SEASONAL DISTRIBUTION, WINTER HABITAT SELECTION AND WILLOW UTILIZATION PATTERNS OF THE SHIRAS MOOSE ON THE MOUNT HAGGIN WILDLIFE MANAGEMENT AREA

by

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ABSTRACT

Moose populations are difficult to manage as moose exist at low population densities compared to other ungulates and may use a variety of habitat types. Local knowledge is needed to effectively manage moose populations and limited research has been conducted recently in Montana. This study took place on the Mount Haggin Wildlife Management Area (MHWMA) in southwestern Montana to assist with the management of moose throughout southwestern Montana and establish a baseline for future research. The objectives of this study were to describe seasonal distribution patterns and habitat selection by adult cow moose, with an emphasis on habitat selection during the winter season, and to quantify patterns in willow browse utilization by moose in winter. To accomplish these objectives, I used data from GPS collars on cow moose to determine the basic habitat use patterns and covariates associated with winter habitat selection. Browse surveys of willow were employed to quantify browse utilization on the study area and to determine which environmental covariates were associated with moose browse utilization in winter. Cow moose on the study area were non-migratory and had small winter and summer home ranges. Moose strongly selected for willow cover types and habitat selection was associated with cover type, distance to conifer, distance to willow, and elevation; these relationships changed when snowpack conditions varied. Current browse utilization was low (~10%) and was associated with previously browsed willow, preferred willow species, and willow community width. Based on the habitat selection analysis, both willow and conifer communities were important to cow moose in winter and these results have management implications for habitat conservation and aerial survey methods. The browse utilization analysis showed that browse was notably heterogeneous and would require a large effort to sample browse utilization accurately. However, browse patterns were associated with habitat covariates and habitat managers should take these covariates into account when placing sites for monitoring of willow browse utilization. Overall, the moose population and willow communities around MHWMA appear to be in good health, but threats from climate change, predation, and the potential for overharvest may create population management challenges in the future.

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CHAPTER 1

INTRODUCTION TO THESIS

Introduction

Management of moose (*Alces alces*) is a challenging enterprise in most habitats throughout its global distribution, including Montana. Moose exist at low population densities and are often solitary in nature, which increases the variability in population trend estimates from various survey protocols (Timmerman and Buss 2007). Furthermore, moose have a low recruitment rate compared to many other managed species (e.g. deer, bobcats, grouse), meaning harvest has to be conservatively applied to maintain a sustainable harvest and stable populations (Timmerman and Buss 2007). Management strategies also have to account for local population dynamics, habitat use patterns, changes in habitat quality and quantity, and high or increasing predation pressure in some locations where native predator populations are expanding. Previous studies of moose ecology in Montana and elsewhere have contributed important insights to guide management strategies and have also identified gaps in our knowledge. Current research is improving our understanding of moose ecology, as well as addressing management challenges and questions that have recently emerged (Crichton et al. 2007) and will hopefully improve the management of moose populations.

Despite being confined to the forests and boreal habitat in the holarctic ecoregion (Franzmann 1981), moose are considered highly adaptive “selective generalists” in terms of habitat use (Peek 2007) and foraging choices (Renecker and Schwartz 2007), meaning

that moose ecology is specialized at a local scale, but globally diverse. As such, moose ecology and population dynamics can be quite variable from population to population (Peek 2007, Ballard and Van Ballenberghe 2007). While insights gained elsewhere have some value to the management of moose in Montana, local knowledge on the subspecies of moose present in Montana (*Alces alces shirasi*, Hundertmark and Bowyer 2004) is most applicable to the management of local populations (Timmermann and Buss 2007).

Moose were initially studied in Montana by McDowell and Moy (1942) and then intensively studied from 1959 to 1973 (Knowlton 1960, Peek 1961, Peek 1962, Smith 1962, Jonkel 1963, Peek 1963, Stevens 1965, Stevens 1966, Stevens 1967, Dorn 1968, Schladweiler 1969, Schladweiler and Stevens 1969, Dorn 1969, Dorn 1970, Schladweiler 1970, Stevens 1970, Stone 1971, Schladweiler 1972, Schladweiler and Stevens 1973a, Schladweiler and Stevens 1973b, Schladweiler 1974, Stevens 1974). These research studies contributed to the foundation for today's management strategies and focused on basic habitat relationships, browse habits, reproduction, and population dynamics of Shiras moose in Montana. From 1973 to 2008, several additional projects were completed, almost exclusively by graduate students (Jenkins 1985, Matchett 1985, Costain 1989, Costain and Matchett 1992, Langley 1993, Langley and Pletscher 1994, Van Dyke 1995, Van Dyke et al. 1995a, Van Dyke et al. 1995b, Tyers 2003, Tyers 2006, O'Reilly 2008). These latter studies had an emphasis on predator/prey interactions, timber management, and the relationship of winter ecology and browse by moose. Overall, these studies have shown that even within the limited distribution of moose in Montana, moose ecology varies greatly and moose exhibit a wide range of strategies

when interacting with their environment, including unique winter habitat use and browse consumption preferences, seasonal use and migration patterns, and responses to habitat disturbance.

The body of knowledge gained from these studies illustrates the diverse ecology of moose in Montana, but also shows how little we know about the local ecology of moose populations in southwestern Montana. While we do have limited knowledge of population demographics and trend from winter aerial surveys in southwestern Montana, little else is known. Knowledge of seasonal use and migration movements (or lack thereof) would be useful for hunting season management, as well as knowledge of current demographic parameters and the impact of predation on moose populations. Moose management could be greatly improved by increasing the effectiveness of aerial surveys to monitor population trend. Understanding the impacts of anthropogenic effects on moose populations (e.g. recreation, habitat loss, climate change) may become increasingly important as humans expand their influence on wildlands and wildlife. Knowledge of critical winter habitat, especially the temporal and spatial use patterns of communities containing key browse species, such as willow, will greatly aid habitat management and conservation. This is especially important in southwestern Montana where extensive willow communities support large moose populations and numerous other species. Knowledge of calving habitat attributes may also play an important role in sustaining moose populations. Investigating any of these topics would help biologists better understand moose population and habitat use dynamics and choose the most appropriate approaches to manage moose populations and their habitats at a local level.

In this study I have addressed some of these management challenges and questions in the Upper Big Hole River Valley, with an emphasis on the impacts of moose browsing on willow communities on the Mount Haggin Wildlife Management Area. Specifically, the objectives of this study were: 1) to describe seasonal distribution patterns and habitat selection by adult cow moose, especially during the winter season and 2) to quantify and investigate patterns in willow browse utilization by moose in winter. For the first objective (Chapter 2), I have described general distribution patterns (winter and non-winter ranges, migration timing, individual home ranges) and tested hypotheses posed in other research to explain the relationship between habitat attributes and winter habitat selection. After examining the findings, I have suggested habitat conservation strategies on moose winter range and improvements to winter aerial survey methods. For the second objective (Chapter 3), I used large-scale, systematic browse surveys to estimate browse utilization on the study area and then tested hypotheses regarding associations between habitat attributes and browse utilization. I used these results to examine the limitations of and potential improvements to browse monitoring methods. The results of these chapters are compared in Chapter 4, along with the overall conservation and management implications and potential directions for future research.

Study Area

The study site was located in southwestern Montana (45° 57’ N, 113° 4’ W), approximately 30 km west of Butte, MT and encompassed the southwest half of the 23,548 hectare Mount Haggin Wildlife Management Area (MHWMA) (Figure 1.1).

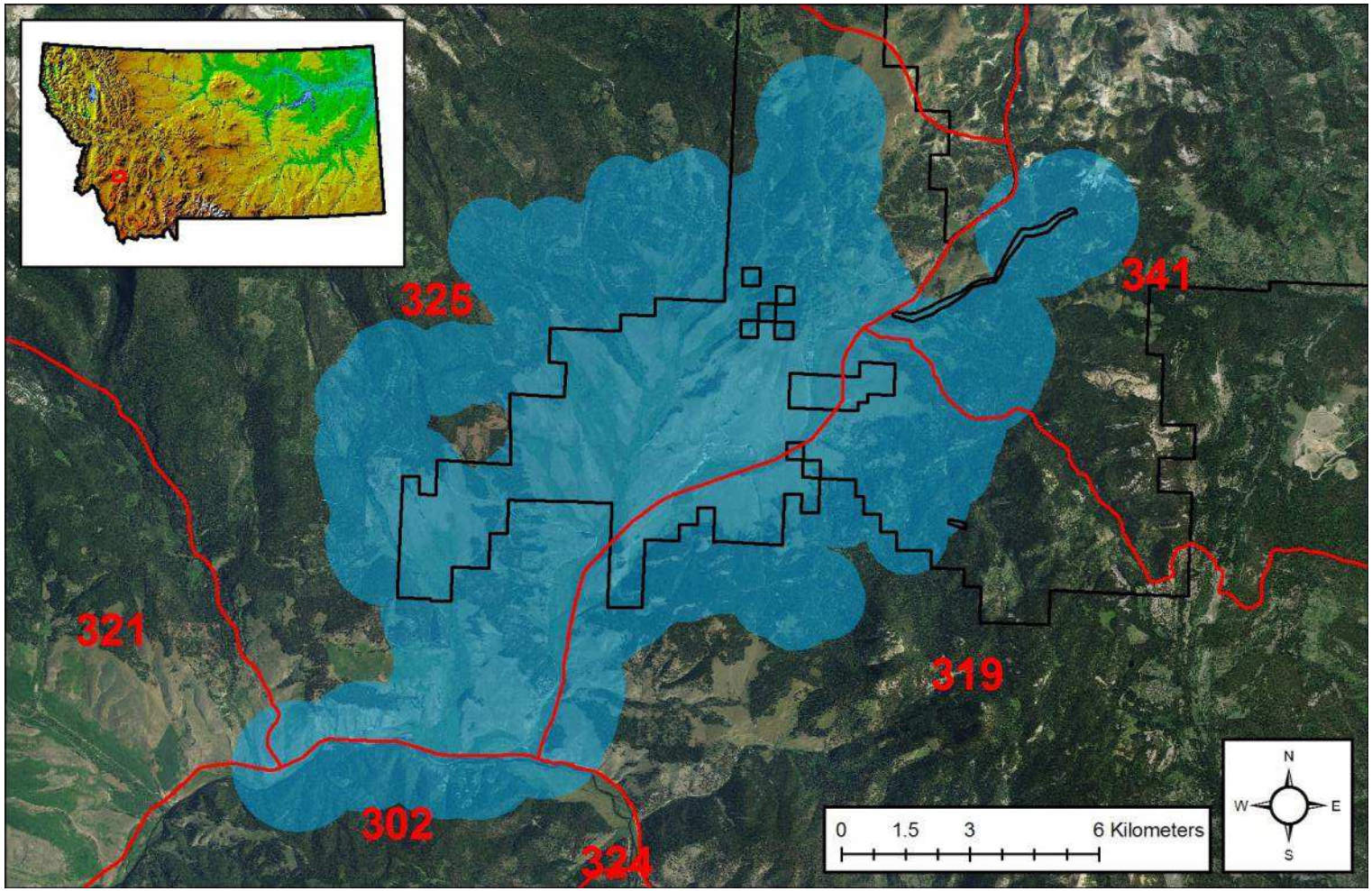

Figure 1.1: A map of the study area on the Mount Haggin Wildlife Management Area (outlined in black) in southwestern Montana. The boundaries of the moose hunting districts overlapping the MHWMA are noted in red and labeled. The transparent blue polygon indicates the winter study area, as calculated in Chapter 2. The background is NAIP aerial imagery (2009). The location of the MHWMA in Montana is indicated with a red rectangle.

The MHWMA straddles the Continental Divide, with streams that flow into the Big Hole and Clark Fork river drainages. The study site was limited to the Big Hole River side of the Divide. Elevation on the study area ranged from 1750 to 2250 meters and the topography varied from rolling hills and flats with meandering streams to steeper slopes at the bases of high mountains (+3200m). Based on climate data from the nearby community of Wisdom, MT for the years 1970-2000 (NOAA, 2004), the mean annual temperature was 1.6°C, with mean daily average temperatures of -10°C and 14°C in January and July, respectively. These mean daily average temperatures were consistent with measurements at the Calvert Creek SNOTEL site (about 10 km west of the study area) of -7°C and 14.5°C in January and July (1992-2010). The average annual precipitation was 48cm at the Calvert Creek SNOTEL site (1980-2010), which was close to the "about 20 inches" (51cm) reported by Frisina and Keigley (2004) for the MHWMA. At the Calvert Creek SNOTEL site (1965 meters in elevation), the mean snow depth in February was 68cm (2004-2011, only years for which snow depth was available). Measurements from this site were used as a surrogate for changes in snowpack condition in this study, although it may have slightly higher amounts of SWE (snow water equivalent) and snow depth compared to the lower elevations on the study area, which were as low as 1750 meters. Additionally, extensive drifting on the study site created notable heterogeneity in snowpack conditions where conifer cover was absent, including within the willow communities across the study area. Snow typically began to accumulate in early or mid-November and was mostly melted by late April or early May (SNOTEL 2011).

Vegetation on the study area included riparian willow bottoms, sagebrush grasslands, pine/fir forests, dry meadows, and nearly barren talus slopes. Riparian willow communities were of particular importance due to heavy moose use in the winter season (noted prior to the initiation of this study). These willow communities were largely represented by six species: Geyer willow (*Salix geyeriana*), Lemmon's willow (*S. lemmonii*), Booth's willow (*S. boothii*), Drummond's willow (*S. drumondiana*), planeleaf willow (*S. planifolia*), and Wolf's willow (*S. wolfii*). Two other willow species, Bebb willow (*S. bebbiana*) and sandbar willow (*S. exigua*), and red-osier dogwood (*Cornus sericea*) were very sparsely distributed and occurred at lower elevations. Other shrubs present in the riparian communities on the MHWMA that may be of importance to moose included snowberry (*Symphoricarpos albus*) and bog birch (*Betula pumila*). The willow communities were actively suppressed for decades while a private livestock operation owned much of the land currently managed as the MHWMA (Keigley et al. 2003). Willow suppression ceased when the state acquired the land in 1976 (Keigley et al. 2003). Under the administration of Montana Fish, Wildlife and Parks, a rest-rotation system for cattle grazing was implemented in 1984 and resulted in a greatly improved condition of upland, riparian, and meadow communities by 1990 (Frisina and Keigley 2004). Willow communities continued to recover and expand under the rest-rotation grazing system in place during this study (MTFWP, unpublished data).

The forest community on the study area was dominated by lodgepole pine (*Pinus contorta*) at lower elevations, with patches of quaking aspen (*Populus tremuloides*) on the edges of conifer stands, and occasional Douglas fir (*Psuedotsuga menziesii*) and

Engelmann spruce (*Picea engelmannii*) stands in more mesic habitats. Scouler's willow (*Salix scouleriana*) and thinleaf alder (*Alnus incana*) were also present in very limited quantities within these lower elevation forest communities. At higher elevations, stands of whitebark pine (*Pinus albicaulis*), Engelmann spruce, and subalpine fir (*Abies lasiocarpa*) became dominant. These species were also occasionally found in conifer riparian areas at lower elevations. Groves of alpine larch (*Larix lyallii*) were found at tree line and in avalanche chutes, occupying more extreme niches. These latter high elevation species primarily existed in communities found outside of the MHWMA and typical moose winter range, while lodgepole/aspen/Douglas fir forests formed a large portion of potential moose winter range adjacent to willow bottoms and open sagebrush grasslands. A substantial portion of the MHWMA and surrounding National Forest lands were logged within the last century (Frisina and Keigley 2004); very few old-growth stands (>300 years) were present. Over the course the study (2007-2010), a mountain pine beetle (*Dendroctonus ponderosae*) outbreak expanded over the entire WMA, starting in the northeast portion and spreading southwest. This outbreak was concurrent with an outbreak across most of southwestern and central Montana. By the summer of 2010, the outbreak had impacted nearly every patch of coniferous forest on the WMA, killing tens of thousands of lodgepole pine trees.

Keigley et al. (2003) reported that *Alces alces* was the only ungulate species that winters on the study area (January to mid-May). Other ungulate species were present during the summer and fall seasons, including pronghorn antelope (*Antilocapra americana*), Rocky Mountain elk (*Cervus canadensis*), mule deer (*Odocoileus*

hemionus), and white-tailed deer (*Odocoileus virginianus*). The presence of elk and deer were of particular importance since in some locations these species may compete with moose for food resources (Jenkins 1985), while in other locations the competition is believed to be minimal (Stevens 1974). Cattle were present in the study area during summer months (June 15-Oct 10), under a strictly managed rest-rotation grazing schedule and stocking rate. Of the predators that may prey upon or otherwise influence moose behavior and survival, black bears (*Ursus americanus*) were present on the study site, while grizzly bears (*Ursus arctos*) had not been confirmed as residents. Wolves (*Canis lupus*) were increasingly present on the study area after recolonizing most of southwestern Montana following reintroductions in central Idaho and Yellowstone National Park in the mid-1990s. The presence or absence of these species may influence moose behavior and habitat use in winter and other seasons. For example, habitat damage due to overutilization of browse species may be especially evident in areas where predators were extirpated or limited (Crete et al. 2001).

Moose hunting districts 319, 325, and 341 encompassed the study area (refer to Figure 1.1). From 2002 to 2010, mid-winter aerial surveys have yielded total observable moose numbers ranging from 52 to 19 (mean = 34.5, SD ± 11.6) combined for the three hunting districts, with a downward trend (MTFWP, unpublished data). It should be noted, however, that these surveys should be interpreted cautiously as they do not provide precise trend data (only a population index) and were highly variable due to confounding factors such as snow depth, temperature, aircraft, observer experience, etc. An average total of 19 licenses (11 antlered, 8 antlerless) were offered in these three districts

(combined) each year from 2002 to 2009 and hunters harvested an average of 15.5 moose annually at an 80% success rate (MTFWP, unpublished data). A total of 10 licenses (7 antlered, 3 antlerless) were issued in these three moose hunting districts for the fall 2010 hunting season, while 9 licenses (6 antlered, 3 antlerless)were issued in 2011, the lowest total number offered in over three decades. The proposal for the 2012 season would eliminate antlerless harvest entirely and retain 6 antlered licenses - 2 in each district.

In summary, the Mount Haggin Wildlife Management Area provided a unique opportunity and study area to research moose. Publicly owned moose winter range is uncommon in southwestern Montana, as is the complete absence of other ungulates during winter, qualities that simplified logistics and minimized confounding factors in this research. The study area was also a representative part of the Upper Big Hole River Valley, which has provided a substantial opportunity for hunters and wildlife watchers alike with large populations of moose inhabiting the valley for the last few decades. By studying moose ecology on the MHWMA, I hope to both improve local management of moose populations around the study area and produce findings and management recommendations that should be applicable to moose populations on other winter ranges in southwestern Montana.

