded by slowly increasing in numbers until the late 1980s (WGFD 1990). Additionally, there were concerns regarding a rise in the number of elk (*Cervus elaphus*) wintering in the Buffalo Valley that may have been competing with moose for winter browse. It was suspected that higher elk numbers were a result of conservative harvest during the 1980s, a series of mild winters, and public feeding programs (WGFD 1988). As a result, elk harvest was increased in 1989 (WGFD 1990) and elk winter range improvement projects were initiated to reduce the potential effects of competition. There was also a need to improve moose winter ranges (WGFD 1991) and several improvement projects were implemented in the early 1990s. Nonetheless, moose trend counts and calf-cow ratios began to decline in the late 1980s and early 1990s and it was suspected that the 1988 wildfires might have been more detrimental to moose than originally believed (WGFD 1991). Since the early 1990s, the population has continued to fluctuate, however, as of 2007, population trend counts were near levels observed in the late 1970s and calf-cow ratios were the lowest observed during the previous 30 years (Figure 1.1).

Because of this decline, research was initiated to determine the factors impacting the north Jackson moose herd. It was suspected that habitat quality had declined due to high moose densities, resulting in pregnancy rates that were among the lowest reported in North America (≈ 75%; Berger et al. 1999, Berger et al. 2001*a*). It was also suspected that because grizzly bears had recently expanded into the study area, naïve moose were more vulnerable to predation (Berger et al. 2001*b*) and, as a result, parturient moose increased their use of areas closer to roads to avoid bear predation (Berger 2007).

Although previous research provided much information regarding certain aspects of moose dynamics in northwest Wyoming, there was a need for research on specific aspects of Shiras moose ecology. Therefore, I utilized global positioning system (GPS) and very high frequency (VHF) radio collars to assess reproductive parameters, calf and adult survival, seasonal distribution, and seasonal habitat selection patterns. Furthermore, I examined the physiological health of this herd via blood, hair, and ultrasonic rump fat measurements. Information provided from this study can be used to assess potential mechanisms limiting the north Jackson moose herd and can provide a framework to direct future research to answer more specific questions.

Research Goals and Objectives

The primary goal of this study was to provide insight into the life-history characteristics of Shiras moose in northwest Wyoming and to use this information to examine potential factors contributing to the possible population declines recently observed in the north Jackson moose herd. The results can assist land and wildlife managers in identifying appropriate management strategies that can benefit moose populations in northwest Wyoming. There were three primary objectives:

(1) Investigate the seasonal distribution and habitat selection patterns of adult female Shiras moose in northwest Wyoming (Chapter 2);

(2) Evaluate the physical condition and nutritional status of adult female Shiras moose (Chapter 3); and

(3) Estimate reproductive parameters, calf survival, adult female and male survival, and the finite rate of population growth for the north Jackson moose herd and make preliminary inferences regarding potential limiting factors (Chapter 4).

In addition to the above objectives, I also investigated the spatial and temporal characteristics of moose highway crossings along a 9.7-km section of U.S. Highway 26/287 that bisects crucial moose winter range in the Buffalo Fork Valley of northwest Wyoming (Appendix A). These results can assist transportation and wildlife managers in identifying, evaluating, and implementing highway designs and mitigation that improve the safety of motorists by reducing the risk of moose-vehicle collisions while maintaining highway permeability for moose.

Thesis Organization

This thesis consists of five chapters, three of which are intended for publication in peer-reviewed scientific journals. Chapter 1 includes a general introduction that provides background information and my research objectives, while Chapter 5 includes general conclusions from my research and provides recommendations for management and future research. Chapters 2, 3, and 4 are in the format required for submission to appropriate scientific journals. The spatial and temporal characteristics of moose highway crossings is included as Appendix A and is in the format required for a final report that has been submitted to the Wyoming Department of Transportation.

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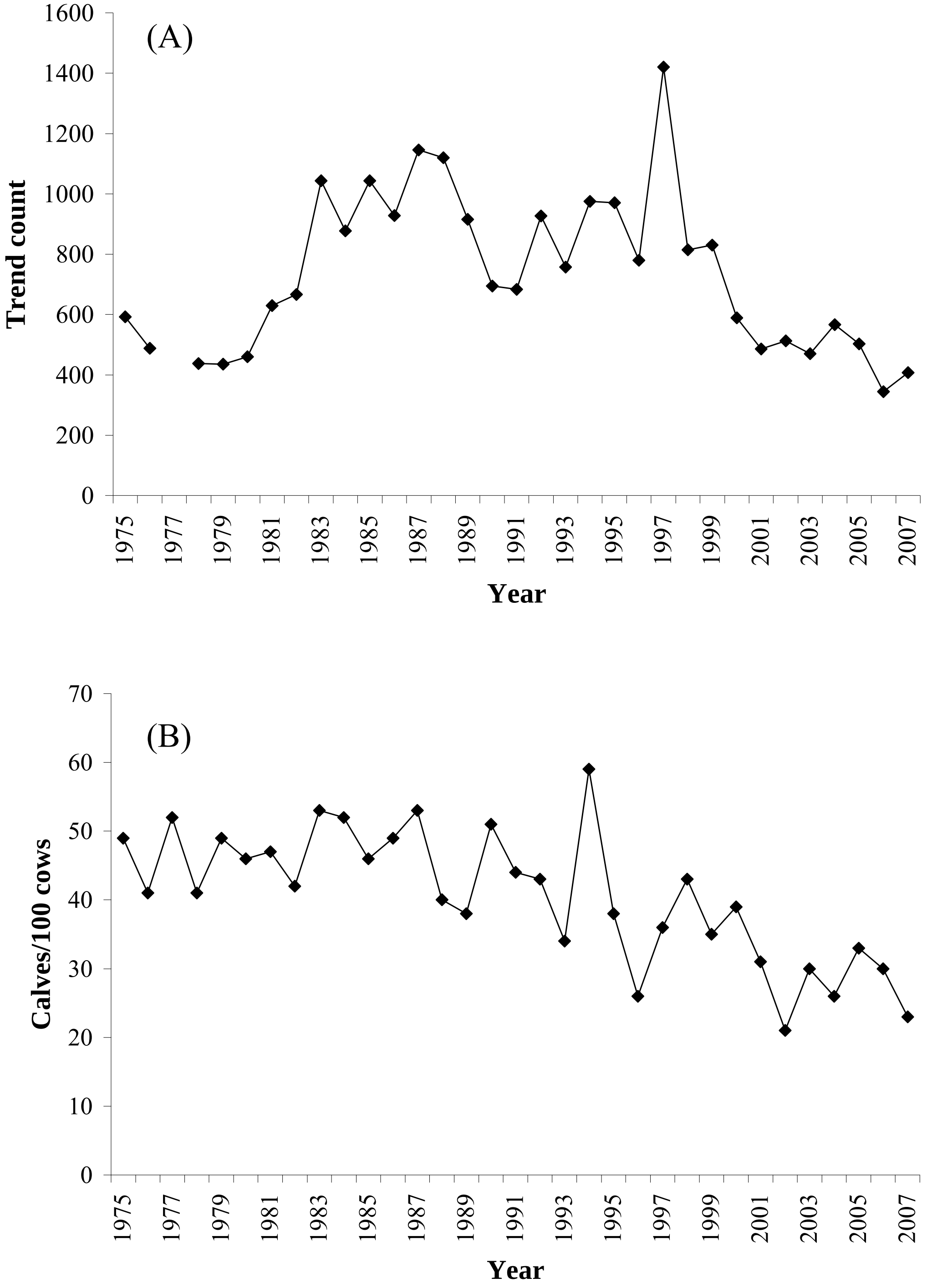

Figure 1.1. Jackson moose herd unit (A) population trend counts and (B) calf-cow ratios compiled from the Wyoming Game and Fish Department Jackson region big game herd unit reports, 1975-2007.

CHAPTER 2

SEASONAL MOVEMENTS AND HABITAT SELECTION OF ADULT FEMALE SHIRAS MOOSE IN NORTHWEST WYOMING

In the format of a paper in the *Journal of Wildlife Management*

INTRODUCTION

Because ungulates can migrate considerable distances between seasonal ranges, understanding their ecology requires the study of year-round habitat use patterns (Nicholson et al. 1997, Unsworth et al. 1998, Nikula et al. 2004). Although researchers and wildlife managers recognize this need, studies often focus on habitat selection during winter when resources are most limited and management actions are likely to benefit a large number of individuals (Hundertmark et al. 1990, Pearson et al. 1995, D'Eon and Serrouya 2005, Poole and Stuart-Smith 2006). However, several aspects of ungulate ecology act to link the dynamics of animals across seasonal ranges. For example, the overwinter survival of bighorn sheep lambs (*Ovis canadensis*) was influenced more by weather, and its potential effects on forage production, the previous spring than by the severity of winter conditions (Portier et al. 1998). Similarly, several studies have suggested that forage limitations on summer range can reduce maternal body condition resulting in decreased reproductive success the following year for elk (*Cervus elaphus*; Cook et al. 2004), caribou (*Rangifer tarandus*; Cameron 1994), muskoxen (*Ovibos moschatus*; Reynolds 2001), and moose (*Alces alces*; Testa and Adams 1998). These interrelationships among seasonal movements and the dynamics of populations challenge our understanding and management of many ungulate species (Gordon et al. 2004).

Moose are typical of temperate ungulates in which individuals within a population have distinct winter and summer ranges linked by migrations of varied distances (Edwards and Ritcey 1956, LeResche et al. 1974, DeMarchi 2003). Different migratory strategies have evolved to maximize individual fitness due to the seasonal availability of forage in temperate environments (Fryxell and Sinclair 1988). Migratory ungulates typically benefit by increasing their access to high quality forage during summer, whereas nonmigratory (i.e., resident) ungulates may remain on lower quality summer range but reduce their risk of predation (Nicholson et al. 1997, Hebblewhite et al. 2006). The availability of forage can also influence the size of seasonal home ranges. Resources are often restricted during winter due to snow accumulations, so moose generally seek winter habitats that provide for a high quantity of forage in a relatively small area (Dussault et al. 2005*a*). In contrast, summer home ranges are typically larger because the availability of forage is not limited by environmental conditions (Houston 1968, Cederlund and Okarma 1988, Kufeld and Bowden 1996). Thus, moose habitat selection patterns may be governed by the amount or quality of resources available on seasonal ranges (Peek 1997). In general, moose select for shrub-dominated, open habitats in winter, but may make use of closed-canopy areas as environmental conditions warrant (Philips et al. 1973, Matchet 1985, Hundertmark et al. 1990, Stephenson et al. 2006). As summer approaches, moose make use of a variety of open habitats then shift use to more closed-canopy areas during late summer possibly due to phenological changes in the quality of forage (Hjelford et al. 1990, Peek 1997). By understanding the spatial distribution of moose across the landscape, managers may be able to gain insight into habitat alterations that impact moose population performance.

The understanding of Shiras moose (*A. a. shirasi*) seasonal distributions and habitat selection in the Intermountain West is limited. Early research was primarily observational in nature and used univariate approaches on a limited number of individuals to assess movement and habitat selection patterns. Nonetheless, Shiras moose have been associated with low-elevation ranges during winter followed by movements of short-to-moderate distances to reach higher elevation ranges during summer (Knowlton 1960, Ritchie 1978, Pierce and Peek 1984, Kufeld and Bowden 1996). Several studies have described the importance of shrub-dominated habitats during winter (Knowlton 1960, Stevens 1970, Van Dyke et al. 1995, Kufeld and Bowden 1996) with a shift to closed-canopy coniferous forests during late winter (Houston 1968, Ritchie 1978, Matchet 1985, Tyers and Irby 1995). Where riparian habitats were limited, the use of mature coniferous forests that provide abundant cover and forage throughout winter were found to be most important (Peek 1974, Pierce 1984, Pierce and Peek 1984). Browse and forbs appeared to dominate summer diets of Shiras moose (Knowlton 1960, Houston 1968, Stevens 1970, Ritchie 1978), but mature coniferous forests, particularly lodgepole pine (*Pinus contorta*), that do not necessarily provide an abundance of forage have been described as an important component of summer habitats (Ritchie 1978, Kufeld and Bowden 1996).

This study was initiated because declining indices of population density and calf-cow ratios suggested a downward trend in Shiras moose numbers in northwest Wyoming. Moose declines have been most evident in the Buffalo Valley, approximately 50 km north of the town of Jackson, Wyoming (Brimeyer and Thomas 2004). Therefore, the goal of this research was to describe seasonal movements, distribution, and habitat selection patterns of adult female Shiras moose captured in the Buffalo Valley. By examining and contrasting Shiras moose habitat use both within and across seasons, I intended to identify potential limiting factors. My specific objectives were to: (1) estimate the dates of winter and summer seasonal range use and the onset of spring and fall migration; (2) describe seasonal space-use patterns including home range size, fidelity, and distances moved; and (3) determine habitat and landscape features that are important predictors of winter and summer habitat selection. Using these data, I mapped population-level predictions of seasonal habitat selection across the winter and summer study area to provide managers with information on important seasonal ranges and to assist with future land-use decisions.

STUDY AREA

The study area encompassed approximately 6,400 km^2 of predominately public land in northwest Wyoming. It was north of the town of Jackson, Wyoming and included portions of Grand Teton National Park (GTNP), Yellowstone National Park (YNP), and the Bridger-Teton National Forest (BTNF) where elevations ranged from 1,866 to 4,197 m. The study area included the upper Snake River and upper Yellowstone River watersheds. Primary moose winter ranges and major tributaries of the Snake River consisted of Pacific Creek, the Buffalo Fork River, and the Gros Ventre River (Houston 1968).

Vegetation types varied with elevation and aspect within the study area (Whitlock 1993, Knight 1994). Lower elevations, and many south-facing slopes at higher elevations, were dominated by sagebrush (*Artemisia* spp.). Mid-elevations were characterized by large stands of lodgepole pine intermixed with Douglas fir (*Psuedotsugia menziesii*) and aspen (*Populus tremuloides*). Engelmann spruce (*Picea* engalmanni) and subalpine fir (*Abies lasiocarpa*) were found on north slopes and more mesic sites. Engelmann spruce, subalpine fir, and lodgepole pine intermixed with smaller stands of whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*), and aspen dominated higher elevations. Alpine tundra occurred at the highest elevations while open forest parks and subalpine meadows occurred at all elevational gradients. Riparian areas dominated by willows (*Salix* spp.) intermixed with narrowleaf cottonwood (*Populus angustifolia*) were located in large, relatively flat flooplain environments at lower elevations and along nearly all drainages within the study area (Wigglesworth and Wachob 2004).

The climate was characterized by short, cool summers and long, cold winters. From 1975-2004, annual precipitation averaged 56 cm (range = 38-79 cm) of which approximately 65% fell as snow between November and May (http://www.cdc.noaa.gov/cgi-bin/Timeseries/timeseries1.pl; accessed 16 October 2005). The Teton Mountains to the west and the northern highlands along the southern boundary of YNP typically receive the greatest amounts of precipitation (Houston 1968, Cole 1969, Boyce 1989).

METHODS

Moose Captures and Data Management

Adult (≥ 2 years) female moose were captured using a helicopter on winter range in the Buffalo Valley of northwest Wyoming during February 2005 and 2006. Moose were darted and immobilized with 10-mg thiafentanil oxalate (A-3080, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA: McJames et al. 1994, Arnemo et al. 2003, Kreeger et al. 2005) and, once handling was completed, thiafentanil was antagonized with 300-mg naltrexone (Trexonil, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) administered intramuscularly at multiple sites. Captures were performed in accordance with approved University of Wyoming Animal Care and Use Committee protocols.

Moose were fitted with TGW-3700 global positioning system (GPS) collars with store-on-board technology and mortality sensing options (Telonics, Inc., Mesa, Arizona, USA). Collars were preprogrammed to attempt a location fix every hour from 15 November to 15 June and every 5 hours from 16 June to 14 November. Location data were collected continuously until 1 March 2007 when the collars were preprogrammed to release from the moose. Location data were examined and all unsuccessful fixes and obvious location errors were removed from datasets (D’Eon et al. 2002, D’Eon and Serrouya 2005). Data were not corrected for fix-rate bias because of high fix-rate success during winter (99.1%) and summer (96.2%, Appendix 2.1; D’Eon 2003, Friar et al. 2004, Hebblewhite et al. 2007). Three-dimensional fixes accounted for a high proportion of winter (83.0%) and summer (60.6%) locations (Appendix 2.2), therefore, data were not differentially corrected because 3-dimensional locations generally have < 20 m error (Di Orio et al. 2003).

Seasonal Home Range Characteristics

Due to variability among individuals in the onset of movements between seasonal ranges, I visually examined the spatial and temporal distribution of location data for individual moose in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) to identify dates and times of seasonal range use (Nikula et al. 2004, D'Eon and Serrouya 2005). Moose were assumed to have left a seasonal range when the distance between sequential relocations increased and the direction of travel suggested movement away from a cluster of locations without returning. Similarly, when the distance between relocations decreased and locations began to cluster, moose were assumed to have arrived at a seasonal range. All locations that occurred outside of these parameters were classified as migration. Based on these assumptions, I identified seasons of use as winter and summer.

If I was unable to estimate movement dates for an individual, I plotted the location data in ArcGIS and examined the number of moose whose seasonal ranges overlapped the location data. I then calculated the mean dates of use for all moose that overlapped the location data and used this as the date of seasonal range use for the individual moose of interest. This was based on the assumption that dates of seasonal range use were comparable among individual moose that utilized similar seasonal ranges during the same year. For moose that arrived on summer range prior to 16 June and left after 14 November, every fifth location was retained prior to and after these dates to maintain a constant fix schedule during summer. I used a Kruskal-Wallis one-way

ANOVA to test for among year differences ($\alpha = 0.05$) in seasonal range arrival and departure dates.

Due to the topographic relief of the study area and the number of locations obtained from the GPS collars, I used the fixed-*k* local convex hull (LoCoH) method to estimate home range size for each moose during each season because it does not require statistically independent location data (Getz and Wilmers 2004, Ryan et al. 2006). This method creates hulls around each location and its *k* nearest neighbors then constructs isopleths by merging these polygons together, beginning with the smallest and ending with the largest (Getz and Wilmers 2004, Ryan et al. 2006). To begin, values of *k* at the 100% isopleth were run in increments of 5 that encompassed the square root of the number of locations for each moose and season. I plotted area estimates against *k* to locate the point at which home range size plateaued (Ryan et al. 2006). Values of *k* were then run in increments of 1 to determine the best *k* value, area estimates were plotted, and shapefiles were created to view the results. To obtain more accurate and unbiased estimates of home range size, 90% LoCoH isopleths were calculated for selected values of *k* for moose during each season (Börger et al. 2006, Elwen et al. 2006). I used a Kruskal-Wallis one-way ANOVA to test for among year differences ($\alpha = 0.05$) in winter and summer home range sizes and if differences were not observed, I pooled annual winter and summer home range sizes, respectively, to test for seasonal differences. If individual moose were monitored during multiple years, home range estimates were averaged to provide a single estimate for each individual prior to testing for seasonal differences.

To estimate the extent of fidelity to seasonal home ranges, I calculated the percent overlap between seasonal ranges for adult female moose that were monitored for 2 consecutive years. Seasonal 90% LoCoH home range polygons were mapped and the total area of overlap for each moose and season was calculated in ArcGIS. The total area of overlap was then divided by the total area encompassed by the 2 seasonal ranges (Scarpitti et al. 2005). To determine the migratory status of radio-collared moose, I estimated overlap between winter and summer ranges within the same year. If < 50% overlap occurred, the moose was considered migratory (MacCracken et al. 1997). For individuals that were considered migratory, I measured the straight-line distance between the mean centers of winter and summer ranges within years. I tested for annual differences ($\alpha = 0.05$) in home range overlap within seasons and straight-line distance moved between seasonal ranges with a Kruskal-Wallis one-way ANOVA.

All 90% LoCoH summer home range polygons were mapped in ArcGIS and if they overlapped at any point, this area was classified as a moose summer range complex. Migration routes were delineated by mapping all transition locations for each moose in ArcGIS and tracing the routes taken from winter to summer range, and back, in both years. To examine the relationship between onset of spring and autumn migration and the elevation of moose summer ranges, I extracted summer elevation data for each moose from a 26 x 26-m digital elevation model (DEM; U.S. Geological Survey [USGS] 1999). I used Spearman rank correlation ($\alpha = 0.05$) to determine if a relationship existed between the onset of spring and autumn migration and the elevation of summer ranges.

Seasonal Habitat Selection

Modeling procedures to estimate resource selection probability functions (RSPF; Manly et al. 2002) followed those outlined by Sawyer et al. (2006) and consisted of 4 basic steps: (1) estimate the relative frequency of use for each GPS-collared moose from a large number of sampling units for each season and year, (2) use the relative frequency as a continuous response variable in a multiple regression analysis (i.e., generalized linear model) that was assumed to have a negative binomial distribution (White and Bennetts 1996) to model the probability of use for each moose as a function of a set of predictor variables, (3) develop a population-level model by averaging the coefficient estimates from the individual moose models for each season, and (4) map the predictions of the population-level model for each season. Individual GPS-collared moose were treated as the experimental unit to avoid spatial and temporal autocorrelation (Aebischer et al. 1993, Otis and White 1999, Millspaugh et al. 2006).

I used the distribution of radio-collared moose from 2005 to 2007 to define winter and summer habitat availability (McClean et al. 1998) by creating a minimum convex polygon around all moose locations for each season using the HOME RANGE TOOLS extension for ArcGIS (Rodgers et al. 2007). I buffered the winter and summer study areas by the average daily distance moved per season (winter = 1,450 m, summer = 1,680 m; Appendix 2.3) to include what could potentially be available to moose within one day's travel. I created a single vegetation layer from 2 existing layers (Homer 1998, Cogan et al. 2005) and reclassified vegetation data into 6 classes: (1) spruce/fir, (2) lodgepole, (3) mixed/other conifer, (4) aspen, (5) riparian/deciduous shrub, or (6) burn/other. Since the vegetation layers did not contain canopy height or percent cover information, I could not estimate canopy height for deciduous shrubs. Therefore, to assess habitat types that could potentially provide thermal cover for moose, cover was defined strictly as conifers in winter and conifers and aspen habitats in summer. I used the SPATIAL ANALYST extension for ArcGIS to estimate distance to cover for each season and to calculate slope (i.e., degrees) and aspect from a 26 x 26-m DEM (USGS 1999).

I created circular sample units with 125-m radii that were systematically distributed with a random start across each study area to measure 11 variables that could potentially influence winter and summer habitat selection. These included the 6 vegetation classes listed above, elevation, slope, aspect, distance to cover, and habitat diversity. I chose 125-m radii circular sampling units because this was approximately the average distance moved by moose in a 2-hour period during both winter and summer. This ensured that the area of the sample unit was small enough to detect changes in animal movement, but large enough to obtain multiple locations within each unit (Sawyer et al. 2006). I extracted vegetation data from each sample unit and calculated the proportion of each vegetation type that occurred within each unit. Elevation, slope, aspect, and distance to cover were obtained from the midpoint of each sample unit. It has been demonstrated that moose select for habitat diversity at a larger spatial scale (Hjelford et al. 1990, Nikula et al. 2004). Thus, I created 250-m-radii circular units centered on the midpoint of each sample unit, extracted vegetation data from each unit, and calculated a Shannon-Weiner diversity index (Krebs 1989) based on the 6 vegetation classes listed above.

To estimate the relative frequency of use for each moose, I counted the number of individual moose locations within each sample unit across the seasonal study areas during each year. Prior to modeling, and to ensure independence of the sample units (Thompson 1992:51), I took a random sample with replacement of approximately 6,000 sample units for winter and 20,000 sample units for summer. I used a forward stepwise modeling procedure to estimate population-level models for each season and used a *t*-statistic to determine variable entry ($\alpha \leq 0.15$) and exit ($\alpha \leq 0.20$; Hosmer and Lemeshow 2000). I considered quadratic terms for slope during winter and elevation and slope during summer. If a quadratic term entered the model then the linear form of each variable was included. Aspect was considered as a categorical variable with the northeast aspect as the reference and if one of the aspect categories (i.e., northwest, southeast, and southwest) was significant ($\alpha \leq 0.15$) all of the categories were included. The burn/other vegetation category was not fitted during the model building process for any season because inference as to selection or avoidance would be difficult to ascertain due to the many different vegetation types that were included in this class. This ensured independence of the vegetation classes and did not violate the unit-sum constraint (Aebischer et al. 1993, Nikula et al. 2004). A Pearson's pairwise correlation analysis was conducted prior to modeling to identify multicolinearities and to identify any predictor variables that should be excluded from analysis ($|r| > 0.60$). Population-level models were developed for each season and year. I used a Spearman's rank correlation analysis ($\alpha = 0.05$) to determine if a significant relationship existed in predicted RSPF values between years for all sample units within each seasonal study area. If no differences were observed, all moose locations were pooled across years for each season and a single winter and summer population-level model was developed using the same techniques described above. All habitat modeling procedures were conducted using the R statistical software package (R Core Development Team 2006).

I mapped RSPF predictions of population-level models across 130 x 130-m pixels for winter and 250 x 250-m pixels for summer that covered each seasonal study area. The RSPF values were assigned values from 1 to 5 representing highest to lowest estimated use probabilities in 20% increments (i.e., highest predicted probability of use = 1 [highest 20%], lowest predicted probability of use = 5 [lowest 20%]; Sawyer et al. 2006, Sawyer et al. 2007).

RESULTS

Moose Captures and Data Management

Twenty adult female moose were captured in February 2005 and 6 additional moose were captured in February 2006. Two GPS collars malfunctioned during this study. One collar partially failed in summer 2005 and averaged < 60% fix-rate success during the remaining seasons. The other partially failed during winter 2006 and again in winter 2007. These collars were removed from all analyses for the seasons they failed except when estimating the dates of seasonal movements.

Seasonal Movements and Home Range Characteristics

Movements between seasonal ranges were identifiable for most moose in both years. I was, however, unable to identify transition from winter to summer range for 3 moose and transition from summer to winter range for 1 moose, thus the mean dates from moose whose summer ranges overlapped these individuals were used to estimate the end of one season and the beginning of the next (Appendix 2.4). Although spring migration began approximately 2 weeks earlier in 2005 ($\bar{x}$ = 8 May ± 4.6 days; $n = 17$) than in 2006 ($\bar{x}$ = 20 May ± 4.3 days; $n = 20$), no statistical difference was observed between years ($P = 0.094$). No significant difference was observed between 2005 ($\bar{x}$ = 18 November ± 3.7 days, $n = 17$) and 2006 ($\bar{x}$ = 22 November ± 3.9 days, $n = 19$) in the onset of fall migration ($P = 0.557$).

Winter home range sizes were estimated for all moose (Appendix 2.5); however, only those moose that successfully left winter range in 2005 ($n = 17$), had a full winter of data in 2006 ($n = 12$), or successfully remained on winter range until collars dropped or were removed during capture efforts in 2007 ($n = 18$) were used to examine annual differences. Mean winter home range size was 4.0 ± 0.5 km^2 in 2005, 5.5 ± 0.9 km^2 in 2006, and 2.9 ± 0.5 km^2 in 2007 (Figure 2.1). There were no differences in winter home range sizes between 2005 and 2006 ($P = 0.268$), but differences were observed when 2007 was compared to 2005 ($P = 0.027$) and 2006 ($P = 0.014$). Therefore, only winter home range sizes from 2005 and 2006 were used for remaining winter home range comparisons. Total mean winter home range size was 4.5 ± 0.5 km^2 ($n = 17$, $\bar{x}$ relocations = 2,720, $k = 62$).

Summer home range estimates were calculated for all moose that had functional collars while on summer range in 2005 ($n = 16$) and 2006 ($n = 19$). Mean summer home range size was 11.9 ± 1.8 km^2 in 2005 and 13.4 ± 2.1 km^2 in 2006 (Figure 2.1). No difference was observed between years ($P = 0.843$). Total mean summer home range size was 13.2 ± 1.9 km^2 ($n = 22$, $\bar{x}$ relocations = 814, $k = 38$). When years were pooled, mean summer home range size was significantly greater than mean winter home range size ($P < 0.001$).

There was a significant difference ($P < 0.001$) between percent winter ($n = 12$, $\bar{x}$ = 21.5 ± 0.03%) and summer home range overlap ($n = 13$, $\bar{x}$ = 44.5 ± 0.03%). All adult female moose were considered migratory in 2005 ($n = 16$) and 2006 ($n = 18$). Only 2 moose had overlapping winter and summer ranges (1 in both years) and the greatest percent overlap observed for an individual moose within a year was 2.9%. There was no significant difference ($P = 0.352$) in the distance traveled between seasonal ranges in 2005 ($\bar{x}$ = 19.8 ± 3.4 km, range = 3.1-38.3 km) and 2006 ($\bar{x}$ = 23.1 ± 3.1 km, range = 3.8-44.0 km).

Seasonal movement patterns involved a general congregation on low elevation winter ranges followed by individual migrations to more dispersed, high elevation summer ranges. All moose traveled along migration routes that paralleled primary drainages or crossed low elevation passes throughout the study area and used the same general routes during spring and autumn (Figure 2.2). Moose that were monitored during migrations in 2005 and 2006 ($n = 12$) used similar routes in both years. Most collared adult female moose occupied 1 of 4 summer range complexes while 3 individuals occupied an area where no other collared moose traveled (Figure 2.2). When the elevations of individual moose summer ranges were regressed against the onset of spring migration, a positive relationship existed, but this correlation was only significant in 2006 ($r_s = 0.728$, $P < 0.001$, Figure 2.3). In general, the onset of fall migration and the elevations of summer ranges were negatively correlated, however, no significant relationship was observed in either year ($P > 0.05$).

Habitat Selection

Winter

Based on movements and distributions of GPS-collared adult female moose during the winters of 2005 to 2007, the winter study area encompassed approximately 1,100 km^2 (Figure 2.4). Population-level habitat selection models were developed for each winter period using 36,485 relocations in 2005 ($n = 17$ moose), 67,160 relocations in 2006 ($n = 21$ moose), and 35,977 relocations in 2007 ($n = 18$ moose). Moose selected winter habitats with a high proportion of riparian/deciduous shrub vegetation, low elevation, high habitat diversity, and near coniferous cover in all years (Appendix 2.6). Moose selected moderate slopes in 2006 and 2007 and avoided northerly aspects in 2005 and 2007. Mixed conifer was avoided in 2006 and 2007 and spruce/fir was avoided in 2007. In 2007, most moose avoided spruce/fir (10 of 18) and mixed conifer (16 of 18). However, individual model coefficients were < -700 for 4 moose and < -800 for 2 moose for the spruce/fir and mixed conifer vegetation classes, respectively, due to a lack of these vegetation types within individual moose winter home ranges. When the coefficients were averaged for the population-level model, estimates for spruce/fir and mixed conifer were not indicative of population-level habitat selection for the GPS-collared sample ($\beta_{\text{spruce/fir}} = -169$, $\beta_{\text{mixed conifer}} = -101$), thus they were removed from the final model (Appendix 2.6). The model was rerun for 2007 and no other variables entered the model. Although each winter model contained different combinations of covariates (Appendix

2.6), the predicted RSPF values for each sample unit were similar between 2005 and 2006 ($r_s = 0.839$, $P < 0.001$), 2005 and 2007 ($r_s = 0.791$, $P < 0.001$), and 2006 and 2007 ($r_s = 0.823$, $P < 0.001$).

Since differences were not observed in the predicted RSPF values among years, all winter relocations were pooled to create a single population-level winter habitat selection model and predictive map of the probability of use. The final pooled model included riparian/deciduous shrub, aspen, and mixed conifer vegetation types, elevation, slope, habitat diversity, and distance to coniferous cover (Table 2.1). Population-level model coefficients indicated that moose selected areas with a high proportion of riparian/deciduous shrub and aspen vegetation, low elevation, high habitat diversity, moderate slopes, close to coniferous cover, and avoided mixed conifer forests (Table 2.1). Areas with the highest predicted probability of moose use were composed of 29% riparian/deciduous shrub, 24% lodgepole, 7% aspen, 6% spruce/fir, and 2% mixed conifer, had an average elevation of 2,114 m, slopes of 4°, and were approximately 151 m from coniferous cover. Predictive maps indicate that the highest probability of use occurred along relatively flat, low-elevation drainages dominated by riparian and deciduous shrub habitats interspersed with patches of conifer and aspen (Figure 2.5).

Summer

Based on movements and distributions of GPS-collared adult female moose during the summers of 2005 and 2006, the summer study area encompassed approximately 3,800 km^2 (Figure 2.6). Population-level habitat selection models were developed for each summer using 13,781 relocations in 2005 (*n* = 16 moose) and 14,915 relocations in 2006 (*n* = 19 moose). Moose selected summer habitats composed of moderate elevations and slopes and avoided mixed conifer forests and aspen in all years (Appendix 2.7). Spruce/fir was avoided in 2005 while lodgepole was avoided in 2006. In 2006, moose also selected summer habitats that offered high habitat diversity, northerly aspects, and were relatively close to cover provided by aspen and conifers. Although the summer 2006 model contained 5 additional covariates (Appendix 2.7), the predicted RSPF values for each sample unit within the summer study area were similar between years ($r_s = 0.924$, $P < 0.001$).

Since differences were not observed in the predicted RSPF values among years, all summer relocations were pooled to create a single population-level summer habitat selection model and predicted probability of use map. The final model included, in the order that they entered, elevation, slope, distance to cover, and lodgepole, mixed conifer, and aspen vegetation types (Table 2.1). Population-level model coefficients indicated that moose selected areas of moderate elevation and slope, close to cover, and avoided lodgepole, mixed conifers, and aspen (Table 2.1). Areas with the highest predicted probability of moose use were composed of 24% lodgepole, 16% spruce/fir, 12% riparian/deciduous shrub, 7% aspen, and 6% mixed conifer, had an average elevation of 2,438 m, slopes of 9°, and were approximately 49 m from cover. Predictive maps indicated that the highest probability of moose use during summer occurred at mid-elevation habitats that were close to cover with relatively flat slopes (Figure 2.7). The low-elevation ranges classified as high or medium-high probabilities of use during winter were classified as low or medium-low probabilities of use during summer.

DISCUSSION

Population-level habitat selection models suggested that adult female moose in the study area selected for low-elevation, riparian habitats dominated by extensive willow communities during winter. Throughout their distribution moose generally seek winter habitats that provide abundant forage (Peek 1997, Månsson et al. 2007). The extensive use of shrub-dominated habitats during winter has been well documented for moose in Alaska (Mould 1979, Hundertmark et al. 1990, MacCracken et al. 1997) and the Intermountain West (Knowlton 1960, Van Dyke et al. 1995, Kufeld and Bowden 1996). Furthermore, past diet and forage studies conducted on Shiras moose in the Greater Yellowstone Area demonstrated the historical preference of willow as winter forage (Rudersdorf 1952, McMillan 1953, Harry, 1957, Houston 1968). Where riparian habitats are less extensive, the use of mature coniferous forests that contain a high diversity of forage species becomes important (Stevens 1970, Pierce and Peek 1984, Matchett 1985, Tyers 2003). Shrub-dominated, riparian habitats provide the greatest abundance of available forage within the study area during the most restrictive time of year. Therefore, these habitats likely reduce the energetic demands of traveling through snow in search of forage and allow moose the opportunity to reduce the negative energy balance typically incurred during winter.

Although moose selected areas dominated by riparian shrubs, they did not select homogenous stands of willows. Adult female moose selected areas with high habitat diversity which suggests that they require a variety of resources to meet their nutritional and energetic requirements during winter. These findings are consistent with results from an experimental study that demonstrated moose selection for a diverse diet even when preferred forage species were highly available (Miquelle and Jordan 1979). On the Kenai Peninsula, Alaska, Oldemeyer et al. (1977) suggested that succession from multi-species to single-species dominated winter range may have contributed to an increased incidence of mortalities associated with malnourishment. Browse quality is generally lower during winter than during summer (Regelin et al. 1987, MacCracken et al. 1997, Schwartz and Renecker 1997); therefore, a variety of resources can better meet the nutritional requirements of moose than a single, highly abundant species (Oldemeyer et al. 1977, Ohlson and Staaland 2001). When browse digestibility, fiber content, protein content, and mineral content were examined among forage species in Alaska, aspen ranked as the highest quality winter browse while willows were intermediate (Oldemeyer et al. 1977). Although browse quality may vary by region, selection by adult female moose for aspen habitats in the study area indicated that moose not only preferred areas with high browse biomass, but they also selected the highest quality browse available during winter.