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CHAPTER 2

SEASONAL DISTRIBUTION AND WINTER HABITAT SELECTION OF MOOSE

Introduction

Animal populations require specific resources to maintain sustainable numbers (Manly et al. 2002). Resource selection studies attempt to identify resources or combinations of resources that are disproportionately used by a population. Understanding habitat selection, whether in the form of seasonal ranges or migration movements of populations or patterns of individuals, allows managers to focus their efforts in conserving habitat at different scales and to choose appropriate methods for managing populations and habitats (Thompson and Stewart 2007). For moose, understanding the importance and use patterns of willow communities is of particular interest as moose benefit from browsing willow extensively on many winter ranges (Peek 2007), but may also cause habitat degradation in areas where willow is overbrowsed (Berger et al. 2001, Pedersen et al. 2007).

Habitat selection by the Shiras moose, as with most species, can be broken down into a series of natural orders, each focusing on a different level of habitat selection. Johnson (1980) identified four spatial scales of habitat selection, of which the second and third orders of selection are most important in the scope of this study. Second order selection is the selection of the home range of an individual within the range of a species. Pooled across individuals within a population, second order selection represents seasonal distributions and movements of a population (migrations). The size of an individual's

home range and home range fidelity are also examples of second order selection (Johnson 1980). Within the home range, the use of various habitat components or "patterns of utilization", such as core areas used by moose (Van Dyke et al. 1995a), form the third order of selection. Studies examining second and third order habitat selection are common, often addressing population and individual level selection of habitats. There is no single correct level of selection to study (Manly et al. 2002) and many researchers have found that different suites of variables are associated with selection at different spatial scales for many species, including moose (Dussault et al. 2006, Poole and Stuart-Smith 2006). Many studies have followed the suggestion of Aebischer et al. (1993) by examining the selection of an individual's home range within a predefined study area (second order) and then the selection of habitat attributes within the individual's home range (third order); this study followed that model.

For moose, multiple variables have been identified as factors of habitat selection and most researchers have focused on how these variables are associated with second and third order selection. During the winter season, these variables include: browse availability (Van Dyke et al. 1995b, Tyers 2003, Poole and Stuart-Smith 2005, Poole and Stuart-Smith 2006, Peek 2007, Baigas 2008, Becker 2008), cover type (Jenkins 1985, Langley 1993, Peek 2007, Baigas 2008), elevation, slope and/or aspect (Matchett 1985, Poole and Stuart-Smith 2006, Becker 2008), distance to conifer or other cover (White et al. 2001, Dussault et al. 2006, Baigas 2008, Becker 2008), predator abundance (Dussault et al. 2005), snow depth and density (Matchett 1985, Peek 2007), and ambient temperature (Schwab and Pitt 1991, Demarchi 1992, Dussault et al. 2004). In different

winter range types as defined by Peek (1974, 2007), these factors may play a greater or lesser role. Snow depth is a key variable that is associated with habitat selection on most winter range types (Peek 2007), but may be difficult to accurately measure or unavailable on many study sites.

Different variables may be more influential at different scales of habitat selection, as has been noted by many researchers for moose (Nikula et al. 2004, Cassing et al. 2006, Dussault et al. 2006, Mansson et al. 2007) and other ungulates (e.g. elk, Boyce et al. 2003 and caribou, Johnson 2002). This may be due to differences in food and cover availability (Dussualt et al. 2006), or differences in selection of habitat for feeding, resting, and traveling (Van Dyke et al. 1995a, Poole and Stuart-Smith 2005), activities in which moose may allocate varying proportions of time and energy, depending on the season or sub-season (e.g. rut, calving, or deep snow seasons).

Furthermore, habitat selection is likely to be variable between sexes and age classes of moose. For instance, adult males and females have been noted to have unique habitat selection patterns (e.g. Miquelle et al. 1992, Cederland and Sand 1994, Oehler et al. 2011), while other studies have documented a notable lack of segregation (e.g. Baigas 2008). In this study, only one age/sex class was used to reduce the variability in habitat selection seen when multiple age and sex classes are sampled. Adult female moose were selected because they have been identified as the most reproductively important age and sex class in other studies (Cederlund and Okarma 1988, Poole and Stuart-Smith 2005).

In this study, locations acquired with GPS collars on adult female Shiras moose were used to determine seasonal distribution and movements for the population, annual

and seasonal spatial use of individual moose, and spatial and temporal habitat selection patterns by individual moose to quantify the distribution and variability of habitat selection patterns. These data were then used to test hypotheses predicting relationships between habitat attributes and habitat selection by cow moose during the winter season. Based on previous habitat selection research on moose, I predicted that cover type, distance to conifer cover, distance to willow cover, elevation, and an indicator for aspect/slope would all be associated with winter habitat selection by moose on the Mount Haggin Wildlife Management Area. I expected that some of these associations would change based on snowpack condition. The goal of this research was to inform decisions by wildlife biologists, including habitat and population management. At the conclusion of this chapter, I have suggested habitat conservation strategies for moose winter range and improvements to winter aerial survey methods based on the findings of this study.

Methods

Moose Capture and Collaring

Eighteen cow moose were collared for this study, 6 each in the winters of 2007, 2008, and 2009, with the last deployment yielding winter location data in both 2009 and 2010. These moose were opportunistically selected from known moose winter range, with an emphasis on sampling moose from across the entire study area. Selected moose were chemically immobilized via hypodermic dart shot from a helicopter. Moose were ear tagged and collared with global positioning system (GPS) collars. Blood and fecal samples were collected to determine pregnancy rates and other health factors and a

reversal was administered. All immobilization and capture techniques used in this project were adapted and developed by Atkinson (2005) with approval from a Montana Fish, Wildlife and Parks Institutional Animal Care and Use Committee.

In 2007, model 3300L collars were deployed (Lotek Wireless, Newmarket, Ontario), while in 2008 and 2009, model TGW 3600 collars were used (Telonics Inc., Mesa, AZ). All collars stored GPS location data in onboard memory and had to be physically recovered to obtain all data. All collars also had mortality sensors, temperature sensors, and timed drop-off devices. The collars in 2007 were programmed to attempt a fix every 30 minutes and to drop off after 52 weeks. The collars in 2008 and 2009 were programmed to attempt a fix every 60 minutes and to drop off after 35 and 67 weeks, respectively. After collar deployment, the moose were monitored with visual relocations or VHF signals 3-5 times monthly to detect any mortality events.

Descriptive Location Analysis

GPS locations were examined and screened for GPS malfunction and restricted to a pre-specified level of accuracy (PDOP < 10, D'Eon et al. 2002). Euclidean distances were calculated between sequential locations at 1, 5, and 10 hour intervals to plot the data at multiple scales. Graphs of these movement rates were constructed to examine seasonal changes in movement rates.

Season Delineation. The location data were split into 2 seasons: winter and summer. Moose movements were used to identify seasons (Wal and Rodgers 2009). The winter season was identified as the period when moose movements were generally

restricted, with rare or no long-range movements (>95th percentile of the annual movement rate distribution). The summer season was determined to be the period when moose rarely stop moving for an extended period (excluding a brief window immediately after calving) and more frequently made long-range movements. The season start and end dates were averaged across all moose within a single year to arrive at population-wide season dates. Departures of a few days to a week were granted for individual moose whose movement rates suggested notable differences from the average.

Home Range Estimations. Two types of home ranges were calculated for this study, using fixed kernel and local convex hull methods. These two methods were selected for different reasons (as explained below), but also to contrast the two methods and the home ranges they produced and to compare to other studies using these methods.

The primary purpose of the fixed kernel home ranges was to define available habitat from which to select available locations for resource selection modeling. Fixed kernel methods were used as opposed to adaptive kernel methods because they provide more accurate and precise estimates at the outer contours of the home range (Kernohan et al. 2001). The href (*h* reference) method (Worton 1989) was used to select initial smoothing parameters to create the fixed kernel home ranges for each individual moose and season. The href method defines a smoothing parameter (*h*) based on the variance (i.e. the spread and distribution) in the location data, also called a reference bandwidth. The smoothing parameter selected was then adjusted ad hoc to reduce gaps in multimodal distributions (Berger and Gese 2007, Jacques et al. 2009, Kie et al. 2010, Oehler et al. 2011). The href method does have a tendency to overestimate home range size and

distribution (Kernohan et al. 2001), but generally produces a satisfactory representation of available habitat for habitat selection studies.

Fixed kernel home ranges were estimated in a geographic information system (ArcGIS 9.3, ESRI, Redlands, CA), using the Hawth's Tools extension (Beyer 2006). Initial href values were increased in increments of 50 until the 95% contour was connected across the entire distribution (creating a single polygon), with the recognition that some individuals could have multimodal home range distributions that could not be linked to create a single polygon. Locations used for this method were subsampled at a 5 hour interval to reduce autocorrelation between locations. Although the autocorrelation was not eliminated, exclusive use of independent data is not necessary for estimating home ranges (Swihart and Slade 1997), especially for robust estimators like kernel methods. However, an adequate time frame must be used to gather a representative sample for a given season/year, which it was in this study as data were collected across the seasons of interest (not just for a month or two). Therefore, a representative sample of locations was obtained, which is a much more important issue than autocorrelation (Otis and White 1999, Fieberg 2007). Further justification for the 5 hour interval can be found in the Used Locations and Autocorrelation section below.

The primary purpose of the local convex hull (LoCoH) home ranges was to delineate and quantify the size of core areas used by moose. These core areas represent the locations and volume of area that moose require to satisfy most of their ecological needs. The LoCoH technique is especially adept at estimating home ranges where hard edges exist (Getz et al. 2007). In this study, I expected that moose would view the edges

of willow communities as hard boundaries and that the LoCoH home ranges would provide the most accurate estimate of home range area and location as other researchers have noted for moose (Baigas 2008, Van Beest et al. 2011).

LoCoH home ranges were estimated in a geographic information system (ArcGIS 9.3, ESRI, Redlands, CA), using the LoCoH Toolbox (Getz et al. 2007). The adaptive local convex hull (a-LoCoH) method was used since it was least affected by changes in sample size and robust to changes in the local hull parameter *a* (Getz et al. 2007). The optimal value of *a* for the seasonal dataset of each moose was estimated as the greatest distance between any two points in the data, as suggested by Getz et al. (2007). As LoCoH home range estimates converge to true values with increasing sample size, all moose locations within a given season were used for home range estimations as opposed to the subsampled locations used in the fixed kernel method.

Resource Selection Analysis

In this study, I was interested in determining which habitat attributes were associated with moose habitat selection. Both spatial and temporal covariates were of interest, specifically spatial covariates related to cover type, elevation, and aspect and a temporal covariate of snow water equivalent (SWE), as snowpack has been shown to be a strong driver of moose habitat selection. Ideally, spatial and temporal data on snowpack condition would be used for resource selection modeling, but no adequate measures of snowpack condition on a spatial scale were available on the study area. Temporal data on snowpack condition were available from a nearby SNOTEL station. Since spatial snowpack data were not available, traditional logistic regression could not be applied to

these data to estimate a resources selection function that included snowpack condition.

The alternative modeling framework employed in this study was conditional logistic regression, also known as discrete choice or matched case-control modeling (Arthur et al. 1996, Cooper and Millspaugh 1999, Durner et al. 2009, and Proffitt et al. 2011). Specific to habitat selection, conditional logistic regression (CLR) compares choices within a group of used and available locations. CLR employs a typical logistic regression formula for binary data with an additional strata covariate and then uses a conditional likelihood to obtain coefficient estimates. The general form of the model is:

$$\text{logit}(p) = \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i + \textit{strata}$$

where p is the probability of habitat selection, the x_i are the explanatory covariates or interactions and their respective coefficients (β_i), and *strata* is a group indicator covariate.

In this study, each stratum consisted of one used location matched with five available locations chosen at random from within the available habitat (see definitions of available habitat below). The available locations within each stratum were assigned the same temporal covariate values as the used location, based on the date and time of day of the used location. Thus, the temporal data were identical within a stratum. This meant that I could not estimate the direct association between any temporal covariates (e.g. SWE) and the probability of habitat selection. However, by using interactions between the temporal and spatial covariates, I was able to estimate the interactive effects of temporal covariates on the spatial covariates. Specific to this study, I was able to examine how SWE influenced the associations between cover type and the probability of habitat selection, but not if cow moose were selecting for areas with lower SWE.

In order to appropriately model resource selection by cow moose, the model needed to account for potential autocorrelation of the location data for each moose. To accomplish this, a two-stage approach was used. The first stage was the selection of the resource selection function (RSF) model structure using Akaike's information criterion (AIC) model selection. In this stage, a sample of locations from all individuals was fitted to an a priori model list and the top model(s) were then used in the second stage. In the second stage, the top RSF model(s) from the first stage were fit to all of the location data for each individual and RSF coefficients estimated. Then, the coefficients were averaged across all individuals to arrive at the population level coefficient estimates. This second stage treated individuals as the sample units, as only the coefficient point estimates were averaged (and individual variance was ignored as it would be biased by any autocorrelation). Population variance was based solely on the variance among the individual coefficient estimates. Thus, the two-stage modeling framework allowed for the estimation of a population-level RSF without precisely modeling within-individual autocorrelation (Fieberg et al. 2010). The key assumptions of this method were that the individual moose monitored were representative of the population and were independent from each other, model selection at the population level was sufficient despite potential individual differences, individual-specific coefficient estimates were unbiased, and that sufficient data existed for each individual moose to create an accurate RSF (Fieberg et al. 2010). These assumptions seemed reasonable in this study.

An alternative to this two-stage approach would be multilevel modeling, which was not used in this study. Multilevel modeling takes into account multiple

measurements (level 1) within individuals (level 2) and allows for inferences about population level and individual resource selection. Multilevel models also account for uncertainty in coefficient estimates at both the population and individual levels, while two-stage modeling ignores uncertainty at the individual level. The application of multilevel models to resource selection is relatively new (Hebblewhite and Merrill 2008, Indermaur et al. 2009, Wagner at al. 2011). In these studies, the heterogeneity in resource selection among individuals was of particular interest and necessitated the use of multilevel modeling. As I was only interested in population level resource selection patterns, I opted to use the simpler and more intuitive two-stage method. Additionally, it should be noted that multilevel modeling methods would be likely to produce similar results and not impact the management implications of this study.

The first stage required a sample of locations from the population to select the model structure. If autocorrelation was ignored at this stage, it could bias the model selection results. Thus, subsampling of the data was still necessary to address autocorrelation in the first stage and has been performed in other studies (e.g. Proffitt et al. 2011). The subsampling method used in this study is explained below. While more sophisticated analyses that explicitly model autocorrelation are being developed (e.g. mixed effects and state-space models), they are not currently feasible for large datasets based on the used-available framework (Fieberg et al. 2010) and therefore were not used in this study.

Used Locations and Autocorrelation. Location data in this study were collected at a relatively fine temporal scale, with locations every 0.5 hours (in 2007) or 1 hour (in

2008, 2009, and 2010). Thus, autocorrelation becomes a potentially serious issue that can bias model selection. To address this issue, I investigated autocorrelation in the data from this study with the goal of using systematic subsampling to reduce autocorrelation.

Autocorrelation was examined using two indices proposed by Schoener (1981) and Swihart and Slade (1985). Data were reduced from a 1 hour interval to 5, 24, 48, 96, and 168 hour intervals to determine at which interval sequential locations were close to or approximately independent. Both indices indicated notable autocorrelation at all intervals based on thresholds identified for these indices, even for the 1 week (168 hour) interval. At the 1 week interval, the subsampled data were reduced to less than 0.6% of the original data, with datasets ranging in size from 10 to 15 locations per moose for the winter season. This would effectively reduce the sample sizes to the point where a large amount of information on habitat selection would be lost. Therefore, I chose not to use the "time to independence" concept to subsample the data to ensure independence.

The alternative concept for data censoring employed in this study was to use a time interval sufficient for an animal to move anywhere in its home range. Based on moose movement rates estimated in this study, a 5 hour interval was determined to be sufficient in most cases for an individual cow moose to traverse its entire home range. Therefore, for both the calculation of fixed kernel home ranges, as explained above, and for creating a sample of used locations to examine habitat selection for each moose, locations were sampled at a 5 hour interval, reducing the data to either 10% (in 2007 - original data collected at 0.5 hour intervals) or 20% (in 2008, 2009, and 2010 - original data collected at 1 hour intervals) of the original datasets. This reduced the

autocorrelation in the data and should have resulted in less biased model selection in the first stage of the two-stage approach for modeling resource selection.

Defining Availability. In order for resource selection functions to be accurate, available locations must be correctly identified (Johnson 1980, McClean et al. 1998, Manly et al. 2002, Boyce 2006, Buskirk and Millspaugh 2006, Fieberg et al. 2010). The definition of availability depends on the question of interest and the scale of selection (Johnson 1980). Defining availability and investigating selection at multiple scales can yield insight into the process of selection (Boyce 2006). In this study, two scales are investigated. The first scale defines availability within individual home ranges, while the second scale defines available habitat as the entire study area.

For the home range scale analysis, availability of winter habitat was defined at an individual level, where the 95% contour of the winter fixed kernel home range for each individual moose delineated the habitat that was available to that moose for that winter. This method is commonly used for both the delineation of available habitat at individual and population scales (e.g. Manly 2002, Mao et al. 2005, McLoughlin et al. 2005, Buskirk and Millspaugh 2006, McDonald et al. 2006, Bleich et al. 2010, Proffitt et al. 2010). Available locations were selected at random (with replacement) in ArcGIS (9.3, ESRI, Redlands, CA), using the Hawth's Tools extension (Beyer 2006). Available locations were selected at a ratio of 5:1 to used locations, following the recommendations of multiple authors using conditional logistic regression modeling (Cooper and Millspaugh 1999, Cooper and Millspaugh 2001, Buskirk and Millspaugh 2006). The available locations were then matched to used locations to create strata (groups) and

temporal covariates were assigned to the available locations, as described above.

For the study area level analysis, availability of winter habitat was defined at a population level, where a winter study area boundary delineated available habitat. Defining a winter study area was more complex than simply creating a population level kernel range or buffering used locations, as both collared and uncollared moose had to be taken into consideration to represent the entire population of moose on this winter range. All points from collared moose during winter were buffered by 930 meters. This distance was five times the 95th percentile of hourly Euclidean distance traveled, on average, by collared moose in this study. The hourly distance was multiplied by five in order to account for the 5 hour interval between used points. Similar methods using movement rates have been employed by Arthur et al. (1996), Gillingham and Parker (2008), Durner et al. (2009) and Proffitt et al. (2011) to define available habitat. The resulting buffer was slightly larger than the previously calculated 95% contour of the fixed kernel home ranges. It should be noted that the single cow moose that migrated off the Mount Haggin winter study area was not included in this calculation.

To account for non-collared moose, ten years (2001-2011, excluding 2009) of location data from moose winter aerial surveys on the study area were digitized from annual flight records (MTFWP, unpublished data). These data were then buffered by 1530 meters. This distance was the population average of the mean distance between all points within a single winter season for each individual moose, effectively the average spread of the home ranges of collared moose. This longer distance seemed to better approximate the available area for the population relative to uncollared moose locations,

as these aerial locations were often singular (vs. clusters of locations from collared moose) and occasionally did not overlap with the winter range as defined by the collared population. The 5 hour movement buffer would not have captured a large enough area to approximate the entire potential winter range for these moose.