Based on my results, there is little evidence to support a shift to habitats with greater canopy cover during late winter even though distance to cover entered the final population-level model. The model developed for winter 2005 could have been interpreted as late winter habitat selection since monitoring was conducted from February 2005 until individual moose left the winter range that year. Adult female moose did select habitats closer to coniferous cover in 2005 ($\bar{x}$ = 95 m) than in 2006 ($\bar{x}$ = 130 m) or 2007 ($\bar{x}$ = 169 m). However, there were no differences in predicted RSPF values among winters suggesting that habitat use was similar for late winter (i.e., 2005), full winter (i.e., 2006), and early winter (i.e., 2007). This indicated that forage availability was more important than cover during the entire winter over the range of conditions observed during this study. Similar results have been described for moose in southeastern British Columbia, Canada (Poole and Stuart-Smith 2006) and in east-central Idaho (Ritchie 1978). This contrasts with other studies where shifts to closed-canopy coniferous forests were observed during late winter due to increased snow accumulations in Alaska (Hundertmark et al. 1990, Ballard et al. 1991, MacCracken et al. 1997, Stephenson et al. 2006), Minnesota (Philips et al. 1973, Peek et al. 1976), Montana (Stevens 1970, Matchett 1985), and Wyoming (Houston 1968). Winter range conditions may not have been severe enough during my study to necessitate selection for coniferous habitats (Poole and Stuart-Smith 2006). Additionally, moose may have utilized tracks of other individuals to reduce the energetic costs of locomotion rather than seeking areas of reduced snow depths under closed-canopy forests (LeSage et al. 2000, Ball et al. 2001). Although conifers appeared to be of minor importance to moose in the study area, the cover that these habitats provide may be important for short periods during the winter. This could especially be true during late winter and early spring when rising ambient temperatures increase thermal stress (Renecker and Hudson 1986, Schwab and Pitt 1991). In winter, moose experience heat stress at -5°C (Renecker and Hudson 1986, Schwartz and Renecker 1997) and generally avoid areas where this threshold is exceeded for extended periods of time (Schwab and Pitt 1991). Thus, during late winter and early spring, moose in the study area may have utilized coniferous habitats during the warmest parts of the day and returned to more open habitats as temperatures cooled.

Summer habitat selection by adult female moose appeared to be associated with habitat and landscape features that may reduce the effects of thermal stress. All moose migrated to higher elevation summer ranges and selected for areas in close proximity to cover provided by aspens and conifers. Areas classified as high-use during summer were > 300 m higher in elevation and were > 100 m closer to cover than high-use areas in winter. In northwest Wyoming, Dirks and Martner (1982) reported a cooling rate of 9.8°C per 1,000 m gain in elevation, thus high-use summer areas were on average 3.2°C cooler than if moose had remained on low-elevation, high-use winter ranges during summer. During summer, moose experience heat stress at 14°C (Schwartz and Renecker 1997) and it has been suggested that regions with temperatures > 27°C for extended periods of time are unsuitable for moose unless there are refugia to provide relief (Kelsall and Telfer 1974). Maximum daily temperatures recorded at the Two Ocean Plateau SnoTel station in the middle of the summer study area (elevation = 2,816 m; approximately 400 m higher than the mean elevation of predicted high-use summer areas) indicated that summer temperatures routinely exceeded the 14°C heat stress threshold, and were very near the upper threshold limit for extended periods of time during the summers of 2005 and 2006 (http://www.wcc.nrcs.usda.gov/snotel/Wyoming/wyoming.html). Therefore, selection for habitats in close proximity to cover may have provided relief from high summer temperatures. This is similar to other research that documented the increased use of closed-canopy forests by moose as summer temperatures rose (Schwab and Pitt 1991, Dussault et al. 2004, Muir 2006). It has also been reported that moose increased nocturnal activity (Dussault et al. 2004) and were more likely to be located in open shrub fields during crepuscular hours in response to increased temperatures (Muir 2006). In north-central Colorado, researchers suggested that lower growth forms of willow at higher elevations provided little cover, thus moose utilized coniferous cover in close proximity to preferred deciduous shrub habitats (Kufeld and Bowden 1996). Although my study cannot prove that mature coniferous forests are critical for moose survival during summer (Balsom et al. 1996), it does lend support for the importance of these habitats in providing cover that could reduce heat stress near the southern extent of their range.

Summer habitats that are closer to cover could provide females tending calves increased protection from predators. It has been documented that parturient female moose seek calving locations that provide greater hiding cover during the neonate phase (Langley and Pletscher 1994, Bowyer et al. 1999, Poole and Stuart-Smith 2007), while only recently has it been reported that females tending calves select habitats that may reduce predation risk during the entire summer (Dussault et al. 2005*b*). While this may have influenced habitat selection for some individuals in the study area, most adult female moose that were fitted with GPS collars were not observed with calves in 2005 or 2006 (Chapter 4). Thus, predation risk likely had little to no effect on the summer habitat selection patterns for the study animals and lends further support for the importance of cover in reducing thermal stress.

The summer habitat selection patterns by moose likely reflect a release from the environmental constraints of deep snow that restrict habitat selection during winter (Dussault et al. 2005*a*, Stephenson et al. 2006). Summer home range sizes were greater than winter and no specific vegetation types were selected for during summer. Habitat diversity did not enter the summer model which suggested that moose were not limited by the availability of forage and could be more selective in their summer habitat use patterns. This is supported by research conducted in Quebec Province, Canada that reported a negative relationship between moose home range size and forage availability in winter, but not during summer (Dussault et al. 2005*a*). When resources are widely distributed and highly available, as they are during summer, moose may seek out patches of the highest quality forage within their home ranges and not necessarily use areas that contain the greatest abundance of forage. Due to differences in elevation, slope, and aspect, changes in plant phenology could have also influenced the choices of feeding sites and habitats used by moose (Hjelford et al. 1990, Mysterud et al. 2001). For example, several researchers have documented high use of forbs by Shiras moose, especially in late spring and early summer even though browse remained a staple of the diet (McMillan 1953, Harry 1957, Knowlton 1960, Houston 1968, Stevens 1970, Ritchie 1978). It is possible that moose used habitat patches within different vegetation classes to take advantage of changes in the quality of forage throughout the summer (Peek 1997). Additionally, summer provided moose with many forage choices resulting in a high level of individual variation in habitat selection patterns across the summer range.

Fidelity to seasonal home ranges may also be influenced by habitat diversity and the spatial distribution of preferred habitat patches. Adult female moose exhibited greater fidelity to larger summer home ranges than to smaller winter home ranges. Higher fidelity to summer home ranges have also been observed in Alaska (MacCracken et al. 1997), New Hampshire (Scarpitti et al. 2005), and Sweden (Andersen 1991*a*). Preferred riparian habitats occur throughout the Buffalo Valley winter range, thus specific knowledge of preferred, high quality habitat patches may not be needed because wherever moose move, they are likely to encounter sufficient forage of similar nutritional value. In contrast, summer range resources are highly available, but the spatial distribution of heterogeneous patches of high quality forage may be more widely dispersed. Over time, moose may have learned where specific patches of high quality resources were located within their summer home ranges resulting in greater fidelity as they frequently visited preferred patches (Forester et al. 2007).

Spring and autumn migrations are influenced by a combination of snow conditions and the availability of forage (Edwards and Ritcey 1957, Coady 1974, LeResche 1974). If elevation was used as a surrogate for snow depth (Poole and Stuart-Smith 2006), moose with higher elevation summer ranges generally began spring migration later, but this relationship was only significant in 2006. During the winter of 2006, snow accumulations were greater and persisted longer into the spring than in 2005 (http://www.wcc.nrcs.usda.gov/snotel/Wyoming/wyoming.html; accessed 16 November 2007). This suggested that after winters with high snow accumulations, spring migrations were highly influenced by snow conditions and the effects this might have in delaying spring green-up, whereas after winters with relatively low snow accumulations, moose may use some other factor to initiate movement. The lack of a relationship between the onset of autumn migration and elevation implies that a rapid accumulation of snow on summer range initiated the return to winter range for all moose regardless of where they summered (Ballard et al. 1991, DeMarchi 2003).

While the timing of movements between seasonal ranges appeared to be influenced by snow, adult female moose exhibited a high degree of individual variability in the onset of spring and autumn migrations. This is similar to research conducted in Alaska (Ballard et al. 1991) and Minnesota (Philips et al. 1973). The variation in movements may be due to the energetic demands of the animals following winters of differing severity. Mule deer (*Odocoileus hemionus*) research in Colorado suggested that improved physical condition following mild winters allowed for earlier migration to summer ranges (Garrott et al. 1987). Nonetheless, a more comprehensive understanding of the timing of seasonal movements and the physical condition of moose prior to migration is needed.

As with application of most modeling procedures to biological data, there were potential weaknesses in the methodology used. Since annual habitat selection models were combined into a single model for each season, some potential for pseudoreplication was introduced because some moose were used to build habitat selection models during all seasons. However, I concluded that the potential for introducing bias was minimal (Oksanen 2001) and that this was the best modeling procedure for the data available. A second area of potential weakness was that all of the available data was used in the modeling procedure in order to produce seasonal models with the highest predictive power possible, thus I was unable to independently validate the model. In the future, I would strongly suggest model validation using independent data in order to verify the predictions of moose habitat selection in northwest Wyoming.

MANAGEMENT IMPLICATIONS

Summer and winter ranges may be equally important components of moose habitat in northwest Wyoming. Managers cannot assume the relative importance of one seasonal range over the other because both are integrally linked into the dynamics of populations. Migration routes are also important components of year-round ranges because access to seasonal ranges would be limited without these and it is unlikely that current population levels could be maintained (Sawyer et al. 2005). Migrations between seasonal ranges generally follow traditional routes and this knowledge is passed from parent to offspring (Sweanor and Sandegren 1988, Andersen 1991*b*), thus it may take several generations for moose to adapt to habitat alterations that impact seasonal movements and the quality of seasonal ranges.

Shiras moose in the study area selected for winter habitats that provided the greatest abundance of, and potentially the highest quality, forage. However, the importance of habitat diversity that includes cover provided by coniferous forests cannot be underestimated, especially during spring when increasing ambient temperatures may limit the foraging activities of moose during the day. Since moose are more concentrated on winter range, habitat improvements could benefit many more individuals, but these projects should not focus strictly on willow-dominated riparian communities. This study suggested that managing for a variety of habitats within the winter range may allow moose to better meet their nutritional and cover requirements.

Shiras moose summer range appears to be highly influenced by habitat and landscape features that limit thermal stress while still securing adequate amounts of high quality forage. Moose are more dispersed on summer ranges and large-scale habitat improvement projects would be impractical. Additionally, most of the summer ranges are relatively protected from human disturbance because much of the area is managed as wilderness by the Bridger-Teton National Forest, Grand Teton National Park, or Yellowstone National Park. However, natural disturbances that can impact moose summer ranges have occurred in northwest Wyoming. Tyers (2003) suggested that the 1988 Yellowstone wildfires were detrimental to moose on the Northern Yellowstone winter range because they removed a large portion of mature coniferous forests. Large-scale wildfires or insect infestations that reduce the amount of mature forests could reduce the physical condition of moose entering winter (Saether 1985, Solberg et al. 1999, Solberg et al. 2004) and may have a detrimental effect on moose populations in the future. A reduction in physical condition could also make moose more susceptible to diseases and parasitic infections by reducing reproductive output and adult survival (Murray et al. 2006). My study was not designed to test how a reduction in the amount of mature coniferous forests may result in population declines (Chapter 1), but indices of moose population density and calf-cow ratios for the north Jackson moose herd suggested the declines began shortly after the 1988 Yellowstone fires. Therefore, due to the continued threat of wildfire and the increased threat of insect infestations that may alter the availability and quality of moose summer ranges through direct destruction of mature coniferous forests, increased monitoring of the availability of mature forests appears warranted. If large-scale habitat alterations occur, moose populations may be negatively impacted and harvest strategies and herd unit objectives may need to be adjusted accordingly.

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Table 2.1. Coefficients for population-level resource selection probability function models of GPS-collared adult female moose winter and summer habitat selection in northwest Wyoming. Variables are in the order that they entered during the winter model-building process.

	Winter			Summer		
Variable	β	SE	*P*	β	SE	*P*
Intercept	11.204	3.775	0.007	-452.987	101.276	<0.001
Riparian	3.559	0.173	<0.001	N.S.[a]		
Elevation (m)	-0.011	0.002	<0.001	0.364	0.088	<0.001
Elevation^2 (m)	N.A.[b]			-0.000	0.038	<0.001
Habitat diversity	0.856	0.143	<0.001	N.S.		
Slope (°)	0.105	0.034	0.005	0.012	0.038	0.752
Slope^2 (°)	-0.006	0.002	<0.001	-0.003	0.001	0.015
Mixed conifer	-2.251	0.995	0.034	-2.427	1.323	0.081
Dist. to cover (m)	-0.002	0.001	0.051	-0.006	0.003	0.041
Aspen	0.590	0.384	0.139	-2.644	1.663	0.127
Lodgepole	N.S.			-0.628	0.293	0.044

[a] Not significant.
[b] Not applicable. Quadratic for elevation was not used during model building process for winter.

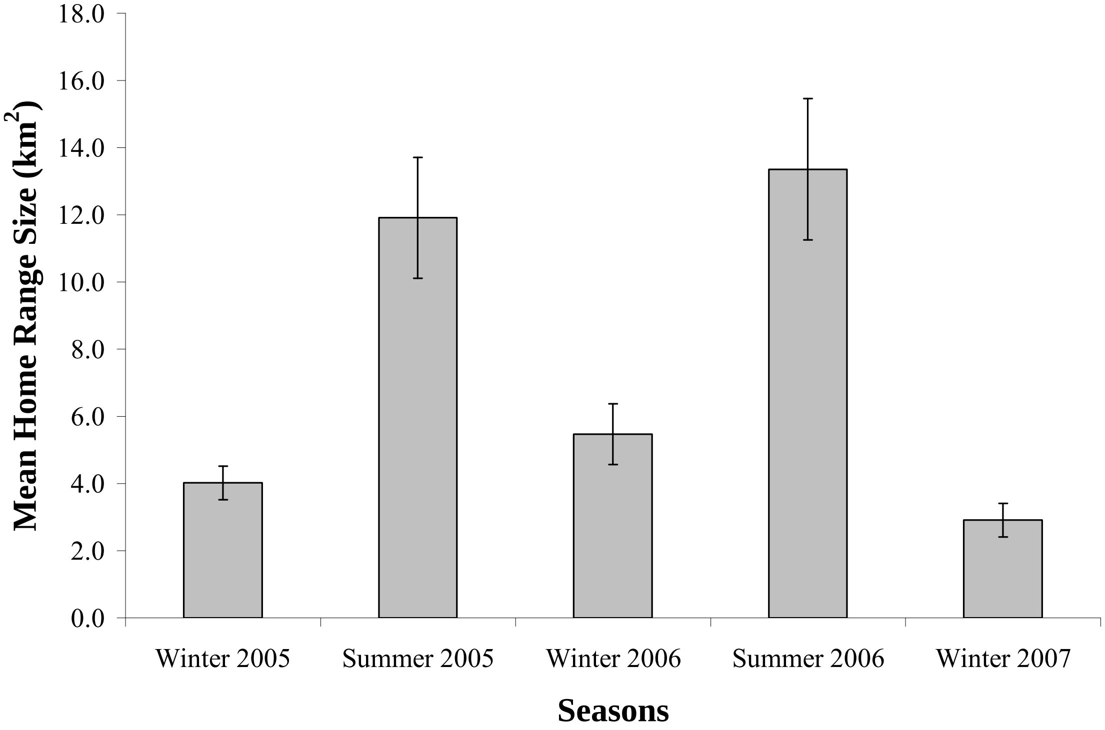

Figure 2.1. Mean 90% LoCoH home range size (km^2) ± standard error by season for GPS-collared adult female moose in northwest Wyoming.

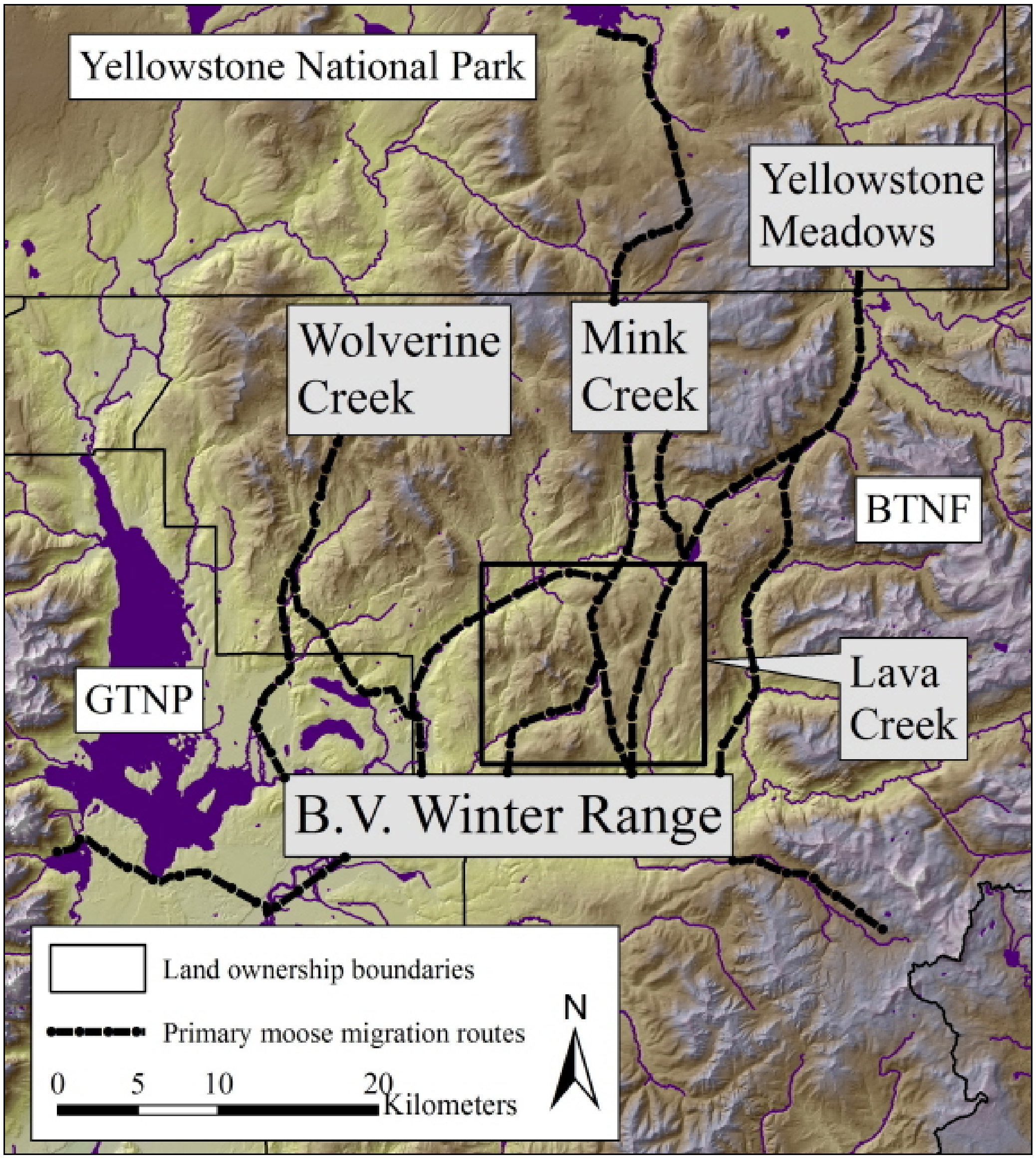

Figure 2.2. Location of major migration routes to and from the 4 identified summer range complexes for GPS-collared adult female moose in northwest Wyoming (2005-2006). Migration routes shown that do not lead to one of the summer range complexes were individuals that used separate summer ranges. The Lava Creek summer range is depicted by the black square and migration routes were not included for moose that used this area because the distance traveled was short. GTNP: Grand Teton National Park; BTNF: Bridger-Teton National Forest.

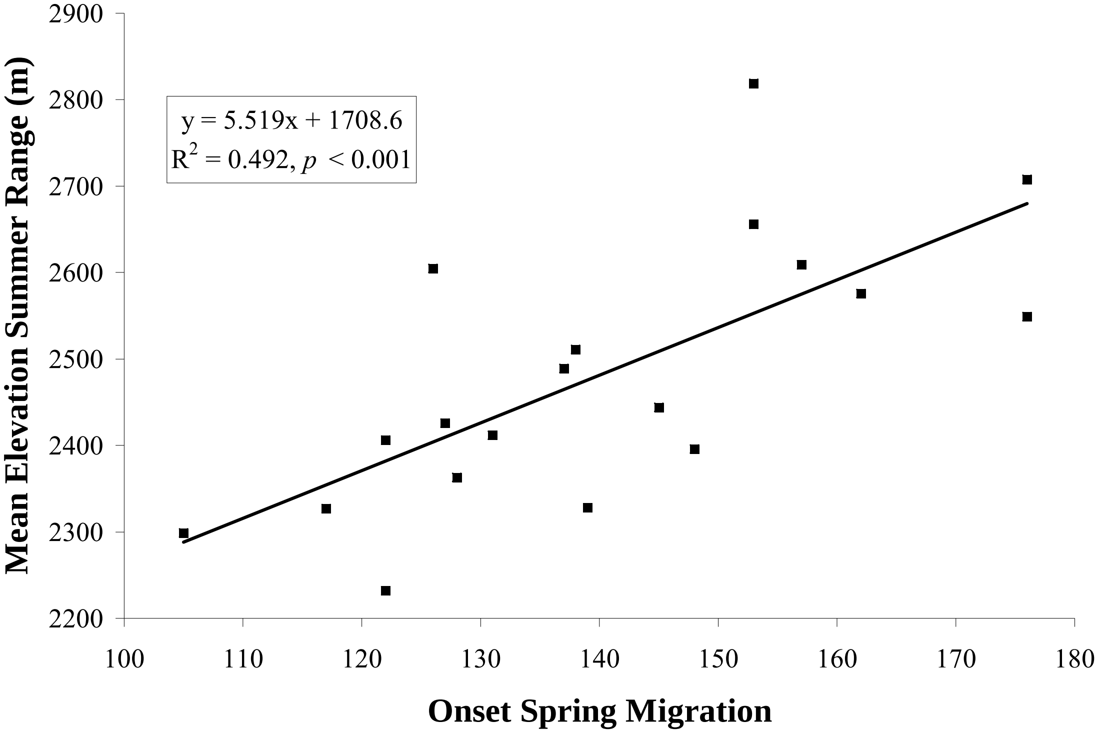

Figure 2.3. Scatterplot of the onset of spring migration (Julian date) against the mean elevation of summer range (m) for individual GPS-collared adult female moose in northwest Wyoming during spring 2006.

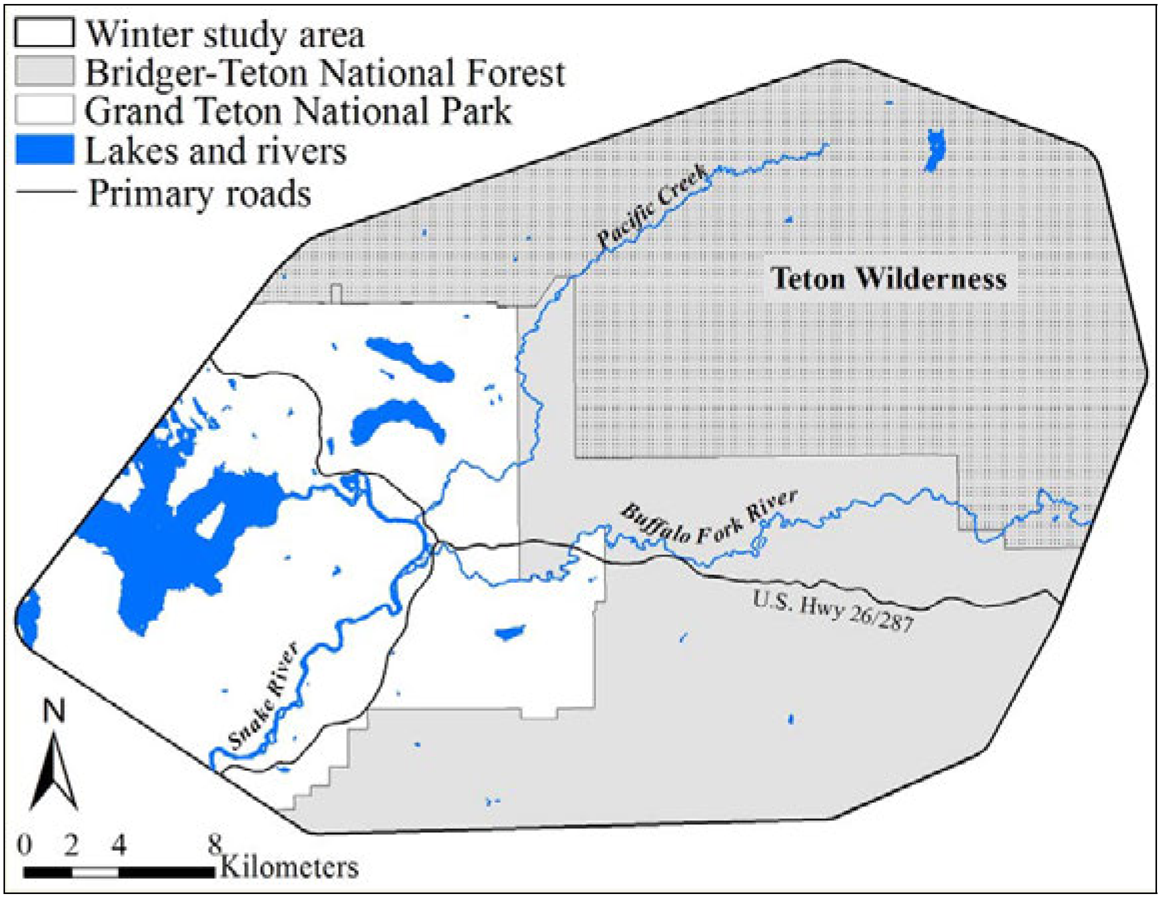

Figure 2.4. Winter habitat selection study area defined by the movement and distribution of GPS-collared adult female moose in northwest Wyoming, 2005-2007.

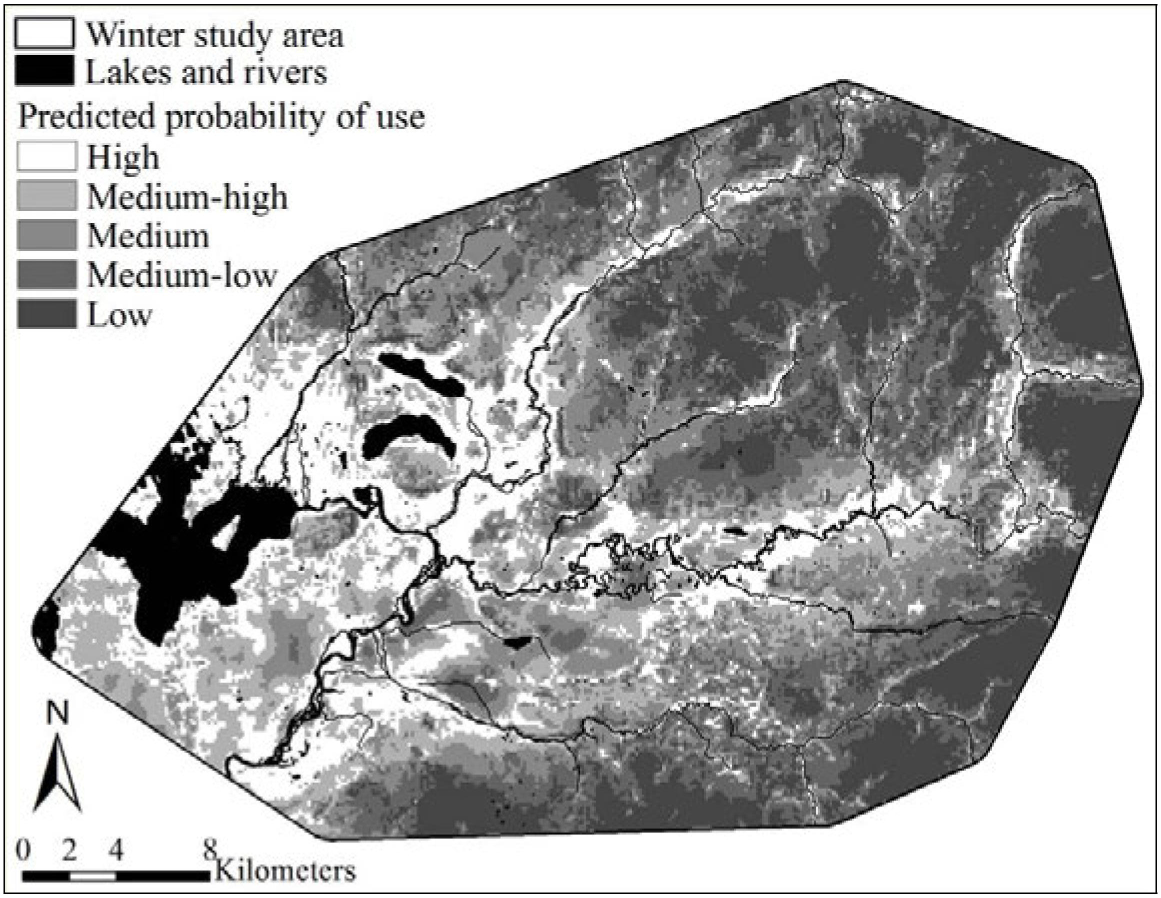

Figure 2.5. Predicted probabilities and associated categories of winter habitat use for adult female moose in northwest Wyoming, 2005-2007.

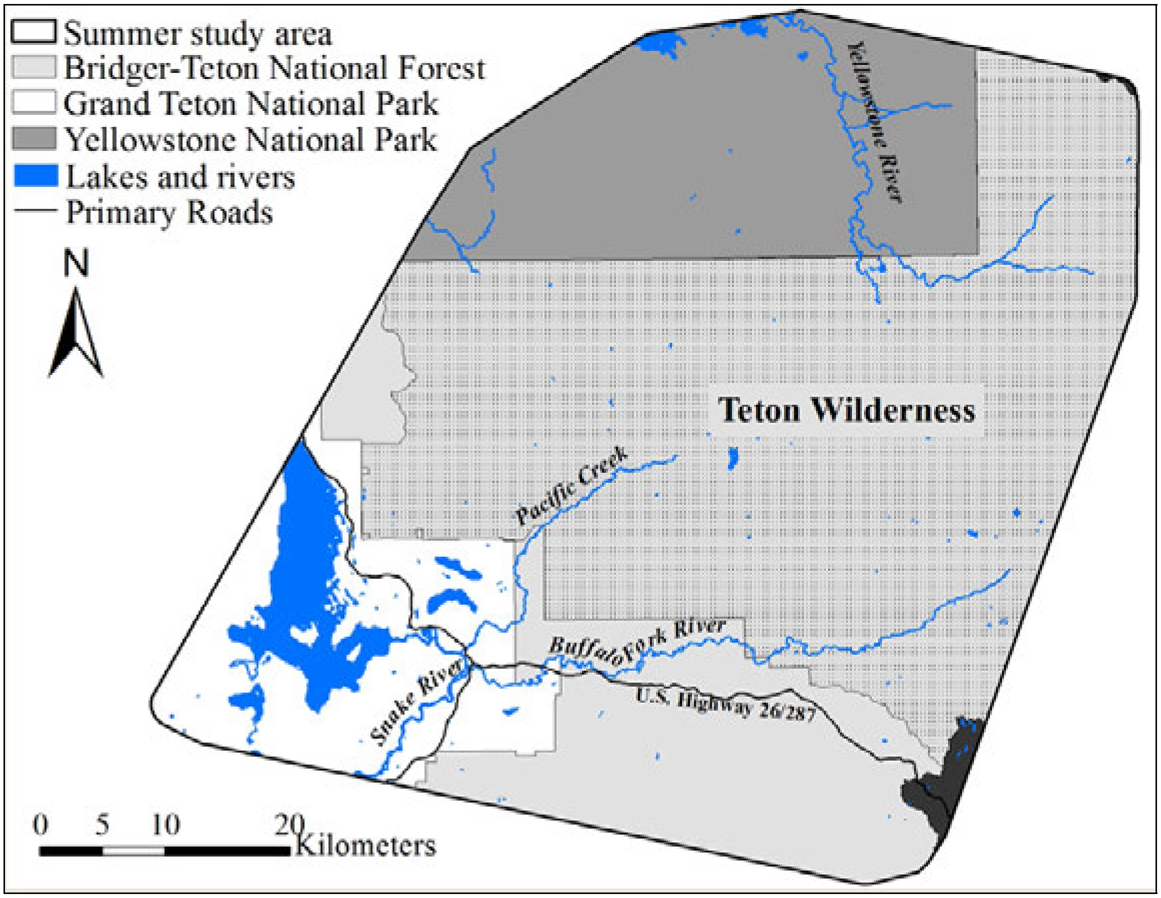

Figure 2.6. Summer habitat selection study area defined by the movement and distribution of GPS-collared adult female moose in northwest Wyoming, summer 2005-2006.

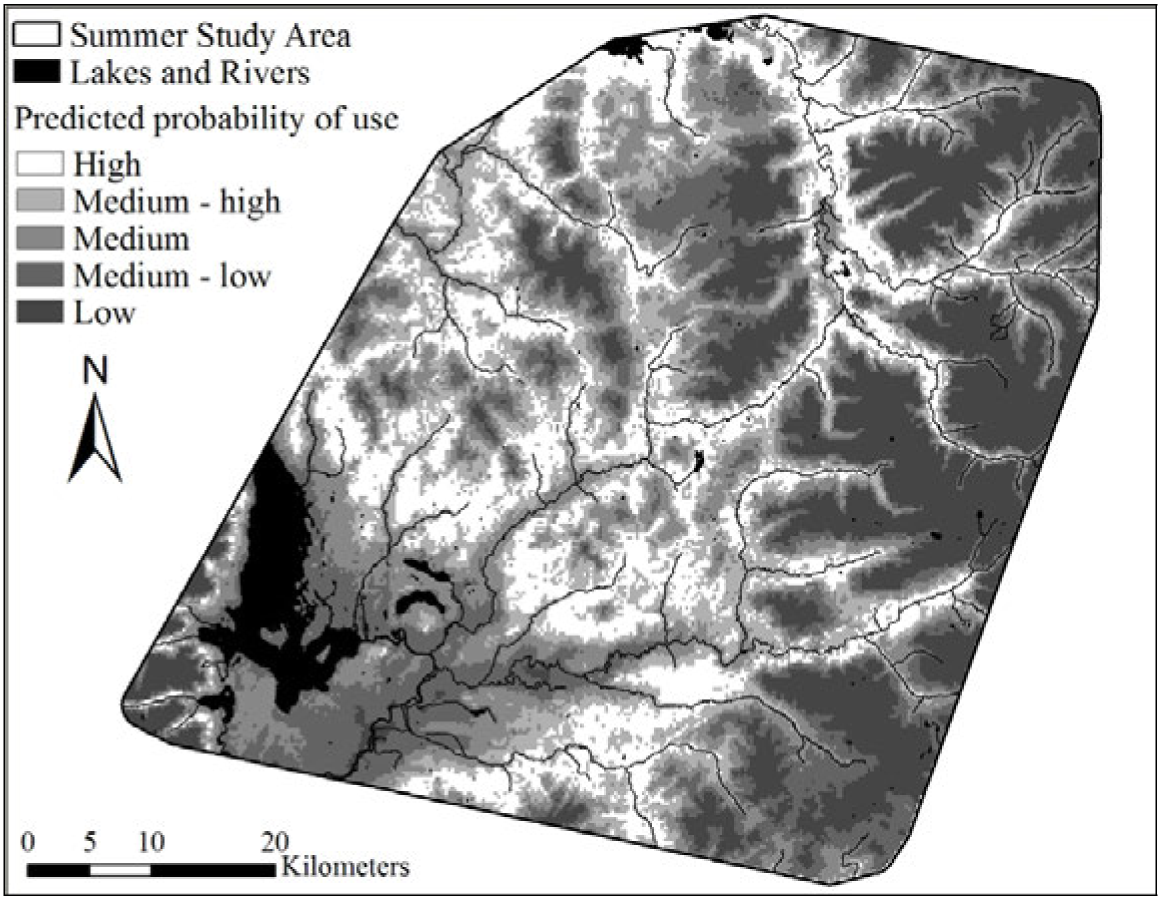

Figure 2.7. Predicted probabilities and associated categories of summer habitat use for adult female moose in northwest Wyoming, 2005-2006.

Appendix 2.1. Total available successful fixes, total number of fix attempts, and percent successful fixes by season and year for GPS-collared adult female moose in northwest Wyoming.

ID	2005						2006						2007		
	Winter			Summer			Winter			Summer			Winter		
	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success
F117	1877	1892	99.21	1921	2022	95.00	4226	4289	98.53	1809	1926	93.93	1498	1500	99.87
F120	2271	2285	99.39	1739	1761	98.75	3767	3801	99.11	1744	1794	97.21	1634	1635	99.94
F122	1878	1882	99.79	1570	1664	94.35	3973	4038	98.39	1582	1658	95.42	2575	2644	97.39
F123	2255	2270	99.34	1215	1269	95.74	4746	4793	99.02	909	966	94.10	2302	2319	99.27
F124	2232	2259	98.80	1254	1310	95.73	4361	4391	99.32	1240	1269	97.71	2379	2411	98.67
F126	1587	1604	98.94	1963	2024	96.99	3883	3909	99.33	2019	2119	95.28	1998	2333	85.64
F127	944	944	100.00	3187	3259	97.79	3006	3011	99.83	2844	2954	96.28	1731	1762	98.24
F128	1941	1973	98.38	1444	1457	99.11	1328	4369	30.40 [a]	1209	1264	95.65	N.A.[a]		
F129	2769	2782	99.53	668	698	95.70	4778	4817	99.19	1017	1098	92.62	2253	2263	99.56
F130	1926	1950	98.77	2530	2589	97.72	1361	1368	99.49	N.A.[b]			N.A.[b]		
F131	2676	2679	99.89	632	674	93.77	1494	1502	99.47	N.A.[b]			N.A.[b]		
F133	1638	1643	99.70	1970	2031	97.00	3736	3764	99.26	2252	2394	94.07	1493	1494	99.93
F134	2076	2093	99.19	1069	1140	93.77	5106	5158	98.99	487	548	88.87	2092	2097	99.76
F135	2082	2108	98.77	1393	1432	97.28	4921	5005	98.32	744	783	95.02	1870	1873	99.84
F142	1585	1597	99.25	1298	1351	96.08	3611	3626	99.59	2108	2145	98.28	1710	1713	99.82
F143	1638	1643	99.70	2305	2346	98.25	1715	1724	99.48	N.A.[b]			N.A.[b]		
F146	1396	1445	96.61	1031	1421	72.55 [a]	2043	4309	47.41 [a]	1312	2246	58.41 [a]	891	1582	56.32 [a]
F173	N.A.[b]			N.A.[b]			2495	2514	99.24	988	1031	95.83	2050	2052	99.90
F174	N.A.[b]			N.A.[b]			1731	1737	99.66	2324	2404	96.67	1688	1692	99.76
F175	N.A.[b]			N.A.[b]			2700	2728	98.97	492	559	88.01	2590	2604	99.46
F176	N.A.[b]			N.A.[b]			1834	1845	99.40	1627	1687	96.44	2043	2171	94.10
F177	N.A.[b]			N.A.[b]			2352	2373	99.12	873	960	90.94	2426	2437	99.55

Appendix 2.1. Continued.

	2005						2006						2007		
	Winter			Summer			Winter			Summer			Winter		
ID	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success	Avail Fixes	Total Fixes	% Success
F178	N.A.[b]			N.A.[b]			2154	2181	98.76	608	655	92.82	2570	2582	99.54
Mean	1928	1944	99.16	1635	1689	96.78	3236	3265	99.09	1363	1427	95.54	1939	1958	99.02

[a] Collar malfunction during all or part of the season, not included in calculation of seasonal means.
[b] Not applicable: moose not radio-collared during these seasons.

Appendix 2.2. Total available successful fixes, total number of 3-dimensional (3D) fixes, and percent 3D fixes by season and year for GPS-collared adult female moose in northwest Wyoming. Total available fixes for summer 2005 and 2006 differs from those in Appendix 2.1 because locations were removed from summer if a moose arrived on summer range prior to 15 June or left after 15 November to maintain a constant fix schedule of 1 fix attempt every 5 hours during the summer period.

	2005						2006						2007		
	Winter			Summer			Winter			Summer			Winter		
ID	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D
F117	1877	1468	78.21	899	520	57.84	4226	3449	81.61	879	432	49.15	1498	1286	85.85
F120	2271	1858	81.81	914	676	73.96	3767	3402	90.31	903	626	69.32	1634	1513	92.59
F122	1878	1686	89.78	809	412	50.93	3973	3506	88.25	776	429	55.28	2575	2217	86.10
F123	2255	1693	75.08	754	435	57.69	4746	3679	77.52	684	366	53.51	1377	1758	76.37
F124	2232	1781	79.79	785	516	65.73	4361	3616	82.92	771	535	69.39	2379	2107	88.57
F126	1587	1313	82.73	939	508	54.10	3883	3319	85.48	923	484	52.44	1998	1232	61.66
F127	944	903	95.66	1189	730	61.40	3006	2813	93.58	1087	628	57.77	1731	1498	86.54
F128	1941	1611	83.00	856	660	77.10	1328	1187	89.38[a]	675	543	80.44	N.A.[a]		
F129	2769	2342	84.58	668	447	66.92	4778	4004	83.80	727	346	47.59	2253	1868	82.91
F130	1926	1291	67.03	1064	658	61.84	1361	1214	89.20	N.A.[b]			N.A.[b]		
F131	2676	2417	90.32	632	426	67.41	1494	1337	89.49	N.A.[b]			N.A.[b]		
F133	1638	1420	86.69	939	523	55.70	3736	3369	90.18	939	464	49.41	1493	1339	89.69
F134	2076	1585	76.35	701	389	55.49	5106	4015	78.63	487	223	45.79	2092	1757	83.99
F135	2082	1618	77.71	814	479	58.85	4921	3977	80.82	669	336	50.22	1870	1574	84.17
F142	1585	1213	76.53	794	588	74.06	3611	3031	83.94	985	700	71.07	1710	1487	86.96
F143	1638	1426	87.06	1024	690	67.38	1715	1507	87.87	N.A.[b]			N.A.[b]		
F146	1396	862	61.75	540	176	32.59[a]	2043	561	27.46[a]	596	163	27.35[a]	891	210	23.57[a]
F173	N.A.[b]			N.A.[b]			2495	2079	83.33	753	447	59.36	2050	1765	86.10

Appendix 2.2. Continued.

	2005						2006						2007		
	Winter			Summer			Winter			Summer			Winter		
ID	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D	Avail Fixes	Total 3D	% 3D
F174	N.A.[b]			N.A.[b]			1731	1479	85.44	1001	587	58.64	1688	1498	88.74
F175	N.A.[b]			N.A.[b]			2700	2168	80.30	492	233	47.36	2590	2194	84.71
F176	N.A.[b]			N.A.[b]			1834	1491	81.30	871	625	71.76	2043	1830	89.57
F177	N.A.[b]			N.A.[b]			2352	1820	77.38	685	377	55.04	2426	2000	82.44
F178	N.A.[b]			N.A.[b]			2154	1581	73.40	608	344	56.58	2570	1996	77.67
Mean	1928	1558	80.82	861	541	62.82	3236	2707	83.67	785	459	58.50	2050	1718	83.79

[a] Collar malfunction during all or part of the season, not included in calculation of seasonal means.

[b] Not applicable: moose not radio-collared during these seasons.

Appendix 2.3. Mean distance moved per day (km) by year and season for GPS-collared adult female moose in northwest Wyoming. Mean winter and summer daily distance moved were calculated by dividing the total distance moved for the season by 24 and 4.75, respectively. Total distance moved per season was estimated in ArcGIS using the Home Range Tools Extension for ArcGIS, Version 1.1 (Rodgers et al. 2007).

	2005		2006		2007
ID	Winter	Summer	Winter	Summer	Winter
F117	1764.7	1481.7	1680.7	1298.4	1120.1
F120	1882.1	2197.6	1272.5	1942.3	1150.3
F122	2057.3	803.3	1411.4	859.3	1721.0
F123	1711.2	2164.5	1587.8	2392.2	1755.8
F124	1668.2	1599.5	1541.5	1746.2	1472.2
F126	1379.5	1449.1	1234.1	1439.9	1425.1
F127	1187.8	1066.1	1001.0	1251.6	1466.4
F128	1958.4	1983.4		1504.7	
F129	2033.3	1741.0	1534.6	2142.8	1402.8
F130	1951.7	1706.5	1023.1		
F131	1124.4	753.5	1039.4		
F133	1337.8	1429.6	1048.3	1373.1	1164.5
F134	1166.6	1678.9	1768.8	1834.9	1755.6
F135	1545.4	1567.2	1520.4	1323.5	1141.9
F142	1837.2	2929.3	1801.7	2611.8	1401.4
F143	1791.8	1977.8	832.8		
F146	1453.9				
F173			931.0	1630.4	1535.0
F174			1339.7	873.2	1451.5
F175			1284.7	1498.8	1428.2
F176			1410.7	1234.2	1393.2
F177			2102.2	2767.9	1660.6
F178			1096.1	2606.4	1706.6
Mean	1638.3	1658.1	1355.4	1701.7	1452.9

Appendix 2.4. Dates of seasonal range use for GPS-collared adult female moose by season and year in northwest Wyoming.

	2005				2006				2007	
	Winter		Summer		Winter		Summer		Winter	
ID	Begin[a]	End	Begin	End	Begin	End	Begin	End	Begin	End[b]
F117	16 Feb	5 May	5 May	27 Nov[c]	30 Nov[c]	28 May	28 May	16 Dec	16 Dec	17 Feb
F120	16 Feb	22 May	24 May	5 Dec	10 Dec	18 May	24 May	6 Dec	9 Dec	15 Feb
F122	16 Feb	5 May	6 May	7 Nov	8 Nov	2 May	4 May	26 Oct	27 Oct	1 Mar
F123	16 Feb	21 May	22 May	4 Nov	10 Nov	2 Jun	3 Jun	3 Nov	21 Dec	17 Feb
F124	16 Feb	21 May	21 May	11 Nov	16 Nov	19 May	22 May	4 Nov	20 Nov	1 Mar
F126	16 Feb	23 Apr	24 Apr	15 Nov	15 Nov	27 Apr	28 Apr	23 Nov	24 Nov	1 Mar
F127	16 Feb	27 Mar	27 Mar	9 Dec	10 Dec	15 Apr	17 Apr	17 Dec	17 Dec	1 Mar
F128	16 Feb	9 May	15 May	12 Nov	16 Nov	17 May	18 May			
F129	16 Feb	11 Jun	15 Jun	8 Nov	16 Nov	6 Jun	8 Jun	22 Nov	26 Nov	1 Mar
F130	16 Feb	8 May	10 May	25 Dec	27 Dec					
F131	16 Feb	7 Jun	16 Jun	3 Nov	16 Nov					
F133	16 Feb	25 Apr[c]	1 May[c]	23 Nov	2 Dec	8 May[c]	9 May[c]	16 Dec	17 Dec	17 Feb
F134	16 Feb	14 May	27 May	2 Nov	14 Nov	25 Jun	30 Jun	22 Oct	3 Dec	1 Mar
F135	16 Feb	14 May	16 May	7 Nov	14 Nov	11 Jun	24 Jun	18 Nov	29 Nov	15 Feb
F142	16 Feb	23 Apr	20 May	12 Nov	30 Nov	2 May	18 May	15 Dec	19 Dec	1 Mar
F143	16 Feb	25 Apr[c]	1 May[c]	6 Dec	12 Dec					1 Mar
F146	16 Feb	17 Apr	16 May	9 Nov	10 Nov	12 May	16 May	17 Dec	25 Dec	1 Mar
F173					23 Feb[a]	6 May	13 Jun	24 Nov	5 Dec	1 Mar
F174					23 Feb[a]	7 May	8 May	16 Dec	20 Dec	1 Mar
F175					23 Feb[a]	25 Jun	29 Jun	23 Oct	4 Nov	1 Mar
F176					23 Feb[a]	11 May	22 May	29 Nov	30 Nov	1 Mar
F177					23 Feb[a]	2 Jun	5 Jun	10 Nov	19 Nov	1 Mar
F178					23 Feb[a]	25 May	16 Jun	31 Oct	9 Nov	1 Mar

[a] Date monitoring began.

[b] Date monitoring ended. Collar was either removed or released from the moose.

Appendix 2.4. Continued.

[c] Unable to identify exact date of transition between seasonal ranges. Dates estimated from the mean dates of movement from moose that overlapped.

Appendix 2.5. Number of relocations (*n*) and nearest neighbors (*k*) used to calculate 90% LoCoH home range (HR) size (km^2) for individual GPS-collared adult female moose by season in northwest Wyoming, 2005-2007.

	2005						2006						2007		
	Winter			Summer			Winter			Summer			Winter		
ID	*n*	*k*	HR Size	*n*	*k*	HR Size	*n*	*k*	HR Size	*n*	*k*	HR Size	*n*	*k*	HR Size
F117	1877	64	3.48	899	34	4.50	4226	73	4.35	879	43	5.37	1498	62	0.86
F120	2271	50	2.26	914	50	17.00	3768	61	2.20	903	54	20.39	1634	47	1.01
F122	1878	44	2.74	809	37	1.75	3973	74	5.61	776	48	1.85	2575	55	2.10
F123	2255	61	4.72	754	29	12.48	4746	68	8.08	684	44	20.41	1377	46	1.86
F124	2232	51	4.40	785	40	15.81	4361	79	9.21	771	43	14.91	2379	65	3.79
F126	1587	53	2.73	939	40	13.37	3883	67	2.86	923	37	12.49	1998	66	2.21
F127	944	41	0.88	1189	41	5.60	3006	73	1.32	1087	39	7.36	1731	59	1.40
F128	1941	53	6.14	856	30	12.51	N.A.[a]			675	36	8.94	N.A.[a]		
F129	2769	67	10.40	668	43	6.17	4778	77	7.59	727	39	7.09	2253	50	3.01
F130	1926	62	5.65	1064	37	9.23	1361	44	1.15	N.A.[b]			N.A.[b]		
F131	2676	64	3.12	632	42	4.28	N.A.[c]								
F133	1638	51	3.02	939	32	10.53	3736	77	3.15	939	48	8.89	1493	68	1.24
F134	2076	59	2.85	701	41	9.95	5106	82	12.34	487	29	9.97	2092	62	3.23
F135	2082	60	3.48	814	34	14.23	4921	87	5.05	669	48	9.44	1870	60	2.14
F142	1585	42	4.89	794	32	25.87	3611	82	3.85	985	41	32.60	1710	52	1.99
F143	1638	58	4.40	1024	32	27.35	1715	46	0.73	N.A.[c]					
F146	1396	46	3.16	N.A.[a]			N.A.[a]			N.A.[a]			N.A.[a]		
F173	N.A.[b]			N.A.[b]			1705	41	0.29	753	29	10.74	2050	48	2.64
F174	N.A.[b]			N.A.[b]			1731	52	2.12	1001	52	5.40	1688	56	4.01
F175	N.A.[b]			N.A.[b]			2700	69	1.65	492	36	6.00	2590	60	1.94
F176	N.A.[b]			N.A.[b]			1834	61	2.77	871	40	13.72	2043	57	4.36
F177	N.A.[b]			N.A.[b]			2352	55	6.62	685	25	35.85	2426	63	6.26

Appendix 2.5. Continued.

	2005						2006						2007		
	Winter			Summer			Winter			Summer			Winter		
ID	*n*	*k*	HR Size	*n*	*k*	HR Size	*n*	*k*	HR Size	*n*	*k*	HR Size	*n*	*k*	HR Size
F178	N.A.[b]			N.A.[b]			2154	59	0.62	608	27	22.26	2570	58	8.36

[a] Not applicable: collar malfunction, home range size not calculated.
[b] Not applicable: moose not radio collared.
[c] Not applicable: mortality, home range size not calculated.

Appendix 2.6. Coefficients for population-level resource selection probability function models developed from GPS-collared adult female moose in northwest Wyoming during winters 2005-2007.

	Winter 2005			Winter 2006			Winter 2007		
Variable	β	SE	*P*	β	SE	*P*	β	SE	*P*
Intercept	5.269	3.443	0.144	9.564	3.920	0.0247	19.875	5.116	0.001
Riparian	2.785	0.363	<0.001	2.584	0.655	<0.001	2.989	0.286	<0.001
Elevation (m)	-0.007	0.002	<0.001	-0.010	0.002	<0.001	-0.015	0.002	<0.001
Habitat diversity	0.442	0.187	0.031	1.114	0.274	<0.001	0.675	0.221	0.007
Dist. to cover (m)	-0.003	0.001	0.013	-0.003	0.001	0.006	-0.002	0.001	0.034
Aspect northwest	-0.638	0.386	0.118	N.S.[a]			-3.563	1.510	0.031
Aspect southeast	-0.063	0.233	0.789	N.S.			-0.042	0.186	0.823
Aspect southwest	-1.453	1.049	0.185	N.S.			-0.217	0.368	0.563
Slope (°)	N.S.			0.033	0.040	0.411	0.112	0.049	0.035
Slope^2 (°)	N.S.			-0.003	0.001	0.059	-0.006	0.002	0.015
Mixed conifer	N.S.			-3.464	1.681	0.053	[b]		
Spruce/fir	N.S.			N.S.			[b]		

[a] Not significant.

[b] Coefficients for mixed conifer and spruce/fir were removed from population-level model in 2007 because estimates were not indicative of population-level selection.

Appendix 2.7. Coefficients for population-level resource selection probability function models developed from GPS-collared adult female moose in northwest Wyoming during summer 2005 and 2006.

	Summer 2005			Summer 2006		
Variable	β	SE	*P*	β	SE	*P*
Intercept	-436.311	91.240	<0.001	-391.534	56.487	<0.001
Elevation (m)	0.348	0.072	<0.001	0.308	0.046	<0.001
Elevation^2 (m)	-0.000	<0.001	<0.001	-0.000	<0.001	<0.001
Mixed	-3.854	1.916	0.063	-1.362	0.449	0.007
Slope (°)	0.062	0.064	0.349	-0.002	0.039	0.969
Slope^2 (°)	-0.004	0.002	0.058	-0.002	0.001	0.116
Aspen	-1.511	0.736	0.058	-1.839	0.932	0.064
Spruce/fir	-1.010	0.563	0.070	N.S.[a]		
Habitat diversity	N.S.			0.570	0.206	0.013
Aspect northwest	N.S.			0.329	0.204	0.124
Aspect southeast	N.S.			0.049	0.174	0.783
Aspect southwest	N.S.			-0.405	0.203	0.061
Lodgepole	N.S.			-1.106	0.357	0.006
Dist. to cover (m)	N.S.			-0.004	0.002	0.085

[a] Not significant.

CHAPTER 3

PHYSIOLOGICAL HEALTH ASSESSMENT OF ADULT FEMALE SHIRAS MOOSE IN NORTHWEST WYOMING

In the format of a paper in the journal *Alces*

INTRODUCTION

The "animal indicator concept" has been used to provide managers with a relative index of a population with respect to the carrying capacity of its habitat (Franzmann 1985). This approach assumes that because an animal is a product of its environment, it will likely reflect the quality of its environment. Early work focused on the use of hematological and serum chemical parameters to assess differences in habitat quality among populations of pronghorn (*Antilocapra americana*; Seal and Hoskinson 1978), white-tailed deer (*Odocoileus virginianus*; Seal et al. 1978), and elk (*Cervus elaphus*; Weber et al. 1984). Franzmann and LeResche (1978) expanded this concept by evaluating blood parameters in relation to indices of physical condition for Alaskan moose (*Alces alces gigas*). This provided a set of baseline data that could be used for comparative purposes to assess population condition and, thus, habitat quality and potential reproductive performance (Franzmann and Schwartz 1985, Stephenson 2003). Packed cell volume (PCV) was the single best predictor of body condition in moose, followed by hemoglobin (Hb), total serum protein (TSP), calcium (Ca), and phosphorous (P; Franzmann and LeResche 1978). These blood parameters identified populations on the extremes (i.e., very good or very poor condition), but were less effective when used to compare populations in moderate condition (Franzmann et al. 1987). More recently, the value of using TSP, Ca, and P has come into question (Keech et al. 1998). Another technique has been developed to evaluate body condition and estimate total body fat using ultrasonography to measure rump fat depth (Stephenson et al. 1993, Stephenson et al. 1998).

The “animal indicator concept” has also been applied to assessment of the nutrient quality of habitat because herbivores acquire minerals from the plants they consume (Franzmann 1985). Even if an animal appears to be in relatively good physical condition, nutritional deficiencies can create physiological imbalances that may impact population performance (Combs 1987, Gogan et al. 1989). Free-ranging herbivores rarely acquire sufficient quantities of particular nutrients because of high variability in forage mineral concentrations among sites and seasons (McDowell 2003). The nutrient quality of browse used by moose is most limited during winter (Kubota et al. 1970, Oldemeyer et al. 1977, Ohlson and Staaland 2001) and mineral concentrations in moose hair show similar temporal trends (Franzmann et al. 1974, Flynn et al. 1977, Stewart and Flynn 1978, Flynn and Franzmann 1987). Therefore, the effects of nutritional deficiencies should be most apparent in winter. Mineral deficiencies can lead to reduced survival, especially among calves and yearlings, and reduced reproductive output among domestic herbivores (WallisDeVries 1998). Clinical deficiencies have rarely been observed in moose populations because a reduction in fitness often predisposes moose to other forms of mortality (O’Hara et al. 2001). Nonetheless, deficiencies of trace elements, specifically Cu, have been suggested as a cause of moose population declines in Alaska (Flynn et al. 1977, O’Hara et al. 2001), Sweden (Frank et al. 1994), and Minnesota

(Custer et al. 2004). Furthermore, O'Hara et al. (2001) suggested that populations experiencing marginal Cu deficiencies may not exhibit clinical symptoms unless additional stressful events occur.

Indices of population density and calf-cow ratios suggest a downward trend in Shiras moose (*A.a. shirasi*) numbers in northwest Wyoming. Potential factors contributing to the decline include a decrease in the quality of summer and winter habitat, increased predation by large carnivores, disease or parasites, or a combination of factors (Berger et al. 1999, Berger et al. 2001, Brimeyer and Thomas 2004). Population declines have been most evident in the Buffalo Fork Valley, approximately 50 km north of the town of Jackson, Wyoming (Brimeyer and Thomas 2004). To address the issues of habitat quality, disease, and parasites, I used the animal indicator concept to investigate the physiological health of adult (≥ 2 years) female Shiras moose in northwest Wyoming via a suite of physiological measurements that can be used to describe the nutritional status of the study population. Although Houston (1969) and Kreeger et al. (2005) have reported blood values for Shiras moose in Wyoming, few data were available from large samples collected over multiple years. Therefore, this work provides baseline data that can be used to aid managers in future evaluation of the health of Shiras moose throughout the Intermountain West. My research objectives were to: (1) compare hematological and serum chemical parameters to baseline data from Alaskan moose, (2) measure maximum rump fat depth with ultrasonography to assess relative health compared to Alaskan moose, (3) examine macronutrient and micronutrient content of moose serum and hair and compare to reported deficiency values for domestic ruminants, (4) evaluate the presence of infectious diseases, and (5) assess endoparasite and ectoparasite loads.

During this study, pregnant adult moose captured during winter experienced reduced parturition rates the following spring (Chapter 4). Consequently, a sixth objective was established to examine the hypothesis that if moose are Cu deficient, a stressful event (i.e., capture) could induce perinatal mortality and influence reproductive success (O'Hara et al. 2001).

STUDY AREA

The study area encompassed approximately 6,400 km^2 of predominately public land in northwest Wyoming. It included the upper Snake River and upper Yellowstone River watersheds and included portions of Grand Teton National Park (GTNP), Yellowstone National Park (YNP), and the Bridger-Teton National Forest (BTNF) where elevations ranged from 1,866 to 4,197 m. Moose wintered in low-elevation, riparian-dominated habitats along the Snake River and its primary tributaries (i.e., Pacific Creek, Buffalo Fork River, Gros Ventre River; Chapter 2). During summer, migratory moose traveled to more dispersed, mid-elevation ranges (Chapter 2), whereas nonmigratory individuals remained on low-elevation ranges (Houston 1968).

Vegetation types varied with elevation and aspect (Whitlock 1993, Knight 1994). Lower elevations, and many south-facing slopes at higher elevations, were dominated by sagebrush (*Artemisia* spp.). Mid-elevations were characterized by large stands of lodgepole pine (*Pinus contorta*) intermixed with Douglas fir (*Psuedotsugia menziesii*) and aspen (*Populus tremuloides*). Engelmann spruce (*Picea engalmanni*) and subalpine fir (*Abies lasiocarpa*) were found on north slopes and more mesic sites. Engelmann spruce, subalpine fir, and lodgepole pine intermixed with smaller stands of whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*), and aspen dominated higher elevations. Alpine tundra occurred at the highest elevations while open forest parks and subalpine meadows occurred at all elevational gradients. Riparian areas dominated by willows (*Salix* spp.) intermixed with narrowleaf cottonwood (*Populus angustifolia*) were located in large, relatively flat floodplain environments at lower elevations and along nearly all drainages within the study area (Wigglesworth and Wachob 2004).

The climate was characterized by short, cool summers and long, cold winters. From 1975-2004, annual precipitation averaged 56.2 cm (range = 37.9-79.1 cm) of which approximately 65% fell as snow between November and May (http://www.cdc.noaa.gov/ cgi-bin/Timeseries/ timeseries1.pl; accessed 16 October 2005). The Teton Mountains to the west and the northern highlands along the southern boundary of YNP typically received the greatest amounts of precipitation (Houston 1968, Cole 1969, Boyce 1989).

METHODS

Adult female moose were captured on winter range within the study area between January and March 2005, 2006, and 2007. Moose were darted from the ground or a helicopter and immobilized with 10-mg thiafentanil oxalate (A-3080, Wildlife Pharmaceuticals Inc., Fort Collins, Colorado, USA; McJames et al. 1994, Arnemo et al. 2003, Kreeger et al. 2005) in 2005 and 2006 and 10-mg carfentanil (Wildnil, Wildlife Pharmaceuticals Inc., Fort Collins, Colorado, USA) in 2007. Immobilization drugs were delivered in a 1-ml dart (Pneu-dart, Williamsport, Pennsylvania, USA) fired from a CO_2-

powered dart rifle (Dan-Inject North America, Fort Collins, Colorado, USA) or a 0.22-caliber-blank dart rifle (Model 193, Pneu-dart, Williamsport, Pennsylvania, USA). Once handling was completed, thiafentanil and carfentanil were antagonized with an intramuscular injection of 300-mg naltrexone (Trexonil, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA; Kreeger et al. 2005) administered at multiple sites. Techniques used to evaluate pregnancy and to determine the presence of a calf in spring were described in Chapter 4. Captures were performed in accordance with approved University of Wyoming Animal Care and Use Committee protocols.

Once immobilized, moose were blindfolded and fitted with global positioning system (GPS; model TGW-3700, Telonics, Mesa, Arizona, USA) or very high frequency (VHF) radio transmitters (model M2710, Advanced Telemetry Systems, Isanti, Minnesota, USA). Numbered, aluminum ear tags were affixed to each ear. Body condition was subjectively evaluated and a score from 0 to 10 was assigned to each moose (Franzmann 1977). Depth of rump fat was measured with an Omega I portable ultrasound unit (E.I. Medical, Loveland, Colorado, USA) in 2005 and a Bantam XLS portable ultrasound unit (E.I. Medical, Loveland, Colorado, USA) in 2006 and 2007 (Stephenson et al. 1993, Keech et al. 1998, Stephenson et al. 1998). Both ultrasound units used a 5-MHz 8-cm linear-array transducer and subcutaneous fat was measured with electronic calipers to the nearest 0.1 cm (Stephenson et al. 1998).

Approximately 50-ml of blood was collected from each moose via jugular venipuncture for hematological analyses, serum chemical analyses, serum trace element screen, and bacterial and viral serology. Hematological analyses included whole blood concentrations of PCV, Hb, mean corpuscular hemoglobin content (MCHC), red blood cells (RBCs), total white blood cells (WBCs), composition of white blood cells, and platelets. Serum chemical analyses included concentrations of albumin (ALB), alkaline phosphate (ALP), aspartate aminotransferase (AST), blood urea nitrogen (BUN), creatine kinase (CK), gamma-glutanyl transferase (GGT), globulins (Glob), glucose (Gluc), lactate dehydrogenase (LDH), TSP, and the macronutrients Ca, magnesium (Mg), and P. Levels of five micronutrients were analyzed with serum trace element screens and included Cu, iron (Fe), manganese (Mn), molybdenum (Mb), and zinc (Zn). Blood was analyzed for the presence of antigens against *Brucella abortus*, *Leptospira*, infectious bovine rhinotracheitis virus, bovine viral diarrhea virus, parainfluenza-3 virus, and bovine respiratory syncytial virus in 2005 while analysis was conducted for only *B. abortus* in 2006 and 2007. Fecal samples and ear swabs were collected to evaluate endo- and ectoparasite loads. A 30-second tick count was performed along the dorsal midline posterior to the neck of each moose to assess the severity of winter tick (*Dermacantor albipictus*) infestations. Hair samples were collected from the dorsal midline between the shoulders and analyzed for concentrations of arsenic (As), barium (Ba), cadmium (Cd), chromium (Cr), cobalt (Co), Cu, Fe, lead (Pb), Mn, mercury (Hg), Mb, nickel (Ni), selenium (Se), thallium (Tl), vanadium (V), tin (Sn) and Zn. All diagnostic analyses were performed at the Wyoming State Veterinary Laboratory (Laramie, Wyoming, USA).

Blood parameter (hematological and serum chemical) values and mineral concentrations (serum and hair macro- and micronutrients) were pooled within years and Table 3.1 was used to assess the nutritional status of the sampled populations based on published reference values. Mean values for PCV, Hb, TSP, Ca, and P were compared to baseline data from Alaskan moose that were considered to be in average to above average condition (Franzmann and LeResche 1978) and the proportion of the sampled population that were below these reported values was presented. Macro- and micronutrient requirements for moose have not been established, so the proportion of the sampled population that was deficient was calculated based on published deficiency thresholds for domestic ruminants (Puls 1994, McDowell 2003). The published reference values for Ca and Mg are not true deficiency thresholds and only represent the lower normal limit for domestic ruminants (Puls 1994, McDowell 2003).

A one-way analysis of variance and a Tukey's Honestly Significant Difference (HSD) test were used to examine among year differences ($\alpha = 0.05$) in rump fat depth, body condition scores (BCS), all blood parameters, and minerals that were above the minimum detection limit (MDL) in order to quantify between year variations. A Spearman rank correlation analysis was conducted to determine if a significant relationship existed between hematological and serum chemical parameters and depth of rump fat ($\alpha = 0.05$). I used logistic regression (Hosmer and Lemeshow 2000) to determine if there was a relationship between Cu levels and parturition rates for pregnant, captured moose and to estimate the level of Cu likely to induce perinatal mortality if a significant relationship was observed. I also used a 2-sample *t*-test with equal variance to test for differences in serum and hair Cu concentrations and rump fat depths for pregnant cows observed with and without calves in the spring. All statistical analyses were performed with Statistix 8.0 software (Analytical Software, Tallahassee, Florida, USA).

RESULTS

Moose Captures, Rump Fat, Disease, and Parasites

Forty-eight adult female moose were captured 61 times during the course of the study. Most captures occurred in February (n = 54) from a helicopter (n = 53). Nearly all ultrasonic rump fat measurements were recorded in February (n = 41) with the exception of 5 that were measured in early to mid-March. There was no attempt to distinguish rump fat depth between cows with and without calves at their side because of inconsistencies in reporting the presence of a calf during capture efforts. Mean rump fat depth did not differ significantly among years (2005-2007; $f_{(2,43)} = 0.9$, $P = 0.399$; Table 3.2). There were no differences between rump fat depth for pregnant cows observed with (n = 8) or without calves (n = 31) in the spring ($P = 0.246$, df =37). Differences were observed in BCS among years ($f_{(2,51)} = 4.8$, $P = 0.012$) and *post hoc* analyses indicated that BCS in 2005 were significantly higher than in either 2006 or 2007 (Table 3.2).

Sampled moose (n = 59) were negative for antigens against *B. abortus* in all years and for *Leptospira*, infectious bovine rhinotracheitis virus, bovine viral diarrhea virus, parainfluenza-3 virus, and bovine respiratory syncytial virus in 2005 (n = 20). Tick loads were relatively low and 30-second counts averaged 2.8 ticks/moose with 55 of 59 moose hosting < 10 ticks. No moose (n = 56) had evidence of ear mites and fluke eggs were not observed in any sample (n = 43). Fecal examinations (n = 44) indicated a low infection (≤ 12 eggs/gm) of *Nematodirus* spp. in 13 moose and *Trichostrongylus* spp. in two moose.

Hematological, Serum Chemical, and Macroelement Analyses

There were no significant differences among years for Hb ($P = 0.053$) or platelets ($P = 0.104$), but differences were evident for PCV ($f_{(2,48)} = 9.5$, $P < 0.005$), MCHC ($f_{(2,48)} = 8.3$, $P < 0.005$), RBCs ($f_{(2,48)} = 6.9$, $P = 0.002$), and WBCs ($f_{(2,48)} = 4.7$, $P = 0.013$; Table 3.3). No consistent increasing or decreasing patterns were observed for PCV, MCHC, or RBCs, but WBCs exhibited a generally increasing trend with 2005 significantly lower than 2007. The percent composition of WBCs did not differ significantly among years for lymphocytes ($P = 0.089$), eosinophils ($P = 0.353$), or monocytes ($P = 0.168$), but significant differences were observed for neutrophils ($f_{(2,48)} = 4.7$, $P = 0.014$) and *post hoc* analyses indicated that 2007 was significantly lower than 2005 and 2006 (Table 3.3).

For serum chemical analyses, there were no significant differences among years for ALP ($P = 0.149$) and GGT ($P = 0.339$), but significant differences were found for ALB ($f_{(2,54)} = 19.0$, $P < 0.005$), AST ($f_{(2,54)} = 10.3$, $P < 0.005$), BUN ($f_{(2,54)} = 4.7$, $P < 0.005$), CK ($f_{(2,53)} = 6.5$, $P = 0.003$), globulins ($f_{(2,54)} = 23.6$, $P < 0.005$), glucose ($f_{(2,54)} = 12.5$, $P < 0.005$), LDH ($f_{(2,54)} = 47.1$, $P < 0.005$), and TSP ($f_{(2,54)} = 48.3$, $P < 0.005$; Table 3.4). No consistent increasing or decreasing patterns were observed for ALB, AST, BUN, globulins, glucose, LDH, and TSP. However, CK values exhibited a generally increasing pattern with 2007 means significantly greater than 2005 (Table 3.4).

Serum analyses showed significant differences among years for all three macronutrients (Ca: $f_{(2,54)} = 35.7$, $P < 0.005$; Mg: $f_{(2,53)} = 16.1$, $P < 0.005$; P: $f_{(2,54)} = 4.93$, $P = 0.011$; Table 3.4), but no consistent increasing or decreasing patterns were observed. Serum Ca annual means exceeded the 8.0 mg/dl threshold (see Table 3.1) in 2006 and

2007, but were just below this level in 2005 (Table 3.4). When moose were compared individually, 18% (11 of 58) had Ca levels below the 8.0 mg/dl threshold. Fifty-seven percent (33 of 58) of sampled moose were below the 4.5 mg/dl threshold (see Table 3.1) for serum P and annual means were below this level in 2005 and 2007 (Table 3.4). Serum Mg annual means exceeded the 1.8 mg/dl threshold (see Table 3.1) during all years (Table 3.4) and only 12% (7 of 57) of individual moose were below this level.

The proportions of moose with PCV, Hb, TSP, Ca, and P values lower than those reported for Alaskan moose considered to be in average to above average condition (see Table 3.1) varied (Table 3.5). Most sampled moose fell below the average moose thresholds for Hb, Ca, and P. Approximately half of the moose sampled were below average for PCV while only one-third were below for TSP. Mean Hb concentrations were lower in all years while PCV was lower in 2006 and 2007 (Table 3.3). Serum levels of Ca and P were lower in all years and TSP was lower in 2005, but higher than the average moose threshold in 2006 and 2007 (Table 3.4).