The two buffers, both the collared moose buffer and the aerial location buffer, were combined to create the study area. As with the home range scale analysis, available locations were randomly selected from within the study area at a ratio of 5:1 to used locations for each individual moose and temporal covariates were assigned to the available locations within strata. The lone cow moose that did not winter on the study area was excluded from this portion of the resource selection analysis.

Model Covariates. To examine patterns in resource selection, I located remotely sensed datasets to calculate covariates of interest. Those covariates were cover type, distance to conifer cover, distance to willow cover, elevation, solar radiation index, snow water equivalent, and temperature (used in the post hoc analysis only). The sources and calculations to obtain these covariates are detailed below. All data were kept in NAD 83 (North American Datum of 1983) using a Lambert Conformal Conic spatial projection.

Cover type, along with the two distance covariates, were derived from the MNHP Montana Land Cover Map (2010). These data consisted of 30 meter pixels classified into hundreds of cover types. Although these data are not recommended for fine scale analysis, I compared hand classified cover types (from aerial photos) to this layer and found that the cover types were very accurate for the broad classes I wanted to examine. For this study, these broad classes of cover types were grouped as follows: conifer,

shrublands/grasslands and meadows, willow, aspen, and other (talus, roads, structures, etc.). These five broad classes were similar to those used by Van Dyke et al. (1995b), Fisher et al. (1998), Osko et al. (2004), and Poole and Stuart-Smith (2006) for moose habitat selection analysis. In order to simplify the cover type classes, the original landcover map was imported into ArcGIS (9.3, ESRI, Redlands, CA) as a raster file and reclassified to combine cover types into the desired groups. The final dataset had the same 30 meter pixels as the original.

In order to calculate the distance to conifer and distance to willow cover covariates, the conifer and willow cover types were extracted from the raster layer created above to form binary conifer/non-conifer and willow/non-willow layers. The straight line distance to the desired cover type was then calculated in ArcGIS using Spatial Analyst. The distance value within the cover type of interest was zero, essentially turning off the impact of this covariate when that cover type was occupied. This calculation produced two datasets with the distance to conifer and willow covariates estimated at a 5 meter pixel scale. While a larger 30 m pixel scale could have been used, that scale had the potential to obscure the small-scale impact of these covariates by essentially creating larger bins of distances (e.g. real distances of 0-30 m represented by the average distance of 15 m versus 0-5 m, 5-10 m, etc. for a 5 m pixel).

Elevation data were sourced from the USGS Digital Elevation Model (USGS 2009). These data were projected in the North American Vertical Datum of 1988 (NAVD 88) vertical projection and are accurate to within a few meters. Pixel size for these data was 1/3-arc second, which on my study area was approximately 9 × 6.3 meter pixels

(vertical × horizontal). For modeling purposes, this covariate was scaled from meters to meters$\times 10^{-2}$. As with the other data, the horizontal projection was NAD 83.

A solar radiation index (SRI) was derived from the DEM dataset. Using the Solar Radiation Area calculator in the Spatial Analyst extension in ArcGIS (9.3, ESRI, Redlands, CA), I calculated the cumulative winter solar radiation. This modeling tool takes into account slope, aspect, topography, latitude, elevation, sun angle, duration (period of cumulative solar radiation in days), and time of year to calculate the SRI (Fu and Rich 2002). To simplify the calculation of this covariate, I used the period of 1 Jan-30 Apr to estimate the amount of solar radiation on my study area during the winter even though winter seasons varied slightly for individual moose and years. Unique maps for each moose or year would have made RSF construction and validation prohibitively difficult. The final dataset had the same 1/3-arc second pixels as the DEM data, with cumulative solar energy in watt hours per meter squared. For modeling purposes, this covariate was scaled to megawatt hours per meter squared (watt hours$\times 10^{-6}$) and ranged from 0.02 - 1.25 MW hours across the study area, with higher values indicating more solar radiation energy striking a pixel over the course of the winter season. This value should be interpreted as a relative index of solar radiation however, as it assumes clear and unobstructed skies and does not account for the effects of vegetation/cover type.

Snow water equivalent (SWE) and temperature data were acquired from the Calvert Creek SNOTEL site (SNOTEL 2011). This site was the closest to the winter study area (10 km west) and should have similar winter weather conditions (e.g. temperature) and be a representative index of the changing snowpack conditions over

time on the study area. Local drifting and spatial snowpack heterogeneity on the study area would not be captured by this index, but overall trends should be similar. The elevation of this site was 1965 meters, compared to the elevation range of approximately 1755-2250 meters on the winter study area. These data consisted of SWE and temperature measurements every 3 hours throughout the winter season. SWE was converted to centimeters and temperature to degrees Celsius for use in this study.

The cover type, distance to conifer cover, distance to willow cover, elevation, and solar radiation index covariates were all stored as raster files for simple extraction of these values to used and available points and for resource selection function map creation. The SWE/temperature measurements were stored as a 1-dimensional shapefile in order to join the used and available location times (at a 5 hour interval) to the nearest SWE/temperature measurement time (at a 3 hour interval).

Cover Type Selection. I used methods outlined by Manly et al. (2002) to calculate simple selection ratios for the cover types available to moose in this study. Selection ratios were calculated at the population level and were also compared with each other to look at significant differences ($\alpha = 0.05$) in the selection of individual cover types. This analysis was completed at both the home range and study area scales, but with separate used and available points for each moose (a Type III design from Manly et al. 2002). Type I and II designs would have used the same available points for all moose and might have obscured individual moose selection patterns or notable differences between individuals. The analysis was completed in R (version 2.13.1, R Development Core Team 2011), with code from the extension *adehabitat* (Calenge 2009).

Two-Stage Modeling and Validation. As mentioned previously, the two-stage modeling framework was used to allow for the estimation of population-level resource selection without needing to precisely model within-individual autocorrelation. This is accomplished by treating individuals as the sampling unit, fitting an RSF to each individual, and then averaging the regression coefficients across individuals to obtain the estimated population level RSF (Fieberg et al. 2010). The following methods explain the application of this process to the moose location data collected in this study

The first stage of this method was to complete model selection at the population level. The subsampled (5 hour interval) data were used to reduce the level of autocorrelation in the data. However, to avoid biasing the model selection results toward moose with a greater number of locations (due to a longer period of monitoring or monitoring for multiple winters), random samples of locations were selected from the subsampled dataset of each moose. The number of locations sampled was equal to the smallest number of locations for any moose (n_s). For moose collared multiple winters, approximately equal samples ($n_s \times$ [1/# of winters]) were randomly selected from each winter, totaling n_s. At this step, 10% of the data ($n_s \times 0.10$) were reserved for model validation. The remaining data ($n_s \times 0.90$) were then combined across all individual moose and fit to a suite of a priori models. Models were fit using conditional logistic regression in R (version 2.13.1, R Development Core Team 2011) with code from the package *survival* (Therneau 2010). Akaike's information criterion (AIC; Burnham and Anderson 2002) was used for model selection with code adapted from the package *bbmle* (Bolker 2011). Models with uninformative parameters were ignored (Arnold 2010).

Uninformative parameters were defined as those that do not explain enough variation to overcome the 2 AIC per parameter penalty and thus should not be interpreted as having an ecological effect (Arnold 2010). As this criterion should not be thoughtlessly applied without evaluating individual models, the estimates and uncertainty of the coefficients in each model were also examined to ensure that parameters with ecological importance were not erroneously excluded.

An a priori model list representing the resource selection hypotheses was developed after taking into account any collinearity between covariates. Pairwise correlations, VIF (variance inflation factors) and scatterplots were examined for potential linear and nonlinear relationships. Pairs of covariates with correlations > |0.6| would not be included in the same model. The a priori models included the five spatial covariates calculated above and SWE interactions with cover type, distance to conifer cover, distance to willow cover, and elevation. The hypotheses for each model covariate and interactions are explained in the Modeling Predictions section below.

For the second stage, the top model (or models if model selection uncertainty suggested competing top models) was fitted to the data for each individual moose and the coefficients averaged across all moose. Separate datasets were fitted for moose that were collared multiple winters, but the resulting coefficients were weighted in the averaging calculation to prevent the final population level coefficients from being biased toward individuals collared for multiple winters. Standard error estimates and 95% CIs for the population level coefficients were based on the variance of the individual coefficients. All calculations were completed in R (version 2.13.1, R Development Core Team 2011).

This process was completed twice, once for the home range scale availability data and once for the study area scale availability data. A full review of this method can be found in Fieberg et al. (2010) and examples of its application can be seen in Nielsen et al. (2002), Sawyer et al. (2006), and Proffitt et al. (2011).

Using the population level coefficients, I constructed RSF maps in ArcGIS (9.3, ESRI, Redlands, CA) that covered the cumulative area of the winter home range estimates or the entire study area (depending on the scale being tested) at varying levels of SWE to predict the relative probability of moose selection (Manly et al. 2002). The probability of moose habitat selection was relative to the other habitat within the home range or study area. Absolute probability could only be estimated if an intercept was estimated, which was not the case with the conditional logistic regression model structure. SWE levels were selected after examining a histogram of the SWE data to identify natural breaks in the data and averaging the SWE data between those breaks. These maps were based on the covariate values at a 5 meter pixel scale in order to preserve the predicted effect of all covariates.

I validated the RSF maps using the reserved data (10% of used locations, equally sampled by moose) to evaluate the ability of the top models to predict used locations (Boyce et al. 2002). The RSF maps were reclassified into 20 equal-area intervals that corresponded to relative probability of habitat selection (0-5%, 5-10%, etc.) and that would be used with equal frequency (5%) by random chance (Durner et al. 2009, Proffitt et al. 2011). I plotted the reserved data on the appropriate SWE level maps (e.g. low, moderate, or high SWE, depending on the SWE value of the reserved location) in ArcGIS

and then imported to the data into R (version 2.13.1, R Development Core Team 2011) to calculate the frequency of the reserved locations within the RSF bins (summed across all SWE levels). The strength of a model was judged on how many of the reserved locations were in the top 25% and top 50% of the RSF bins. This simple validation procedure did not take into account the variance of the model coefficients (the extrapolated RSF maps only used the point estimates).

Modeling Predictions. I evaluated possible relationships between moose winter habitat selection and six environmental covariates. Five of these covariates were spatially defined: cover type, distance to conifer cover, distance to willow cover, elevation, and solar radiation index. The sixth covariate, SWE, only varied temporally and therefore I could not determine the direct association of this covariate with habitat selection, but I could discern its interactive effect with the spatial covariates by using conditional logistic regression. Thus, the predictions for the interactive effects of SWE can be found within the predictions for the individual spatial covariates. There was strong evidence in published literature that all of these covariates would be associated with moose habitat selection in winter. A seventh covariate, temperature, was only examined post hoc, as there were limited and conflicting studies supporting an association between temperature and habitat selection in winter. Temperature, like SWE, was a temporal covariate with no spatial data and only the interactive effects were estimated; no predictions were made for the temperature interactions.

Cover type may be the greatest determinant in explaining moose habitat selection (Jenkins 1985, Langley 1993, Peek 2007, Baigas 2008). Moose tend to select for two

types of cover in winter, those with abundant forage and those with substantial canopy cover. No matter the type of winter range (e.g. floodplain, riparian, or conifer), the presence of a few key browse species is critical, which in the Northern Rockies includes a wide variety of willow species, aspen, other deciduous shrubs, and even conifers like subalpine fir and Douglas-fir (e.g. Peek 1974, Jenkins 1985, Langley 1993, Van Dyke et al. 1995b, Tyers 2003, Poole and Stuart-Smith 2005, Poole and Stuart-Smith 2006, Baigas 2008, Becker 2008). On my study area, the willow community provided an abundant and highly palatable browse source and moose were expected to use this community above all others for browsing. Aspen were also present, but the distribution of this community was relatively limited. The second cover type of potential importance on my study area were the conifer communities, which has been noted as a refuge from harsh snow conditions and thermal cover in other studies and is often heavily used in late winter when snowpack is greater (e.g. Houston 1968, Stevens 1970, Pierce and Peek 1984, Matchett 1985, Jenkins and Wright 1988, Langley 1993, Tyers 2003, Peek 2007) or when temperatures exceed thermal limits, either on a hourly (Demarchi 1992) or seasonal scale (Schwab and Pitt 1991). However, the importance of conifer cover as snowpack increases has been debated, as a few studies have not detected a change in cover type selection with increasing snow depths (Poole and Stuart-Smith 2006, Becker 2008). Additionally, one study found that the use of thermal cover by moose was notably absent in some populations (Lowe et al. 2010) and another found that thermal cover may be more critical in summer than in winter (Dussault et al. 2004). In terms of scale of selection, other studies have shown that cover type selection has been stronger at the

within home range scale than at the landscape (study area) scale (Nikula et al. 2004), particularly for cover types with dense forage resources (Dussault et al. 2006).

Based on these previous studies, I hypothesized that moose would strongly select for willow and aspen cover types, although the degree of selection may decrease with increasing SWE. I also hypothesized that moose would select for conifer types, at least during high SWE levels; at low SWE levels there could be no selection for conifer cover. Grasslands and other habitat would be selected against, no matter the snowpack conditions. Finally, I hypothesized that the selection for willow, aspen, and conifer (with high SWE) cover types would be greater at the home range scale.

Winter moose habitat selection has been noted by many studies to be impacted by the distance to conifer cover or other cover types with closed canopies (Van Ballenberg and Peek 1971, White et al. 2001, Dussault et al. 2006, Peek 2007, Baigas 2008, Becker 2008). Generally, moose prefer distances close to conifer cover, with increasing selection as snowpack increases. This observation parallels those studies that found that moose tend to select for conifer cover, especially during periods of heavy snowpack. As for the impact of scale, Dussault et al. (2006) found that edge effects were weaker at smaller scales. Thus, I hypothesized that moose would select for closer distances to conifer cover, and that this relationship would strengthen at higher SWE levels. I also hypothesized that this selection would be greater at the study area scale.

A few studies have directly quantified the association between distance to willow cover and habitat selection (Van Dyke et al. 1995b, Kufeld and Bowden 1996, Baigas 2008), with moose preferring closer distances to willow cover. Therefore, I hypothesized

that moose would select for closer distances to willow cover. There were no direct studies looking at the interaction between distance to willow and snowpack changes, but since moose selection for willow cover decreases with increasing snowpack (e.g. Jenkins 1985, Tyers 2003, Baigas 2008), I hypothesized that the strength of selection for closer distances would decrease with increasing snowpack. As with conifer cover, I hypothesized that this selection for an edge would be greater at the study area scale.

Moose selection for lower elevations has been documented, often as a surrogate for spatial differences in snow depth (Matchett 1985, Poole and Stuart-Smith 2006, Becker 2008). Unsurprisingly, a number of studies have shown that moose use lower elevations as snow depths increase, particularly in late winter (Stevens 1970, Kufeld and Bowden 1996, Poole and Stuart-Smith 2006). I hypothesized that moose would select for lower elevations, and that this selection would increase as SWE increased. Since elevations were likely to vary more at a study area scale than at the home range scale, I hypothesized that selection for lower elevations would be greater at the study area scale.

The final spatial covariate of interest was a solar radiation index (SRI). This metric accounted for both slope and aspect, which have been shown to be influential on moose habitat selection (Langley 1993, Van Dyke 1995, Poole and Stuart-Smith 2005, Baigas 2008, Becker 2008). As the study area was relatively flat, the SRI probably better represented changes in aspect and snowpack condition (reduced due to melting) than slope. There was no evidence in the literature suggesting a change in the association between SRI and probability of habitat selection by moose at different levels of SWE, so no interaction was included in the models tested. I hypothesized that moose would select

for locations with greater SRI, as this would potentially ameliorate snow conditions. As literature was scant, I did not have a hypothesis regarding the different scales of selection.

An additional temporal covariate, temperature, was examined post hoc. As with the SWE covariate, the association between temperature and habitat selection could only be modeled in the form of interactions with the spatial covariates. As discussed above in the cover type predictions, a few studies found that moose would seek thermal cover during warmer times of day (Demarchi 1992) or warmer periods within a season (Schwab and Pitt 1991). However, the impact of temperature was absent in some populations (Lowe et al. 2010) and moose may be more temperature sensitive in summer than in winter (Dussault et al. 2004). As there was conflicting evidence, this covariate was only addressed after the a priori modeling effort. For the post hoc modeling exercise, a temperature and cover type interaction and a temperature and distance to conifer interaction were added in all combinations to the top model(s). Improvement to the top models was determined by examining the ΔAIC scores.

The hypothesized a priori relationships noted above are listed in Table 2.1 for quick reference. In the first column, a '+' indicates a relationship where increasing the value of the covariate would increase the probability of habitat selection. A '–' indicates a relationship where increasing the value of the covariate would decrease the probability of habitat selection. A '0' indicates no relationship. These signs correspond with the predicted signs of the coefficients in the logistic regression models. In the second column, either HR, SA, or UNK represent predictions as to which scale (home range, study area or unknown) will have the larger coefficient (more positive or more negative,

Table 2.1: The predicted relationships between the explanatory variables examined in this study and cow moose habitat selection based on current literature. The sign in the first column corresponds with the predicted signs of the coefficients in the logistic regression models. The second column indicates at which scale selection will be greater.

Coefficient	Predicted Relationship with Habitat Selection	Scale with Greater Selection
WILLOW	+	HR
ASPEN	+	HR
CONIFER	0	HR
GRASSLANDS	−	HR
OTHER	−	HR
DISTANCE TO CONIFER	−	SA
DISTANCE TO WILLOW	−	SA
ELEVATION	−	SA
SRI	+	UNK
WILLOW×SWE	−	HR
ASPEN×SWE	−	HR
CONIFER×SWE	+	HR
GRASS×SWE	0	HR
OTHER×SWE	0	HR
DIST TO CONIFER×SWE	−	SA
DIST TO WILLOW×SWE	+	SA
ELEVATION×SWE	−	SA

depending on the predicted relationship in the first column), representing greater selection for that covariate at that scale of habitat selection.

Results

Descriptive Location Analysis

Eighteen collars were successfully deployed over the course of this study and no capture mortalities occurred. Sixteen of the eighteen collars were recovered and captured

recoverable data. Two collars were lost due to a technical error. The six Lotek collars deployed in 2007 malfunctioned, causing complete collar failure within 4-6 months (including the VHF beacon). Despite the malfunction, Lotek was able to retrieve the GPS location data from all four of the recovered collars, but these data were limited to an average of 18 out of 52 weeks scheduled (early February to mid-June), after which the GPS was no longer functioning. All of the collars from the 2008 and 2009 deployments were recovered and they collected data as programmed; all drop off mechanisms from 2008 and 2009 performed as designed and on schedule (within 1-2 hours). Detailed data of the capture and collar recovery can be found in Appendix A.

Over the four winters when collars were deployed, 44,572 locations were acquired after censoring for accuracy. An additional 51,009 locations were acquired during the three summer seasons after censoring for accuracy. Including the locations acquired between seasons, a grand total of 106,543 accurate locations were collected. In total, 99.4% of the programmed locations were acquired (109,219 of 109,930, excludes locations in the non-winter season of 2007 when collars malfunctioned and thousands of locations were missed). When the locations were censored, 2.5% of the acquired locations were discarded (2,676 of 109,219). These percentages varied only slightly from moose to moose, although cow moose that used more conifer cover types had slightly higher percentages of censored locations (see Appendix B).

The failure of the VHF beacons in 2007 prevented any visuals or monitoring of marked moose in that year. For the winter 2008 and 2009 deployments, moose were monitored regularly and 69 and 119 visuals (or track encounters in winter) were obtained

in those deployments. As part of this monitoring, I determined parturition timing and calf survival for the collared cow moose. Data on mid-winter pregnancy rates from blood drawn at capture indicated that of the 18 cow moose tested from 2007 to 2009, 15 were pregnant (83.3 %). In 2008, 5 of 5 pregnant cows gave birth, and 5 of 5 pregnant cows also gave birth in 2009; cows were not monitored in 2007 due to equipment failure. No twins were observed. The average date of parturition was estimated to be May 25 for data collected in 2007, 2008, and 2009 (range: May 17 – June 11). For the summer periods in 2008 and 2009, 10 calves were monitored and 7 survived until late September when calf monitoring ceased for the summer season. For the winter periods in 2008, 2009, and 2010, 6 calves were monitored and only 1 survived to the start of the summer season. Individual calf survival data can be found in Appendix C.

A total of 15 individual cow moose were monitored during this study. Of those moose, 13 had known fates at the end on monitoring; two fates were unknown due to collar failure. Seven of the 13 moose were alive at the end on monitoring. Of the other six, three were legally harvested by hunters, two were killed by predators, and one died from accidental entrapment in a frozen pond. The cow moose which did not survive are noted in Appendix A and mortality reports for the non-hunting related mortalities can be found in Appendix D.

Season Delineation. Based on movement rates, the winter season was defined as starting at collar deployment for 2007, 2008, and 2009. Moose movements were already restricted on these dates. In 2010, the winter season began on January 1, the date when moose movements for the 3 moose remaining in the study became restricted. This

corresponded with increasing snowpack on the study area in 2010. The end of the winter season was determined to be April 10, April 30, April 30, and April 15 for 2007-2010, respectively. The dates for the end of winter also corresponded with the period of high snowmelt at the nearby Calvert Creek SNOTEL site (SNOTEL 2011) and an increasing percentage of bare ground on the study area (observational data, this study). These dates were also in line with the data from one moose that migrated to a unique winter range separate from the Mount Haggin Wildlife Management Area during this study.

For about 10-14 days after the end of winter, moose still occasionally localized and were only making a few long range movements. After this period, moose movements were more constant and included more frequent long range movements, indicative of a summer pattern (but not a spring migration). Thus, the summer season started on April 24, May 10, and May 10 for 2007, 2008, and 2009, respectively. The end of the summer season was largely determined by the end of data collection, either from collar failure, mortality, or drop off (early summer in 2007 and October 10 in 2008). In 2009, four collared moose were alive at the end of the summer season, which was determined by the start of noticeable localization to be around November 10. Based on field observations, this date corresponded with the end of the rut, but otherwise very few differences in movement rates were seen across the calving, mid summer, and rut periods, excluding a brief period of extreme localization which was contemporaneous with parturition in late May or early June (Testa et al. 1999). No summer season was determined for 2010 as all collars had dropped off on April 15. All of these data are summarized by individual moose in Appendix E, including notes on slight departures from the population dates.

Home Range Estimations. Based on the seasons defined above, winter and summer home ranges were calculated. In general, winter home ranges were relatively compact and were highly associated with willow communities and adjacent conifer stands. Summer home ranges were slightly larger and more expansive, but were still highly associated with willow communities. For 19 moose/winters of data, the average 95% fixed kernel home range size was 9.726 km^2 (range: 2.436-28.134 km^2), while the average 90% LoCoH home range was 1.170 km^2 (range: 0.202-4.060 km^2). For 15 moose/summers of data, the average 95% fixed kernel home range size was 21.114 km^2 (range: 9.045-51.824 km^2), while the average 90% LoCoH home range was 2.805 km^2 (range: 0.996-7.268 km^2). Due to the failure of the 2007 collars, only limited data were collected with which to estimate home ranges during the summer season of that year; if those data are excluded, the average summer home range sizes for the 95% fixed kernel and 90% LoCoH methods increased slightly to 22.443 km^2 and 2.980 km^2, respectively. These data are summarized by individual moose in Appendix F.

Cow moose during this study stayed almost exclusively on the winter range during the summer season, often overlapping their individual winter home range by a substantial amount. Moose used on average 56.0% of their 95% fixed kernel winter range in the following summer (range: 24.6%-100% overlap), excluding one moose which migrated and had zero percent overlap (moose 11 in 2009). Five cows were collared for multiple winter seasons, while 8 cows were collared for a single winter. All five cows collared for multiple winters showed seasonal range overlap across years, averaging 50.4% overlap (range: 16.0%-85.0%) in the 95% fixed kernel home ranges

from consecutive winters. These seasonal home ranges, along with the location data used to produce them, are displayed in the figures in Appendix G.

There was a notable relationship between the winter home range size averaged for all moose within a winter and the average SWE for the winter season. When SWE was higher, home ranges were smaller, and when SWE was lower, home ranges were larger on average. This relationship is shown in Figure 2.1. It should be noted that sample sizes for the average winter home range size were small; data from 4, 6, 6, and 3 moose were used to estimate average winter home range sizes in 2007, 2008, 2009, and 2010, respectively. The linear correlation between these two measures was r = -0.95.

Resource Selection Modeling

Available Locations. For the within home range scale of habitat selection, available locations for each moose were selected at random from within the home range of that moose. These available locations for each moose can be seen in Appendix H. For the study area scale of habitat selection, a winter study area was defined with collared cow and additional aerial moose locations. This final study area and the aerial moose locations used to create the area are displayed in Figure 2.2. An example of the available locations selected for each moose from within the study area is displayed in Figure 2.3.

Cover Type Selection. If cover types were used at the same rate as their availability, the selection ratio would be 1.0. A section ratio of 2.0 would mean that a cover type was selected for at twice the rate than would be expected if it were used at the same rate as its availability (at random). The use of the word “significant” in the section

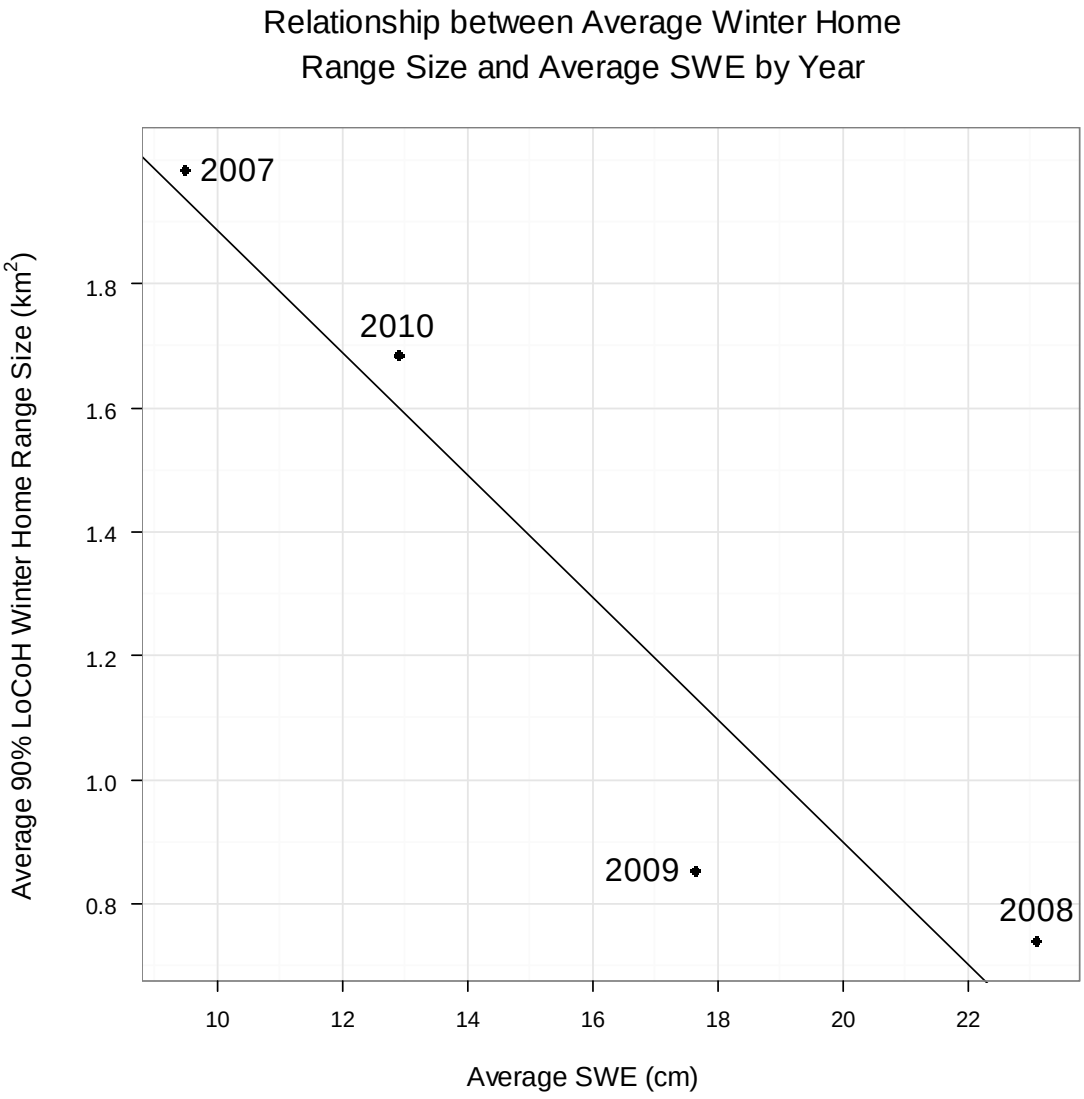

Figure 2.1: A plot showing the relationship between SWE and winter home range size for the four winters when cow moose were collared, 2007-2010. There was a strong negative relationship between the average SWE for each winter and the average 90% LoCoH home range size.

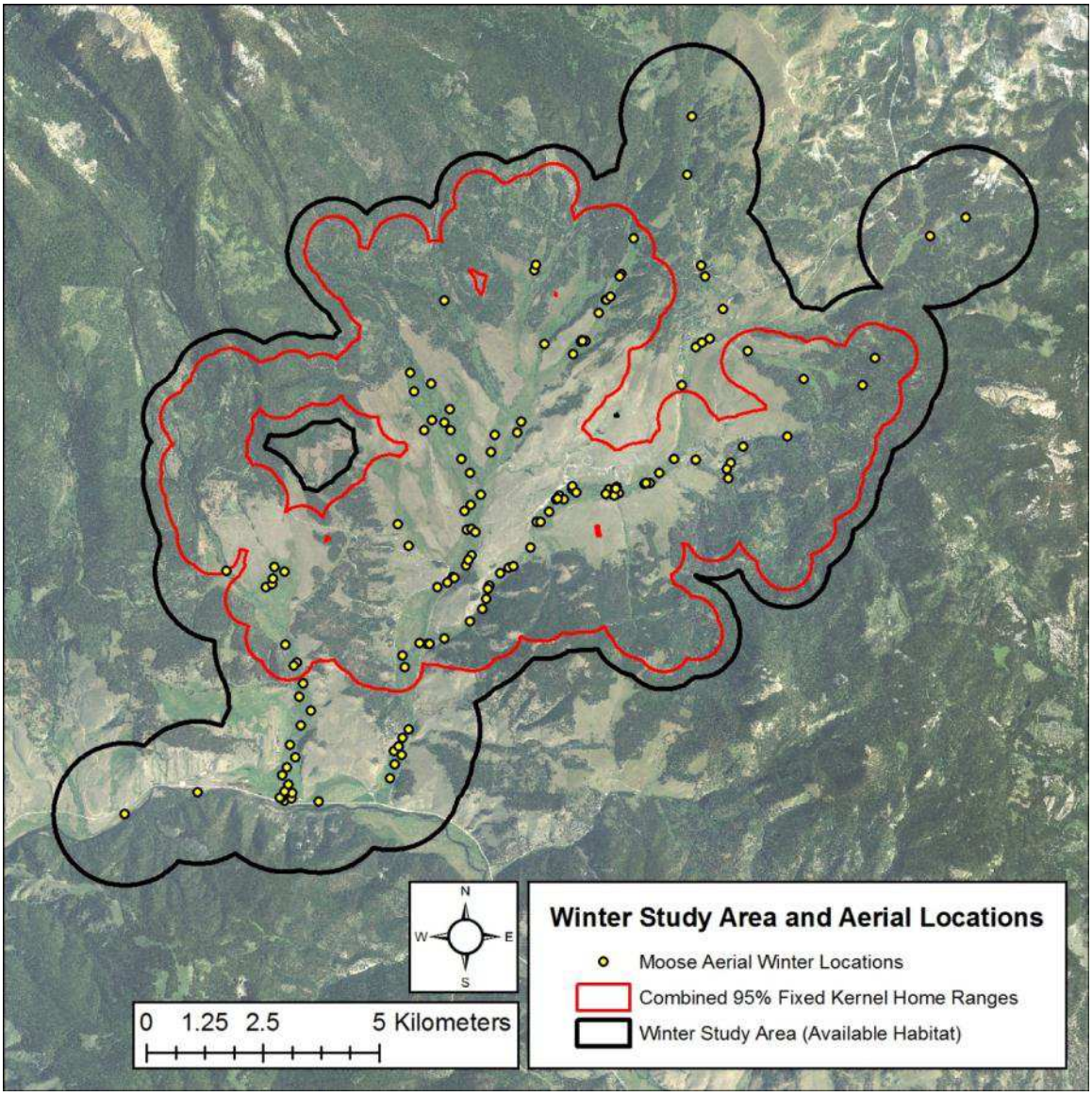

Figure 2.2: The entire winter study area, representing available habitat at the study area scale, is displayed above in black. For comparison, the combined 95% fixed kernel home ranges are shown in red (excluding the lone moose which migrated off the study area). The winter aerial locations (2001-2008, 2010, & 2011) used in part to define the study area are also displayed as yellow dots.

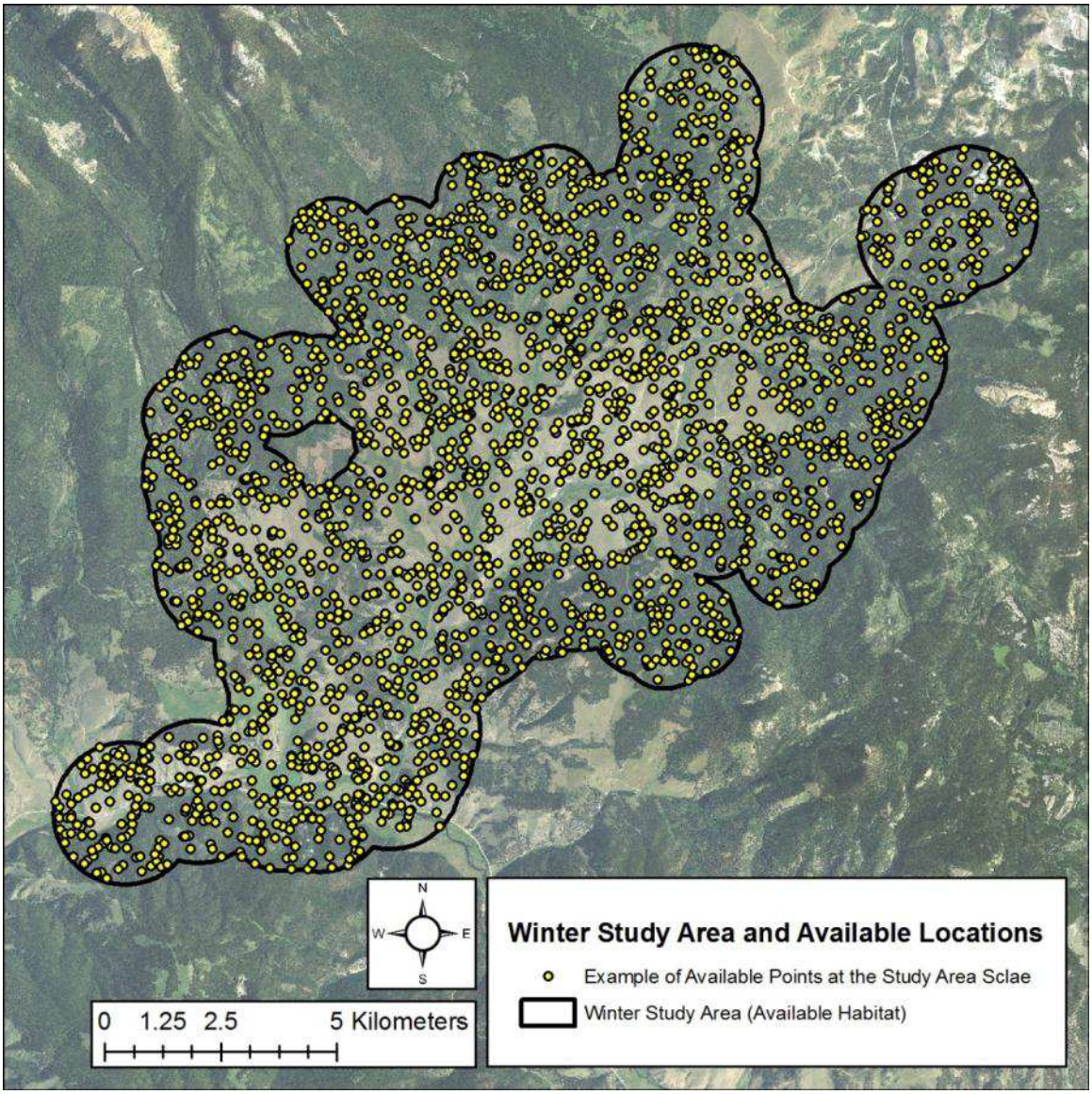

Figure 2.3: An example of the random locations generated within the study area, which represented the available habitat resources at the study area scale.

refers to a 95% confidence interval (CI) or a comparison of selection ratios at an alpha level of $\alpha = 0.05$ based on the methods of Manly et al. (2002). Bonferroni confidence intervals ($1- \alpha/n$) were used when comparing multiple (n) selection ratios simultaneously to test for differences between selection ratios.