Of the 13 serum chemical parameters analyzed, 2 exhibited a significant relationship with rump fat depth ($n = 43$). Aspartate aminotransferase ($r_s = -0.339$, $P = 0.041$; Figure 3.1) and LDH ($r_s = -0.327$, $P = 0.049$; Figure 3.2) were both inversely correlated with depth of rump fat. The enzyme CK revealed a partial correlation that was negatively related to rump fat ($r_s = -0.317$, $P = 0.057$; Figure 3.3) when all moose were included. However, when one moose with a CK value >1000 U/l was removed from analyses, the direction of correlation reversed and the relationship became insignificant ($r_s = 0.237$, $P = 0.130$). No significant relationship was observed between rump fat and any hematological parameters ($n = 38$).

Serum and Hair Trace Mineral Analyses

Serum Cu, Fe, and Zn were detected in all moose (Table 3.6), whereas Mn and Mb had levels below the MDL and were not detected in any sample. There was not a significant difference among years in Cu ($P = 0.329$), but significant differences were observed for Fe ($f_{(2,47)} = 3.79$, $P = 0.030$) and Zn ($f_{(2,47)} = 25.1$, $P < 0.005$). No consistent increasing or decreasing patterns were observed for the annual means of Fe and Zn. When compared to domestic ruminants (see Table 3.1), sampled moose were deficient in Cu during all years and deficient in Zn in 2005 and 2007 (Table 3.6). When examined individually, a high proportion of moose were deficient in Cu and Zn (Table 3.6) and all moose above the Zn deficiency threshold were sampled in 2006 ($n = 15$). Serum Fe annual means exceeded the 1.1 ppm threshold (see Table 3.1) during all years and only 2% (1 of 50) of individual moose were below this level (Table 3.6).

Hair concentrations of As, Cd, Co, Hg, Mb, Ni, Se, Tl, V, and Sn were consistently below MDL whereas all samples had detectable levels of Ba, Cr, Cu, Fe, Mn, Pb, and Zn (Table 3.6). There were no significant differences among years in Cu ($P = 0.279$), Mn ($P = 0.429$), and Pb ($P = 0.080$), but significant differences were evident for Ba ($f_{(2,56)} = 3.34$, $P = 0.043$), Cr ($f_{(2,56)} = 4.80$, $P = 0.012$), Fe ($f_{(2,56)} = 4.52$, $P = 0.015$), and Zn ($f_{(2,56)} = 11.80$, $P < 0.005$). No consistent increasing or decreasing patterns were observed in concentrations of Ba, Cr, and Zn, but Fe concentrations showed a generally decreasing pattern with 2007 means significantly lower than 2005. Hair annual means for Cu, Fe, Zn, and Mn were below deficiency thresholds for domestic ruminants (see Table 3.1) during all years (Table 3.6). When examined individually, all moose were deficient in Cu, Zn, and Mn while all but 3 moose were below the deficiency threshold for Fe (Table 3.6).

In order to test the hypothesis that a stressful event (i.e., captures) may increase the incidence of perinatal mortality, I examined the relationship between serum and hair Cu concentrations collected from adult female moose in winter and the presence of a calf in spring. All years were pooled and logistic regression failed to reveal a significant relationship between mean serum (P = 0.275, df = 35; Figure 3.4) or hair (P = 0.231, df = 44; Figure 3.5) Cu concentrations and the presence of a calf in the spring. The mean serum Cu concentration for pregnant cows observed with a calf was 0.52 ppm (SD = 0.08, n = 9) and for pregnant cows not observed with a calf was 0.47 ppm (SD = 0.11, n = 28). The mean hair Cu concentration for pregnant cows observed with a calf was 4.62 ppm (SD = 0.69, n = 11) and for pregnant cows not observed with a calf was 4.56 ppm (SD = 0.70, n = 35). There were no significant differences between mean serum (t = -1.22, df = 35, P = 0.230) or hair (t = -0.23, df = 44, P = 0.821) Cu concentrations and the presence of a calf in the spring.

DISCUSSION

Blood Parameters and Rump Fat

Although PCV, Hb, TSP, Ca, and P have been used to evaluate habitat quality and the nutritional status of Alaskan moose (Franzmann and LeResche 1978), none of these parameters were correlated with rump fat depth of Shiras moose in this study. My results suggest that the serum enzymes AST and LDH may be good predictors of Shiras moose condition as indexed by ultrasonic rump fat measurements. Similar to my study, AST was found to be negatively correlated with rump fat of Alaskan moose (Keech et al. 1998). The authors suggested that decreased AST levels reduced moose susceptibility to disease since they were generally in better physical condition. Although this may be true, AST and LDH are indicators of muscle or organ damage generally associated with exertional myopathy (EM; Williams and Thorne 1996). Levels of AST for Shiras moose were not indicative of EM and were well below values reported for bighorn sheep (*Ovis canadensis*) that were stressed or subsequently developed EM (Kock et al. 1987). Additionally, levels of AST were well below values reported for normal moose (Haigh et al. 1977) which suggests that EM had little influence on these relationships. The inverse relationships that I observed between AST, LDH, and rump fat are consistent with increased utilization of body proteins from muscle and organ tissues as lipid reserves decline in lean animals. Indeed, Cherel et al. (1992) observed a similar trend in that lean rats utilized greater amounts of muscle protein during phase II fasting (i.e., protein sparing) than did obese rats. While I observed a significant relationship between two serum enzymes and rump fat depth, similar to research conducted on caribou (*Rangifer tarandus*; Messier et al. 1987), elk (Cook et al. 2001) and moose (Keech et al. 1998), I cannot conclude that a set of blood parameters has been identified that accurately reflects Shiras moose nutritional status as indexed by rump fat at this time.

Maximum rump fat depth indicated that moose in the study area were in relatively good physical condition. When compared to rump fat of moose captured during early to mid-March in Alaska (Keech et al. 1998, Bertram and Vivion 2002, Boertje et al. 2007), the study population displayed nearly two times more rump fat. Although I was unable to compare rump fat for moose with and without calves at side, several studies have reported that cow moose with greater amounts of rump fat were not tending calves (Testa and Adams 1998, Keech et al. 2000). Therefore, it might be that fewer cows had calves at side which resulted in the higher rump fat depths observed in the study area. While rump fat may be a useful predictor of reproductive success within moose populations, it appears to be an insensitive index of fitness when compared across populations (Boertje et al. 2007). Heard et al. (1997) suggested that moose populations living in relatively harsh environments or in areas with low forage quality or quantity may have a higher fat-fertility threshold than moose populations living in milder climates with good quality forage. Thus, the higher rump fat depths observed for the study population may be a result of a lack of quality forage and a need for moose to maintain a greater fat threshold so that reproductive potential was maximized. Nonetheless, a larger sample of rump fat measurements collected across multiple locations may provide a more accurate assessment of baseline rump fat levels and the subsequent impacts on reproductive performance for moose in Wyoming. Similar to evaluations of elk condition (Cook et al. 2001), the thickness of specific muscles measured via ultrasonography could provide an additional index that may be used in association with rump fat depth to provide a more accurate assessment of the physical condition (i.e., protein versus fat catabolism) of Shiras moose populations.

Moose in the study area appeared to be in moderate physical condition based on the five blood parameters (PCV, Hb, TSP, Ca, and P) considered to be good predictors of moose nutritional status (Franzmann and LeResche 1978). This indicated that habitat conditions may be slightly suboptimal, but it is not very good or very poor. When compared to Alaskan moose considered to be in good to excellent condition (Franzmann and LeResche 1978), most adult female moose sampled were below reference values for PCV, Hb, Ca, and P and above the reference value for TSP. When these five blood parameters were further compared to an expanding, highly productive population and one that was in poor condition from Alaska (i.e., populations on the extremes; Franzmann et al. 1987), moose from the study area were intermediate. Due to the high variability in these blood parameters for populations that fall within the extremes and annual variation potentially caused by the severity of winters (Ballard et al. 1996), ranking one population against another may be impractical (Franzmann et al. 1987).

Macro- and Micronutrients

Adult female moose in the study area exhibited annual variation in nearly all macro- and micronutrients. These results indicate that the nutritional quality of moose browse exhibits similar annual variation. Indeed, researchers in Alaska and Sweden have reported high annual variation in the mineral content of moose browse even in the same plant (Oldemeyer et al. 1977, Ohlson and Staaland 2001). It has been suggested that a diversity of browse species can better meet the nutritional requirements of moose than a single, highly abundant species (Oldemeyer et al. 1977, Miquelle and Jordan 1979, Ohlson and Staaland 2001). Moose in the study area utilized low-elevation, riparian habitats dominated by large communities of willow intermixed with small stands of conifers and aspen during winter (Chapter 2), thus it may be assumed that willow composed a high proportion of the winter diet as well. Therefore, if willows are deficient in certain nutrients, moose that consume high quantities of willow will also be deficient in these elements. Analysis of forage quality is a more precise indicator of deficiency in most cases (McDowell 2003), thus future investigations that explore potential links between diet diversity and nutritional deficiencies in Shiras moose will likely be informative.

Since moose acquire nutrients directly from the plants they consume (McDowell 2003), low concentrations of some minerals in serum and hair indicated nutritional limitations associated with moose habitat in the study area. My results indicated that moose winter forage may have been limited in Cu, Zn, Mn, and P. Deficiencies in any nutrient are most likely to occur during winter when the availability and mineral content of forage is most limited (Kubota et al. 1970, Oldemeyer et al. 1977, Ohlson and Staaland 2001). Furthermore, increased intra- and interspecific competition for limited winter forage (O'Hara et al. 2001) may exacerbate existing nutritional deficiencies due to overutilization of resources (Barboza et al. 2003). Moose may be highly susceptible to nutritional deficiencies (Murray et al. 2006) and, although Cu, Zn, Mn, and P deficiencies are difficult to diagnose in wild populations, the physiological imbalances that they may create could have had a considerable impact on the performance of the population, particularly for the developing fetus and calf.

While I cannot conclude that low or marginal Cu has contributed to recent moose declines, it remains a possibility. Copper concentrations in serum and hair indicated a potential deficiency among moose in the study area. Most Cu is stored in the liver, but when levels fall below 20 μg/g, serum and hair become sensitive indicators of Cu deficiency among domestic ruminants (Combs 1987, Blakley et al. 1992, McDowell 2003). Copper is an essential nutrient for the developing fetus and fetal Cu demands greatly increase during the final trimester of pregnancy (Puls 1994, McArdle 1995, Rombach et al. 2003), which could increase the likelihood of reproductive failure if maternal Cu is deficient (Hidiroglou and Knipfel 1981, McDowell 2003). Serum Cu levels in moose from the study population were similar to levels observed by Gogan et al. (1989) in Cu deficient elk that experienced decreased adult survival and poor recruitment. Although direct comparisons cannot be made due to differences in dates of sample collection, faulty hoof keratinization and decreased reproductive output have been linked to a Cu deficiency in moose from the Kenai Peninsula, Alaska (Flynn et al. 1977). Several other studies have also suggested the possibility of reduced Cu intake as a cause of moose population declines in Sweden (Frank et al. 1994), Alaska (O'Hara et al. 2001), and Minnesota (Custer et al. 2004).

There was no relationship between low or marginal serum and hair Cu levels and the reproductive output of pregnant moose captured during winter. This contrasts with the hypothesis proposed by O'Hara et al. (2001) who suggested that populations experiencing marginal Cu deficiencies may not exhibit clinical symptoms (i.e., decreased reproductive success) unless an additional stressful event occurred. Moose captured in southeast Wyoming with similar Cu concentrations did not experience decreased reproductive performance (E. Wald, University of Wyoming, unpublished data), but they were captured two months prior to moose in my study. It may be that the cumulative effects of stressors (i.e., low quality forage, moderate physical condition, environmental conditions) near the third trimester of pregnancy combined with potential deficiencies in several other nutrients (i.e, Mn, Zn, P) create physiological imbalances (Frank et al. 1994) that compromised reproductive performance.

Concentrations of Mn in hair and Zn in serum and hair indicated a potential deficiency among moose within the study area. All moose hair samples indicated a deficiency in these nutrients while approximately two-thirds of moose were serum Zn deficient. All moose that were above serum Zn deficiency thresholds for domestic ruminants were sampled in 2006 and the higher levels observed were likely a result of sample contamination from incorrect collection procedures (Puls 1994). In domestic ruminants, clinical signs of Mn and Zn deficiencies include reduced reproductive performance and calf survival (Hidiroglou 1979, Hidiroglou and Knipfel 1981, McDowell 2003). To my knowledge, clinical signs of Zn deficiency have not been observed in wild moose populations. Although direct comparisons cannot be made to the current study, Stewart and Flynn (1978) reported low Mn concentrations from moose hair in Saskatchewan, Canada even though clinical signs of deficiency were not observed. The reliability of using serum and hair to assess dietary intake of Mn and Zn is relatively low (Smart et al. 1981, Combs 1987, McDowell 2003), but the possibility remains that deficiencies may have impacted moose in the study area.

The low serum P observed in the sample population from 2005 and 2007 may have been partially due to the effects of capture. Although Franzmann and LeResche (1978) did not observe changes in P concentrations during their study, Karns and Crichton (1978) did observe a decrease in P from the time of capture to release in caribou. The capture techniques used during my study may have delayed sample collection in some moose causing a decrease in P concentrations. Nonetheless, McDowell (2003) noted that P had to be consistently below the deficiency threshold to consider a population deficient. Since moose were not deficient in all three years of the study, there is only an indication of a potential deficiency that warrants continued evaluation.

Parasites and Disease

Insignificant loads of endoparasites were detected in some fecal samples and tick counts indicated a relatively low infestation of winter ticks in the study area. The low tick counts observed may have been partially due to inexperience in identifying the nymph stage which was common during captures in February. However, patterns of hair discoloration and loss in March and April (Lankester and Samuel 1997, Samuel 2004) also indicated relatively low tick loads on moose from the northern part of my study area while moose that occupied ranges to the south appeared to carry higher tick loads. In Alberta, Canada, Drew and Samuel (1986) noted that snow cover during April adversely affected tick survival, but warm, dry spring conditions may enhance tick reproductive success resulting in an increased abundance the following autumn (Delguidice et al. 1997, Samuel 2004). Field observations indicated that snow cover remained longer into spring on the northern ranges, but disappeared rapidly to the south. Similar to what has been observed on Isle Royale (Delguidice et al. 1997) and in central Alberta (Samuel and Baker 1979), an increase in ambient temperatures during spring could reduce snow cover which may result in an increased number of ticks and, potentially, an increased incidence of tick-induced mortalities the following spring (Lankester and Samuel 1997, Samuel 2004).

Diseases did not appear to be impacting moose in the study area. Elk seroprevalence for brucellosis was 12.5% in the Buffalo Valley (Barbknecht 2008), thus there was potential for disease transmission on winter range. However, experimental studies of brucellosis in moose indicated that they may be a dead-end host for the disease because infection leads to rapid mortality (Forbes et al. 1996). Deaths associated with brucellosis infection have not been observed among moose in the GYE (Cook and Rhyan 2003), but clinical symptoms of infection may not be observed prior to death due to the rapid progression of the disease in moose.

MANAGEMENT IMPLICATIONS

Measures of physiological health of adult female Shiras moose in the study area indicated that they were in moderate physical condition and appeared to have deficiencies of several important nutrients. Consequently, they may be more susceptible to environmental stressors that could result in increased mortality and decreased reproductive performance. These effects may be most evident during spring following a severe winter. Indeed, this population has experienced increased spring mortalities before and it was suspected that the combination of severe winters and habitat quality may have contributed to population fluctuations from 1950-1966 (Houston 1968). Therefore, habitat improvement projects could be initiated on primary moose winter ranges to improve habitat quality. This could be completed on a large-scale over multiple years so that high numbers of moose do not reduce the growth potential of preferred forage and the amount of available forage remains sufficient even during high snow years. In addition to twinning rates and age of first reproduction, the percent utilization of current annual growth of preferred forage has been identified as an additional measure to assess the nutritional status of a population (Boertje et al. 2007), thus managers could also expand current habitat monitoring programs to document browse removal rates of preferred winter forage as well as the nutritional quality of the habitat.

Because the combination of nutritional deficiencies and relatively high rump fat levels indicated a high fat-fertility threshold for this moose population (Heard et al. 1997), the continued collection of rump fat measurements and reproductive performance data remains paramount. Only after sufficient baseline data are available on rump fat depths can interpretation of the fat-fertility threshold for the population be evaluated. Rump fat measurements could be collected from harvested moose at check stations which may provide managers with a general index of the nutritional condition within herd units statewide. Blood samples can also be collected to further examine the relationship between rump fat depth, AST, and LDH. If after further evaluation this relationship appears valid, managers may be able to assess the nutritional condition of moose without the need for an ultrasound.

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Table 3.1. Reference values used in application of the animal indicator concept for Shiras moose in northwest Wyoming.

Parameter (units)	Sample type	Reference
Packed cell volume (%)	Blood	50.0[a]
Hemoglobin (g/dl)	Blood	18.6[a]
Total serum protein (g/dl)	Serum	7.5[a]
Calcium (mg/dl)	Serum	10.4[a]
	Serum	< 8.0[c]
Phosphorous (mg/dl)	Serum	5.2[a]
	Serum	< 4.5[b]
Copper (ppm)	Serum	< 0.6[b,c]
	Hair	< 6.7[c]
Iron (ppm)	Serum	< 1.1[b]
	Hair	≤ 40.0[c]
Magnesium (mg/dl)	Serum	< 1.8[b]
Manganese (ppm)	Hair	< 5.0[b]
Zinc (ppm)	Serum	< 1.0[b]
	Hair	< 100.0[b]

[a] Values for Alaskan moose in average to above average condition (Franzmann and LeResche 1978).

[b] Deficiency level for cattle and sheep; Mn levels are indicative of slight deficiency, lower normal limit for serum Mg and may not be indicative of true deficiency (McDowell 2003).

[c] Deficiency level for cattle; lower normal limit for serum Ca and may not be indicative of true deficiency (Puls 1994).

Table 3.2. Count (*n*), mean ($\bar{x}$) ± standard error (SE), and 95% confidence intervals (CI) for rump fat depth and body condition scores (BCS) by year for adult female moose captured in northwest Wyoming during winter 2005-2007.

Year	Parameter	*n*	$\bar{x}$ ± SE	95% CI[a]
2005	Rump fat (mm)	13	27.6 ± 3.5	19.9 – 35.3
	BCS	17	7.5 ± 0.3	6.9 – 8.2
2006	Rump fat (mm)	18	26.4 ± 1.3	23.7 – 29.0
	BCS	19	6.6 ± 0.2	6.1 – 7.0
2007	Rump fat (mm)	15	23.6 ± 1.3	20.8 – 26.5
	BCS	18	6.6 ± 0.2	6.1 – 7.0

[a] Upper and lower confidence interval.

Table 3.3. Mean ± standard deviation for hematological analyses of adult female moose captured in northwest Wyoming during winter 2005-2007.

	Year		
Parameter[a] (units)	2005 (*n* = 19)	2006 (*n* = 16)	2007 (*n* = 16)
PCV (%)	54.7 ± 7.9	45.6 ± 4.5	49.7 ± 5.2
Hb (g/dl)	16.5 ± 2.1	15.6 ± 1.6	17.2 ± 1.7
MCHC (g/dl)	30.6 ± 4.8	34.2 ± 1.9	34.7 ± 2.0
RBC (x 10^6/µl)	7.9 ± 1.3	6.8 ± 0.6	7.3 ± 0.7
Total WBC (/µl)	5296.8 ± 1581.2	5967.5 ± 1466.2	6952.5 ± 1706.7
Lymphocytes (%)	56.1 ± 9.6	56.4 ± 9.9	63.7 ± 13.2
Neutrophils (%)	36.2 ± 8.7	37.3 ± 8.9	27.9 ± 11.2
Eosinophils (%)	4.4 ± 3.2	3.7 ± 2.9	5.4 ± 4.1
Monocytes (%)	3.3 ± 1.8	2.7 ± 1.1	2.4 ± 1.0
Platelets (x 10^3/µl)	189.4 ± 53.0	148.4 ± 58.5	177.8 ± 58.7

[a] PCV = packed cell volume; Hb = hemoglobin; MCHC = mean corpuscular hemoglobin concentration; RBC = red blood cell; WBC = white blood cell.

Table 3.4. Mean ± standard deviation for serum chemical analyses of adult female moose captured in northwest Wyoming during winter 2005-2007.

	Year		
Parameter[a] (units)	2005 (*n* =20)	2006[b] (*n* = 18)	2007 (*n* = 17)
Albumin (g/dl)	2.9 ± 0.5	3.8 ± 0.5	3.4 ± 0.4
ALP (U/l)	255.9 ± 99.1	338.1 ± 151.1	297.3 ± 125.5
AST (U/l)	62.4 ± 17.5	87.1 ± 18.6	103.7 ± 42.5
BUN (mg/dl)	3.4 ± 1.0	5.0 ± 2.4	3.4 ± 1.9
Ca (mg/dl)	7.9 ± 1.2	10.2 ± 0.4	10.5 ± 0.9
CK (U/l)	111.8 ± 76.6	238.8 ± 175.6	328.9 ± 267.1
GGT (U/l)	10.2 ± 5.7	16.2 ± 6.2	15.5 ± 22.3
Globulins (g/dl)	3.3 ± 0.8	4.6 ± 1.0	5.1 ± 0.7
Glucose (mg/dl)	102.6 ± 20.3	79.7 ± 20.6	72.0 ± 18.8
LDH (U/l)	161.5 ± 37.8	275.2 ± 58.2	310.5 ± 53.3
Mg (mg/dl)	2.0 ± 0.1	2.4 ± 0.1	2.4 ± 0.1
P (mg/dl)	3.7 ± 0.2	4.7 ± 0.3	4.3 ± 0.2
TSP (g/dl)	6.1 ± 1.1	8.4 ± 0.8	8.5 ± 0.6

[a] ALP = alkaline phosphate; AST = aspartate aminotransferase; BUN = blood urea nitrogen; Ca = calcium; CK = creatine kinase; GGT = gamma-glutanyl transferase; LDH = lactate dehydrogenase; Mg = magnesium; P = phosphorous; TSP = total serum protein.

Table 3.4. Continued.

[b] ALP, CK, and Mg ($n = 17$).

Table 3.5. Total moose sampled (*n*), range, and the proportion of the sample that was below the reference value for moose considered to be in average to above average condition for five blood parameters used for condition assessment.

Parameter[a] (units)	*n*	Range	Reference[b]	Proportion below reference
PCV/HCT (%)	51	35.1 – 82.3	50.0	0.51
Hb (g/dl)	51	12.1 – 20.7	18.6	0.88
TSP (g/dl)	58	3.6 – 10.3	7.5	0.33
Ca (mg/dl)	58	5.2 – 13.0	10.4	0.81
P (mg/dl)	58	2.1 – 6.6	5.2	0.78

[a] PCV = packed cell volume; Hb = hemoglobin; TSP = total serum protein; Ca = calcium; P = phosphorous.

[b] Values for Alaskan moose in average to above average condition (Franzmann and LeResche 1978).

Table 3.6. Annual mean ± standard deviation, published deficiency levels, and the proportion of sampled adult female moose that were deficient in macro- and micronutrients analyzed in serum and hair from northwest Wyoming during winter 2005-2007. No published deficiency levels are reported for barium, chromium, and lead.

Element (units)	Sample type	Year			Published deficiency levels (ppm)	Proportion below deficiency level
		2005	2006	2007		
Copper (ppm)	Serum	0.51 ± 0.09	0.46 ± 0.14	0.45 ± 0.10	< 0.6[a,b]	0.84
	Hair	4.76 ± 0.72	4.63 ± 0.56	4.43 ± 0.65	< 6.7[b]	1.00
Iron (ppm)	Serum	2.78 ± 0.38	2.33 ± 0.74	2.32 ± 0.46	< 1.1[a]	0.02
	Hair	26.35 ± 16.7	19.12 ± 8.32	15.37 ± 6.54	≤ 40[b]	0.95
Zinc (ppm)	Serum	0.58 ± 0.13	1.42 ± 0.60	0.71 ± 0.09	< 1.0[a]	0.70
	Hair	82.64 ± 7.74	89.49 ± 3.52	89.86 ± 2.98	< 100[a]	1.00
Manganese (ppm)	Hair	1.09 ± 0.16	0.79 ± 0.08	1.00 ± 0.25	< 5.0[a]	1.00
Barium (ppm)	Hair	1.29 ± 0.74	1.79 ± 0.63	1.73 ± 0.64		
Chromium (ppm)	Hair	1.73 ± 0.55	1.39 ± 0.20	1.57 ± 0.29		
Lead (ppm)	Hair	0.17 ± 0.09	0.11 ± 0.06	0.26 ± 0.35		

[a] Deficiency level for cattle and sheep; Mn levels are indicative of slight deficiency (McDowell 2003).
[b] Deficiency level for cattle (Puls 1994).

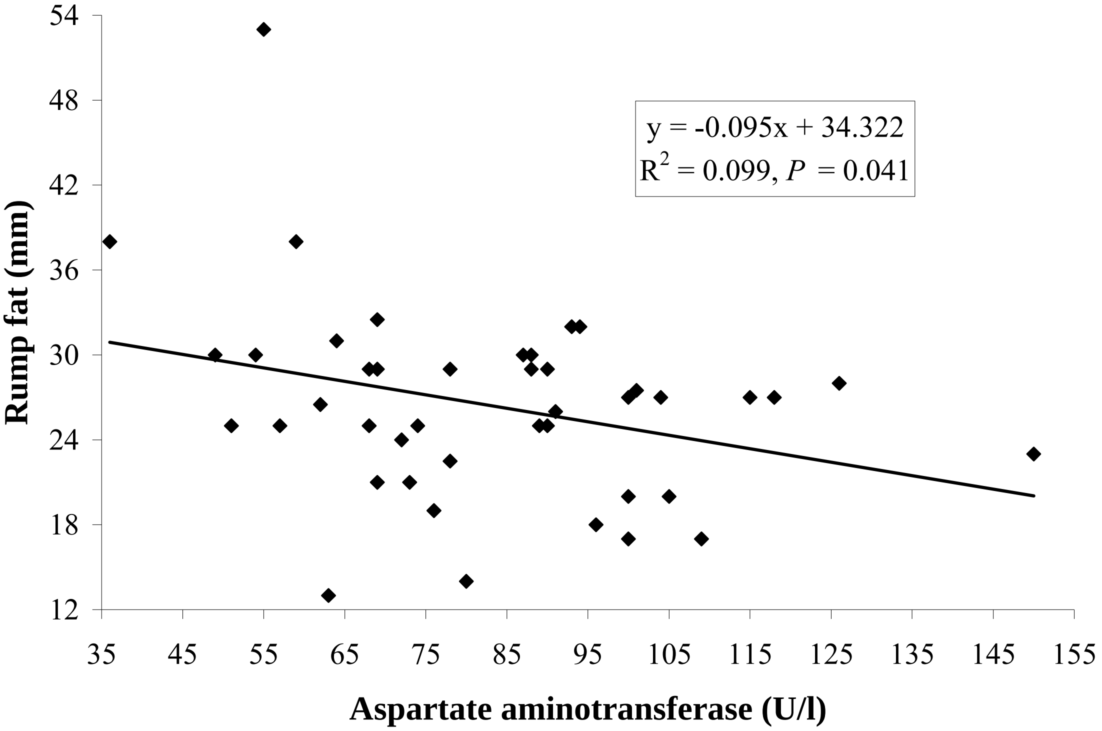

Figure 3.1. Scatterplot describing the relationship between rump fat depth (mm) and aspartate aminotransferase (U/l) concentrations of captured adult female moose in northwest Wyoming, winter 2005-2007 (*n* = 43).

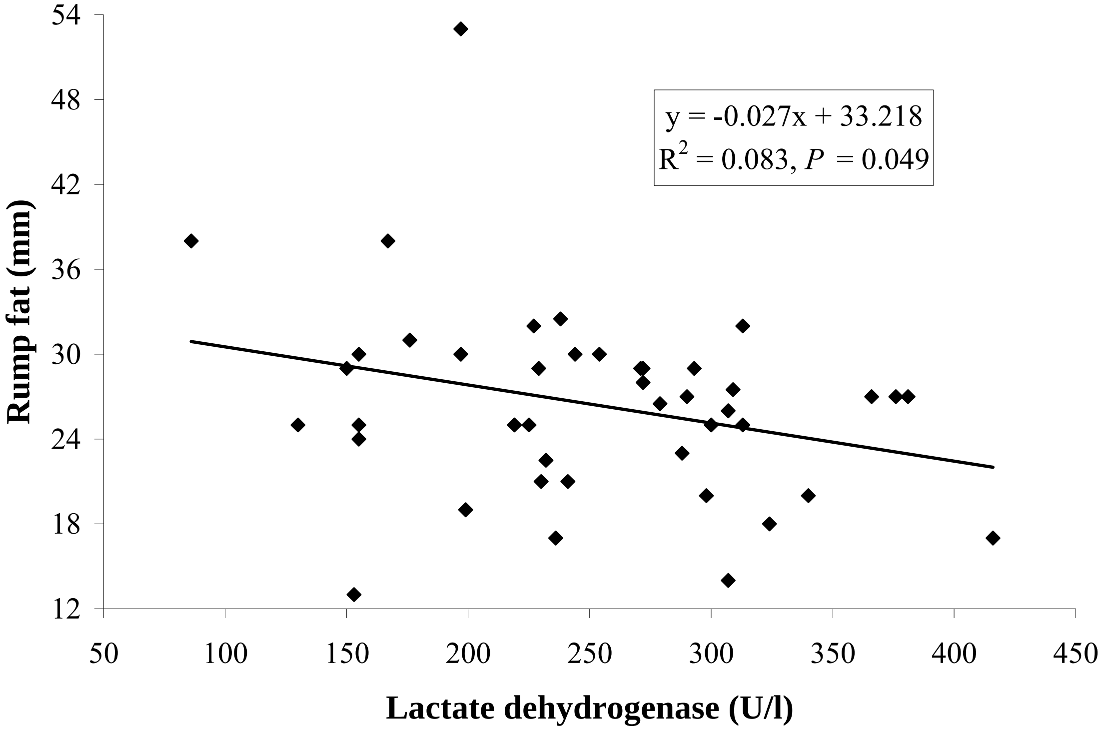

Figure 3.2. Scatterplot describing the relationship between rump fat depth (mm) and lactate dehydrogenase (U/l) concentrations of captured adult female moose in northwest Wyoming, winter 2005-2007 (*n* = 43).

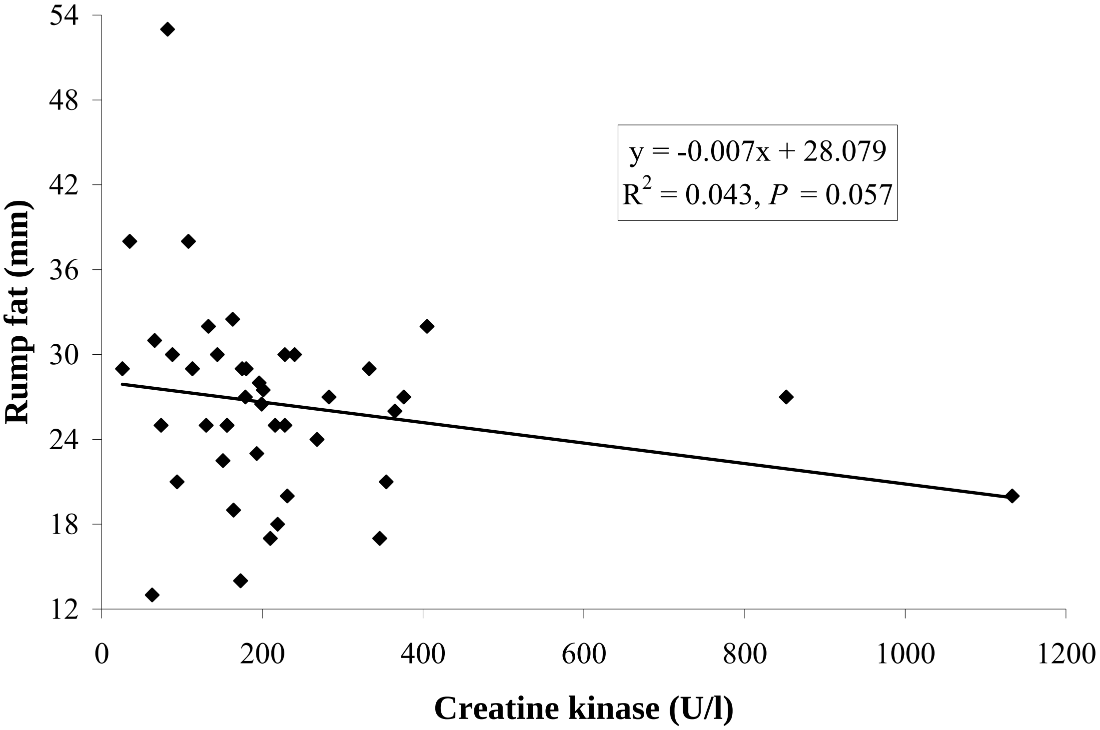

Figure 3.3. Scatterplot describing the relationship between rump fat depth (mm) and creatine kinase (U/l) concentrations of captured adult female moose in northwest Wyoming, winter 2005-2007 (*n* = 43). When the outlier was removed, this relationship became insignificant (*P* = 0.130).

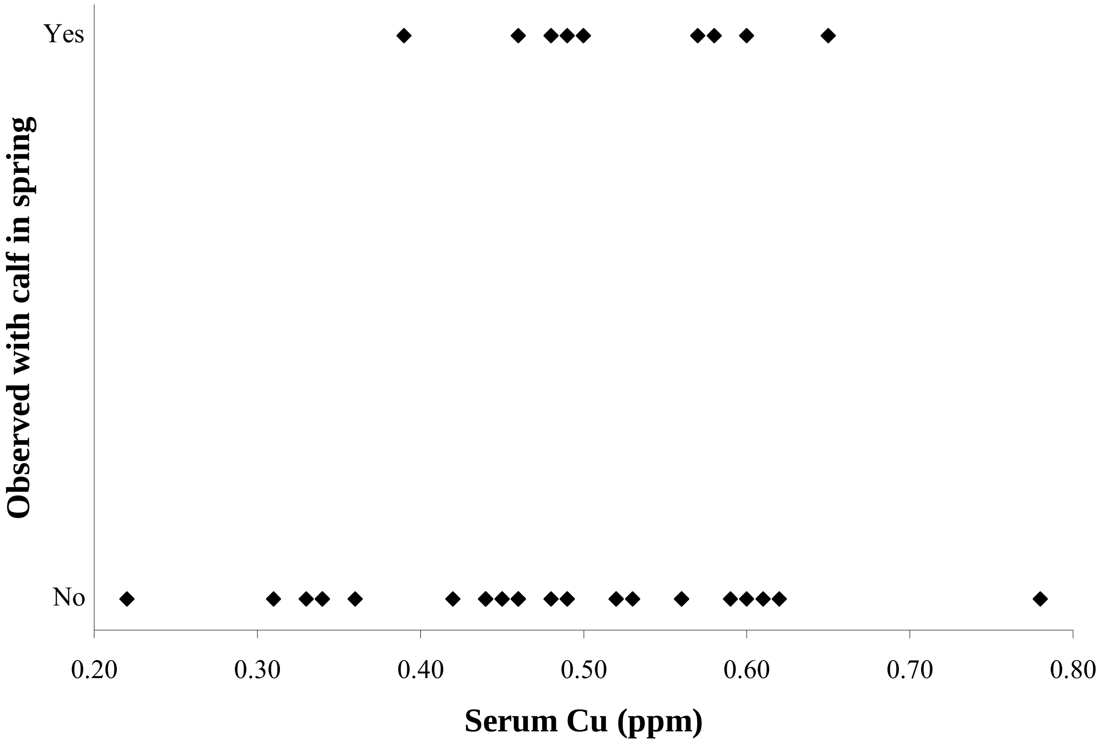

Figure 3.4. Regression of calf presence in spring on serum Cu concentration (ppm) for pregnant adult female moose captured in northwest Wyoming, 2005-2007. The top row represents Cu concentrations for cows observed with a calf in the spring (*n* = 9) and the bottom row represents Cu concentrations for cows not observed with a calf in the spring (*n* = 28).

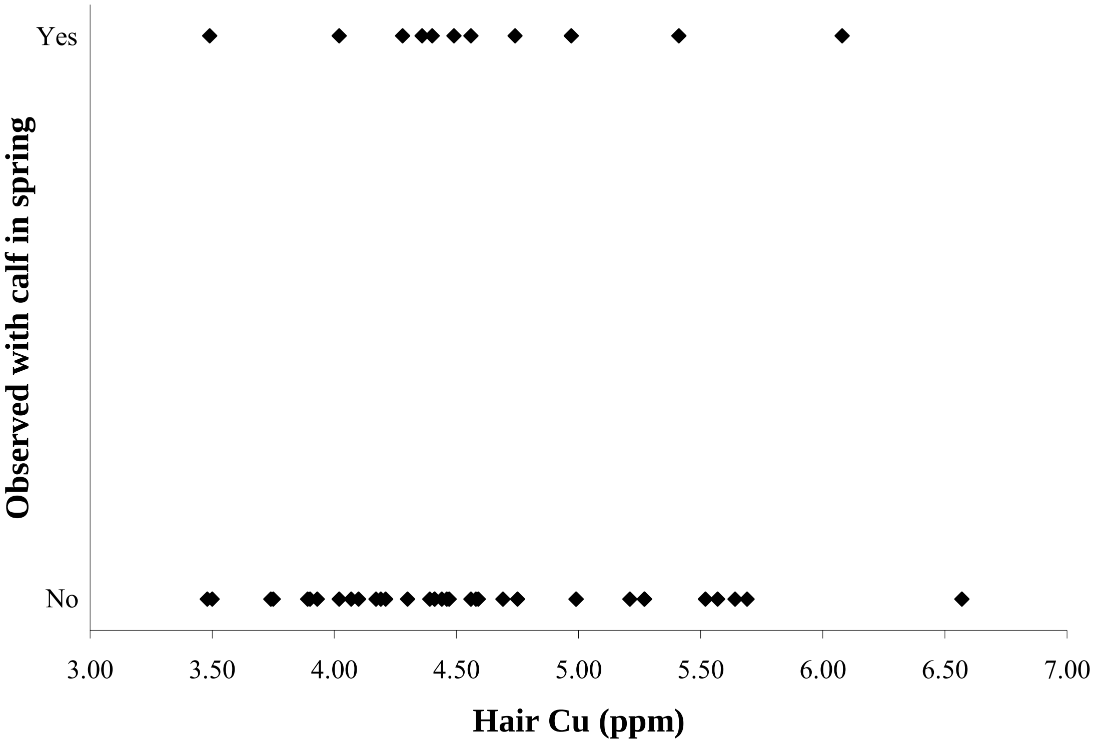

Figure 3.5. Regression of calf presence in spring on hair Cu concentration (ppm) for pregnant adult female moose captured in northwest Wyoming, 2005-2007. The top row represents Cu concentrations for cows observed with a calf in the spring (*n* = 11) and the bottom row represents Cu concentrations for cows not observed with a calf in the spring (*n* = 35).

CHAPTER 4

THE DYNAMICS OF A SHIRAS MOOSE POPULATION IN A MULTIPLE PREDATOR AND PREY ECOSYSTEM IN NORTHWEST WYOMING

In the format of a paper in the *Journal of Wildlife Management*

INTRODUCTION

Estimating population growth and demographic rates are fundamental to the study of animal populations. By understanding demographic parameters, managers can make more informed decisions regarding management practices that may reduce the effects of factors limiting population growth. Limiting factors can be broadly defined as aspects of the environment or interactions among species that alter vital rates resulting in a change in the observed population growth rate (Messier 1991, Messier 1994, Van Ballenberghe and Ballard 1994). While experimental determination of the relative forces that control population growth is difficult, insights into causal mechanisms may be inferred by detailed demographic studies. In comparison to analyses of population trend data, demographic studies (i.e., estimation of individual vital rates) can reveal the proximal factors that may influence population growth such as resource limitation, predation, disease, competition, or several factors working in combination. Although controversy remains in regards to population limitation or regulation of ungulates (Boutin 1992, Van Ballenberghe and Ballard 1994), the two factors most often identified as influencing the rate of population growth, either singly or in combination, are habitat and predation (Messier 1991, Testa 2004).

Moose (*Alces alces*) are an important game species and play a vital role in complex ecosystems with multiple predator and prey assemblages. While much research has been devoted to the population dynamics of moose, including some of the seminal work in population ecology (Peterson 1977), there is considerable variation regarding the relative influence of habitat and predation as limiting factors. For example, in interior Alaska, one moose population appeared to be limited primarily by density-dependent factors (Keech et al. 2000), while an adjacent population appeared to be limited by predation on calves (Bowyer et al. 1998).

Much of the research conducted in North America on the dynamics of moose populations has involved ecosystems where moose were the dominant prey for large predators (Bergerud et al. 1983, Gasaway et al. 1992, Bertram and Vivion 2002). However, where moose are not the dominant prey, the factors influencing population dynamics may vary considerably (Gasaway et al. 1983, Ballard and Larsen 1987, Van Ballenberghe 1987, Kunkel and Pletscher 1999). The complexity of systems with multiple prey and predator species makes inferences about single species interactions more difficult. Nonetheless, through the examination of demographic rates, researchers can infer potential mechanisms that may limit population growth. For example, moose twinning rates and the age of first reproduction are two parameters used by managers as a measure of the nutritional status of moose populations (Franzmann and Schwartz 1985, Keech et al. 2000, Boertje et al. 2007). Furthermore, the selective behavior of certain predators during specific life stages can be used to infer the potential effects of predation on a population. For example, predation by either black bears (*Ursus americanus*) or grizzly bears (*U. arctos*) typically accounts for the majority of neonatal moose calf mortalities (Ballard et al. 1991, Osborne et al. 1991, Bertram and Vivion 2002, Swenson et al. 2007), whereas the impact of wolf (*Canis lupus*) and cougar (*Puma concolor*) predation occurs primarily after the neonate phase (Larsen et al. 1989, Ross and Jalkotzy 1996).

Relatively little research has been conducted on the demography and population dynamics of Shiras moose (*A. a. shirasi*) in the Intermountain West. Kufeld and Bowden (1996) estimated Shiras moose survival in northcentral Colorado where legal and illegal harvest accounted for 91% of all mortalities. Olterman and Kenvin (1998) described the reproduction and survival of Shiras moose transplanted to southwestern Colorado where black bears and cougars occurred at relatively low densities. Kunkel and Pletscher (1999) studied the dynamics of elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), and moose in a multipredator ecosystem in and near Glacier National Park, Montana, USA. They reported that moose survival rates were higher where alternate prey was abundant. The Greater Yellowstone Ecosystem (GYE) provides an opportunity to explore further the complex dynamics of a population of Shiras moose where alternate prey is abundant (Boyce 1989, Lubow and Smith 2004), grizzly bears continue to expand their range (Schwartz et al. 2006), and gray wolves were recently reintroduced (Bangs and Fritts 1996).

Indices of population density and calf-cow ratios since the late 1980s have suggested a declining trend in Shiras moose numbers in northwest Wyoming, USA (Chapter 1). This population was previously thought to be limited by density-dependent factors (Berger et al. 1999, Berger et al. 2001), but the recent expansion of grizzly bears and gray wolves into the area has led to questions regarding the relative influence of predation (Brimeyer and Thomas 2004). Therefore, my goal was to estimate the reproductive parameters and demographic rates of the north Jackson moose herd and use these estimates to evaluate the relative influence of factors that may be limiting population growth. My objectives were to: (1) estimate reproductive parameters, neonate survival, and annual calf survival, (2) estimate adult (≥ 2 years) female and male annual survival rates, (3) use the estimated vital rates to calculate the finite rate of growth and conduct associated sensitivity analyses, and (4) make inferences as to the relative influence of limiting factors based on study results and information from previous research. My results may assist managers with decisions regarding the management of Shiras moose populations in multiple predator and prey ecosystems.

STUDY AREA

The study area encompassed approximately 6,400 km^2 of predominately public land in northwest Wyoming (Figure 4.1). It was north of the town of Jackson, Wyoming and included portions of Grand Teton National Park (GTNP), Yellowstone National Park (YNP), and the Bridger-Teton National Forest (BTNF) where elevations ranged from 1,866 to 4,197 m. The study area included the upper Snake River and upper Yellowstone River watersheds. Moose wintered in low-elevation, riparian-dominated habitats along the Snake River and its primary tributaries (i.e., Pacific Creek, Buffalo Fork River, Gros Ventre River; Houston 1968, Chapter 2). During summer, migratory moose traveled to more dispersed, mid-elevation ranges (Chapter 2), whereas nonmigratory individuals remained on low-elevation ranges (Houston 1968). Dominant vegetation types varied with elevation and aspect (Whitlock 1993, Knight 1994) and were described in Chapter 2 of this thesis.

The climate was characterized by short, cool summers and long, cold winters. From 1975 to 2004, annual precipitation averaged 56 cm (range 38-79 cm; http://www.cdc. noaa.gov/cgi-bin/Timeseries/timeseries1.pl; accessed 16 October 2005), with most of the annual precipitation falling as snow between November and May. The Teton Mountains to the west and the northern highlands along the southern boundary of YNP typically received the greatest amounts of precipitation (Houston 1968, Cole 1969, Boyce 1989).

The study area contained several other populations of large ungulates. The Jackson elk herd consisted of 14,000-18,000 elk, of which approximately 70% were supplementally fed on the National Elk Refuge or state-run feedgrounds during winter. These elk migrated to more dispersed ranges during summer (Boyce 1989, Lubow and Smith 2004). Resident populations of bison (*Bison bison*) and mule deer (*Odocoileus hemionus*) inhabited the Jackson Valley and a migratory population of pronghorn (*Antilocapra americana*) traveled to the area during summer (Sawyer et al. 2005). Grizzly bears occurred throughout the study area and have steadily expanded their range in the GYE since the early 1990s (Schwartz et al. 2006). Gray wolves dispersed from YNP to the Jackson Valley during the winter of 1997-1998 (Smith et al. 1999) and as of 2007, seven packs ($n \approx 82$ wolves), consisting of at least six breeding pairs, inhabited portions of the study area (Jimenez et al. 2008). It was suspected that cougar populations also increased in recent years (Wyoming Game and Fish Department [WGFD] 2006, H.

Quigley, Beringia South, personal communication) while harvest data indicated that black bear populations in the study area remained relatively stable (WGFD 2007*a*).

The study area included the northern portion of the Jackson moose herd unit and encompassed WGFD hunt areas 7, 14, 15, 17, and 32 (Figure 4.1), as well as hunt area 8 in the Absaroka moose herd unit. Hunt areas 7, 14, and 32 in the Teton Wilderness were closed to all moose harvest during the 2005 and 2006 hunting seasons and in 2007, these areas were opened to limited quota, antlered only moose harvest (WGFD 2007*b*). The remaining hunt areas in the study area allowed antlered only, limited quota harvest for the duration of the study. At the end of biological year 2006, the population estimate for Jackson moose herd unit was 1,785 moose and the population objective for the entire herd unit was 3,600 moose (WGFD 2007*b*).

METHODS

Moose Captures

Adult moose were captured on winter range between January and March 2005-2008. Moose were darted from the ground or a helicopter and immobilized with 10-mg thiafentanil (A-3080, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA; McJames et al. 1994, Arnemo et al. 2003, Kreeger et al. 2005) in 2005 and 2006 and 10-mg carfentanil (Wildnil, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) in 2007. Immobilization drugs were delivered in a 1-ml dart (Pneu-dart, Williamsport, Pennsylvania, USA) fired from a CO_2-powered dart rifle (Dan-Inject North America, Fort Collins, Colorado, USA) or a 0.22-caliber-blank dart rifle (Model 193, Pneu-dart, Williamsport, Pennsylvania, USA). Once handling was completed, thiafentanil or carfentanil were antagonized with an intramuscular injection of 300-mg naltrexone (Trexonil, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA; Kreeger et al. 2005) administered at multiple sites. In 2008, adult female moose were captured via helicopter net-gunning. Age was estimated from incisor tooth wear (Hindelang and Peterson 1994) and numbered, aluminum ear tags were affixed to each ear. Approximately 50-ml of blood were collected from all moose via jugular venipuncture and fecal samples were collected from adult females in 2007. Adult females were fitted with either global positioning system (GPS; model TGW-3700, Telonics, Mesa, Arizona, USA) or very high frequency (VHF) radio transmitters (model M2710, Advanced Telemetry Systems, Isanti, Minnesota, USA) and all adult males were fitted with VHF collars. All radio collars were equipped with mortality-sensing options and VHF collars were fitted with a cotton spacer that would rot away in 3-4 years which allowed for collar retrieval prior to termination of battery life. Captures were performed in accordance with approved University of Wyoming Animal Care and Use Committee protocols.

Adult Survival

In addition to moose captured during this study, I monitored 18 adult female moose that had been fitted with VHF collars in previous years (Berger et al. 1999, Berger et al. 2001). Radio-collared moose were monitored monthly from fixed-wing aircraft during May to December of each year. While moose were concentrated on winter range, ground surveys were conducted to monitor survival from January to May. Although cause of mortality was not a primary study objective, all mortality signals were investigated on foot and site investigations and field necropsies were performed to determine cause of death where possible. I assessed moose condition at time of death based on the color and consistency of femur bone marrow and scored the moose into 1 of 3 classes that generally represented percent femur marrow fat (Peterson 1977:30). I examined all available bones for evidence of abnormalities (i.e., arthritis, healed breaks, jaw necrosis). If available, two incisors were collected and age was determined by cementum annuli (Sargeant and Pimlott 1959) at the WGFD Laboratory (Laramie, Wyoming, USA). I considered predation to be the cause of death when subcutaneous hemorrhaging and evidence of a chase or struggle were present (Kunkel et al. 1999, Atwood et al. 2007). I identified the predator species responsible for the mortality using predator-specific characteristics such as injury patterns, point of attack, method of killing, and carcass location (Atwood et al. 2007) and used a key adapted from Kunkel et al. (1999) to categorize predator-related mortalities as being possible, probable, or positive predation by cougar, wolf, or bear (black or grizzly). If evidence of predation was not present, mortalities were characterized as being of natural causes and were classified as malnutrition, disease, or other natural cause. Mortalities were classified as unknown if site evidence and carcass inspection were inconclusive as to cause of death. If mortalities occurred within 30 days post-capture and no cause of death could be determined, the death was classified as a capture-related mortality (Kreeger et al. 2005). If the date of death was unknown, it was estimated using the midpoint between the last time the signal was active and the first time a mortality signal was heard (Modafferi and Becker 1997). Dates of death for moose fitted with GPS collars were estimated by downloading the collar and locating the first known location in a point cluster where the carcass was found.

I attempted to maintain 20-25 radio-collared females and males at the beginning of each biological year (BY; 1 June – 31 May) during the study (Garton et al. 2001). I used the staggered entry Kaplan-Meier procedure to estimate annual survival rates of adult females and males on a monthly basis for each BY and used log-rank tests to compare sex-specific survival among BYs (Kaplan and Meier 1958, Pollock et al. 1989). Capture-related mortalities were censored from survival analyses and all moose censored due to radio failure were removed the month that radio contact was lost. Adult male survival rates were estimated with harvest censored and with all forms of mortality included to examine differences in survival with and without harvest. The number of moose at risk at the beginning of each month was pooled across BYs to estimate sex-specific survival rates for the duration of the study even if annual differences were observed. The adult female survival rate estimate was used to evaluate the population growth rate during the entire study period (see below). I then used a log-rank test to compare female and male survival rates for the duration of the study (Pollock et al. 1989).

Reproduction and Calf Survival

Pregnancy status was determined by analysis of blood sera for concentrations of pregnancy-specific protein B (PSPB) by BioTracking (Moscow, Idaho, USA; Stephenson et al. 1995, Huang et al. 2000). Fecal samples were analyzed for progestagen concentration at the Smithsonian Institute Conservation Research Center (Front Royal, Virginia, USA) following methods described by Monfort et al. (1993) and Schwartz et al. (1995). Due to differences among populations in fecal progestagen cutoff values for pregnant and nonpregnant moose (Muir 2006), I used a regression tree analysis (De'ath and Fabricius 2000) to estimate a fecal progestagen cutoff value from fecal samples collected at capture in 2007. For this analysis, the dependent variable was the fecal progestagen value and the response variable was pregnancy status based on PSPB. This gave an estimated fecal progestagen cutoff value and the probability that this value would accurately predict pregnant and non-pregnant status. To estimate the timing of potential fetal mortalities and the efficacy of progestagen in determining pregnancy status, additional fecal samples were collected from handled and unhandled moose 1-2 months post-capture in 2006 and 2007. Fecal progestagen concentrations were compared to the pregnancy cutoff value to determine if losses occurred prior to or after the date of collection.

All radio-collared adult female moose were surveyed from the ground or air during late May to early June of each year (Van Ballenberghe and Ballard 1997, Boertje et al. 2007) to assess parturition rates because peak parturition typically occurs around 25 May across much of North America (Hauge and Kieth 1981, Schwartz and Hundertmark 1993, Bowyer et al. 1998, Testa et al. 2000, Bertram and Vivion 2002). Helicopter surveys were conducted with the pilot and two observers between 31 May and 7 June 2005-2007. Radio-collared cows not observed with a calf during initial aerial observations were surveyed again from the air usually within 1 or 2 days. Prior to concluding that a cow was not accompanied by a calf, attempts were made to obtain the clearest view of the cow possible on the second survey and the behavior of the cow (i.e., standing, running, or aggressiveness) was noted. If I was unable to conclude from aerial observations that a cow was accompanied by a calf, a ground search was conducted on foot or horseback. To assess parturition rates for moose that were not captured during winter (i.e., unhandled), I first estimated the number of pregnant unhandled moose by multiplying the known pregnancy rate of captured moose by the total number of unhandled moose surveyed in each year. Parturition rates were calculated by dividing the total number of unhandled cows observed with calves by the total number surveyed that were assumed to be pregnant. Twinning rates were assessed by dividing the number of cows observed with twins by the total number of cows with calves.

All radio-collared females were surveyed from the ground or air approximately 8 weeks after parturition surveys to estimate neonate survival. Protocols for these surveys were the same as parturition surveys. I chose to survey all radio-collared females so that late births could be observed. Late births were included in estimates of parturition rates, but neonate survival was estimated only from those calves that were observed in June. Ground surveys of all radio-collared females observed with calves during neonate surveys were conducted during late March and April 2006-2008 to assess annual calf survival. Since calves were not collared, the fate of calves that were lost due to death or radio failure of the collared cow were unknown, thus, these calves were censored from analyses. Surveys of females that lost calves between parturition and neonate surveys were also made to assess the efficacy of neonate surveys.

I used the Kaplan-Meier procedure and the log-rank test (Kaplan and Meier 1958, Pollock et al. 1989) to estimate neonate and annual calf survival rates and to test for differences among years. I also used the log-rank test (Pollock et al. 1989) to assess among-year variation in pregnancy rates. To determine if capture had an effect on parturition rates, neonate survival, and annual calf survival, I used the log-rank test (Pollock et al. 1989) to compare these parameters between the handled and unhandled samples of moose within years.

Population Modeling

I used a simple post-birth, Lefkovich matrix model for females that assumed constant vital rates over time to characterize moose population growth during the study period (Caswell 2001, Skalski et al. 2005). The matrix was parameterized into 3 stage classes (i.e., calf, yearling, adult). The top row of the matrix (i.e., productivity elements) was the product of survival, parturition, and fecundity rates for yearlings and adults. Because calves do not reach sexual maturity by autumn (Edwards and Ritcey 1958, Schladweiler and Stevens 1973, Schwartz and Hundertmark 1993), they were not allowed to breed in the model. The adult fecundity rate was calculated by dividing the total number of calves produced by the total number of parturient, radio-collared females. In Alaska, calf sex ratios at birth did not differ (Schwartz and Hundertmark 1993), so I assumed a 50:50 sex ratio and divided fecundity by 2 to estimate the number of female calves produced per parturient female. Since yearlings were not monitored, I assumed yearling parturition and survival from the literature. Houston (1968) estimated a yearling pregnancy rate of 0.057 in the Jackson Valley, Wyoming based on corpora lutea counts of 35 harvested 2.5-year-old moose. I used this pregnancy rate for yearlings and assumed that yearling parturition rates were a similar fraction of the adult parturition rate. Yearling fecundity was assumed to be 0.50 because yearlings rarely produce twins

(Pimlott 1959, Schwartz 1997). Although several researchers have described lower yearling survival rates when compared to adults (Dodge et al. 2004, Testa 2004, Murray et al. 2004), researchers in Alaska indicated that yearling survival rates were similar to adult survival rates (Ballard et al. 1991), thus, I assumed that yearling and adult survival rates were equal.

From the parameterized matrix, I calculated a deterministic estimate of the finite rate of population growth (λ; Caswell 2001, Skalski et al. 2005). To examine the influence of each vital rate on λ, I calculated the elasticity of each matrix element using PopTools (G. M. Hood, 2004; PopTools version 3.0.2. http://www.cse.csiro.au/poptools). I used a parametric bootstrap procedure to estimate 95% confidence intervals (CI) for λ. I assumed a binomial distribution of vital rates and generated 1,000 random replicates of each vital rate based on the mean and the total number of experimental units used to estimate each vital rate during the study. I then generated 1,000 simulated Lefkovich matrix replicates to estimate λ from random combinations of each vital rate. The mean λ estimate was calculated from the simulated data and 95% CI were estimated from the distribution of resulting λ values.

RESULTS

Moose Captures

Eighty adult female moose were captured 93 times during the course of the study. From 2005 to 2007, 53 of 61 adult females were darted from a helicopter. Thirty-two females were captured with helicopter net-gunning in 2008. Most adult males were darted from a helicopter ($n = 21$) and radio-collared in 2005 ($n = 27$) and 2006 ($n = 4$). Four suspected capture-related mortalities (2 female, 2 male) occurred during the study and these individuals were censored from survival analysis. One female moose died 9 days post-capture in 2005. Field necropsy was unable to reveal an apparent cause of death and no problems were recorded during handling. One male died at 3 weeks and another at 4 weeks post-capture in 2005 after being darted from the ground. The first male that died was relatively old (12 yrs) and field necropsy revealed severe malnutrition (i.e., no body or organ fat, depleted femur marrow). Necropsy revealed gross lesions on the lungs of the second male consistent with pneumonia that was possibly caused by aspirated rumen contents during handling. In 2006, a single female was euthanized 1 day post-capture. Although serum enzymes (i.e., aspartate aminotransferase, creatine kinase, and lactate dehydrogenase) did not reveal exertional myopathy as the cause, it was suspected due to partial paralysis of the front limbs.

Pregnancy and Reproduction

Analyses of PSPB from moose captured during winters 2005-2007 indicated a high annual pregnancy rate that was not different among years ($P > 0.05$; Table 4.1). To assess parturition rates, all radio-collared adult female moose were surveyed from the ground or air between 25 May and 19 June 2005-2007. Two sets of twins in 2006 and one set of twins in 2007 were observed, while no twins were observed in 2005 (Table 4.1). When years were pooled, the average twinning rate was 0.07 (SE = 0.04, $n = 45$). The fecundity rate was estimated as 1.07 calves per parturient female. There was a significant difference in parturition rates between moose that were captured (i.e., handled) in winter and those that were not captured (i.e., unhandled) in 2005 ($\chi^2 = 5.01$, 1 df, $P = 0.025$) and 2006 ($\chi^2 = 5.53$, 1 df, $P = 0.019$), but a significant difference was not observed in 2007 ($\chi^2 = 2.86$, 1 df, $P = 0.091$), possibly due to high variance in the estimates (Table 4.1). When compared within groups (i.e., handled and unhandled) among years, parturition rates did not differ ($P > 0.05$; Table 4.1). Therefore, within group estimates were pooled among years and a significant difference was observed in the estimated parturition rates between handled and unhandled females ($\chi^2 = 13.43$, 1 df, $P < 0.001$; Table 4.1).

Because of differences in parturition rates between handled and unhandled females, a second parturition survey was conducted from the helicopter two weeks after the initial survey in 2005, but no additional calves were observed. Furthermore, no additional calves were observed during neonate survival surveys in July 2005 or annual calf survival surveys in March and April 2006 indicating that survey protocols adequately detected calf presence. To test the effects of capture techniques using the same immobilization drug (i.e., thiafentanil), 7 adult females were darted from the ground and 13 were darted from a helicopter in 2006. Sample sizes were small, but no females captured from the ground were observed with a calf (0 of 5), whereas 36% (4 of 11) of adult female moose immobilized by helicopter were observed with a calf. In 2007, all moose were captured via helicopter with a different immobilization drug (i.e., carfentanil) and a similar trend was observed (Table 4.1).

Using pregnancy status as determined by PSPB and the fecal samples collected at capture in 2007 ($n = 19$), the regression tree analysis indicated that the pregnancy cutoff value for fecal progestagen was 2.52 μg/g (Figure 4.2). The probability that this value would accurately predict pregnancy at capture from fecal progestagen was 100%, whereas the probability that it would predict non-pregnancy was 60% (Figure 4.2). During 2006 and 2007, fecal samples were collected from 21 handled and 12 unhandled females > 1 month post-capture. Of the 14 pregnant, handled moose that were not observed with calves the following spring, 79% (n = 11) were determined not to be pregnant when fecal samples were collected based on the fecal progestagen cutoff value (Figure 4.3). The fecal progestagen cutoff value accurately predicted whether an unhandled female would be observed with a calf the following spring 92% (11 of 12) of the time (Figure 4.3). One unhandled and 3 handled moose appeared to lose their fetus or calf at a later date because progestagen indicated that these females were pregnant at time of sample collection. One handled female observed with a calf in the spring was misclassified as not pregnant (Figure 4.3).

For moose that were handled and lost a calf in the year of capture, the probability that they would be observed with a calf the following year after not being captured was 80% (8 of 10). For unhandled moose observed with a calf in any given year, the probability that they would be observed with a calf the following year was 33% (6 of 18). When all moose were pooled regardless of being handled or unhandled, the probability that they would be observed with a calf in consecutive years was 31% (13 of 42).

Neonate and Annual Calf Survival

Because of small sample sizes for handled moose observed with calves, no comparisons were made of neonate and annual calf survival between handled and unhandled moose, thus all calves produced each year were pooled to examine annual differences. All radio-collared adult female moose were surveyed from the ground or air between 17 and 24 July 2005-2007 to document neonate survival and late births. There were 3 late births observed in 2006 and 1 in 2007. One calf was censored in 2006 due to loss of radio contact with the cow between parturition and neonate surveys. No significant differences were observed in neonate survival among years ($P > 0.05$; Table 4.1). When years were pooled, 16 of 42 calves were lost between parturition and neonate surveys for an average survival rate of 0.62 (SE = 0.08; Table 4.1).

In March and April 2006-2008, radio-collared cows observed with calves in June and July of the previous year were surveyed on winter range to estimate annual calf survival rates. No calves that were lost between parturition and neonate surveys were observed with the cow on winter range. Six calves were censored from analysis due to radio failure (1 in 2006, 3 in 2007) or death of the radio-collared cow prior to surveys (2 in 2008). All late births observed were included in analyses of calf survival and 2 of 3 successfully returned to winter range while 1 was lost due to radio collar failure of the cow. No significant differences were observed in annual calf survival among years ($P > 0.05$; Table 4.1). When years were pooled, 19 of 41 calves successfully returned to winter range yielding an average annual calf survival rate of 0.46 (SE = 0.08; Table 4.1). Of 28 adult female moose monitored for ≥ 2 years, 11% returned to winter range with a calf at side 2 years in a row.

Adult Survival

To estimate annual survival rates, adult female moose were monitored for four consecutive BYs (i.e., 2004, 2005, 2006, 2007). Annual female survival rates ranged from 0.77 (SE = 0.07) in BY 2006 to 0.94 (SE = 0.04) in BY 2005 (Table 4.2). The survival rate estimate for BY 2005 was significantly different from estimates for BY 2006 ($\chi^2 = 4.34$, 1 df, $P = 0.037$) and BY 2007 ($\chi^2 = 3.92$, 1 df, $P = 0.048$; Table 4.2). No significant differences were observed in annual survival rates among any other years ($P > 0.05$; Table 4.2).

Survival rates were estimated for adult male moose for all BYs (i.e., 2004, 2005, 2006, 2007), but comparisons and interpretations were limited to BY 2005 and BY 2006 because these years contained a full year of data and adequate sample sizes. There were no significant differences in survival rate estimates between BY 2005 and BY 2006 when harvest was included as a mortality factor ($\chi^2 = 0.01$, 1 df, $P = 0.92$) or when harvest was censored ($\chi^2 = 0.00$, 1 df, $P > 0.99$; Table 4.2). When survival rates were compared between harvest included and harvest censored males within years, no significant differences were observed in estimated survival rates for BY 2005 ($\chi^2 = 0.82$, 1 df, $P = 0.365$) or BY 2006 ($\chi^2 = 0.50$, 1 df, $P = 0.48$; Table 4.2).

When years were pooled, the adult female survival rate estimate was 0.83 (SE = 0.03; Table 4.2). Pooled annual (i.e., all years) survival rate estimates for males with harvest included was 0.82 (SE = 0.05) and with harvest censored it was 0.89 (SE = 0.04; Table 4.2). There was no significant difference between annual survival rates of females and males when harvest was included ($\chi^2 = 0.06$, 1 df, $P = 0.806$) or when harvest was censored ($\chi^2 = 2.18$, 1 df, $P = 0.140$; Table 4.2).

Adult female mortalities peaked during late winter and early spring with 85% (22 of 26) of the observed mortalities occurring during the months of March, April, and May (Figure 4.4). Most female mortalities were classified as unknown due to high levels of scavenging or lack of site evidence. Predation accounted for 8 mortalities while 5 females appeared to have died of natural causes not related to predation (3 malnutrition, 1 disease, 1 other natural causes; Figure 4.5). One female moose killed by a cougar in March 2005 had evidence of jaw necrosis, but no evidence of any other bone abnormalities were found on the remaining individuals, whether female or male. There was no apparent temporal pattern to nonharvest-related adult male mortalities, but when harvest was included as a mortality factor, survival declined from September to November (Figure 4.6). Most male mortalities were classified as unknown primarily due to the remote locations of the mortality sites (Figure 4.5). The mean age of adult female and male mortalities was 7.1 years (SE = 0.84; $n = 11$) and 9.3 years (SE = 2.25; $n = 2$), respectively. The mean female bone marrow class was 1.8 ($n = 15$) and male bone marrow class was 2.40 ($n = 5$).

Population Modeling

Due to the differences observed in parturition rates between handled and unhandled moose, I used the unhandled moose parturition rates to estimate calf production. Based on adult pregnancy and parturition rates, the expected yearling parturition rate was 0.05 and this was used to estimate yearling productivity. Using pooled vital rates estimated during the study, λ was calculated to be 0.973 (Figure 4.7). This indicated that the moose population may be subject to a modest decline of approximately 2.7% annually. The mean λ estimate derived from 1,000 matrix replicates of randomly generated vital rates was 0.972 (SE = 0.002) with 95% CI of 0.907-1.062 (Figure 4.9). This indicated that the moose population was slightly decreasing to stable during the study period, but there was some uncertainty in the estimate. Based on simulations, there was a 17% chance that the population had a positive growth rate and a 76% chance that it had a negative growth rate in any given year. Adult female survival had the highest elasticity (0.658), followed by calf survival (0.114), adult fecundity and yearling survival (0.113), and yearling fecundity (0.001; Figure 4.8).

DISCUSSION

Demographic data from this study indicated that the north Jackson moose herd may be limited by habitat quality or availability, and its effects on the survival and reproductive performance of adult females, more than predation by grizzly bears and wolves. However, my findings do not support the classic concept of density-dependence as a limiting factor for this population as proposed by Berger et al. (1999, 2001). Indices of moose density indicated that the north Jackson moose herd has been declining since the late 1980s (Chapter 1) and evidence from the current study suggested that continued population declines appear to be more likely than a stable or increasing population (λ = 0.972, 95% CI = 0.907-1.062). This indicated that the nutritional quality, rather than the availability, of habitat may be the most important determinant limiting population growth because a reduction in moose numbers, no matter the cause, should have resulted in increased physical condition and reproductive success if this population occupied productive habitat (Bowyer et al. 2005). Potential moose population declines may have occurred concurrently with a reduction in habitat quality, due to unidentified causes, which might explain the marginal nutritional condition (Chapter 3) and low reproductive output observed in the study population. Because my study was not designed to evaluate cause-specific mortality, I could not rule out the potential additive effects of gray wolf or grizzly bear predation on adults and calves. But such effects, if present, appeared to be secondary to the influence of habitat quality possibly due to the abundance of alternate prey in the GYE.

The pattern of adult female mortality in this study was indicative of a population that is nutritionally limited. Consistent with other demographic studies of ungulates, adult female survival had the most significant influence on population growth, but contrary to these studies, there was high annual variation in survival rates (Gaillard et al. 2000) primarily due to variation in mortality during late winter and early spring (March-May). Increased spring mortality was suggestive of habitat limitations because the nutritional demands of female moose increase as winter progresses and peaks during late winter in association with parturition and lactation (Schwartz et al. 1984, Schwartz et al. 1987). Therefore, if the nutritional demands of females were not met during this critical period or environmental factors increase the energetic demands of locomotion and reduce the availability of forage, decreased survival may occur. Bender et al. (2007) observed increased spring mortality in a mule deer population following a dry spring that reduced the availability of quality forage. Likewise, Modafferi and Becker (1997) observed decreased female moose survival in late winter following years with heavy and persistent snow accumulation in Alaska. In the Jackson Valley, Houston (1968) suggested that moose populations fluctuated from 1950 to 1966 in response to willow conditions and periodic die-offs that occurred during severe winters. This indicated that moose in good physical condition were likely buffered against the effects of increased winter severity, whereas moose in poor physical condition were more susceptible (Bowyer et al. 2000).

While this study was not designed to evaluate cause-specific mortality, I did observe a relatively-high proportion of deaths due to natural causes that were not related to predation (19%, see Figure 4.5) which was indicative of poor habitat quality resulting in reduced physical condition. In other moose populations where predation was found to be a significant mortality factor for adults, no deaths associated with natural causes were reported (Bergerud et al. 1983, Gasaway et al. 1992). Similar to other studies (Boertje et al. 1988, Larsen et al. 1989), I observed some spring grizzly bear predation on adult female moose, but a reduction in physical condition due to poor habitat quality may have predisposed moose to predator-related mortalities. Therefore, it is likely that if habitat quality were improved, the physical condition of moose would also improve which may result in increased survival rates.

Although my modeling indicated that the Jackson moose population may be in a slow rate of decline ($\lambda = 0.973$), consistent with trends since the late 1980s (Chapter 1), the low twinning rates observed during the study (see Table 4.1) indicated that habitat quality had not improved as moose numbers declined. Moose twinning rates are used by managers as an indicator of the nutritional status of the population (Franzmann and Schwartz 1985, Boertje et al. 2007). Twinning rates have been reported to be as high as 70% for moose populations that occupy highly productive habitat (Franzmann and Schwartz 1985) and as low as < 1% for moose that occupy poor quality habitat (Albright and Keith 1987). When Shiras moose were expanding in the GYE during the early 20th century, twins were more common than singletons (Bailey 1930), but, in the Jackson Valley, twinning rates declined to approximately 15% by the 1940s (Denniston 1956) and were 4.5% in the 1960s (Houston 1968). High moose densities during the 1950s may have resulted in overutilization of resources (Harry 1957) which may have reduced female condition and, thus, twinning rates. The low twinning rates observed for this Shiras moose population may have been due to the relatively stable environments (i.e., lack of disturbances) that these moose inhabit (Peek 1974, Schwartz 1997). The lack of disturbance may result in high forage biomass, but that forage may be of low nutritional value. Additionally, twinning rates during this study were also much lower than those observed for moose populations that appeared to be held at low densities by predation in Alaska (range 39-63%; Ballard et al. 1991, Osborne et al. 1991, Gasaway et al. 1992, Bertram and Vivion 2002) and Canada (54%; Bergerud et al. 1983) which again suggested nutritional constraints that limit reproductive output in this population.