Moose strongly selected for the WILLOW cover type at both scales, with selection ratios of 3.53 (95% CI: 2.75, 4.31) and 5.40 (95% CI: 4.53, 6.45) at the home range and study area scales, respectively. The WILLOW cover type was also selected for at a significantly greater ratio than any other cover type. ASPEN was also used at a slightly greater frequency than expected, with ratios of 1.75 (95% CI: 0.78, 2.73) and 1.27 (95% CI: 0.60, 1.93) at the home range and study area scales, respectively. However, the 95% CIs for the ASPEN cover type included one at both scales, indicating no significant selection for or against ASPEN. The selection ratios for the FOREST and GRASSLAND indicated that these cover types were used less than expected at both scales. The 95% CIs for FOREST and GRASSLAND both excluded one. The OTHER category was used equal to its availability at the study area scale (1.07), but selected less often then expected at random at the home range scale (0.69). These data are shown in Table 2.2, including the selection ratios, 95% CIs, and the pairwise comparisons of the selection ratios. Due to relatively small sample sizes, both the ASPEN and OTHER cover type selection ratios and comparisons should be interpreted cautiously. Differences in selection ratios between individual moose were small and are not presented here.

Two-Stage Modeling and Validation. Initial examination of the habitat selection covariates revealed that no pairs of covariates had correlations > |0.6|. The largest

Table 2.2: The population-level selection ratios, standard errors, and 95% confidence intervals for cover type selection at both scales of availability examined in this study. The results of the pairwise comparison of selection ratios are also shown.

Scale		Selection Ratio and CIs				Selection Ratio Comparison[1]				
Home Range	Cover Type	W_i	SE	(95% CI)		Willow	Aspen	Other	Forest	Grass
	Willow	3.53	0.30	2.75	4.31	NA				
	Aspen	1.75	0.38	0.78	2.73		NA			
	Other	0.69	0.08	0.49	0.88			NA	X	
	Forest	0.70	0.06	0.56	0.85			X	NA	
	Grassland	0.46	0.04	0.36	0.56					NA
Study Area	Cover Type	W_i	SE	(95% CI)		Willow	Aspen	Other	Forest	Grass
	Willow	5.49	0.37	4.53	6.45	NA				
	Aspen	1.27	0.26	0.60	1.93		NA	X		
	Other	1.07	0.27	0.38	1.76		X	NA		
	Forest	0.52	0.09	0.30	0.75				NA	X
	Grassland	0.54	0.06	0.38	0.69				X	NA

[1] An 'X' indicates that the selection ratios for the pairwise comparison of cover types using Bonferroni CIs were **not** significantly different at a 95% confidence level ($\alpha = 0.05$); this comparison does not apply within a single cover type (NA).

correlation between covariates was -0.496, between the ELEVATION and DISTANCE TO CONIFER COVER. Scatterplots of all covariate pairs did not reveal any notable nonlinear issues. No covariates had variance inflation factors (VIFs) > 5. The largest VIF was 1.24 (ELEV). Therefore, no covariates or pairs of covariates were excluded from the final a priori model list, which totaled 79 models (Appendix I).

Due to the rarity of two cover types, ASPEN and OTHER (see Figure 2.4), the cover types had to be further consolidated. As some moose did not have used or available points in one or both of these categories, the respective coefficients could not be estimated in the two-stage modeling framework (Fieberg et al. 2010). ASPEN was combined with WILLOW, as both cover types provided potential browse resources but minimal closed canopy cover in winter. The OTHER cover type was consolidated with

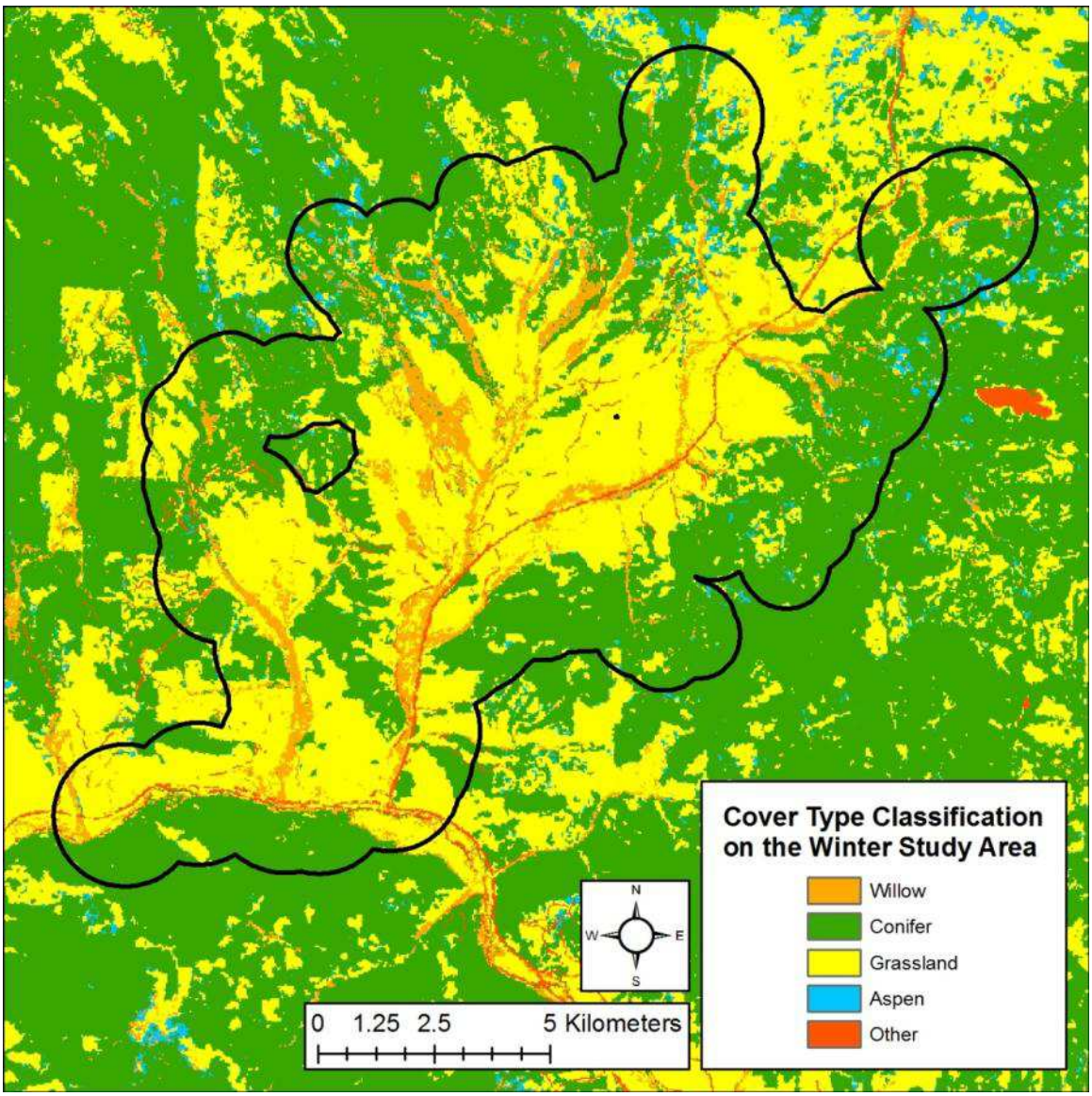

Figure 2.4: A map showing the cover types classified on the study area and surrounding terrain (based on consolidated cover types from the Montana Land Cover Map, MTNHP 2010). This map contains the cover types as originally reclassified, prior to consolidating the cover types to WILLOW & ASPEN, CONIFER, and GRASSLAND & OTHER. Note the relative rarity of ASPEN and OTHER cover types on the study area.

GRASSLAND, as these cover types would largely be buried in snow and not provide any cover or foraging opportunity. These intuitive combinations were confirmed by the cover type selection ratios at both scales, as both ASPEN and WILLOW were selected for by moose, while neither the OTHER nor the GRASSLAND cover types were selected for at a rate greater than their availability. After combining the cover types, indicator variables were created, one for WILLOW & ASPEN, the other for CONIFER cover. Therefore, the GRASSLAND & OTHER category was used as the reference category with which to compare moose habitat selection in other cover types. These indicator variables were then used to model cover type selection.

At the home range scale of habitat selection modeling, two models had ΔAIC scores < 4 (Table 2.3), out of the a priori model list of 79 models. However, the second model (Model 1) contained the uninformative interaction of COVERTYPE×SWE, which only reduced the model deviance by 0.542 AIC and did not overcome its 4.0 AIC penalty (Arnold 2010). An examination of the COVERTYPE×SWE coefficients in Model 1 confirmed that these coefficients should not be interpreted as having any ecological importance (uncertainty was high and coefficient values were small). This left a single top model (Model 38) from which to draw inference. The coefficients and 95% CIs from this first stage of modeling are shown in Table 2.4 in the Original Coefficients column.

Using Model 38, the second stage of analysis was completed by fitting the data for individual moose to estimate coefficients and obtain population level coefficient means and standard errors from the distribution of individual coefficients. These data are displayed in Table 2.4 in the Averaged Coefficients column.

Table 2.3: Model selection results for winter habitat use by cow moose on the Mount Haggin WMA analyzed at the home range scale. All models are ranked according to AIC and presented along with the number of parameters (k), the ΔAIC value (the change in AIC value relative to the best model), and the relative model weight (w_i). Abbreviations are: COVERTYPE (either WILLOW & ASPEN, CONIFER, or GRASSLAND & OTHER), DIST_CON (distance to conifer cover edge, in meters), DIST_WIL (distance to willow cover edge, in meters), ELEV (elevation in meters), SRI (solar radiation index summed across the winter season, in megawatt hours per meter squared), and SWE (snow water equivalent). Models highlighted in gray are those which do not have uninformative parameters (Arnold 2010).

ID	Model	K	AIC	ΔAIC	w_i
38	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI	9	7913	0.000	0.750
1	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI	11	7916.4	3.458	0.133

Table 2.4: Coefficient values (β_i) and 95% confidence intervals (in parentheses) for the covariates in the top model explaining winter habitat selection analyzed at the home range scale. Abbreviations are the same as those in Table 2.3. Coefficients in bold have confidence intervals that do not span zero.

	Model 38	
Coefficient	Original Coefficients	Averaged Coefficients
CONIFER	**0.64538**	0.30433
	(0.5053, 0.78547)	(-0.02169, 0.63035)
WILLOW_ASPEN	**1.24768**	**0.87821**
	(1.12642, 1.36894)	**(0.64927, 1.10715)**
DIST_CONIFER	**0.00383**	0.01219
	(0.00276, 0.00491)	(-0.00623, 0.0306)
DIST_WILLOW	**-0.01478**	-0.01687
	(-0.01768, -0.01188)	(-0.04753, 0.0138)
ELEV	0.16365	1.34337
	(-0.21975, 0.54705)	(-2.90711, 5.59385)
SRI	**0.41773**	**0.59438**
	(0.26162, 0.57384)	**(0.17639, 1.01237)**
DIST_CON×SWE	**-0.00030**	**-0.00107**
	(-0.00036, -0.00023)	**(-0.00197, -0.00018)**
DIST_WIL×SWE	**0.00033**	-0.00013
	(0.00018, 0.00048)	(-0.00168, 0.00141)
ELEV×SWE	**-0.02746**	-0.06153
	(-0.04915, -0.00577)	(-0.27637, 0.15332)

At the study area scale of habitat selection modeling, four models had ΔAIC scores < 4 (Table 2.5) out of the a priori model list of 79 models. However, the third and fourth models contained the uninformative parameter of SRI, which only reduced the model deviance by 0.138 and 0.167 AIC (third and fourth models, respectively) and did not overcome its 2.0 AIC penalty (Arnold 2010). This left two competing top models (Model 2 and Model 39) from which to draw inference, the difference being that Model 2 included the COVERTYPE×SWE interaction while Model 39 excluded that interaction. The coefficients and 95% CIs from this first stage of modeling are shown in Table 2.6 in the Original Coefficients columns for these two models.

Table 2.5: Model selection results for winter habitat use by cow moose on the Mount Haggin WMA analyzed at the study area scale. All models are ranked according to AIC and presented along with the number of parameters (k), the ΔAIC value (the change in AIC value relative to the best model), and the relative model weight (w_i). Abbreviations are: COVERTYPE (either WILLOW & ASPEN, CONIFER, or GRASSLAND & OTHER), DIST_CON (distance to conifer cover edge, in meters), DIST_WIL (distance to willow cover edge, in meters), ELEV (elevation in meters), SRI (solar radiation index summed across the winter season, in megawatt hours per meter squared), and SWE (snow water equivalent). Models highlighted in gray are those which do not have uninformative parameters (Arnold 2010).

ID	Model	K	AIC	ΔAIC	w_i
2	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE	10	6101.7	0.000	0.396
39	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE	8	6102.4	0.629	0.289
1	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI	11	6103.6	1.862	0.156
38	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI	9	6104.2	2.462	0.116

Table 2.6: Coefficient values (β_i) and 95% confidence intervals (in parentheses) for the covariates for the top two models explaining winter habitat selection analyzed at the study area scale. Abbreviations are the same as those in Table 2.5. Coefficients in bold have confidence intervals that do not span zero.

	Model 02		Model 39	
Coefficient	Original Coefficients	Averaged Coefficients	Original Coefficients	Averaged Coefficients
CONIFER	**1.13271**	1.49109	**0.74299**	0.26037
	(0.6382, 1.62721)	(-2.50653, 5.4887)	**(0.5953, 0.89067)**	(-0.63619, 1.15692)
WILLOW_ASPEN	**1.24269**	4.85742	**1.34984**	**0.97799**
	(0.80203, 1.68335)	(-1.72949, 11.44433)	**(1.21372, 1.48596)**	**(0.59497, 1.36101)**
DIST_CONIFER	**0.00508**	0.00227	**0.00462**	0.00218
	(0.00387, 0.00629)	(-0.02268, 0.02721)	**(0.00353, 0.00571)**	(-0.01699, 0.02135)
DIST_WILLOW	**-0.01419**	-0.01750	**-0.01299**	-0.02866
	(-0.01721, -0.01116)	(-0.0669, 0.0319)	**(-0.01567, -0.01031)**	(-0.07984, 0.02251)
ELEV	**-0.00330**	-1.55320	**-0.29982**	-1.38207
	(-0.00549, -0.0011)	(-3.89938, 0.79298)	**(-0.51425, -0.08538)**	(-3.29524, 0.5311)
CONIFER×SWE	-0.02116	-0.03505		
	(-0.04715, 0.00483)	(-0.24024, 0.17015)		
WIL_ASP×SWE	0.00609	-0.17547		
	(-0.01767, 0.02985)	(-0.45735, 0.10641)		
DIST_CON×SWE	**-0.00034**	-0.00069	**-0.00032**	-0.00069
	(-0.00042, -0.00027)	(-0.00183, 0.00044)	**(-0.00038, -0.00025)**	(-0.00158, 0.00021)
DIST_WIL×SWE	**0.00026**	-0.00003	**0.00019**	0.00045
	(0.00011, 0.00041)	(-0.00232, 0.00226)	**(0.00006, 0.00033)**	(-0.00185, 0.00275)
ELEV×SWE	**-0.00018**	0.02279	**-0.01947**	0.01513
	(-0.00030, -0.00006)	(-0.0839, 0.12949)	**(-0.03078, -0.00816)**	(-0.06972, 0.09998)

Using Models 2 and 39, the second stage of analysis was completed by fitting the data for individual moose to estimate coefficients and obtain population level coefficient means and standard errors from the distribution of individual coefficients. These data are displayed in Table 2.6 in the Averaged Coefficients columns of the respective models.

In the paragraphs and figures below, interpretations of individual covariates are presented. Although these interpretations only reference individual covariates, the statements must be taken in the context of all other covariates in the model (e.g. the association between distance to willow and habitat selection was negative, after

accounting for all other covariates in the model). No individual covariate can be interpreted independently from the other covariates in the model.

The original coefficient signs were largely in line with predictions. For all models at both scales, WILLOW & ASPEN and CONIFER were selected over GRASSLAND & OTHER, with the WILLOW & ASPEN coefficient being larger than the CONIFER coefficient. The only model that included a cover type interaction was Model 2 at the study area scale. In this model, the coefficients for the WILLOW & ASPEN×SWE and CONIFER×SWE both appeared to have a large amount of uncertainty and the plausible values for both included both negative and positive coefficients. This suggested that the effect of these coefficients may be negligible in terms of ecological impact. Examining the uninformative COVERTYPE×SWE interactions at the home range scale produced a similar conclusion. This subject is revisited in the RSF map discussion below.

For all models at both scales of selection, the DIST_CONIFER and the DIST_CONIFER×SWE covariates were included in the top models. In all models, the interaction coefficient was negative, meaning that greater distances to conifer cover were selected against as SWE increased. This was in line with my predictions. However, at low SWE levels, the association between distance to conifer cover and habitat selection was positive, meaning that greater distances from conifer were selected for when SWE was low. This can be seen in the plots in Figure 2.5, which show the impact of the SWE interaction on the association between distance to conifer and relative habitat selection. These plots are derived from Model 38 at the home range level of selection, but plots from the top study area scale models produce similar results.

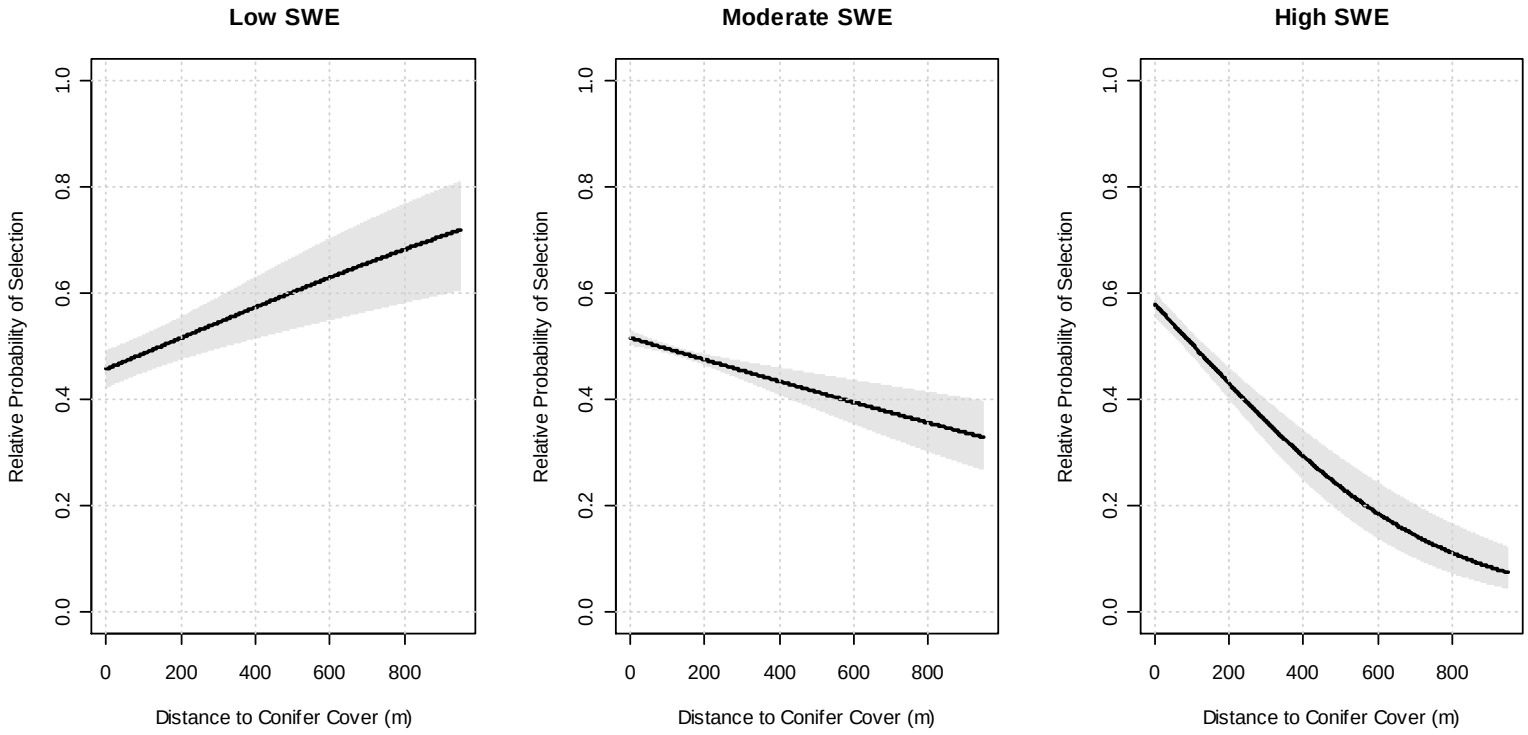

Figure 2.5: A plot showing the interactive effect of SWE on the predicted relationship between distance to conifer cover and relative selection by cow moose, after accounting for all other covariates in the model. The gray band represents the 95% confidence interval. This plot is based on the original coefficients from the top home range selection model (Model 38). All other covariates were held at their respective means for this plot, excluding SWE which was plotted at SWE = 8.96, 15.66, and 23.00 cm to represent low, moderate, and high levels of SWE.