There appeared to be a low probability (0.33) that unhandled moose in the study population would be observed with a calf in consecutive years, which was indicative of nutritional limitations that may have resulted in reproductive pauses. Successful reproduction in ungulates is highly dependent on maternal condition and, in turn, maternal condition may be affected by habitat quality and past reproductive performance (Clutton-Brock et al. 1983, Testa and Adams 1998, Keech et al. 2000, Reynolds 2001). Thus, if habitat quality in the study area was inadequate to support both lactation and fat accretion in consecutive years, successful reproduction may have been compromised (Clutton-Brock et al. 1983, Cook et al. 2004*a*). Reproductive pauses (whether caused by an inability to conceive, lost pregnancy, or neonatal calf mortality) may benefit this moose population by allowing the female to accrue sufficient body fat to produce a viable offspring that has a greater chance of survival the following year (Cameron et al. 1993, Testa 1998, Testa and Adams 1998, Keech et al. 2000). Similar to the current study, a low percentage (18%) of consecutive-year calf production was observed for a population of moose in Newfoundland, Canada affected by poor winter nutrition and severe winter weather. Additionally, Reynolds (2001) observed an increased reproductive interval (from 1 to every 2-3 years) in musk-oxen (*Ovibos moschatus*) resulting from increased densities that likely affected forage. Although direct comparisons cannot be made, Cameron (1994) observed a 24% frequency of reproductive pauses in caribou and Clutton-Brock (1983) observed lower calf production in red deer the year following successful reproduction (68.9%) than in years following failed reproduction (89.5%).

The mechanisms responsible for the decreased reproductive success of pregnant female moose captured during winter may have been related to marginal physical condition more than capture and handling techniques. The observed difference in parturition rates between handled (24%) and unhandled females (79%) as well as the high proportion of females known to be pregnant at capture that lost their fetuses at some point 1-2 months post-capture (79%) was somewhat unique among documented moose captures. My findings contrast with those from an expanding moose population in southeast Wyoming where 9 pregnant adult female moose were captured 2 months prior to the current study using the same immobilization techniques, but 8 were observed with calves the following summer (E. Wald, University of Wyoming, personal communication). My results also contrasted with findings by Larsen and Gauthier (1989) who reported no decrease in parturition rates when moose were captured during late pregnancy. Only one other study documented significantly lower parturition rates for mammals captured during winter and this occurred in moose from Alaska (Ballard and Tobey 1981). The authors suggested that stress associated with immobilization without the use of a tranquilizer may have increased the incidence of fetal mortality. Although female moose handled during the first year of the study did not exhibit signs of capture-related stress (Kreeger et al. 2005), handling moose appeared to artificially induce a reproductive pause regardless of the immobilizing agent or capture technique. Indeed, for moose that were captured and lost their calf, there was a high probability (0.80) that they would be observed with a calf the following year after not being handled. It has been posited that moose may be highly susceptible to nutritional deficiencies (Murray et al. 2006), thus, the combination of capture and marginal physical condition with deficiencies in several nutrients (Chapter 3) may have pushed moose over a physiological threshold that induced the reproductive pause post-capture.

The reduced reproductive success observed in the study population indicated that a reduction in the physical condition of adult females as winter progressed may have contributed to a concurrent reduction in reproductive output. Contrary to previous research (Berger et al. 1999), the observed pregnancy rate for moose (92%) was relatively high when compared to the North American average (84%; Boer et al. 1992) while the mean parturition rate (79% for unhandled moose) was on the lower end of the distribution (range = 75- 90%; Stenhouse et al. 1995, Keech et al. 2000, Testa 2004, Berger et al. 2007, Boertje et al. 2007). Although female moose with high body fat are more likely to become pregnant (Heard et al. 1997, Testa and Adams 1998, Keech et al. 2000) pregnancy rates appear to be relatively constant across a range of geographic areas, population densities, and environmental conditions (Edwards and Ritcey 1958, Boer et al. 1992). Therefore, high pregnancy rates may only indicate that moose had sufficient body fat during the breeding season to become pregnant (Cook et al. 2004*a*, Cook et al.

2004*b*). However, the nutritional deficiencies observed in the study population indicated that moose may have a higher fat-fertility threshold than other populations (Heard et al. 1997, Chapter 3) and if the lower limit of this threshold was reached prior to parturition, there may be a greater potential for abortion or resorption. Indeed, during spring 2008 (i.e., BY 2007), WGFD personnel responded to 2 separate instances of female moose aborting calves and a third cow that died while aborting a calf near the town of Jackson, Wyoming (S. Kilpatrick, WGFD, personal communication).

The high neonate (62%) and annual calf survival (46%) rates indicated that predation pressure on moose calves was relatively low. This may be due to the abundance of alternate prey available in the GYE. Mattson (1997) reported that elk calves were used more than expected by grizzly bears in the GYE while both black bears and grizzly bears were significant predators of neonatal elk calves before (Smith et al. 2006) and after (Barber-Meyer et al. 2008) wolf restoration. Since elk calving grounds contain a relatively high abundance of animals, and the potential nutritional rewards are high, bears may prefer to forage near these areas during calving season (French and French 1990). In contrast, moose are solitary by nature, thus the potential nutritional reward may be less because of the greater search time that might be required by bears to locate moose calves. The high neonate survival and the abundance of alternate prey suggest that bear predation on neonatal moose calves may be more opportunistic (Zager and Beecham 2006). Cougar (Ross and Jalkotzy 1996) and wolf predation (Larsen et al. 1989) on moose calves generally occurs after the neonate life stage. The impact of these predators on calf survival appeared to be minimal based on the proportion of potential mortalities that occurred between neonate and annual calf survival surveys (≈ 0.16).

Using comparable data where predation on calves was a primary source of mortality, neonate survival ranged from 17-39% in Alaska (Ballard et al. 1990, Ballard et al. 1991, Gasaway et al. 1992, Bowyer et al. 1998, Testa et al. 2000, Bertram and Vivion 2002) and Canada (Larsen et al. 1989). Not surprisingly, annual calf survival was also higher than observations from Alaska where rates ranged from 13-33% (Ballard et al. 1991, Osborne et al. 1991, Gasaway et al. 1992, Testa et al. 2000, Bertram and Vivion 2002), but it was similar to a low-density moose population in Canada where some calf predation occurred (44%; Stenhouse et al. 1995) and a high-density population that was influenced primarily by density-dependent processes in Alaska (53%; Keech et al. 2000).

Although wolves did account for some adult female moose mortalities, the effect of wolf predation on this population appeared to be minimal. This may have been due to the abundance of alternate prey, specifically elk, in the study area. In a multipredator ecosystem in northwest Montana, adult female moose survival rates were higher where alternate ungulate prey were available (Kunkel and Pletscher 1999). Likewise, in Mantioba, Canada where elk and moose occurred sympatrically, wolves preferred elk disproportionately more than moose (Carbyn 1983). In the Jackson Valley, elk represented > 90% of wolf kills (Jimenez et al. 2008), which indicated a similar trend. The apparent preference for elk by wolves in the GYE was likely due to the greater abundance of elk in the area. To reduce the potential effects of predation on moose and other large ungulates, wolves were selected for reintroduction from source populations where elk or deer were the primary prey (Bangs and Fritts 1996).

When harvest was included in survival analyses, adult male survival appeared to decline in autumn, but survival exhibited no specific temporal patterns when harvest was censored. The lack of a temporal pattern of male mortality suggested that males were able to acquire sufficient forage prior to the onset of winter to recoup losses incurred during autumn rut (Modafferi and Becker 1997). Non-harvest related survival rates were similar to those observed for males in Colorado (Olterman and Kenvin 1998) and Alaska (Modafferi and Becker 1997). When all forms of mortality were included, male survival was slightly higher than a moose population in Alaska where vulnerability to harvest increased with age (Ballard et al. 1991), but was much greater than a population in Newfoundland, Canada where harvest was heavily biased towards males (Albright and Kieth 1987).

Although evidence indicated that a declining moose population was more probable than a stable or increasing population in the study area, caution should be used when interpreting the finite rate of growth. All yearling input parameters were estimated from previous research and I assumed that parturition rates for unhandled moose were representative of the population. Boer (1992) reported that twinning rates were significantly correlated with the proportion of pregnant yearlings in a population. Yearling pregnancy rates were estimated for the study population based on work conducted in the Jackson Valley by Houston (1968). Twinning rates during my study were similar to those observed by Houston (1968), thus I assumed that yearling pregnancy was also similar and that the estimated yearling fecundity rate may be fairly accurate. Even though it was assumed that yearling survival equaled adult survival, several studies have reported that yearling survival was lower than adults (Dodge et al. 2004, Testa 2004, Murray et al. 2006). Therefore, my estimate of population growth may have been biased high. Furthermore, although parturition rate estimates were consistent across years for the handled and unhandled groups of moose, neonatal calf losses that may have occurred prior to parturition surveys would have biased my parturition estimates low and my annual calf survival estimates high. Based on the accuracy of fecal progestagen in predicting whether a female would be observed with a calf in the spring (see Figure 4.3), the introduction of bias associated with unrecorded neonatal losses appeared to be minimal and likely had little effect on my estimates of annual calf survival and population growth.

Additional moose research in northwest Wyoming could be used to further assess the nutritional status of the population. In addition to multi-year twinning rates that average < 10%, Boertje et al. (2007) suggested that the nutritional status of moose populations could be evaluated by obtaining short-yearling (i.e., a moose that has almost completed its first year of life) mass, age of first reproduction, and annual browse biomass removal rates. Although the value of using criteria developed in Alaska to assess the nutritional condition of Shiras moose populations based on short-yearling mass may be limited due to differences in body size among species, radio-collaring short-yearling female moose would provide an accurate estimate of the age of first reproduction. It would also provide estimates of survival for the yearling age class and a measure of yearling reproductive success that could be used to more accurately assess the finite rate of growth. Efforts to assess the condition of moose winter ranges may assist managers in evaluating the quality of the habitat. In addition to research that could provide more insight into the nutritional status of the population, increased monitoring to estimate cause-specific mortality for adult female moose, especially in the spring, would be an important step to further evaluate the extent of potential limiting factors resulting from predation and other causes.

MANAGEMENT IMPLICATIONS

The low reproductive potential and decreased spring survival of adult female moose in this population indicated that habitat may be the primary limiting factor in the study area. Therefore, population and habitat management strategies designed to increase the quality of moose habitat could be evaluated relative to their impacts on reproductive output and survival of adult females (Bender et al. 2007). Although this population may be in decline, increased reproductive output and female survival may not be realized until a disturbance (i.e., fire, mechanical treatment) acts to improve the quality of moose winter range. Habitat improvement projects could be completed on a large-scale over multiple years so that high numbers of moose do not reduce the growth potential of preferred forage and the amount of available forage remains sufficient even during high snow years. Improvements to moose summer ranges may be limited in scope because much of the area is managed as a naturally regulated system by the U.S. Forest Service and the National Park Service. Mature coniferous forests are an important component of Shiras moose habitat selection in winter (Tyers 2003) and summer (Chapter 2), thus disturbances that reduce the amount of mature forests (i.e., wildfires, insect outbreaks) could negatively affect moose population performance. Therefore, large-scale disturbances and their potential impacts on moose population dynamics could be closely monitored.

Although most elk use feedgrounds (Boyce 1989, Lubow and Smith 2004), there are relatively high numbers of free-ranging elk in the Jackson Valley that also utilize moose winter ranges and during periods of heavy and persistent snow accumulation, elk may compete with moose for browse (Miller 2002). Increasing elk harvest and improving elk winter ranges may reduce the competitive interactions of these species. However, caution should be used if elk harvest is increased to alleviate some of the competitive pressure because a reduction in elk numbers on winter range may increase the impact of predators on moose (Gasaway et al. 1983, Ballard and Larsen 1987, Kunkel and Pletscher 1999) potentially creating a predator-pit scenario. Managing wildlife populations in ecosystems that contain multiple prey and predators is a highly-complex endeavor that requires active management and long-term research to make informed decisions. By closely examining long-term demographic data in relation to interactions with other ungulates, predators, habitat, and environmental factors, managers and researchers can gain a better understanding of ecosystem dynamics. Nonetheless, this study provided a framework with which future research can now be directed to answer more cause-specific questions regarding the dynamics of moose in northwest Wyoming.

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Table 4.1. Number of moose sampled (*n*), mean rate ($\bar{x}$), and 95% confidence intervals (95% CI) for adult female moose reproductive parameters and calf moose survival in northwest Wyoming, biological years 2004-2006.

	2004			**2005**			**2006**			**Total**		
Parameter	*n*	$\bar{x}$	95% CI	*N*	$\bar{x}$	95% CI	*n*	$\bar{x}$	95% CI	*n*	$\bar{x}$	95% CI
Pregnancy[a]	21	0.91	0.78-1.00	19	0.95	0.85-1.00	19	0.90	0.76-1.00	59	0.92	0.84-0.99
Parturition												
Handled[b]	16	0.19	0.00-0.38	16	0.25	0.04-0.46	13	0.31	0.06-0.56	45	0.24	0.12-0.37
Unhandled[c]	14	0.79	0.57-1.00	19	0.79	0.61-0.97	10	0.80	0.55-1.00	43	0.79	0.67-0.91
Twinning[d]	14	0.00	0.00-0.00	19	0.11	0.00-0.24	12	0.08	0.00-0.24	45	0.07	0.00-0.14
Neonate survival[e]	14	0.50	0.24-0.76	17	0.71	0.49-0.92	11	0.64	0.35-0.92	42	0.62	0.47-0.77
Annual calf survival[f]	13	0.39	0.12-0.65	18	0.56	0.33-0.79	10	0.40	0.10-0.70	41	0.46	0.31-0.62

[a] *n* = number females captured. Pregnancy rate calculated from pregnancy-specific protein B of handled moose only.
[b] *n* = number of pregnant, handled moose alive at start of parturition surveys.
[c] *n* = number of parturient females calculated from the number of unhandled, female moose alive at start of parturition surveys multiplied by the pregnancy rate for handled moose during each year.
[d] *n* = total number of cows observed with calves.
[e] *n* = number of calves that were observed during parturition surveys. One calf was censored in 2006 due to radio failure of cow.
[f] *n* = early and late births combined. Six calves censored (2005 = 1; 2006 = 3; 2007 = 2) due to radio failure or death of cow.

Table 4.2. Adult annual (i.e., biological year [BY]) and study period (i.e., total) survival rates and 95% confidence intervals (CI) estimated using the Kaplan-Meier staggered entry design for radio-collared female and male Shiras moose in northwest Wyoming. Male BY 2004 included February, March, April, and May only and was not an estimate for the entire BY. Male survival rates were estimated separately with harvest included and harvest censored in BY 2005 and BY 2006.

Year	Number alive at start	Number added	Number deaths	Number censored	Survival rate	95% CI
			Female			
BY 2004	18	21	6	1	0.84	0.73-0.96
BY 2005	32	12	2	4	0.94	0.86-1.00
BY 2006	38	15	8	20[a]	0.77	0.62-0.91
BY 2007	25	32	10	1	0.79	0.66-0.91
Total	113	80	26	26	0.83	0.77-0.89
			Male			
BY 2004	0	27	0	2	1.00	1.00-1.00
BY 2005						
Harvest included	25	4	7	0	0.74	0.57-0.90
Harvest censored	25	4	4	3	0.84	0.70-0.98
BY 2006						
Harvest included	22	0	5	1	0.77	0.60-0.95
Harvest censored	22	0	3	3	0.86	0.72-1.00
BY 2007	16	0	0	3	1.00	1.00-1.00

Table 4.2. Continued.

Year	Number alive at start	Number added	Number deaths	Number censored	Survival rate	95% CI
			Male			
Total						
Harvest included	63	31	12	6	0.82	0.73-0.91
Harvest censored	63	31	7	11	0.89	0.82-0.97

[a] Fifteen global positioning system collars released from adult female moose on 1 March 2007.

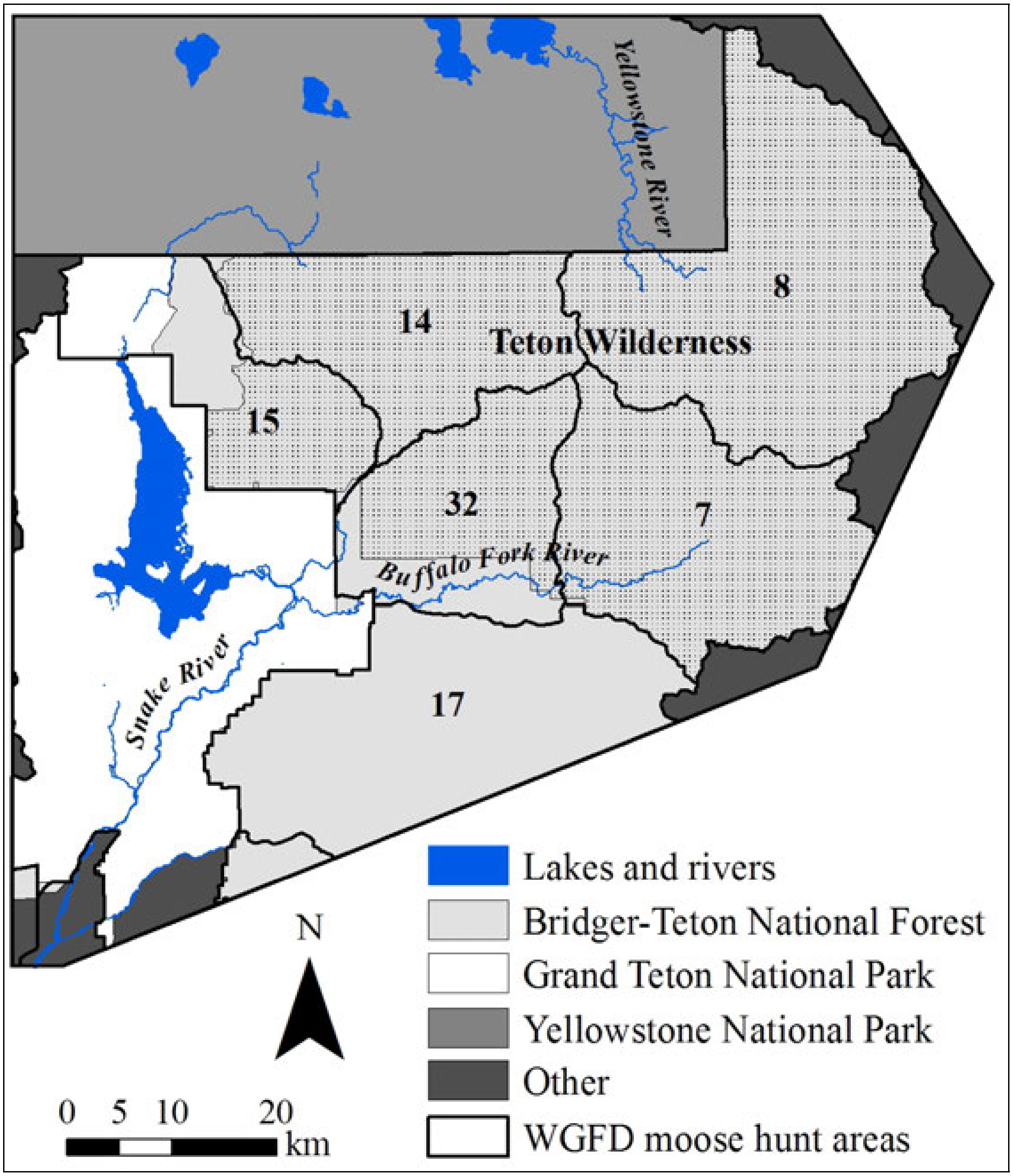


Figure 4.1. Study area located in northwest Wyoming. The Buffalo Fork River is approximately 50 km north of Jackson, Wyoming, USA. Moose hunt areas 7, 14, and 32 were closed to hunting during 2005 and 2006, but opened to limited quota, antlered harvest in 2007.

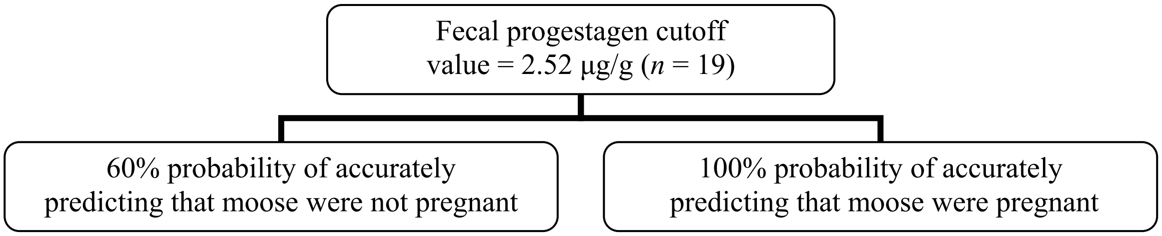


Figure 4.2. Results of fecal progestagen regression tree analysis used to predict the pregnancy status of adult female moose at capture in February 2007. Initial pregnancy status was determined using pregnancy-specific protein B. This cutoff value was used to determine pregnancy status of adult female moose approximately 1-2 months post-capture, but prior to parturition.

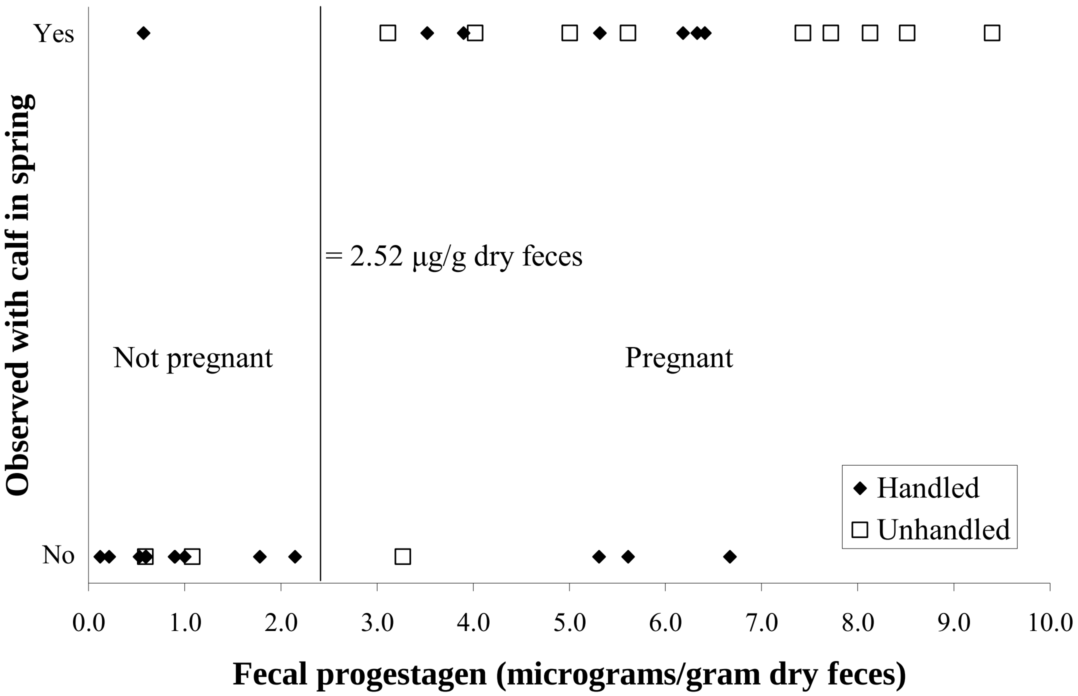


Figure 4.3. Progestagen concentrations from fecal samples collected > 1 month post-capture for handled and unhandled adult female moose in northwest Wyoming, 2006-2007. The handled sample was for moose that were pregnant at capture based on pregnancy-specific protein B while the pregnancy status of unhandled moose was estimated using the fecal progestagen cutoff value (vertical line). The top row represents female moose that were observed with calves (*n* = 7 handled, *n* = 9 unhandled) and the bottom row represents female moose that were not observed with calves (*n* = 14 handled, *n* = 3 unhandled) during spring parturition surveys.

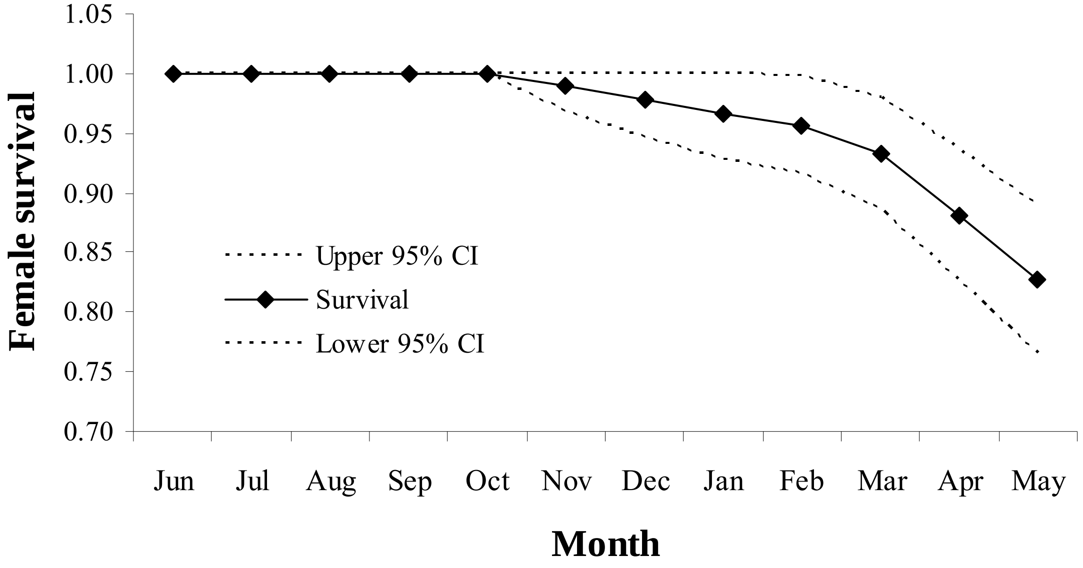


Figure 4.4. Pooled annual survival curve and upper and lower 95% confidence intervals (CI) by month for radio-collared adult female moose in northwest Wyoming, biological years 2004-2007.

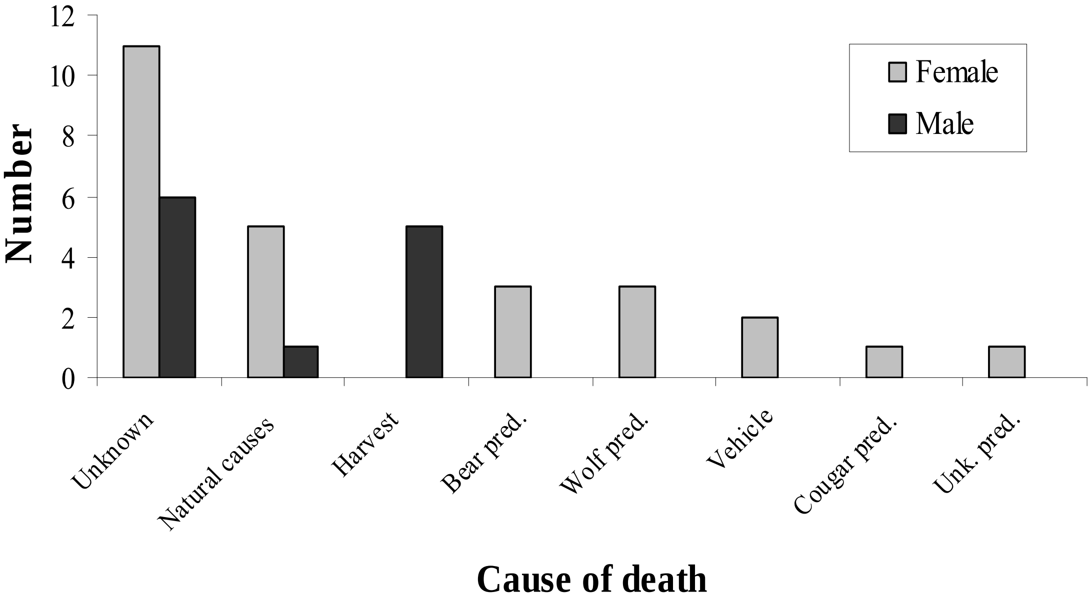
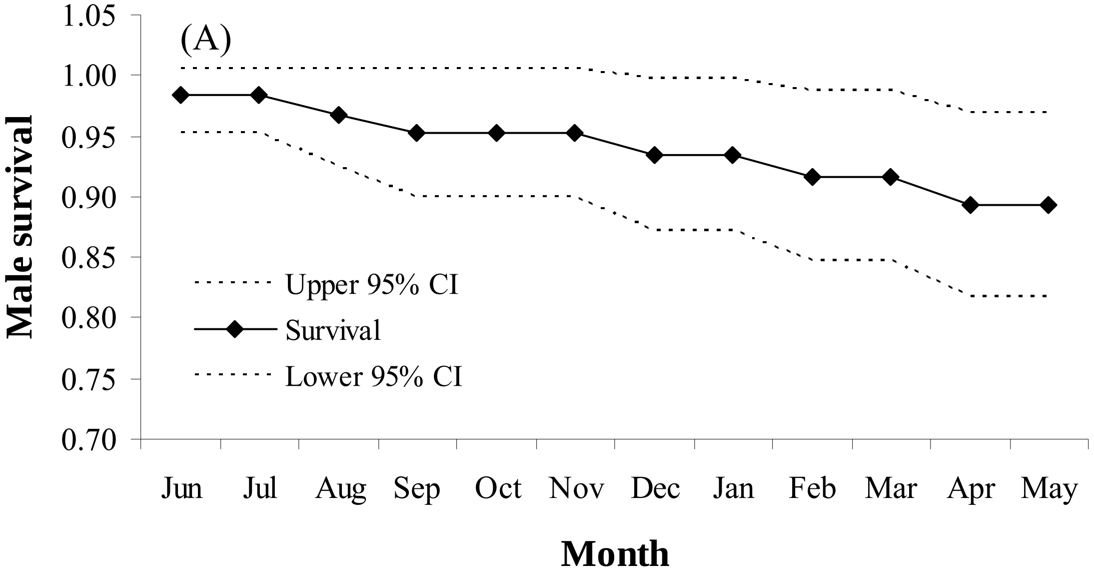


Figure 4.5. Cause-specific mortality by sex for radio-collared adult moose in northwest Wyoming, February 2005 to May 2008.



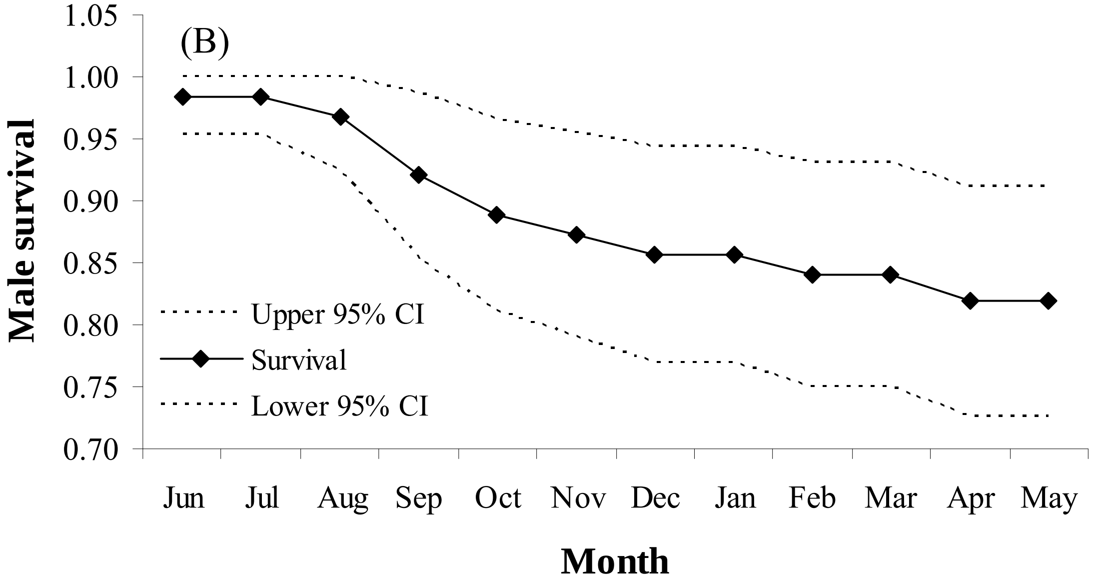


Figure 4.6. Pooled annual survival curves and upper and lower 95% confidence intervals (CI) by month for radio-collared adult male moose when (A) harvest was censored and (B) harvest was included in survival analyses, biological years 2004-2007.

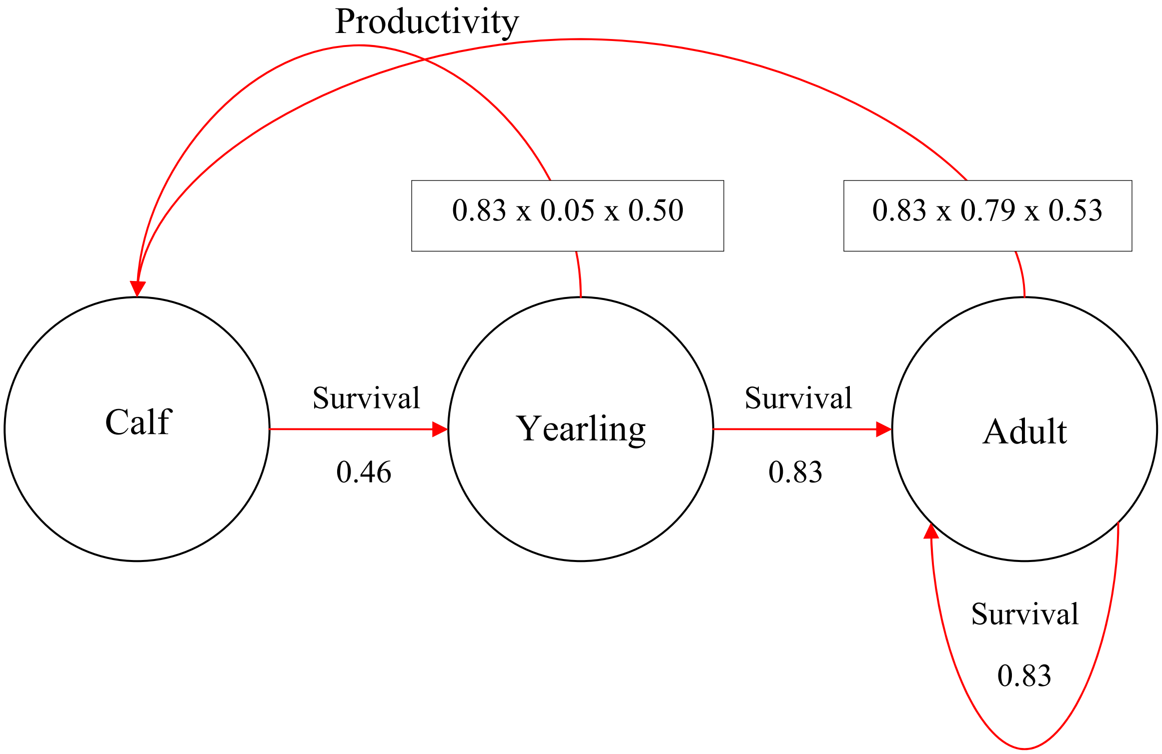


Figure 4.7. Schematic of female-based, Lefkovich matrix model with 3 stage classes using the demographic data estimated (i.e., calves and adults) or assumed (i.e., yearlings) for moose in northwest Wyoming. Productivity equals the product of stage-specific survival, parturition, and fecundity for yearlings and adults.