For all models at both scales, DIST_WILLOW coefficient sign was negative as predicted, indicating that greater distances from willow were selected against. When the interaction with SWE was interpreted, this negative relationship became less strong at greater SWE levels, as predicted. The predictive plots of this relationship can be found in Figure 2.6, which demonstrated strong selection for short distances to conifer at all SWE levels and small changes in this association as SWE increased. These plots are derived from Model 38 at the home range level of selection, but plots from the top study area scale models produced similar results.

The ELEVATION and ELEVATION×SWE interaction coefficients were as predicted for the study area models, with higher elevations selected against and with increasing intensity at higher SWE levels. At the home range scale, the ELEVATION and ELEVATION×SWE coefficients showed that higher elevations were actually selected for when SWE < 6 cm, which was a rare occurrence during the winter season. Under most circumstances (SWE > 6 cm), higher elevations were selected against. Aside from the selection for higher elevations at low snowpack, these associations were as predicted at the home range scale. Plots of the predicted association between ELEVATION and the probability of habitat selection for different levels of SWE are shown in Appendix J. These plots are derived from Model 38 at the home range level of selection, but plots from the top study area scale models produce similar results as the SWE levels used for these plots were > 6 cm (SWE levels were 8.96, 15.66, and 23.00 cm).

Finally, the SRI coefficient for the home range model was positive as predicted, with areas receiving greater solar radiation being selected for. This covariate was absent

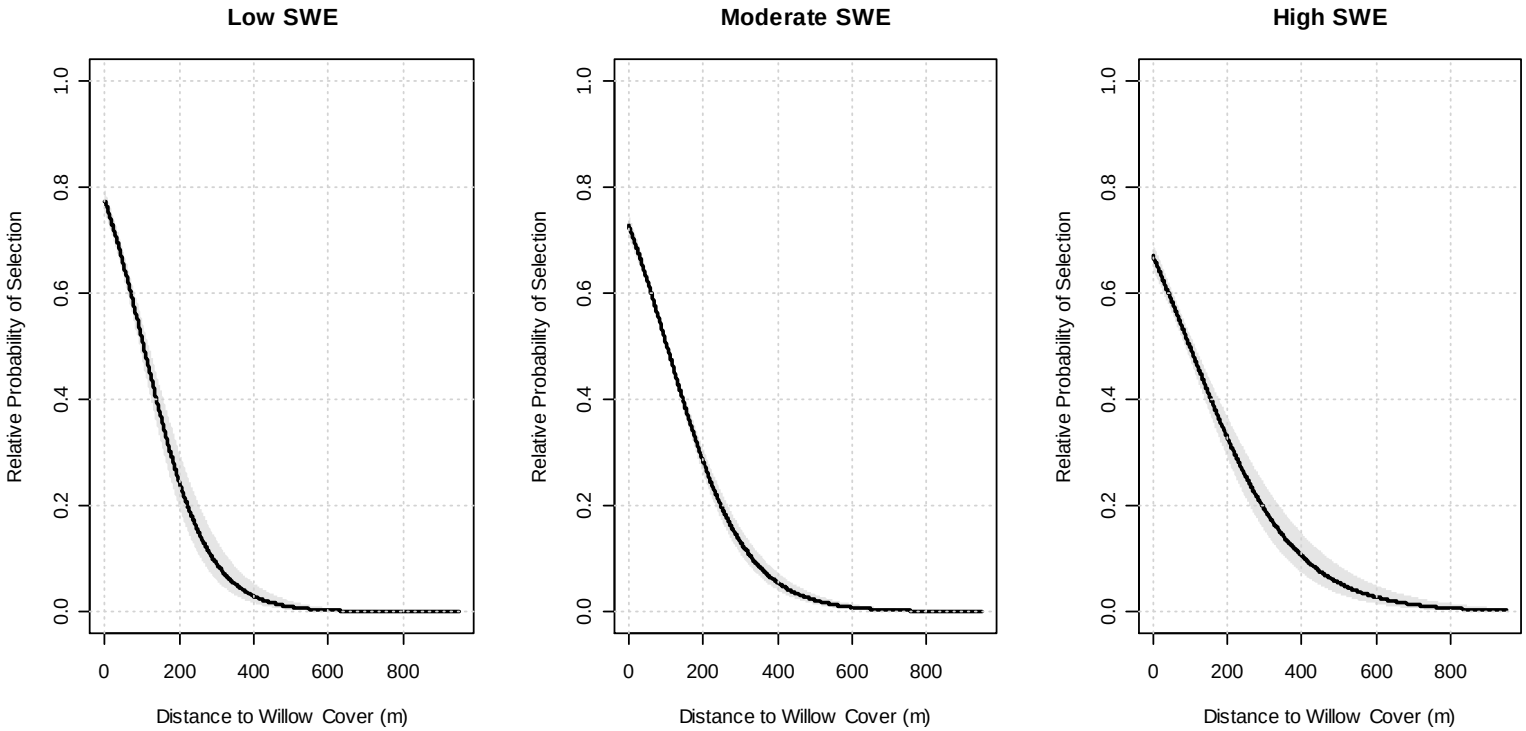

Figure 2.6: A plot showing the interactive effect of SWE on the predicted relationship between distance to willow cover and relative selection by cow moose, after accounting for all other covariates in the model. The gray band represents the 95% confidence interval. This plot is based on the original coefficients from the top home range selection model (Model 38). All other covariates were held at their respective means for this plot, excluding SWE which was plotted at SWE = 8.96, 15.66, and 23.00 cm to represent low, moderate, and high levels of SWE.

from the top study area models, suggesting minimal or zero association with moose habitat selection at that scale.

Aside from the absence of the SRI covariate in top models at the study area scale, there were no other major differences between the top models at the home range and study area scales. Both scales included all other covariates in the top models, including the COVER TYPE×SWE interaction (which was included in the second, nested model in the home range scale analysis – see Table 2.3). None of the coefficients in comparable models (e.g. Model 38 and Model 39 from the home range and study area scales, respectively) were notably different. In fact, the coefficient values were quite similar, often differing by only negligible amounts, suggesting that the covariates were not associated with greater selection at one scale or the other, counter to what I had predicted.

A comparison of the original (stage 1) and averaged coefficients (stage 2, averaged across individual moose) revealed that the averaged coefficients were only slightly different from the original coefficients, but that the estimated variability in averaged coefficients was higher, as demonstrated by the larger CIs (Tables 2.4 and 2.6). The only notable and unexpected sign change was for the ELEVATION×SWE interaction at the study area scale, but the uncertainty in this coefficient was so large that both positive and negative values were equally plausible. Although the averaged coefficients showed higher variability, they were used to create the RSF maps as these averages were more likely to be representative of the population means.

In order to produce RSF maps, I needed to define multiple SWE levels to produce representative maps for different SWE values and for validating the models. I examined

a smoothed histogram of the SWE values in the dataset (Figure 2.7) and identified two natural breaks in the data, at SWE values of 12.5 cm and 18.5 cm. Splitting the distribution at these points created three SWE ranges (0-12.5, 12.5-18.5, 18.5-26.5), which had average values of 8.96, 15.66, and 23.00 cm. These values corresponded to the 10^{th}, 37^{th}, and 75^{th} percentiles of the SWE distribution. The three average SWE values were then used to model periods of low, moderate, and high SWE.

Using the averaged coefficients from the top home range and study area scale models, I created sets of three RSF maps using the low, moderate, and high SWE levels. These maps were then used to validate the models using the randomly selected reserved used locations (10%). The reserved locations were plotted on the map with the SWE level (low, moderate, high) corresponding to the SWE value of that reserved location. Approximately 20%, 35%, and 45% of the reserved locations had SWE values that corresponded to the SWE ranges of the low, moderate, high SWE maps. Then the bin values (1-20) were extracted to the reserved locations and pooled across the SWE levels to determine the total accuracy of the models.

For the home range scale model, Model 38, 64.0% of the reserved locations fell within the top 25% of RSF bins. Additionally, 90.5% of the locations were within the top 50%. The top study area scale model, Model 2, had 75.3% and 88.3% of the reserved locations within the top 25% and 50% of RSF bins, respectively. For the other top study area scale model, Model 39, 74.0% and 88.3% of the reserved locations fell within the top 25% and 50% of RSF bins, respectively. The data for each model are broken down by RSF bins in Appendix K.

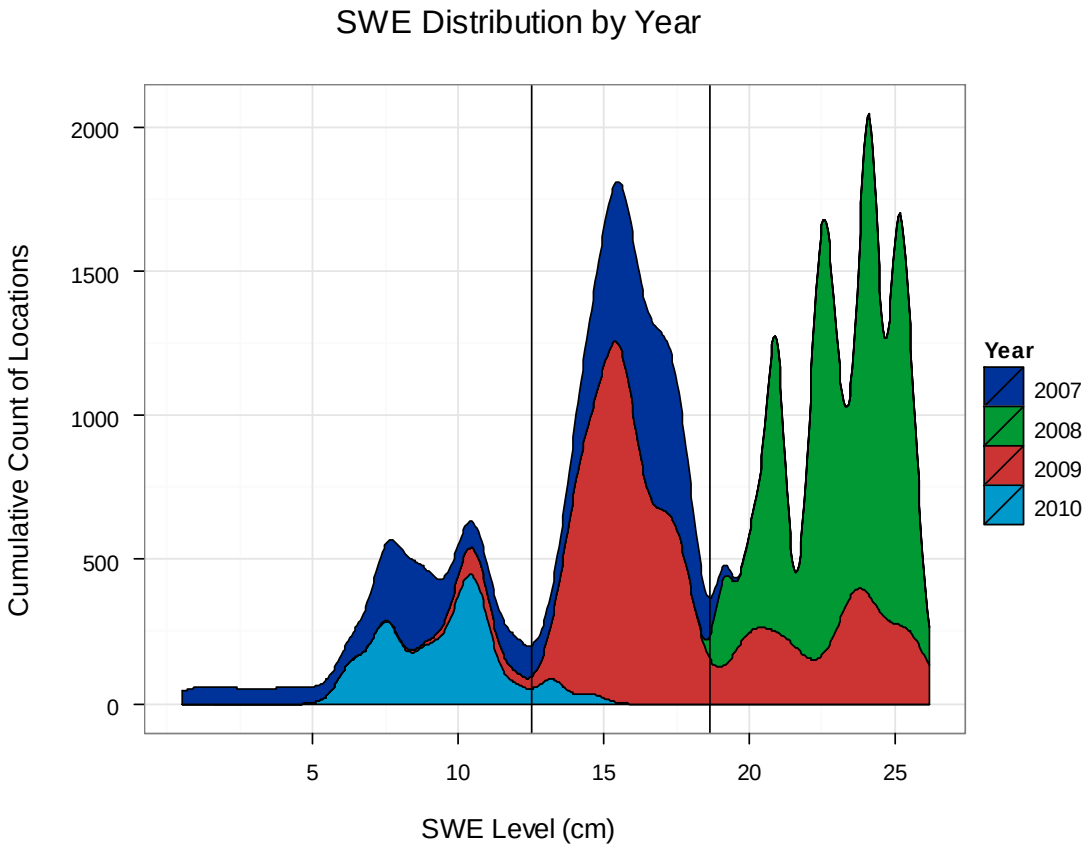

Figure 2.7: A smoothed histogram of the SWE values observed during this study, broken down by year the data were collected. These values are strictly for the winter periods when the collared moose locations were recorded (e.g. January 2008 is not represented). Note the natural breaks at SWE values of 12.5 cm and 18.5 cm (vertical lines).

Additionally, the study area scale RSFs were extrapolated beyond the study area to show potentially suitable habitat outside of the study area boundary. Most of the habitat with a high probability of moose use was within the study area. A set of RSF maps depicting low to high SWE conditions for the top study area scale model (Model 2) are displayed in Figures 2.8, 2.9, and 2.10. A corresponding set of maps for the other top model (Model 39) are available in Appendix L. There were minimal differences in the sets of maps between these two models.

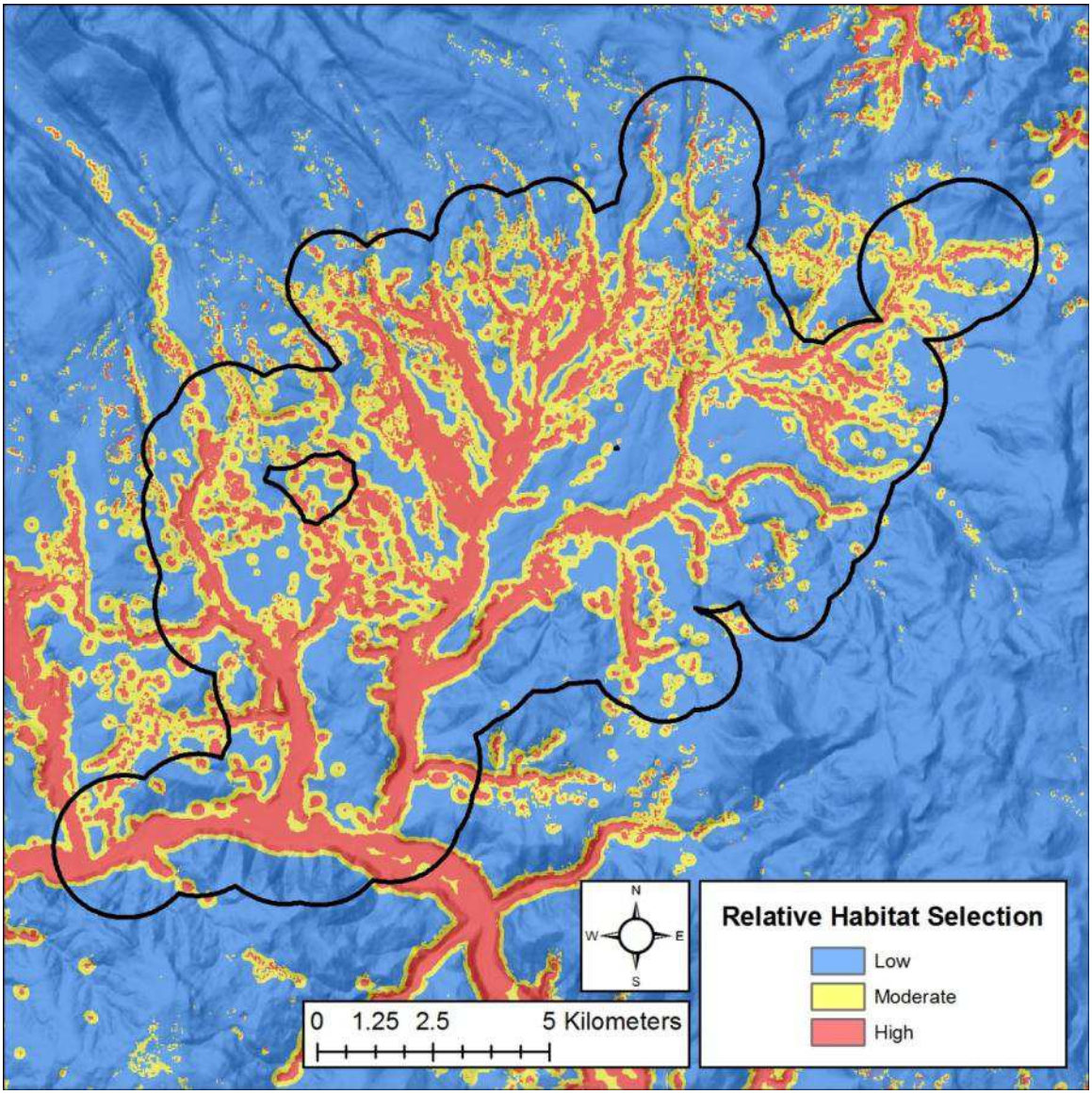

Figure 2.8: This map shows the relative habitat selection across the study area and surrounding area by cow moose during periods of low snowpack (SWE = 8.96 cm). Model 2 from the study area scale analysis was used to create this map. The RSF values were grouped into 3 bins: low probability (0-50%), moderate probability (50-75%), and high probability (75-100%).

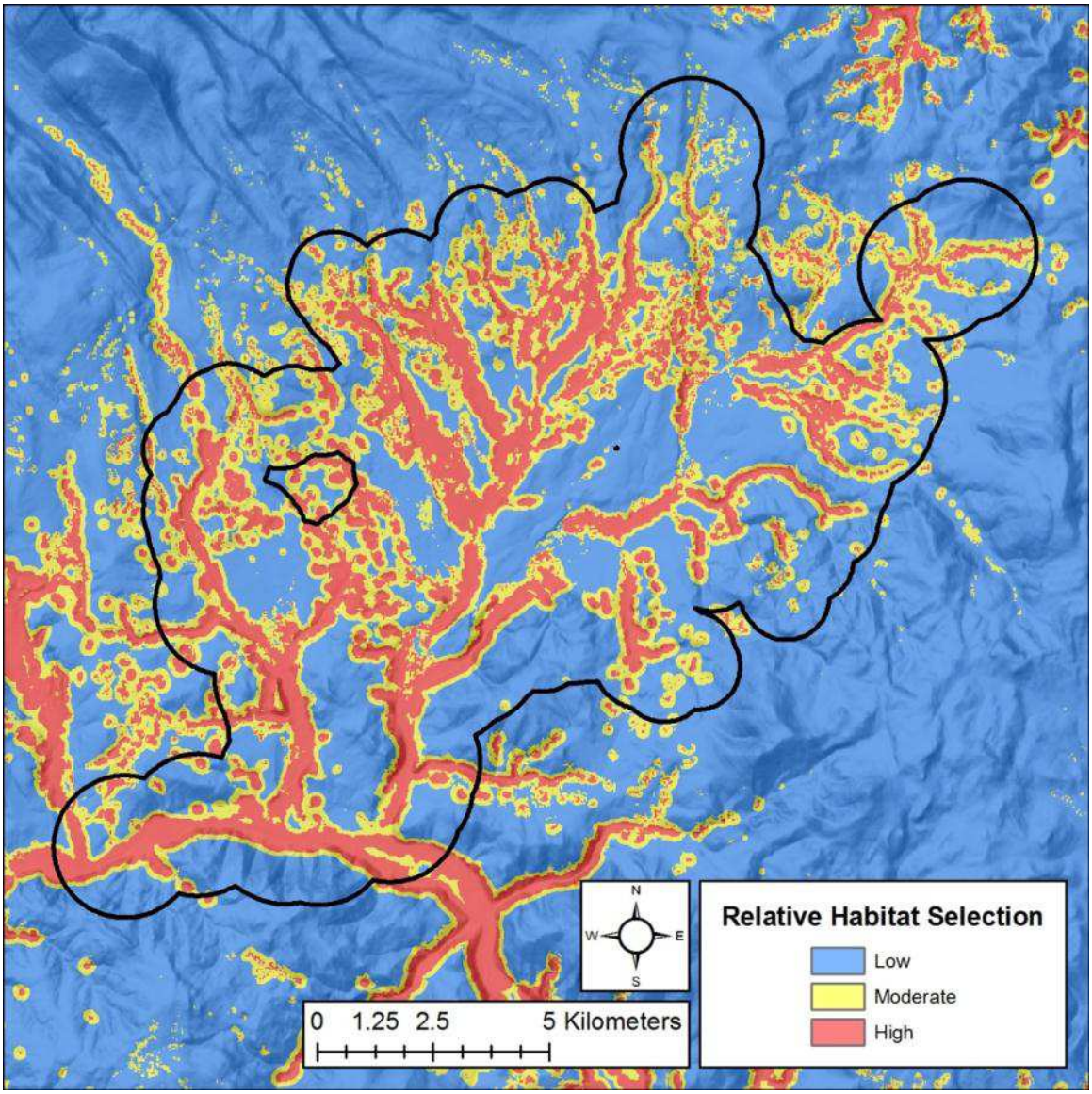

Figure 2.9: This map shows the relative habitat selection across the study area and surrounding area by cow moose during periods of moderate snowpack (SWE = 15.66 cm). Model 2 from the study area scale analysis was used to create this map. The RSF values were grouped into 3 bins: low probability (0-50%), moderate probability (50-75%), and high probability (75-100%).

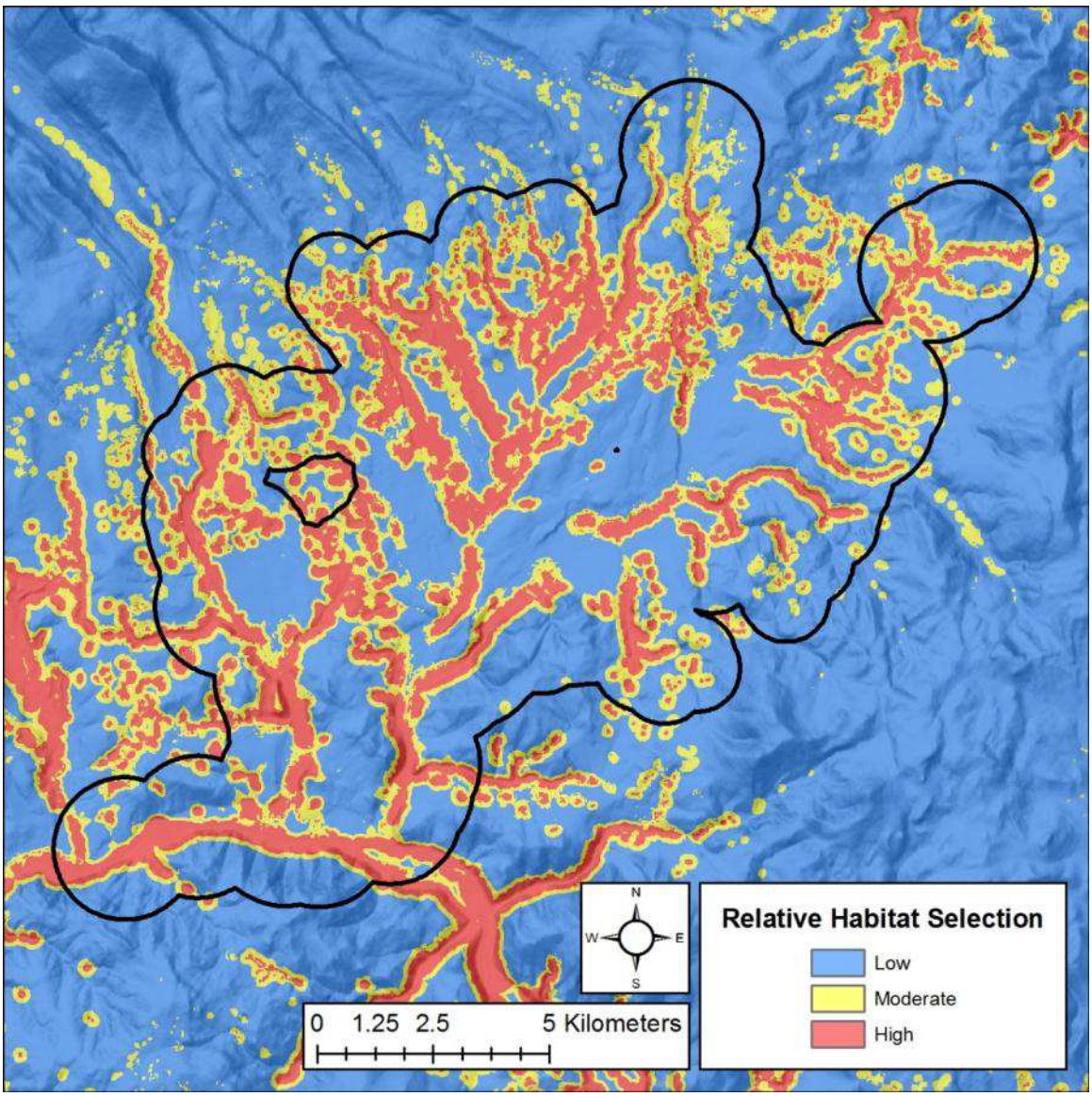

Figure 2.10: This map shows the relative habitat selection across the study area and surrounding area by cow moose during periods of high snowpack (SWE = 23.00 cm). Model 2 from the study area scale analysis was used to create this map. The RSF values were grouped into 3 bins: low probability (0-50%), moderate probability (50-75%), and high probability (75-100%).

The post hoc analysis of interactive effect of temperature showed that an interaction between temperature and distance to conifer cover (DIST_CONIFER×TEMP) did substantially improve model fit of the top home range scale model, reducing the AIC score of Model 38 by 24.47 AIC units. Distances closer to conifer cover were selected for when temperatures increased. A COVER TYPE×TEMP improved slightly fit as well (a reduction of 6.82 AIC units), but a model with both interactions did not perform better than the model that only included the DIST_CONIFER×TEMP interaction. A set of plots showing the relationship between distance to conifer cover and habitat selection at low, moderate and high temperatures can be found in Appendix J.

Slightly different post hoc analysis results were obtained at the study area scale, where the combination of the DIST_CONIFER×TEMP and COVER TYPE×TEMP interactions showed the greatest improvement. As with the home range scale, distances closer to conifer cover were selected for when temperatures increased, and selection for conifer cover increased when temperatures increased (willow cover selection did not change). The addition of these two interactions to the two top models reduced the AIC scores of Models 2 and 39 by 16.60 and 17.07 AIC units, respectively.

Discussion

In this study, my objectives were to define the seasonal distribution and habitat use for the moose population on the Mount Haggin Wildlife Management Area and surrounding public and private lands, as well as determining the habitat selection patterns of these moose. Specifically, I tested hypotheses in the form of resource selection

function models regarding the associations between habitat attributes (e.g. cover type, distance to conifer cover, elevation) and habitat selection by cow moose during the winter season. Interactions with a temporal variable for snow water equivalent (SWE) were also examined, since changes in snowpack have been shown to drive moose habitat selection patterns. The goal of this research was to improve biologists' understanding of the importance of specific habitat attributes to local moose populations by estimating resource selection functions at multiple scales and interpret those results to improve management techniques and strategies.

As part of the descriptive portion of this research, seasons were estimated and home ranges calculated. The winter and summer seasons were determined from the movement rates of the population of moose on the study area since the moose were non-migratory. These dates were comparable to seasons used in other studies of moose ecology and habitat selection. In this study, winter began in early January and ended in mid to late April. The date range of 1 Jan to 15 Apr or 30 Apr is frequently used by moose researchers for the winter season for both migratory and non-migratory populations as it coincides with snow conditions (e.g. Schwab and Pitt 1991, Dussault et al. 2005, Pool and Stuart-Smith 2006, Baigas 2008), although winter dates as early as mid-November and as late as early June have been noted by others with migrating moose populations (Langley 1993, Becker 2008). Like other studies, I found that moose movements that indicated restricted use during winter were largely tied to snowpack conditions. Researchers should be cautious in applying arbitrary season dates, especially across years, as snow conditions are likely to vary from year to year, and therefore would

affect the length and dates of a winter season. Dates for individual moose seasons may be necessarily in some situations as it was for a few individuals in this study (see also Matchett 1985 and Becker 2008), since variability among individuals is common and may bias results if ignored (Wal and Rodgers 2009).

Home ranges for moose generally consist of core areas of use connected by travel between those areas (Van Dyke et al. 1995a, Hundertmark 2007). Local convex hull (LoCoH) methods for defining home ranges are particularly well suited to delineating these core areas and the approximate spatial extent (size) of these areas that are critical for moose winter range requirements. LoCoH home ranges also excel in identifying hard edges, for example between cover types, where moose may strategically choose to use one cover type but avoid another. In this study, the LoCoH home ranges demonstrated that moose were confining most of their use to core areas in willow cover types, in many cases near conifer cover. The LoCoH home ranges in the figures in Appendix G highlight this pattern of use. This was further confirmed by the cover type selection analysis, which showed strong selection for willow cover types.

In terms of size, the LoCoH home ranges calculated for cow moose during the winter and summer seasons in this study were similar to those noted elsewhere. I calculated the average 90% LoCoH home ranges to be 1.170 km^2 and 2.805 km^2 for winter and summer, respectively. These compare to 4.5 km^2 and 13.2 km^2 for winter and summer ranges for cow moose near Jackson Hole, Wyoming (Becker 2008) and 2.19 km^2 winter ranges for cow moose in the Snowy Range of Wyoming (Baigas 2008). The Jackson Hole study was on a floodplain riparian winter range, similar to the MHWMA,

while the Snowy Range was a mix of riparian and conifer winter range types. Evidently, moose on the MHWMA did not use as much area during the winter and summer seasons compared to other recent studies of moose in the Northern Rockies. This suggests that moose on the MHWMA winter range were able to fulfill their needs in a relatively small area and, consequently, could have a substantial impact on the browse species in areas occupied, especially during the winter season.

Perhaps one of the most surprising findings from this study was that cow moose collared on the MHWMA winter range were using the area as summer range. Aside from one moose that migrated to a winter range off the study area, there was minimal evidence of migration and significant overlap between winter and summer ranges. On average, 56.0% of a winter range for an individual moose was used as summer range. This pattern in habitat use is not unique to the MHWMA, as Peek (2007) notes that multiple floodplain riparian winter ranges have been shown to support year-round populations of non-migratory moose (e.g. Becker 2008). Additionally, the summer ranges in this study were centered on the willow communities, identical to the winter ranges. The summer LoCoH home ranges presented in Appendix G highlight this pattern. This finding emphasizes the importance of the willow communities on the MHWMA, and perhaps in other similar winter and summer habitats nearby.

The winter selection ratios of cover types show that cow moose were selecting for willow habitat types at 3.53 and 5.40 times the rate expected (at the home range and study area scales, respectively) if moose were only using willow at random. This was in line with my predictions that moose would strongly select for this cover type due to its

abundant, palatable browse source. Numerous other studies have found this selection pattern, which is a consistent preference for all moose subspecies across the holarctic ecoregion. Based on the selection ratios, cow moose selected against conifer cover ($w_i < 1.0$), but this simple analysis did not account for any other covariates that may impact selection of conifer cover, particularly the temporal variables addressed in the modeling discussion below. As I predicted, grasslands were selected against, which is unsurprising as they provide few resources when buried in snow that may exceed 100 cm in depth.

In terms of model selection for the RSF, most covariates examined were associated with moose habitat selection. These positive and negative associations between the covariates and moose habitat selection were generally in the predicted direction for the original and averaged coefficients and supported findings from other moose populations (e.g. Jenkins 1985, Langley 1993, Van Dyke et al. 1995b, Tyers 2003, Poole and Stuart-Smith 2005, Peek 2007). The top models for habitat selection at both scales included almost all of the covariates, the exception being the exclusion of SRI from the top models at the study area scale. Additionally, the COVERTYPE×SWE interaction was included in top models at both scales, but this coefficient had CIs (using the original SEs) that included zero, suggesting that the evidence for including this covariate in the model structure was weak after accounting for all the other variables in the model. This was particularly obvious in the model selection results at the home range scale, as it was clearly an uninformative parameter at this scale (Arnold 2010).

After obtaining averaged coefficients and their standard errors from the individual moose model fits, I noted that there was a large degree of variability in the coefficient

estimates, so much so that almost all of the variables had 95% CIs that included zero. This finding is not unusual, as other researchers have noted high variability among individuals when using the two-stage modeling framework (Neilsen et al. 2002, Sawyer et al. 2006, Proffitt et al. 2011) or creating individual-level RSFs (Gillingham and Parker 2008). In fact, Fieberg et al. (2010) specifically point out that variance estimators will be biased high in some instances, but do not offer a specific solution to this issue as variances are not explicitly used in RSF calculations and validation. There were two possible reasons for this unexpectedly high level of variability.

First, two-stage modeling assumes homogeneity in RSF model structure across individual moose. Only one model is applied to the collared individuals to obtain the averaged coefficients. It does not account for the fact that some moose may select habitat based on different covariates. In reality, individual moose are likely to take into account different covariates and may ignore some covariates altogether, either due to individual preference or differences in habitat availability. A quick post hoc examination of model selection using only individual data confirmed this: the model selection results were different across individual moose. However, at the individual level, model selection uncertainty was very high (large numbers of competing models) and in most cases, similar models were selected by individual moose, but the order of models in the selection results differed slightly. The use of multi-level modeling in future research of moose habitat selection instead of two-stage modeling could account for and quantify any heterogeneity among individuals and result in a more accurate assessment of moose habitat selection.

The second possible reason for high variability in coefficient estimates was that moose in different years would be subjected to different ranges of snowpack conditions. Therefore, it was possible that limited SWE ranges experienced by some moose were affecting the coefficients for the estimated SWE interactions and the covariates that had SWE interactions. Therefore, I experimentally eliminated the SWE interactions post hoc from the top model for the home range scale data and then obtained the averaged coefficients for that model (i.e. a model identical to Model 58, which included all covariates but SWE). The resulting coefficients had reduced standard errors (with minimal changes to the coefficients themselves) and the 95% CIs for the DISTANCE TO CONIFER and DISTANCE TO WILLOW coefficients now excluded zero, along with the WILLOW_ASPEN and SRI coefficients. The CONIFER cover type CI barely included zero at the 95% confidence level. Therefore, it appeared as though the high variability in the averaged coefficients for the top models at both scales was likely due, in part, to the interactions of most of the covariates with SWE. This makes sense, as some moose were only subjected to high SWE conditions in some years (e.g. 2008 in this study), while in other years moose encountered a wider range of SWE levels (e.g. 2009 in this study). The data in Figure 2.7 show what SWE levels were recorded for each year in this study. Hypothetically, the interactive effect of SWE with the spatial covariates could be different at different SWE levels and thus, variability in the individual moose coefficient estimates may be due to data collection over different SWE ranges for individual moose in different years. A YEAR variable was not examined here as it varied on a temporal scale, like SWE, and the direct effect could not be modeled within the conditional logistic

regression framework (a YEAR covariate would have been the same for the used and available points within a cluster). Also, the sample sizes for any individual year were small (n = 3-6) and the coefficient estimates for individual years (i.e. if the coefficients were only averaged within a specific year) would have been highly variable due to these small sample sizes.

Despite the substantial variability in averaged coefficients of the RSFs at both scales, the RSFs validated well. A substantial majority of locations fell within the top 25% of RSF bins for all models validated. Sixty-four percent of the reserved locations for the top home range scale model were within the top 25% of RSF bins. The study area scale models performed slightly better with approximately 75% of the reserved locations within the top 25% of RSF bins for both models. Surprisingly, the top study area models performed equally well, even though the top model included a COVERTYPE×SWE interaction, while the other model did not. The RSF maps for these two models were also quite similar (Figures 2.8-2.10 and Appendix L). While it would be ideal to validate these models with data from other moose not included in the model training, no independent data were available from my study area with the spatial precision necessary to test the models. Thus, internal validation was the only option and as such, the strong validation results should be interpreted cautiously.

Unsurprising, the RSF maps showed a strong association between areas with a high probability of cow moose selection and willow communities. As SWE increased, the selection for closer distances to conifer cover became apparent, with some willow communities further from conifer cover dropping from high to low probability of

selection. Differences in selection for high or low elevations at different SWE levels were not obvious in the RSF maps, nor were the effects of the distance to willow cover.

The extrapolated study area level RSFs showed that most of the high probability moose habitat fell within the study area boundary, while a large portion of the low probability habitat was outside of the study area. This indicates that the study area was probably well defined, and included almost all of the habitat with the highest probability of selection by moose. However, it should be noted that moose monitored in this study were sampled from the willow communities on the study area, and the possibility exists that a small portion of this moose population used the high conifer forests outside of the designated study area and was not represented in my sample. This strategy has been noted in other studies (Tyers 2003, Baigas 2008).

Lastly, I would caution against the direct application of these models to other moose populations and winter ranges elsewhere in the Northern Rockies. The transferability of RSFs and their predictive ability in other populations can be marginal, even when similar resources are available (Proffitt et al. 2011). Of course, if these RSFs can be validated with independent data from another moose population, then transferability or lack thereof to that population can be determined.