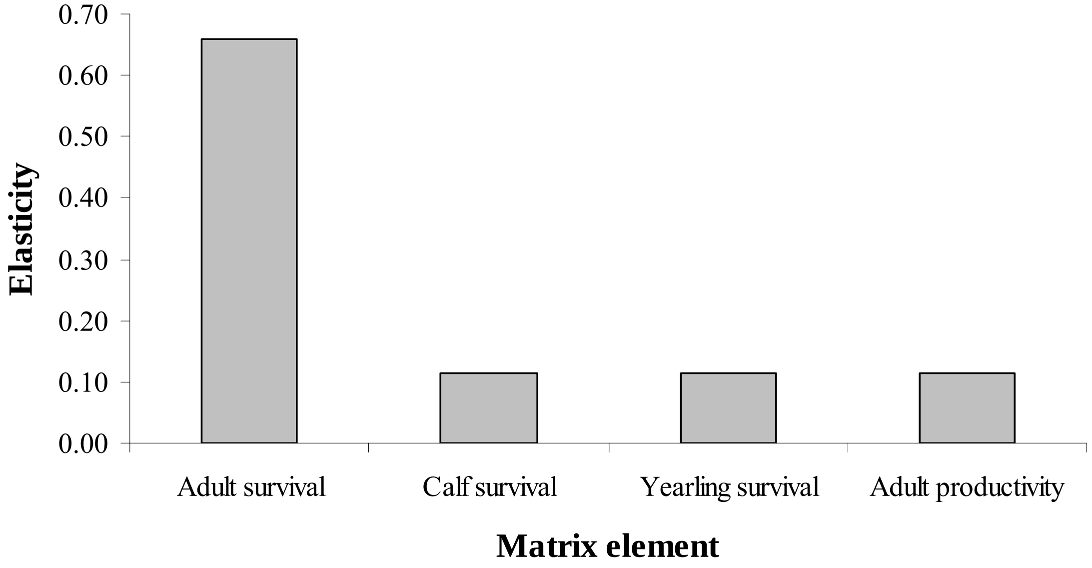


Figure 4.8. The deterministic elasticity of matrix elements calculated from the pooled vital rates from the demographic study. Adult productivity was the product of adult survival, parturition, and fecundity rates. The elasticity for yearling productivity was < 0.01.

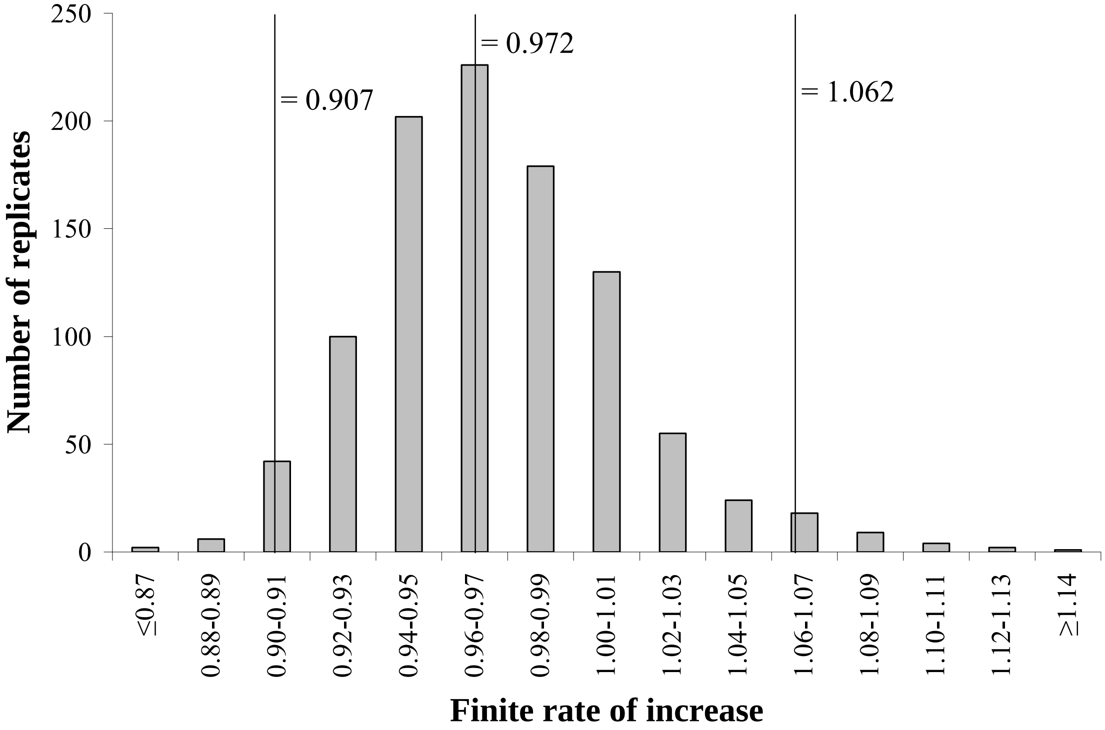


Figure 4.9. Distribution and range of the finite rate of increase (λ) for Shiras moose in northwest Wyoming, biological year 2004-2007, based on 1,000 replicates of a Leslie matrix population model with vital rates selected randomly from a binomial distribution. The middle vertical line represents the mean λ estimate. The left and right vertical lines represent the lower and upper 95% confidence intervals, respectively.

CHAPTER 5

GENERAL CONCLUSIONS

Summary

Throughout their circumpolar distribution, moose (*Alces alces*) generally seek winter habitats that provide abundant forage (Peek 1997, Månsson et al. 2007). Shiras moose (*A.a. shirasi*) in northwest Wyoming appeared to follow a similar pattern and selected low-elevation, riparian habitats dominated by willow (*Salix* spp.) communities. In Alaska, aspen (*Populus tremuloides*) ranked as the highest quality winter forage (Oldemeyer et al. 1977), thus selection for aspen indicated that moose not only preferred habitats with high forage biomass, but they also selected for the highest quality browse available during winter. Moose also selected for areas with high habitat diversity which indicated that they require a variety of resources to meet their nutritional and energetic requirements during winter. I observed little evidence to support a shift to more closed-canopy habitats as winter progressed, but winter range conditions may not have been severe enough to necessitate selection for coniferous habitats during late winter (Poole and Stuart-Smith 2006).

Summer habitat selection by adult female moose in the study area appeared to be associated with habitat and landscape features that limited the effects of thermal stress. Areas classified as high-use during summer were > 300 m higher in elevation and > 100 m closer to cover than areas classified as high-use in winter. Selection for habitats in close proximity to cover may have provided refugia from high summer temperatures that typically exceeded the heat stress threshold for moose. Although my data do not prove that mature coniferous forests are critical for moose survival during summer (Balsom et al. 1996), they do lend support to the notion that these habitats are important in providing cover and reducing the potential effects of heat stress near the southern extent of their range.

Moose exhibited a high degree of individual variability in the onset of spring and autumn migrations. In general, there was a relationship between the onset of spring migration and the elevation of summer ranges in 2006 which indicated that snow conditions may be a factor in the timing of migration in some years. There was no relationship between autumn migration and the elevation of summer range which indicated that a rapid accumulation of snow initiated migration regardless of summer range elevation. Photoperiod may also affect the timing of migratory events in the study population (Garrott et al. 1987).

Based on comparisons of blood parameters compiled for Alaskan moose (*A.a. gigas*; Franzmann and LeResche 1978), adult female moose in the study area appeared to be in moderate physical condition. Ultrasonic rump fat measurements were relatively high, but there was evidence that moose winter forage was deficient in copper, zinc, manganese, and phosphorous. Because of nutritional deficiencies, the study population may require greater fat depths than other moose populations to maximize reproductive potential (Heard 1997). Rump fat levels indicated that moose were able to obtain sufficient quantities of forage, but these resources were not of the highest quality. I observed a significant negative relationship between rump fat levels and two blood parameters, aspartate aminotransferase and lactate dehydrogenase. Both of these parameters are indicators of muscle and organ damage generally associated with exertional myopathy (EM; Williams and Thorne 1996), however, concentrations were not indicative of EM. The negative relationships that I observed were consistent with increased utilization of body proteins as lipid reserves decline in lean animals. Diseases and parasites appeared to have minimal population-level effects. However, the impacts of the winter tick (*Dermacentor albipictus*) may increase in years following warm, dry springs.

The north Jackson moose herd appears to have been declining since the late 1980s based on indices of moose density (Chapter 1) and modeling efforts from my study indicated that a declining population was more likely than a stable or increasing population. The population growth rate was influenced by late winter and early spring adult female mortality. Although increased predation may have partially contributed to the observed decline, its influence was likely limited by the abundance of alternate prey, specifically elk (*Cervus elaphus*), in the Greater Yellowstone Ecosystem. Additionally, the study population exhibited low reproductive potential in the form of low twinning rates, reproductive pauses, and relatively low parturition rates. This indicated that the nutritional quality of available forage may be the most important determinant in limiting population growth because a reduction in moose numbers over a 20-year period, no matter the cause, should have resulted in increased physical condition and reproductive success (Bowyer et al. 2005). Moose populations may have slowly declined in response to gradually declining habitat quality over this time period.

In addition to the 1988 Yellowstone fires and its effect on moose summer ranges, another explanation for the declining population performance with reduced moose numbers could be drought and climate change (Murray et al. 2006). Although a loss of vigor and even death has been observed due to drought in a riparian tree species from eastern Montana, the plains cottonwood (*P. deltoides*; Knight 1994), to my knowledge, no work has been conducted to examine the effects of drought on the growth potential and nutritional quality of riparian vegetation in the Intermountain West. In northwest Wyoming, there has been a series of relatively mild winters and dry summers since the 1990s, and if the nutritional quality of riparian vegetation preferred by moose was altered due to drought, this may have had a negative effect on the physical condition and overall population performance of the north Jackson moose herd.

While habitat quality and its effects on the physical condition, survival, and reproductive success of adult female moose appeared to be the primary factor limiting population growth, I cannot discount the potential effects of predation. Although evaluating cause-specific mortality was not a primary objective during this study, grizzly bears (*Ursus arctos*) and gray wolves (*Canis lupus*) were responsible for some mortalities. However, a relatively high proportion of deaths were attributed to natural causes not related to predation which suggested that predation pressure was insufficient to account for the nutritional limitations of the habitat.

Management Implications

Shiras moose population declines in northwest Wyoming began shortly after the 1988 Yellowstone fires (Chapter 1) and moose selection for areas in close proximity to coniferous cover indicated that a reduction in this habitat feature may have been detrimental to moose. Similar patterns were observed on the northern Yellowstone winter range after the 1988 wildfires (Tyers 2003). A reduction in coniferous cover on summer range may have reduced the amount of available forage and increased thermal stress that, ultimately, resulted in reduced physical condition and lower reproductive potential. The continued threat of disturbances (i.e., wildfires, insect outbreaks) that have the potential to greatly reduce the availability of coniferous forests may negatively affect moose populations near the southern extent of their range. Because much of the summer range used by moose in northwest Wyoming is managed for natural regulation, little can be done to improve these habitats. Therefore, continued monitoring of moose populations and the potential effects of reduced coniferous cover appear warranted.

Although winter range habitat improvements occurred during the early 1990s in the Jackson Valley, these were relatively small in scale. Thus, improvements in fitness may only have been observed at the individual rather than the population-level. To benefit moose at the population-level, large-scale improvement projects could be initiated. However, because of differences in management strategies among state and federal agencies in the Jackson Valley, this may be a difficult task. Nonetheless, through cooperation and planning, efforts to improve moose winter ranges on a large-scale could be implemented. Prescribed burns or mechanical treatment of preferred riparian shrubs would improve growth as well as the nutritive value of forage for moose and other ungulates. Aspen was also an important component of moose winter range and projects that encourage growth and regeneration could benefit this population. Habitat improvements would likely lead to improved herd health and may result in increased adult female survival, reproductive success, and population growth.

Future Research

Given insights from this study, future research can be directed to answer more specific questions in regards to the ecology and dynamics of moose populations in northwest Wyoming. Global positioning system collars could be used to further assess the importance of coniferous cover for moose on summer ranges by examining habitat selection patterns between day and night. If thermal stress during summer influences habitat selection, one would expect to see more use of coniferous cover during the day when temperatures are high and less use during night (Muir 2006). This could also be evaluated during late winter and early spring because moose may select habitats that reduce thermal stress as spring temperatures increase. Although the predictive-probability-of-use map provided a framework to estimate where moose are most likely to be located during winter, it did not take into account environmental factors such as snow depths or ambient temperatures. Some areas classified as high-use during winter may not support moose because of greater snow depths than what occurs in the Buffalo Valley. This would greatly reduce the availability of forage and increase the energetic cost of locomotion which would likely result in reduced physical condition. Areas in and around Pacific Creek in Grand Teton National Park may need to be reassessed due to this factor.

Further evaluation of the physiological health of this population appears warranted. By evaluating blood parameters in relation to individual habitat selection patterns, researchers may have a clearer picture of habitat components that could reduce moose fitness. Continued evaluation of blood parameters that are correlated with rump fat depth may provide managers with an easy assessment of physical condition without the need for an ultrasound. Rump fat depths or blood parameters can be used to assess the health of moose herds statewide by collecting this information at check stations during the autumn. This would provide managers with a relative index of the nutritional status of moose populations entering winter. This information could also be used to assess fat catabolism as a function of winter severity or reproductive status if moose were to be captured again during mid to late winter. To gain a better understanding of the relationship and utilization rates between protein and fat reserves during winter, I would strongly recommend using ultrasonography to measure the thickness of specific muscles from captured moose (Cook et al. 2001). Preferably, this would be accomplished at the beginning and near the end of each winter season so that accurate assessments of utilization rates could be conducted. Nutritional deficiencies are best examined through direct evaluation of the mineral content of forage (McDowell 2003). Therefore, future research could assess the mineral content of preferred moose forage, both during winter and summer. This could also provide information that may be used to assess the potential effects of drought and climate change on moose browse in the Jackson Valley. Furthermore, estimating annual browse biomass removal rates could provide an additional assessment of the nutritional status of this population. Boertje et al. (2007) suggested that, in addition to multi-year twinning rates < 10%, annual browse biomass removal rates of > 35% may be indicative of low nutritional status of a moose population.

Long-term studies of the dynamics of this moose population appear warranted. Because of the reduced parturition rates of moose captured during this study, capturing and radio-collaring a large sample of moose at once, then not handling them again for the duration of the study, could provide estimates of survival and reproductive success over a very long time period. This could be used to further assess the reproductive output (i.e., parturition rates, twinning rates, reproductive pauses) of this population on an annual basis by removing capture effects completely. Additionally, capturing a sample of short-yearlings over the course of 2-3 years could be used to estimate yearling survival and parturition rates as well as the age of first reproduction. Yearling survival and parturition rates could be used to estimate more accurately the growth rate of this population. The age of first reproduction could be used to evaluate further the nutritional status of the population (Boertje et al. 2007).

More effort could be made to estimate cause-specific mortality and further evaluate the potential effects of grizzly bear and gray wolf predation as well as the impacts of condition in predisposing moose to predator-related mortality. Although I used a simple technique to evaluate condition at time of death, it did not appear to be very useful because it was too general. Collecting marrow samples and evaluating percent marrow fat would be a better assessment of condition at time of death (Neiland 1970, Ballard 1995). Increasing the frequency of aerial relocations, especially during spring, could expedite the ability of researchers to determine cause of death prior to significant scavenging. Bear sign was evident at mortality sites, but there was an insufficient amount of moose remains to determine cause-specific mortality. Thus, in many cases, I was unable to determine if the moose died due to some other factor prior to the arrival of the bear or if the bear was the proximate cause of death.

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APPENDIX A

SPATIAL AND TEMPORAL CHARACTERISTICS OF MOOSE HIGHWAY CROSSINGS IN THE BUFFALO FORK VALLEY, WYOMING

A final report submitted to the *Wyoming Department of Transportation*

FINAL REPORT

FHWA-WY-08/03F

State of Wyoming Department of Transportation

U.S. Department of Transportation Federal Highway Administration

SPATIAL AND TEMPORAL CHARACTERISTICS OF MOOSE HIGHWAY CROSSINGS IN THE BUFFALO FORK VALLEY, WYOMING

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February 2008

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Report No. FHWA-WY-08/03F	Government Accession No.	Recipients Catalog No.
Title and Subtitle: Spatial and temporal characteristics of moose highway crossings in the Buffalo Fork Valley, Wyoming		Report Date February 2008
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Author(s) Scott Becker, Matthew Kauffman, and Wayne Hubert		Performing Organization Report No.
Performing Organization Name and Address U.S. Geological Survey Wyoming Cooperative Fish and Wildlife Research Unit University of Wyoming Department 3166, 1000 East University Avenue Laramie, WY 82071		Work Unit No. RS01(205) Job No. B29Y
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Sponsoring Agency Name and Address Wyoming Department of Transportation 5300 Bishop Blvd. Cheyenne, WY 82009-3340 WYDOT Research Center (307) 777-4182		Type of Report and Period Covered Final Report February 2005 – February 2008
		Sponsoring Agency Code
Supplementary Notes WYDOT Technical Contact: Cody Beers, Public Involvement Specialist, District 5, Riverton.		

Abstract: The purpose of this study was to provide the Wyoming Department of Transportation (WYDOT) and the Wyoming Game and Fish Department (WGFD) with information that could be used to assess the importance of habitat, landscape, and anthropogenic features that are essential determinants in evaluating moose crossing locations in northwest Wyoming.

Approximately 30 moose were captured, tranquilized, and collared using global positioning system (GPS) collars. The collars were programmed to provide a fix every hour from 15 November to 15 June, and every five hours from 16 June to 14 November.

The results of this study demonstrated that models developed to assess adult female moose winter habitat selection could be used at a finer spatial scale to accurately identify areas where moose are most likely to cross U.S. Highway 26/287 in the Buffalo Valley. The moose crossing events were not randomly distributed, but occurred at predictable locations that could be estimated by examining winter habitat selection parameters that contained an abundance of forage provided by aspen and willow-dominated, riparian habitats, on either side of the road.

Key Words Wyoming, GPS, collar, moose, habitat, vegetation, structure, roadway design, crossing, migration.		Distribution Statement Unlimited	
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SI* (Modern Metric) Conversion Factors

Approximate Conversions **from** SI Units

Symbol	When You Know	Multiply By	To Find	Symbol
Length				
mm	millimeters	0.039	inches	in
m	meters	3.28	feet	ft
m	meters	1.09	yards	yd
km	kilometers	0.621	miles	mi
Area				
mm^2	square millimeters	0.0016	square inches	in^2
m^2	square meters	10.764	square feet	ft^2
m^2	square meters	1.195	square yards	yd^2
ha	hectares	2.47	acres	ac
km^2	square kilometers	0.386	square miles	mi^2
Volume				
ml	milliliters	0.034	fluid ounces	fl oz
l	liters	0.264	gallons	gal
m^3	cubic meters	35.71	cubic feet	ft^3
m^3	cubic meters	1.307	cubic yards	yd^3
Mass				
g	grams	0.035	ounces	oz
kg	kilograms	2.202	pounds	lb
Mg	megagrams	1.103	short tons (2000 lbs)	T
Temperature (exact)				
°C	Centigrade temperature	1.8 C + 32	Fahrenheit temperature	°F
Illumination				
lx	lux	0.0929	foot-candles	fc
cd/m^2	candela/m^2	0.2919	foot-Lamberts	fl
Force and Pressure or Stress				
N	newtons	0.225	poundforce	lbf
kPa	kilopascals	0.145	pound-force per square inch	psi

Approximate Conversions **to** SI Units

Symbol	When You Know	Multiply By	To Find	Symbol
Length				
in	inches	25.4	millimeters	mm
ft	feet	0.305	meters	m
yd	yards	0.914	meters	m
mi	miles	1.61	kilometers	km
Area				
in^2	square inches	645.2	square millimeters	mm^2
ft^2	square feet	0.093	square meters	m^2
yd^2	square yards	0.836	square meters	m^2
ac	acres	0.405	hectares	ha
mi^2	square miles	2.59	square kilometers	km^2
Volume				
fl oz	fluid ounces	29.57	milliliters	ml
gal	gallons	3.785	liters	l
ft^3	cubic feet	0.028	cubic meters	m^3
yd^3	cubic yards	0.765	cubic meters	m^3
Mass				
oz	ounces	28.35	grams	g
lb	pounds	0.454	kilograms	kg
T	short tons (2000 lbs)	0.907	megagrams	Mg
Temperature (exact)				
°F	Fahrenheit temperature	5(F-32)/9 or (F-32)/1.8	Celsius temperature	°C
Illumination				
fc	foot-candles	10.76	lux	lx
fl	foot-Lamberts	3.426	candela/m^2	cd/m^2
Force and Pressure or Stress				
lbf	pound-force	4.45	newtons	N
psi	pound-force per square inch	6.89	kilopascals	kPa

ACKNOWLEDGMENTS

A project of this magnitude could not have been accomplished alone. Scott Becker would first like to thank the late Dr. Stanley H. Anderson for his belief in my abilities to accomplish this task and for providing me the opportunity to study a fascinating critter, the moose. Scott Becker would also like to thank my three remaining committee members Dr. Fred Lindzey, Dr. Chuck Anderson, and Dr. Tom Thurow for stimulating discussions and for providing helpful edits to this final report. This project would not have been possible without the funding and support provided by the Teton County Conservation District, Wyoming Animal Damage Management Board, Wyoming Department of Transportation (WYDOT), Wyoming Game and Fish Department (WGFD), and the Wyoming Governor's Big Game License Coalition/Wildlife Heritage Foundation of Wyoming.

The success of this project was also due in large part to the contributions of many individuals from multiple agencies. Cody Beers, WYDOT public involvement specialist, and Michael Patritch, WYDOT research manager, provided needed data, guidance, assistance, and were always available to answer questions. Ryan Nielson and Hall Sawyer of Western Ecosystems Technology, Inc. for discussions and assistance with the habitat selection modeling procedures and for providing data used to validate the highway crossing model. Doug Brimeyer, Steve Kilpatrick, Sarah Dewey, Terry Kreeger, Andrea Barbknecht, and members of the WGFD Moose Working Group cannot be thanked enough for providing guidance, support, and field assistance. We would also like to thank the many WGFD, Bridger-Teton National Forest, and Grand Teton National Park employees who assisted with housing, moose captures, and flights during the course of this study. Finally, but certainly not least, we would like to thank our pilots – Gary Lust (retired) of Mountain Air Research, Dave (and Nora and Ashes) Savage of Savage Air Services, and Dave Stinson of Sky Aviation. Without your skills and abilities in the air, we would not have been able to accomplish half of what we set out to do.

EXECUTIVE SUMMARY

To accommodate rises in traffic volume and to address highway safety concerns, transportation managers often need to expand existing travel corridors which may result in an increased risk of wildlife-vehicle collisions. Wildlife-vehicle collisions are not random events and appear to be related to the daily and seasonal activity patterns of animals. By examining the spatial and temporal patterns of wildlife crossings, managers can apply appropriate mitigation to reduce collision risk and maintain highway safety. The U.S. Highway 26/287 reconstruction project provided an opportunity to examine the influence of habitat, landscape, and man-made features that determine moose crossing locations in northwest Wyoming. A previous model developed to assess moose winter habitat selection was used at a smaller spatial scale to determine if it could accurately identify moose crossing locations along a 9.7 km (6.0-mi) section of U.S. Highway 26/287 that bisects a high-density moose winter range in the Buffalo Fork Valley. We used an independent sample of moose crossing locations to validate the predictive highway crossing map. We also examined temporal patterns of moose crossings and the influence of fence types.

The predictive map indicated that areas classified as high or medium-high predicted probabilities of use occurred between mileposts 3.2-4.5, 6.1-6.7, and 7.0-9.0. These areas were characterized by a high proportion of aspen and riparian/deciduous shrub habitat with little coniferous cover, low elevation, relatively flat slope, and moderate distance to cover. Of the 201 moose crossings recorded from the independent sample, 81% (*n* = 162) occurred in high to medium-high probability of use areas. Moose used high-use areas more than expected, medium-high and medium-low use areas as expected, and low-use areas less than expected. Although we were unable to directly measure the use of the Buffalo Fork and Blackrock Creek bridges, mileposts on either side of these structures were classified as high-use areas which suggest a high likelihood that moose utilized these structures to cross U.S. Highway 26/287. Moose crossed the highway more than expected during afternoon to early evening and less than expected during mid-day. A high proportion of fencing occurred along private lands adjacent to the highway that were not preferred moose habitat, therefore, moose crossed the highway more than expected in areas that contained no fencing and less than expected in areas that contained fencing. Fencing along the highway was not constructed to prevent moose movements and preferred habitat and landscape features appeared to have more influence in determining crossing locations than the presence of fencing.

Because aggregations of moose crossings occurred at predictable locations and the risk of collisions were highest during periods of limited visibility, managers could reduce speed limits and erect temporary warning signs during winter in areas classified as high and medium-high predicted probabilities of use to warn motorists of the increased risk of encountering a moose on the highway. Due to the low number of moose-vehicle collisions during this study (*n* = 1), major and costly mitigation may not be justified in the Buffalo Fork Valley unless collisions increase following highway reconstruction. Lengthening existing bridges over rivers and streams may facilitate animal movements

under these structures. Moose are not the only animals that inhabit the Buffalo Fork Valley, thus, managers could develop mitigation to benefit multiple species while continuing to maintain motorist safety.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

PROBLEM DESCRIPTION

Rising human populations create an increasing need to expand transportation corridors to accommodate the concurrent rise in traffic volume. This can lead to sharp increases in the number of wildlife-vehicle collisions (McDonald 1991, Oosenbrug et al. 1991, Groot Bruinderink and Hazebroek 1996, Farrell and Tappe 2007). In the United States, Conover et al. (1995) estimated that approximately 726,000 deer (*Odocoileus* spp.)-vehicle collisions occurred in 1991 resulting in an estimated 211 human fatalities. In 1991, deer-vehicle collisions cost an estimated $1,500 (U.S.) per accident and human injuries occurred in approximately 4% of collisions (Conover et al. 1995). Because not all accidents are reported, the actual number of deer-vehicle collisions may be much higher (Conover et al. 1995). When collisions occur with larger animals (i.e., moose [*Alces alces*]), the risk of human injury and increased property damage rises significantly (Joyce and Mahoney 2001). Methods to reduce wildlife-vehicle collisions have had mixed results. Mitigation to reduce the number of collisions or prevent animals from entering the roadway (i.e., roadside clearing, fencing, overpasses and underpasses) appear to be the most effective, but maintenance and repair costs often limit their implementation (Bashore et al. 1985, Feldhammer et al. 1986).

Wildlife-vehicle collisions can rarely be associated with a single factor, but the spatial and temporal patterns of accidents are not random events and appear to be related to daily and seasonal activity patterns of animals (Bashore et al. 1985, Belant 1995, Waller and Servheen 2005). In addition, traffic volume, speed limits, driver awareness, and weather conditions have been implicated as influencing the risk of collisions (Lavsund and Sandegren 1991, Modafferi 1991, Joyce and Mahoney 2001, Seiler 2005). Numerous studies have used modeling approaches to identify habitat, landscape, and anthropogenic (i.e., man-made) features that predict high collision risk areas (Hubbard et al. 2000, Nielsen et al. 2003, Malo et al. 2004, Seiler 2005, Dussault et al. 2007). These models aid managers in determining where animal travel corridors occur and where appropriate mitigation can be applied so that collision risk is reduced and habitat linkages are maintained (Clevenger et al. 2002, Ng et al. 2004, Kindall and Van Manen 2007).

Most studies of wildlife-vehicle collisions examined habitat and landscape characteristics once the frequency of accidents became socially unacceptable. Many roads in North America bisect important seasonal ranges of ungulates where few collisions have recently occurred, but the importance of identifying areas of potential increased collision risk can be valuable in addressing possible problem locations before they become chronic. By examining spatial and temporal patterns of animal movements associated with a roadway, proactive engineering can be implemented into existing roadway design or incorporated into the design phase of proposed highway reconstruction projects to reduce the chances that wildlife-vehicle collisions will reach a socially unacceptable level (Groot Bruinderink and Hazebroek 1996, Finder et al. 1999). The U.S. Highway 26/287 reconstruction project from Moran Junction to Dubois, Wyoming (Young and Sawyer

2006) is an example where mitigation can be incorporated into the design phase. A portion of this highway bisects a high-density moose winter range in the Buffalo Fork Valley (Houston 1968, Brimeyer and Thomas 2004) in northwest Wyoming.

Core moose crossing areas have been identified by snow-track surveys in the Buffalo Fork section of the U.S. Highway 26/287 reconstruction project (Young and Sawyer 2006). However, the influence of habitat, landscape, and anthropogenic features in determining crossing locations has not been investigated. We used global positioning system (GPS) collars to collect fine scale movement data for adult (≥ 2 years) female moose that winter adjacent to U.S. Highway 26/287 in the Buffalo Fork Valley during winter 2005-2007. Using habitat and landscape variables that were deemed important predictors of winter habitat use, we developed a model to estimate habitat selection by adult female moose over the entire winter range (Chapter 2). We used this model at a smaller spatial scale to determine whether winter habitat selection patterns of moose could accurately identify crossing locations by moose along a 9.7-km (6.0-mi) section of U.S. Highway 26/287 that bisects winter range in the Buffalo Fork Valley. We also examined temporal patterns of moose crossing events and the influence of fence type in determining crossing locations.

CHAPTER 2

OBJECTIVES

The purpose of this study was to provide the Wyoming Department of Transportation (WYDOT) and the Wyoming Game and Fish Department (WGFD) with information that could be used to assess the importance of habitat, landscape, and anthropogenic features that are essential determinants in evaluating moose crossing locations in northwest Wyoming. The results will assist WYDOT in identifying, evaluating, and implementing highway designs and mitigation that improve safety to moose and motorists by reducing the risk of moose-vehicle collisions while maintaining highway permeability for moose. With an improved understanding of the spatial and temporal characteristics of moose crossings, a more efficient approach to mitigation can be applied to future highway redevelopment projects.

The primary objective of this study was to apply a model developed to estimate winter habitat selection by adult female moose to a 9.7-km (6.0-mi) stretch of U.S. Highway 26/287 in the Buffalo Fork Valley to determine if the model could be used to accurately identify crossing locations for a migratory moose population that winters adjacent to the highway. We also quantified the influence of fence types associated with moose crossing events and estimated the frequency and timing of crossings that occurred along U.S. Highway 26/287 and U.S. Highway 26/89/187 during the study period. To formally address the above objectives, we tested the following hypotheses: (1) moose crossing events are randomly distributed and occur in equal proportions throughout the day, (2) the location of moose crossings occur in equal proportion to the predicted probability of use (i.e., preferred habitat) within the highway study area, and (3) fence types are crossed in proportion to availability by moose.

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CHAPTER 3

TASK DESCRIPTION

Study Area

The study area was located about 50 km (30 mi) north of the town of Jackson, Wyoming and encompassed approximately 1,100 km^2 (425 mi^2; Chapter 2) of predominately public land in northwest Wyoming (Figure 1). It was defined by the winter distribution of GPS-collared adult female moose (Chapter 2) and included portions of Grand Teton National Park (GTNP) and Bridger-Teton National Forest (BTNF). Primary moose winter ranges occurred along the Buffalo Fork River, the Snake River, and Pacific Creek. Major roads within the study area included U.S. Highway 26/287, U.S. Highway 26/89/187, and U.S. Highway 89/287 (Figure 1). All were two-lane highways with speed limits ranging from 88 km/h (55 mi/h) in GTNP to 105 km/h (65 mi/h) outside of Park boundaries. From January 2005 to December 2007, mean daily traffic was estimated to be 952 vehicles/day along U.S. Highway 26/287 with a peak in traffic volume occurring during the tourist season from June through September (WYDOT 2006, 2007, 2008).

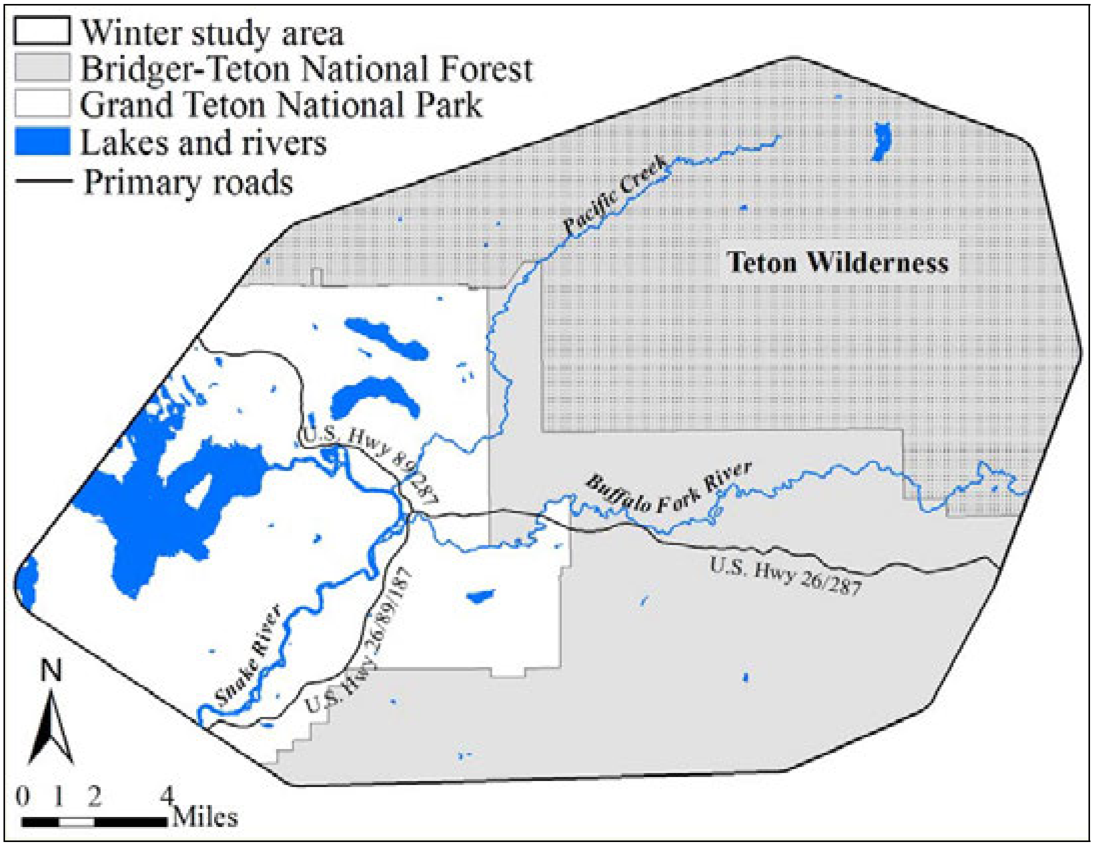

Figure 1. Study area in northwest Wyoming defined by the winter distribution of GPS-collared adult female moose ($n = 22$), 2005-2007.

Vegetation types occur along an elevational gradient (Whitlock 1993, Knight 1994) within the study area. Lower elevations and many south-facing slopes at higher elevations are dominated by big sagebrush (*Artemisia tridentata*). Mid-elevations are characterized by large stands of lodgepole pine (*Pinus contorta*) intermixed with Douglas fir (*Psuedotsugia menziesii*) and aspen (*Populus tremuloides*). Engelmann spruce (*Picea engalmanni*) and subalpine fir (*Abies lasiocarpa*) are found on north slopes and more mesic sites at lower elevations. Engelmann spruce, subalpine fir, and lodgepole pine intermixed with smaller stands of whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*), and aspen dominate higher elevations. Alpine tundra occurs at the highest elevations while open forest parks and subalpine meadows dominated by grasses and forbs (i.e., flowering plants) occur at all elevations. Riparian areas are dominated by willows (*Salix* spp.) intermixed with narrowleaf cottonwood (*Populus angustifolia*) and occur in large, flooplain environments at lower elevations and along nearly all streams within the study area (Wigglesworth and Wachob 2004).

The climate is characterized by short, cool summers and cold winters. From 1975-2004, annual precipitation averaged 56.2 cm (22.1 in; range = 37.9 cm [14.9 in] – 79.1 cm [31.1 in]; http://www.cdc.noaa.gov/cgi-bin/Timeseries/timeseries1.pl; accessed 16 October 2005), but most of the annual precipitation falls as snow between November and May. The Teton Mountains to the west and the northern highlands along the Yellowstone National Park (YNP) boundary typically receive the greatest amounts of precipitation (Houston 1968, Cole 1969, Boyce 1989).

Moose Captures and Data Management

Adult female moose were captured from a helicopter on winter range in the Buffalo Fork Valley of northwest Wyoming during February 2005 and 2006. Moose were darted and immobilized with 10-mg thiafentanil oxalate (A-3080, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA; McJames et al. 1994, Arnemo et al. 2003, Kreeger et al. 2005). Once handling was completed, thiafentanil was antagonized with an intramuscular injection of 300-mg naltrexone (Trexonil, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA). All captured moose were fitted with TGW-3700 GPS collars with store-on-board technology (Telonics, Mesa, Arizona, USA) that were programmed to attempt a location fix every hour from 15 November to 15 June and every 5 hours from 16 June to 14 November. Location data were collected until 1 March 2007 when the collars were programmed to release from the moose. Upon retrieval of GPS collars, location data were examined and all unsuccessful fixes and obvious location errors were removed (D'Eon et al. 2002, D'Eon and Serrouya 2005). Data were not corrected for fix-rate bias because of the high fix-rate success observed (Chapter 2; D'Eon 2003, Friar et al. 2004, Hebblewhite et al. 2007). Three-dimensional fixes accounted for a high proportion of winter locations (Chapter 2), therefore, data were not differentially corrected because 3-dimensional locations generally have < 20 m error (Di Orio et al. 2003). Captures were performed in accordance with approved University of Wyoming Animal Care and Use Committee protocols.

Frequency and Timing of Highway Crossing Events

To estimate the number of highway crossing events during winter within the study area, we mapped winter locations of moose from 2005 to 2007 in ArcMap 9.2 (Environmental Systems Research Institute, Redlands, California, USA) and used the HOME RANGE TOOLS extension for ArcGIS (Rodgers et al. 2007) to create movement paths for each individual. We determined that a crossing occurred when the straight line between 2 consecutive locations crossed either U.S. Highway 26/287 or U.S. Highway 26/89/187. We did not investigate crossings that occurred along U.S. Highway 89/287 between Moran Junction and YNP because of limited traffic volume due to seasonal road closures within GTNP.

Because winter locations were collected every hour, the timing of crossing events were estimated to have occurred within the time period between 2 consecutive locations. The timing of moose crossings were grouped into 4 distinct time periods to reflect when moose-vehicle collisions were most likely to occur. These time periods were 0300 – 0859 hrs (early to mid-morning), 0900 – 1459 hrs (mid-day), 1500 – 2059 hrs (afternoon to early evening), and 2100 – 0259 hrs (night). A chi-square test ($P \leq 0.05$) was used to determine if crossing events occurred at random during each time period throughout the day.

Predicting Moose Crossing Locations in the Buffalo Fork Valley

To create the highway study area, we used a hand-held GPS unit to mark the location of mileposts 3 through 9 and plotted these in ArcGIS. We digitized a 9.7-km (6.0-mi) stretch of U.S. Highway 26/287 from a U.S. Geological Survey 1:24,000 scale digital orthophoto quarter quadrangle map and divided each 1.6-km (1.0-mi) section into 10 equal segments that represented secondary mile markers to the nearest 0.16-km (0.1-mi). The highway study area was defined as that area within a 1.5-km (0.9-mi) buffer around the highway, which represented the average daily distance moved by radio-collared adult female moose during winter (Chapter 2).

The final population-level model developed to estimate adult female moose winter habitat selection included coefficients for the proportion of riparian/deciduous shrub, mixed/other conifer, and aspen habitats, elevation, habitat diversity, slope, and distance to coniferous cover (Chapter 2). To measure these variables, we created circular sample units with 25-m (82-ft) radii that were systematically distributed across the highway study area. We extracted vegetation data from each sample unit with HAWTHs ANALYSIS TOOLS (Beyer 2004) and calculated the proportion of each vegetation type that occurred within each unit. We used SPATIAL ANALYST to estimate slope from a 26 x 26-m digital elevation model (U.S. Geological Survey 1999) and to create a distance to cover layer from the existing vegetation map. Cover was defined strictly as coniferous habitats that could potentially provide thermal cover during winter. Estimates for elevation, slope, and distance to cover were extracted from the midpoint of each sample unit. We used 250-m (820-ft) radii circular units centered on the midpoint of each

sample unit to calculate a Shannon-Weiner habitat diversity index based on the proportion of spruce/fir, lodgepole pine, mixed/other conifer, aspen, riparian/deciduous shrub, and other habitat types that occurred within each circular sample unit.
We used the R statistical software package (R Core Development Team 2006) to estimate resource selection probability functions (RSPF; Manly et al. 2002) for each sample unit using population-level coefficients developed to assess winter habitat selection by adult female moose (Table 1; Chapter 2). The RSPF predictions were mapped across 50 x 50-m pixels for the highway study area. The RSPFs were assigned to 1 of 4 categories based on the quartiles of the distribution of predictions (Sawyer et al. 2006, Sawyer et al. 2007). Pixels were assigned values from 1 to 4 representing the highest to lowest estimated use probabilities in 25% increments (i.e., highest use probability = 1 [highest 25%], lowest use probability = 4 [lowest 25%]).

To determine the validity of the predictive map in delineating moose crossing locations in the highway study area, we used an independent sample of 201 crossing events collected during winter 2003-2004 and 2004-2005 that were recorded to the nearest 0.16-km (0.1-mi) marker (Young and Sawyer 2006). Since it was unknown exactly where the moose crossed the highway relative to the nearest mile marker, we created 80-m buffers around each 0.16-km (0.1-mi) marker and estimated an average RSPF class from all the predicted probability-of-use classes within each buffer. The 80-m buffer represented the mean probability-of-use for each mile marker given that a moose could have crossed anywhere within that buffer and still be classified as having crossed at the mile marker. Markers with mean RSPF classes from 1.00 to 1.50 were assigned to class 1 and were classified as high-use areas, markers with mean RSPF classes from 1.51 to 2.50 were assigned to class 2 and were classified as medium-high-use areas, markers with mean RSPF classes from 2.51 to 3.50 were assigned to class 3 and were classified as medium-low-use areas, and markers with classes from 3.51 to 4.00 were assigned to class 4 and were classified as low-use areas. We joined the RSPF class and the number of crossing events associated with each secondary mile marker from the independent sample and calculated the proportion of crossing events that occurred within each RSPF class. We estimated a chi-square statistic ($P \leq 0.05$) for each RSPF class to determine if moose selected highway crossings associated with preferred habitat.

Fence Types and Moose Crossings

To determine if fence type influenced moose movement across U.S. Highway 26/287 in the Buffalo Fork Valley, we created a GIS layer that depicted three different fence types that occurred within the highway study area: (1) bighorn fence, (2) four-strand, barbed wire fence, and (3) buck-and-rail fence. The bighorn fence was a two-pole, two-wire fence that stands approximately 1.1 m (43 in) in height (Figure 2). Sections of four-strand, barbed-wire fence were primarily located along stretches with permanent standing water. A small section of buck-and-rail fencing was located west of the GTNP boundary (Figure 3). No fencing occurred within GTNP, from the bridge over Blackrock Creek (milepost 8.45) to milepost 9 on the north side of the highway, and from mileposts 8 to 9 on the south side of the highway.

Because fence types differed on either side of the roadway in a number of locations, we examined the north and south side of the highway separately then combined both sides for analysis. We assumed that the straight line used to depict moose movements accurately reflected the fence type that was crossed by moose. Only those crossing events that occurred between mileposts 3 and 9 were used to assess the possible effects of fence type. We used a chi-square test ($P \leq 0.05$) to estimate if moose crossed fences in proportion to what was expected throughout the study area.

Table 1. Coefficients (β) and standard errors (SE) for a population-level winter habitat selection model developed from global-positioning system (GPS)-collared adult female moose in northwest Wyoming, 2005-2007.

	Winter		
Variable	β	SE	*P*
Intercept	11.204	3.775	0.007
Riparian	3.559	0.173	<0.001
Elevation (m)	-0.011	0.002	<0.001
Habitat diversity	0.856	0.143	<0.001
Slope (°)	0.105	0.034	0.005
Slope^2 (°)	-0.006	0.002	<0.001
Mixed conifer	-2.251	0.995	0.034
Dist. to cover (m)	-0.002	0.001	0.051
Aspen	0.590	0.384	0.139

Figure 2. Bighorn fence (view facing west). This was the primary type of fence found east of the Grand Teton National Park boundary within the highway study area.

Figure 3. Radio-collared adult female moose crossing buck-and-rail fencing. This type of fence was found west of the Buffalo Fork bridge and the Grand Teton National Park boundary in the highway study area.

CHAPTER 4

RESULTS

Frequency and Timing of Highway Crossing Events

Twenty-two adult female moose were monitored to estimate the frequency and timing of crossing events within the winter study area. A total of 257 crossing events were recorded with 19 moose crossing U.S. Highway 26/287 or U.S. Highway 26/89/187 at some point during the study period. Only 8 moose crossed the highway ≥ 10 times and these moose accounted for 84% of all crossing events (*n* = 217). Adult female moose crossed the highway more than expected during afternoon to early evening ($\chi^2 = 10.32$, df = 1, $P = 0.001$), less than expected during mid-day ($\chi^2 = 18.26$, df = 1, $P < 0.001$), and as expected during the night ($\chi^2 = 0.52$, df = 1, $P = 0.473$) and early to mid-morning ($\chi^2 = 0.12$, df = 1, $P = 0.732$; Table 2).

Table 2. Comparison of observed and expected moose highway crossings by time of day in the Buffalo Fork Valley, Wyoming, winter 2005-2007.

Time	Observed number of highway crossings	Expected number of highway crossings	χ^2	*P*	Observed/ expected[a]
Afternoon to early evening	90	64.25	10.32	0.001	>
Night	70	64.25	0.52	0.473	=
Early to mid-morning	67	64.25	0.12	0.732	=
Mid-day	30	64.25	18.26	<0.001	<

[a] ">": use greater than expected; "=": use equal to expected; "<": use less than expected.

Predicting Moose Crossing Locations in the Buffalo Fork Valley

The highway study area covered approximately 34 km^2 (13 mi^2; Figure 4) within the Buffalo Fork Valley moose winter range. Private land encompassed approximately 11 km^2 (4 mi^2) with the remaining area managed by GTNP and BTNF. The predictive map indicated that areas classified as high or medium-high probabilities of use occurred between mileposts 3.2 and 4.5, 6.1 and 6.7, and 7.0 and 9.0 (Figure 5). These areas were characterized by a high proportion of aspen and riparian/deciduous shrub habitat with little coniferous cover, low elevation, relatively flat slope, and moderate distance to cover. Private land used for cattle and horse grazing occurred between mile markers 4.5 and 6.1, while private land held in conservation easements occurred between mile markers 6.1 and 6.9. The predictive map indicated that moose were less likely to cross private land that was used for grazing, but were more likely to cross on private land that was held in a conservation easement (Figure 5). Mileposts that occurred on either side of the Buffalo Fork bridge and the Blackrock Creek bridge were each classified as high-use areas. This indicates a high likelihood that moose may have utilized bridges to cross U.S. Highway 26/287 because preferred habitat occurred on either side.

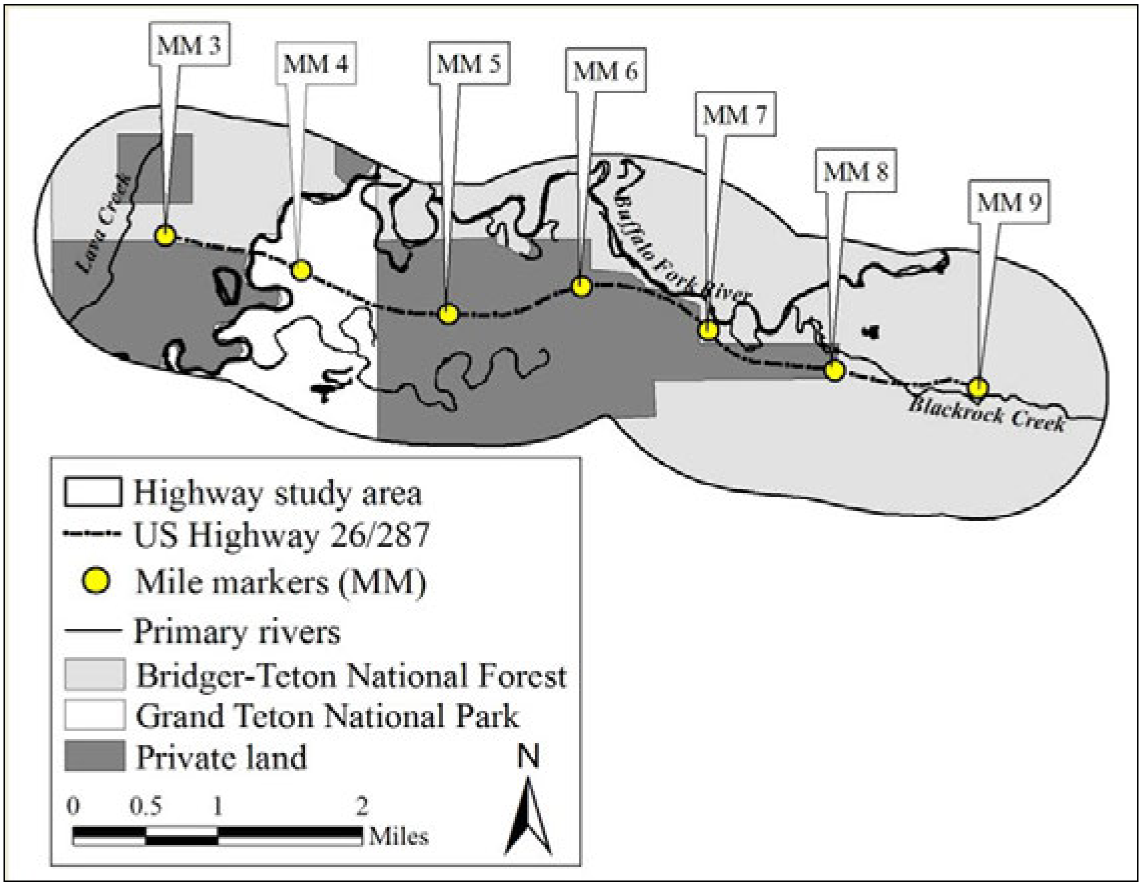

Figure 4. Highway study area in the Buffalo Fork Valley, Wyoming, used to measure habitat and landscape variables when creating a predictive map of winter habitat selection along a 9.7-km (6.0-mi) stretch U.S. Highway 26/287 during winter 2005-2007.

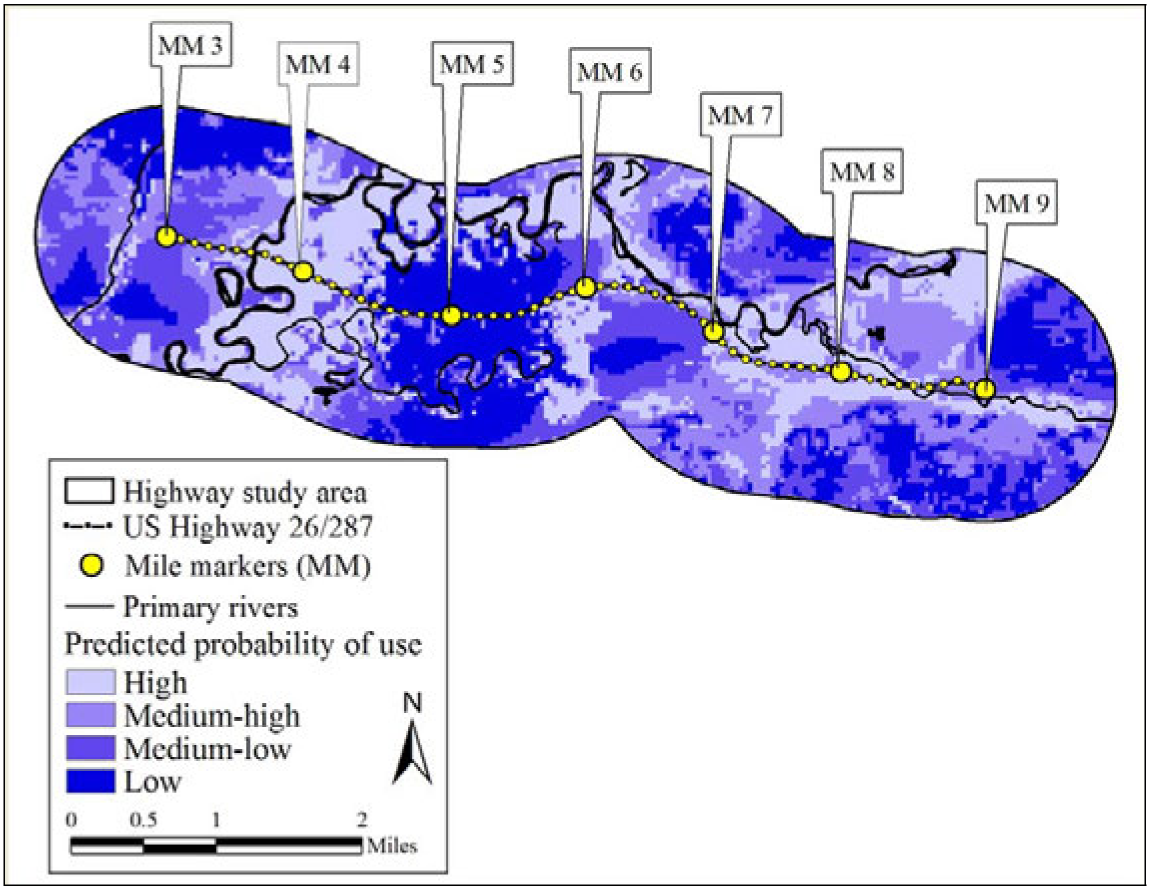

Figure 5. Relative predicted probabilities and associated categories (low = 0-25%, medium-low = 26-50%, medium-high = 51-75%, high = 76-100%) of habitat use for the highway study area developed from a model of winter habitat selection for adult female moose in northwest Wyoming during winter 2005-2007.

Of the 201 moose crossings recorded from the independent sample, the highest proportion of crossing events occurred in areas classified as high or medium-high predicted probabilities of use (81%, *n* = 162), while fewer crossings occurred in areas classified as medium-low or low predicted probabilities of use (19%, *n* = 39; Table 3). Moose crossed the highway in areas categorized as high-use areas more than expected (χ^2 = 6.92, df = 1, *P* = 0.009), as low-use areas less than expected (χ^2 = 5.40, df = 1, *P* = 0.020), and in proportion to what was expected in medium-high-use (χ^2 = 0.36, df = 1, *P* = 0.550) and medium-low-use (χ^2 = 3.64, df = 1, *P* = 0.056) areas (Table 3). Although areas classified as medium-low were used approximately as expected, the actual number of crossings (*n* = 22) were lower than the number of expected crossings (*n* = 33).

Table 3. Comparison of observed and expected moose highway crossings associated with the mean predicted probability of use for each 0.16-km (0.1-mi) mile marker along U.S. Highway 26/287 in the Buffalo Fork Valley, Wyoming, winter 2005-2007. The predicted probability of use was calculated by extracting RSPF class values from an 80-m buffer around each milemarker and averaging these values. Markers with mean RSPF classes from 1.00 to 1.50 were classified as high-use areas, markers with mean RSPF classes from 1.51 to 2.50 were classified as medium-high-use areas, markers with mean RSPF classes from 2.51 to 3.50 were classified as medium-low-use areas, and markers with classes from 3.51 to 4.00 were classified as low-use areas.

Predicted probability of use	Proportion of mile markers	Number highway crossings[a]	Proportion of highway crossings	χ^2	*P*	Observed/ expected[b]
High	0.23	64	0.32	6.921	0.009	>
Medium-high	0.46	98	0.49	0.357	0.550	=
Medium-low	0.16	22	0.11	3.639	0.056	=
Low	0.15	17	0.08	5.401	0.020	<
Total	1.00	201	1.00			

[a] Data from an independent sample collected during winter 2003-2005 (Young and Sawyer 2006).

[b] “>”: use greater than expected; “=”: use equal to expected; “<”: use less than expected.

Fence Types and Moose Crossings

Along the 9.7-km (6.0-mi) stretch of U.S. Highway 26/287, there was approximately 6.4 km (4.0 mi) of fencing on the north and the south side of the highway for a total of 12.9 km (8.0 mi). About 6.6 km (4.1 mi) of highway was fence free with most occurring within GTNP and east of Blackrock Creek. One section of barbed-wire fence that was less than 0.16 km (0.1 mi) in length was assumed to be bighorn fence in this analysis. Bighorn fence was the primary fence type within the study area while buck-and-rail fence and barbed-wire fence each occurred along equal proportions of highway (Table 4).

A total of 311 fence crossings were recorded with 19 of 22 moose crossing fences along U.S. Highway 26/287 at some point during the study period. Only 9 moose crossed fences ≥ 10 times and these accounted for 87% of all crossing events ($n = 269$). Adult female moose crossed sections of highway that contained no fencing more than expected ($\chi^2 = 41.55$, df = 1, $P < 0.001$) and crossed less than expected along sections with bighorn ($\chi^2 = 11.47$, df = 1, $P < 0.001$), buck-and-rail ($\chi^2 = 5.87$, df = 1, $P = 0.004$), and barbed-wire ($\chi^2 = 8.33$, df = 1, $P = 0.015$) fence types (Table 4).

Table 4. Comparison of observed and expected moose highway crossings by fence type crossed in the Buffalo Fork Valley, Wyoming, winter 2005-2007. The number of fence crossings were calculated for the north and south side of U.S. Highway 26/287 separately and then combined to estimate significance.

Fence type	Proportion fence type	Number of fence crossings	Proportion fence crossings	χ^2	*P*	Observed/ expected[a]
No fencing	0.34	171	0.55	41.548	<0.001	>
Bighorn	0.56	129	0.41	11.477	<0.001	<
Buck and rail	0.05	6	0.02	5.865	0.015	<
Barbed wire	0.05	5	0.02	8.330	0.004	<
Total	1.00	311	1.00			

[a] ">": use greater than expected; "<": use less than expected.

CHAPTER 5

DISCUSSION AND RECOMMENDATIONS

Discussion

This study demonstrated that models developed to assess adult female moose winter habitat selection can be used to identify areas where moose are most likely to cross U.S. Highway 26/287 in the Buffalo Fork Valley. Moose crossing events were not randomly distributed along the highway. Aggregations of moose crossings occurred at locations that could be predicted by examining winter habitat selection parameters. Similarly, the number of grizzly bear (*Ursus arctos*) highway crossings in Alaska (Graves et al. 2006) and Montana (Waller and Servheen 2005) were clustered at specific locations while most wildlife-vehicle collisions typically occur along a relatively small proportion of the roadway (Bashore et al. 1985, Joyce and Mahoney 2001, Malo et al. 2004, Seiler 2005). The spatial aggregation of crossings may increase the risk of collisions between motorists and moose in areas identified as high or medium-high predicted probabilities of use. Mitigation that may potentially increase highway safety for motorists, as well as maintain highway permeability for moose, can be applied to sections of highway where crossing locations are most likely to occur.

Moose crossings were aggregated in areas where preferred habitat and landscape features occurred on either side of the highway. In northwest Wyoming, adult female moose selected for low-elevation habitats during winter that contain an abundance of forage provided by aspen and willow-dominated, riparian habitats (Chapter 2). Other studies have noted the importance of preferred habitat and landscape features in predicting crossing locations and collision risk for moose (Gundersen et al. 1998, Seiler 2005), elk (*Cervus elaphus*; Dodd et al. 2007), white-tailed deer (*Odocoileus virginianus*; Carbaugh et al. 1975, Feldhammer et al. 1986, Finder et al. 1999, Hubbard et al. 2000), and black bear (*Ursus americanus*; Clevenger et al. 2002, Kindall and Van Manen 2007). Dussault et al. (2007) indicated that the proportion of forage was greatest where moose crossed roads in Quebec, Canada, yet moose selected crossing locations that provided abundant cover rather than food resources. However, snow accumulations during their study were some of the highest in the world (Dussault et al. 2007) and it has been well documented that, when the availability of forage decreases and the energetic cost of locomotion increases due to increased snow depths, moose generally seek cover provided by mature coniferous forests (Matchett 1985, Hundertmark et al. 1990, MacCracken et al. 1997, Stephenson et al. 2006). In northern Sweden, snow depth influenced the availability of food which in turn influenced the peak in moose-vehicle collisions during winter (Lavsund and Sandegren 1991). In Norway and Alaska, a similar trend was observed concerning moose-train collisions (Modafferi 1991, Andreassen et al. 2005). In the Buffalo Fork Valley, snow accumulations may not have been severe enough to cause a shift in use to closed canopy coniferous forests. Additionally, the Buffalo Fork Valley provided abundant winter forage and moose may have utilized tracks of other individuals to reduce the cost of locomotion in deep snow (Ball et al. 2001), thus crossing locations may be consistent among years even with varied degrees of winter severity. Nonetheless, in years of deep snow, increased monitoring of moose crossing locations may be warranted to determine if there is a shift in preferred habitat and, consequently, highway crossing locations.

Although moose crossings typically occurred in low elevation areas that contained a high proportion of aspen and riparian habitats, moose selected for areas with high habitat diversity. This suggests that moose require a mix of riparian, aspen, and coniferous habitats to meet forage and cover requirements and that the distribution of all habitat types across the landscape likely influenced the probability that a crossing event occurred in a specific location. Private lands used for grazing adjacent to the highway were composed primarily of herbaceous cover and contained little habitat diversity or preferred forage, thus very few moose crossings occurred in these areas. In contrast, private lands held in conservation easements were composed of a mix of riparian and coniferous habitats and, not surprisingly, moose use and crossing events associated with these areas were relatively high. Areas of high habitat diversity have also been implicated with the increased risk of vehicle collisions for white-tailed deer in Illinois (Finder et al. 1999), Iowa (Hubbard et al. 2000), and Minnesota (Nielsen et al. 2003) and roe deer (*Capriolus capriolus*), wild boar (*Sus scrofa*), and red deer (*Cervus elaphus*) in Spain (Malo et al. 2004). However, in areas where preferred habitat is common and habitat diversity is relatively low, highway crossings, and thus wildlife-vehicle collisions, were more randomly distributed (Allen and McCullough 1976, Bashore et al. 1985, Feldhammer et al. 1986).

Bridges over the Buffalo Fork River and Blackrock Creek were both identified as having a high probability of use suggesting that moose may utilize these structures to cross beneath the highway. Young and Sawyer (2006) documented and photographed several moose crossing the highway underneath these structures. Bridges may facilitate wildlife crossings which could ultimately reduce the risk of wildlife-vehicle collisions along short sections of highway near these structures (Seiler 2004, Seiler 2005). However, Hubbard et al. (2000) indicated that bridges acted as "major edge-creating landscape features" that increased the risk of collisions with white-tailed deer in Iowa. Furthermore, low to intermittent traffic volume caused a reduction in passage rates for elk using wildlife underpasses in Arizona that was possibly caused by the sudden auditory and visual stimuli created by a vehicle crossing over the underpass during an otherwise quiet period (Gagnon et al. 2007*a*). Even though moose relocations were obtained every hour during the winter period, this location frequency was insufficient to confirm whether or not a moose actually used bridges to cross the highway. All that could be determined is that habitat and landscape features on either side of the bridges were classified as high use areas and the probability that a moose used these habitats, and thus the bridges, was also high.

Moose crossed the highway more frequently in areas that were not fenced when compared to areas that contained any of the three other fence types. Although fences within the Buffalo Fork Valley were not designed to prevent moose from crossing the highway, these results concur with those of Seiler (2005) who described the risk of moose-vehicle collisions being greatest along sections of road that did not contain moose-proof fencing. Furthermore, in South Africa, the ratio of total accidents to animal-related accidents was significantly less along sections of highway that had a higher proportion of fencing (Eloff and Van Niekerk 2005). In contrast, fencing along an interstate highway in Pennsylvania reduced the number of deer observed in the right-of-way, but it did little to reduce the number of deer-vehicle collisions (Feldhammer et al. 1986). We suggest that preferred habitat and landscape features had much more influence in determining moose crossing locations given that the fence-types present in the Buffalo Fork Valley were not high enough to prevent moose crossings. The predictive map indicated that the unfenced section of highway, located within GTNP, contained a high proportion of preferred habitat on either side of the roadway. Likewise, from mile marker 7 to approximately 8.5 (i.e., Blackrock Creek), preferred habitat can be found on both sides of the highway even though the majority of this area primarily contains bighorn fence. Approximately 8.1 km (5.0 mi) of fence, nearly two-thirds of the total length of fencing along the highway, was along private land that was not preferred moose winter habitat. Thus, the likelihood that a moose would cross a fence in these areas was significantly reduced due to habitat features rather than fence presence. Lack of fence structures in areas of quality moose habitat may have inhibited our assessment of the influence of fence type on moose movements associated with U.S. Highway 26/287.

Approximately 88% of all moose crossing events in the Buffalo Fork Valley occurred from afternoon to mid-morning (i.e., 1500 – 0859 hours), which coincided with peaks in daily moose activity patterns (Renecker 1986). Light conditions during these time periods are relatively poor or non-existent which can increase the risk of moose-vehicle collisions. In Newfoundland, approximately 75% of all moose-vehicle collisions were observed between sunset and sunrise while severe injuries or death to motorists were twice as likely to occur after dark (Joyce and Mahoney 2001). Similarly, other studies have demonstrated that highway crossings and the potential of collisions increased significantly from dusk to dawn for ungulates (Carbaugh et al. 1975, Belant 1995, Groot Bruinderink and Hazebroek 1996) and grizzly bears (Waller and Servheen 2005, Graves et al. 2006). In contrast, caribou (*Rangifer tarandus*) were observed to cross roads more frequently during the day (Dyer et al. 2002), which may minimize collision-risk due to increased motorist visibility.

Concurrent with increased highway crossings during evening and early morning hours is a reduction in traffic volume during these time periods. Grizzly bears have been observed to cross more frequently at night when traffic volume was low (Waller and Servheen 2005, Graves et al. 2006). Elk shifted use away from highways during the day when traffic volume was high and returned to areas near the highway at night when traffic volumes decreased (Gagnon et al. 2007*b*). Furthermore, research along the Trans-Canada Highway in Banff National Park, Canada, has shown reduced permeability of the highway for all wildlife due to very high traffic volume (Alexander and Waters 2000, Alexander et al. 2005). Increased traffic volume has also been implicated in preventing bighorn sheep (*Ovis canadensis*) from reaching important mineral sites in Rocky Mountain National Park, Colorado (Keller and Bender 2007) and with an increased risk of deer-vehicle collisions in Arkansas (Farrell and Tappe 2007). Although traffic volume was not analyzed within the context of moose crossing probabilities in our study, when compared to other studies, the relatively low number of vehicles on U.S. Highway 26/287 during winter does not appear to impede moose movements across the road at the present time. However, the risk of moose-vehicle collisions is likely increased at night due to reduced motorist visibility and a concurrent increase in moose crossing events.

Recommendations

Application of the winter habitat selection model developed for moose in northwest Wyoming should be used with caution if applied to other sections of highway in the state. The model worked well to identify areas along U.S. Highway 26/287 that have a high risk of moose-vehicle collisions, but the model may not work well if habitats available to moose differ from those found in the Buffalo Fork Valley. If the model is to be used in other areas, it should be tested using an independent sample of crossing locations for validation prior to making assumptions concerning potential mitigation. Snow-track surveys, similar to those conducted by Western Ecosystems Technology, Inc. (Young and Sawyer 2006), would work well in determining the efficacy of the model for other locations. If this is done and model performance is not satisfactory, the results of the snow-track survey may be used because areas identified as core moose crossing locations in the Buffalo Fork Valley by Young and Sawyer (2006) were basically the same as those identified in the present study. However, if a more complete understanding of habitat, landscape, and anthropogenic features used by moose to select highway crossings is needed, a new study utilizing GPS technology may be warranted if the risk of moose-vehicle collisions is high.

Although numerous moose crossing events were observed in the Buffalo Fork Valley, only one moose-vehicle collision was recorded during the study. This occurred near milepost 7.4 which was classified as a high probability of use area. The collision occurred on 12 June 2005 and involved an uncollared, adult female moose that died as a result of the accident. While some accidents may go unreported, moose-vehicle collisions are relatively rare events in the Buffalo Fork Valley with only 5 collisions reported from 1995 to 2004 (Young and Sawyer 2006). All radio-collared moose that wintered in the Buffalo Valley were migratory and most summered at higher elevations to the north (Chapter 2). Thus, the greatest risk of collisions occurred during winter when traffic volume was much lower than during summer.

Within the Buffalo Fork Valley, speed limits could be reduced and seasonal use of large, temporary warning signs with flashing lights could be erected in areas classified as high or medium-high predicted probabilities of use during winter to warn motorists of the increased risk of encountering moose on the highway (Groot Bruinderink and Hazebroek 1996, Gordon et al. 2004, Sullivan et al. 2004). Speed limits have been identified as an important determinant in the number and severity of moose-vehicle collisions, especially during night when motorist visibility is reduced (Joyce and Mahoney 2001, Seiler 2004, Seiler 2005), but they have also been difficult to enforce (Lavsund and Sandegren 1991, Joyce and Mahoney 2001). Since local residents primarily drive the road during winter, a public awareness program could be implemented to educate people about the risk of moose-vehicle collisions (Joyce and Mahoney 2001) if traffic volume increases and the number of moose-vehicle accidents concurrently rise following highway reconstruction. The message could be conveyed to the public by hosting informational workshops or conducting essay or poster contests at local schools (Del Frate and Spraker 1991). Bumper stickers and information packets describing moose and their behavior could also be distributed to local residents and offered to patrons at gas stations and shops throughout the area. Many tourists come to northwest Wyoming to observe moose, so the packets could also be used to show areas where they are most likely to see moose. Public service announcements could be broadcast over the radio to inform motorists of areas where the risk of collisions is highest (Del Frate and Spraker 1991).

Major and costly mitigation may not be justified in the Buffalo Fork Valley at the present time unless moose-vehicle collisions increase following highway reconstruction. Vegetation removal along the highway right-of-way to increase motorist visibility may be the most easily-applicable and socially-acceptable form of large-scale mitigation (Jaren et al. 1991, Gundersen et al. 1998, Rea 2003, Andreassen et al. 2005). However, this type of mitigation must be maintained routinely because of moose preference for early seral vegetation (Loranger et al. 1991, Peek 1997). Moose-proof fencing has proven effective, but may only be justified in areas where traffic volume is high due to the high costs associated with construction and maintenance (Lavsund and Sandegren 1991, McDonald 1991, Groot Bruinderink and Hazebroek 1996). Caution must be used though because dependent upon where fences terminate, new high-collision-risk areas may be created due to animal movements along fence lines. In extreme cases, electric fencing has proven effective in reducing moose-vehicle collisions (Leblond et al. 2007). When used in conjunction with fencing to funnel animals to areas where they are most likely to cross a highway (Ng et al. 2004), the use of overpasses and underpasses that facilitate animal movements has also proven successful (McDonald 1991, Foster and Humphrey 1995, Clevenger and Waltho 2005, Gagnon et al. 2007*a*). Crossing structures that greatly improved rates of passage for large animals are high, wide, and short in length (Clevenger and Waltho 2005) and provide suitable habitat at the crossing points (Ng et al. 2004). Similar to the expansion of the Buffalo Fork Bridge in 2007, lengthening of existing bridges over rivers and streams that act as natural travel corridors may be a cheaper way of facilitating animal movements across the highway rather than erecting costly underpasses and overpasses at important crossing locations (Hubbard et al. 2000, Ng et al. 2004, Sawyer and Rudd 2005, Seiler 2005).

Moose are not the only animals that inhabit the Buffalo Fork Valley or cross U.S. Highway 26/287. A suite of large and small carnivores, ungulates, and small rodents have also been documented to cross the highway (Young and Sawyer 2006). Hence, potential crossing aggregations should be identified for all wildlife that may cross the highway and mitigation that benefits multiple species should be employed (Sawyer and Rudd 2005). For example, within the Buffalo Fork section of U.S. Highway 26/287, core elk crossing areas were similar to those identified for moose (Young and Sawyer 2006). Thus, mitigation to prevent moose-vehicle collisions will also assist in preventing elk-vehicle collisions in the Buffalo Fork Valley. Mitigation for multiple species will certainly increase the difficulty in planning appropriate, and potentially expensive, mitigation, but it will ultimately benefit motorists by increasing highway safety and wildlife by maintaining habitat linkages (Ng et al. 2004).

Numerous studies have demonstrated the effects of transportation corridors on wildlife, but some animals appear to have a higher tolerance of traffic than others. Alexander et al. (2005) noted that highway permeability was much lower for large carnivores than ungulates along the Trans-Canada Highway in Banff National Park, Canada. They indicated that 300-500 vehicles/day decreased highway permeability for large carnivores whereas ungulates demonstrated a higher tolerance to increased traffic volume. They also suggested that mitigation should be implemented at the threshold for carnivores to maintain habitat linkages and reduce habitat fragmentation for all wildlife (Alexander et al. 2005). Carnivores may be impacted by current traffic volume along U.S. Highway 26/287 during all seasons while ungulates may be affected during the summer months. Coordination with state and federal land and wildlife management agencies should continue after highway reconstruction so the impacts of the traffic corridor on wildlife can be determined and appropriate mitigation can be implemented to maintain motorist safety and highway permeability for wildlife.

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