In summary, willow cover types were strongly selected for on the MHWMA moose winter range and moose home ranges were centered on willow communities. Conifer was also an important cover type in winter, but mostly in terms of its relative distance to willow cover, especially when SWE levels were high. However, there was minimal evidence of shifting cover type selection with changing SWE levels. A post hoc

analysis revealed increasing temperatures were associated with increasing selection for conifer cover and closer distances to conifer cover in winter. The RSF model structure and coefficient values were quite similar at the home range and study area scales of selection, although SRI was not included in the top study area scale models. The models validated well, despite notable variability in coefficient estimates derived from the two-stage modeling framework.

Management Implications

In this study, I found that cow moose on the Mount Haggin Wildlife Management Area were largely non-migratory. This was an unexpected finding and has interesting implications for moose population and habitat management at this site and possibly other areas with abundant willow communities that can support year-round moose populations. Specific management implications for moose population and habitat management based on the non-migratory finding, cover type selection patterns, and the associations between covariates and habitat selection examined in this study are detailed below.

The pattern of strong selection for willow communities in this study highlights the importance of this resource when it is readily available. This importance is magnified by the fact that moose used the same areas and willow communities for calving and summer range. Managers should strive for abundant and healthy willow communities in areas where huntable moose populations are desired and encourage land management agencies and private land owners to manage for maximum willow cover in riparian areas. Disturbances (e.g. winter recreation trails, roads, logging operations) near willow communities should be minimized in both winter and summer to reduce stress on cow

moose overwintering or calving in these areas. However, the sole importance of willow cover should not be over emphasized, as conifer cover near willow communities may be critical in years with average to above average snowpack conditions and could be important for thermal cover when winter temperatures exceed the thermal limits of moose. Based on the RSFs and modeling covariates, conifer edge near willow has a higher probability of selection than the interior of a conifer stand as moose selected for close distances to willow in this study.

As would be expected with strong cover type selection where a highly palatable browse source is available in great abundance, managers should not be surprised if moose populations with high population densities have a negative impact on willow community composition and structure. This impact has been observed in multiple locations and can affect numerous species that utilize willow cover (Berger et al. 2001, Keigley et al. 2002, Boertje et al. 2007, Pedersen et al. 2007). The results of this study show that managers should expect to see these impacts in willow communities where moose winter at lower elevations and near conifer edges, particularly during years with higher SWE levels. This impact may be amplified if the population is non-migratory and moose are consuming willow outside of the winter season (although leaf stripping in these seasons may not negatively impact willows as much as browsing). It should be noted that the RSFs developed in this study used location data from cow moose during a period of low to moderate moose population density, and the possibility exists that moose may select for habitats differently at higher population densities. Therefore, the associations between the covariates examined here and moose winter resource selection may be stronger or

weaker at population densities that would be of greater interest to wildlife managers.

The results of this study have interesting implications for the timing and value of aerial surveys. Since moose selected for closer distances to conifer cover as SWE levels increased, periods with greater snowpack may cause moose populations to have reduced sighting probabilities due to obstruction by nearby conifer cover (Bowden and Kufeld 1995, Anderson and Lindzey 1996, Drummer and Aho 1998, Quayle et al. 2001, Peters 2010). However, the important caveat here is that the RSF models suggested that moose were not using conifer cover with a greater frequency, but rather just habitats closer to conifer cover. Still, it may be advantageous for wildlife managers to fly earlier in the winter season when moose are less likely to be in close proximity to conifer cover. This parallels the recommendations from other studies that suggest avoiding mid-winter aerial surveys (Baigas 2008). However, this guideline must be balanced with the need for snow cover, which may also influence sightability (Timmerman and Buss 2007), although not nearly as much as vegetative cover (Anderson and Lindzey 1996, Quayle et al. 2001).

Secondly, temperature may influence aerial surveys. The post hoc analysis of the temperature interactions suggest that moose were likely to change their habitat selection when temperatures changed. Conifer cover and distances closer to conifer cover were selected for with greater intensity when temperatures increased. Thus, aerial surveys are likely to be biased if temperatures are higher as moose seek thermal cover, similar to the implications of SWE on aerial surveys, but on a finer temporal scale (daily).

The last important implication for aerial surveys relates to the relationship between the hunted population in the fall and the surveyed population in the winter. Due

to the general lack of migration in this population, it is reasonable to assume that the population available during the hunting season is nearly identical to the population surveyed each winter (at least for cow moose). Thus, at this site, trends in the winter survey population are likely parallel to trends in the population available for hunter harvest. This may become increasingly important if the impacts of other predators can be estimated or demonstrated. For instance, a lack of positive population response after a reduction of hunter opportunity may indicate that other forces (e.g. predation, habitat condition) are influencing moose population declines more than hunter harvest, as have been noted in some areas (Becker 2008, MTFWP, unpublished data).

In conclusion, I have confirmed that cow moose do select for certain habitat attributes on the Mount Haggin Wildlife Management Area moose winter range. These selection patterns are similar to those that have been noted elsewhere in the Northern Rockies and may apply to similar moose winter ranges in southwestern Montana. Willow communities were a key resource for moose populations on this type of winter range, but must be managed in tandem with conifer cover to fulfill moose winter range requirements. These results will allow biologists to improve habitat management recommendations on both public and private lands and adjust the timing of aerial surveys to more accurately track moose population trends.

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CHAPTER 3

BROWSE UTILIZATION PATTERNS IN WILLOW COMMUNITIES

Introduction

Moose populations across Montana have expanded in the last century, both in geographic range and in population size. This expansion has had a negative impact on moose winter range in some locations where moose have overutilized key browse species such as aspen and willow (Keigley et al. 2002, Boertje et al. 2007). Unsustainable or excessive browsing has the potential to reduce local biodiversity and carrying capacity for moose and other ungulates (Berger et al. 2001, Pedersen et al. 2007, Peek 2007). Understanding browse utilization is important for balancing management objectives between moose populations and vegetative community health where moose browse.

Moose primarily eat the twig tips of shrubs and trees when browsing, although they occasionally consume forbs and grasses, depending on season and forage availability (Renecker and Schwartz 2007). Similar to habitat selection, moose have been described as "selective generalists" when it comes to diet. In North America alone, moose have been documented feeding upon 221 different plant species and/or genera (Renecker and Schwartz 2007). However, individual moose typically focus their browsing on only a few species, and certain genera and species are preferred over others when available. For the Shiras moose of the Rocky Mountains, willow (*Salix* sp.) species are both highly preferred and abundant on some types of winter range, where it may represent up to 90% of the browse consumed (Peek 2007). Other common winter browse species of the

Shiras moose include aspen, Douglas fir, lodgepole pine, subalpine fir, gooseberry, and buffaloberry (e.g. Tyers 2003, Baigas 2008).

Peek (1974) described three common types of winter range in a review of winter habitat use by Shiras moose. He labeled these types as riparian, floodplain riparian, and conifer (Peek 2007). Riparian winter range is characterized by willow bottoms mixed with conifers on high gradient streams; moose browse on both willow and conifer species in this type. Floodplain riparian systems yield more expansive willow communities on low gradient streams, which form a vast majority of browse consumption. In some cases, floodplain systems may support year-round moose populations. Conifer type winter range occurs in areas with minimal or no willow communities; aspen and conifers are important browse items in this type. All three of these winter range types are utilized by moose in Montana (see Stone 1971, Stevens 1967, and Stevens 1970 for use patterns in riparian, floodplain riparian, and conifer types, respectively).

Peek (2007) classified the Upper Big Hole River Valley as a typical floodplain riparian winter range. The winter range on the southwestern half of the Mount Haggin Wildlife Management Area (MHWMA) is likely an extension of this floodplain riparian type, with extensive low-gradient willow communities. Furthermore, willow is most likely the primary source of browse for moose in this area, due to its abundance, its selection by moose where available (Renecker and Schwartz 2007), and the observation of heavily browsed willow on the MHWMA in the past (Keigley et al. 2003). Winter habitat selection data from this study showing strong willow cover type selection (Chapter 2; Table 2.2) and extensive willow cover use by moose in summer (including

calving) has confirmed that the MHWMA is most likely a floodplain riparian winter range. It is important to note that this type of winter range can be year-round range (Peek 2007) and this appears to be the case in this area. The need for understanding browse utilization patterns on this type of winter/year-round range is emphasized by the fact that it supports some of the most substantial moose populations and hunter opportunity in Montana (e.g. Upper Big Hole Valley, Centennial Valley) and may also be more susceptible to browse overutilization, especially as moose may consume and impact willow in summer as well, although summer consumption by moose is typically leaf stripping and not twig browsing (Dorn 1970, Renecker and Schwartz 2007, Stolter 2008).

Willow browse selection and utilization patterns during the winter season have been studied by a number of researchers in recent years across all winter range types. Factors influencing browse selection have included: 1) the species of willow, with some species preferred over others (Dorn 1970, Kovalchik et al. 1988, Tyers 2003, Dwire et al. 2006, Månsson et al. 2007); 2) if the willow was previously browsed, with more preference toward previously browsed individual plants and even branches (Molvar et al. 1993, Bowyer and Bowyer 1997, Stolter 2008); 3) willow canopy density, with some researchers reporting decreasing browse at increasing densities (Singer and Zeigenfuss 2003) and others reporting increasing browse at increasing densities (Dassault et al. 2006); 4) browse (biomass) production and availability (Tyers 2003, Månsson et al. 2007); 5) elevation and snow depth, with increasing values corresponding with decreasing willow browse utilization (Tyers 2003); 6) distance to conifer edge (Dussault et al. 2006), with greater distance yielding lower browsing; and 7) willow community

height, with selection for increasing with height in one study as mechanical protection (snow) reduced availability (Tyers 2003) and decreasing in another (Singer and Zeigenfuss 2003). As a general observation, the use of habitat and consumption of available browse by moose is generally patchy (Van Dyke et al. 1995) and moose spend more time in food-rich habitat types (Dussault et al. 2005).

Thus, browse utilization patterns are hypothesized to be heterogeneous in nature, with some patches preferred over others depending on habitat attributes within and around those patches (Van Dyke et al. 1995, Tyers 2003, Peek 2007, Renecker and Schwartz 2007). If present, this heterogeneity could create an additional challenge for monitoring browse utilization, as some areas or even individual plants may be chronically heavily browsed due to favorable conditions (Bowyer and Bowyer 1997, Stolter 2008), while other patches or plants remain unbrowsed. Heterogeneity in browse utilization needs to be understood if biologists want to accurately monitor willow community health and relate browse utilization to moose population size or trends. The amount of heterogeneity will also affect how much sampling effort is needed to accurately capture trends in browse utilization and monitor willow community health where moose browse.

The goal of this study was to improve understanding of how moose browse willow communities in southwestern Montana by evaluating the patterns of browse utilization on the Mount Haggin Wildlife Management Area. In order to more effectively monitor willow community health, biologists need to understand how certain habitat attributes relate to moose browse utilization and how much sampling effort is required for effective monitoring. The results of this research will help biologists understand moose

impacts on willow communities and how and where to monitor willow browsing by informing biologists of appropriate sample sizes and optimal placement of willow browse monitoring sites. The results will also allow biologists to stratify willow monitoring locations based on key habitat attributes if desired (e.g. species, evidence of previous browsing, etc.) or to account for the possibility of bias in the browse utilization results at historic monitoring locations.

Methods

Browse Utilization Survey Structure

Forty transects were established in a systematic distribution across the willow communities on the MHWMA to measure browse utilization by moose. A color aerial photo (NAIP 2009) of the sampling universe with the willow communities highlighted in white can be found in Figure 3.1. These transects were placed perpendicular to the stream in major drainages at 1 km intervals within the WMA boundaries. Transects extended from the edge of the willow community through to the other edge in 50 m segments (the sampling unit for browse utilization), resulting in transects of variable lengths (50-500 m) depending on the width of the willow community. No partial segments shorter than 50 m were established as they would not provide sufficient twig sample sizes for browse utilization. This method allowed for systematic sampling while accounting for the amount of willow available at each site (as represented by willow community width) to provide a representative sample of the entire willow community on the study area. This setup also allowed for maximized efficiency as many transects were

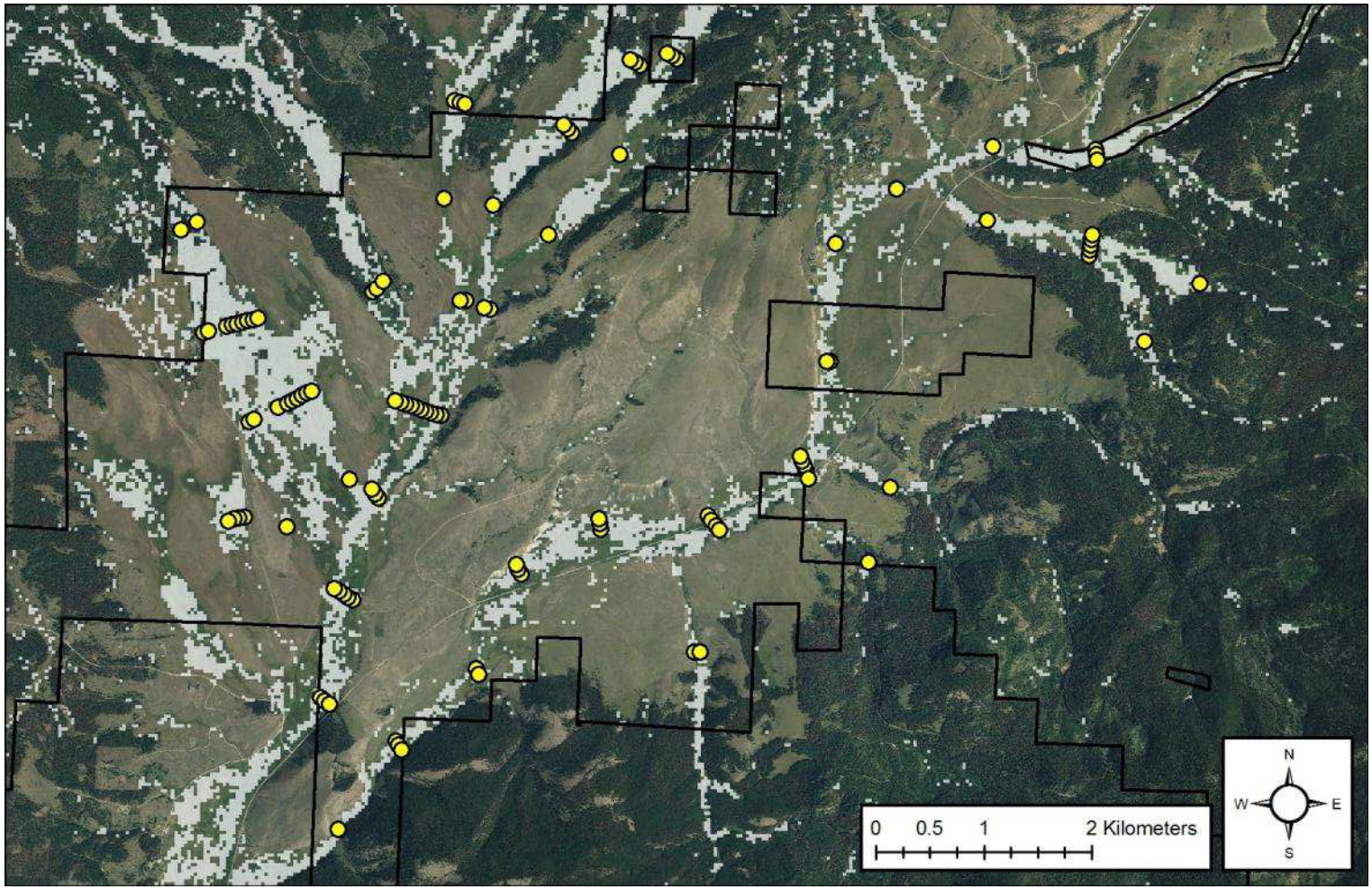

Figure 3.1: Sampling locations for the browse utilization surveys on the Mount Haggin Wildlife Management Area in southwestern Montana. The WMA boundary is in black. The center of each segment is represented by a yellow dot. Willow communities are highlighted in white, as estimated from remotely sensed land cover data (MTNHP 2010). The background is NAIP aerial imagery (2009).

only accessible by foot and as far as 3 km from motorized access during the survey period. The start and end of each segment were marked with plastic flagging and their locations were recorded with a GPS. Approximately 5.5 km of transects were established, comprised of 111 segments, each 50 m in length.

In early May 2008, 2009, and 2010, winter browse utilization was measured along these transects. Early May was selected as the browse survey period to prevent any potentially confounding moose, elk or cattle browsing on willow, which has been documented on rare occasions outside of the winter season (Roath and Krueger 1982, Singer et al. 1994, Peinetti et al. 2001, Brookshire et al. 2002), and to avoid agitating moose during the calving season (May 15 - June 15). Within each 50 m segment the willow community was systematically sampled at 20 points, starting at the origin and for every 2.5 m thereafter at a predetermined bearing (perpendicular to the overall stream course). Sample points were established with a standardized 2.5 m rod as measurement with a standard 50 m tape was not feasible in dense willow stands. At each point, a sampling protocol was followed to objectively sample the percent of twigs browsed from the nearest willow to that point, if a willow was available for sampling. The sampling protocol used in this study and definitions of this methodology can be found in Appendix M. Selected branches were marked with aluminum tags so the same willows and twigs could be measured each year of the study. Twenty twigs were sampled from each willow and noted as either unbrowsed, browsed (only previous year's growth removed by browsing) or heavily browsed (more than previous year's growth removed by browsing). If all twenty sample points had a willow eligible for survey, then 400 twigs were

examined on each 50 m segment.

The branch/twig sampling method used in these surveys was adapted from a method developed by Stickney (1966) and was originally applied to deer browse on serviceberry and chokecherry, both shrubs with a growth form comparable to the large willow species present on the study area. Others have used the percent of twigs browsed method for measuring browse utilization on various species of shrubs and trees (Jensen and Scotter 1977, Wikeem and Pitt 1987, Singer et al. 1994, Romme et al. 1995, Kielland and Bryant 1998, Rooney and Waller 2003, Singer and Zeigenfuss 2003), often to estimate biomass consumed. Biomass consumed was not estimated in this study as time was limited and it was necessary to sample a large area in a relatively short time frame.

Moose Browse Utilization and Response Variable Calculation

The standard calculation for percentage of twigs browsed along each segment (browse utilization) would be as follows (Jensen and Scotter 1977):

$$\text{Browse utilization (\% twigs browsed)} = \frac{\text{Browsed twigs (browsed and heavily browsed twigs)}}{\text{All twigs examined (unbrowsed, browsed, and heavily browsed)}}$$

This calculation produced a browse utilization response that ranges between 0.0 and 1.0 (0% and 100%). The calculation, however, gave equal weight to both browsed twigs and heavily browsed twigs. It was necessary to calculate an intensity-adjusted browse utilization since heavy browsing by moose actually represents the consumption of multiple previous year's growth twigs. I noted during these surveys that a heavily browsed twig generally accounted for the consumption of 2-5 (average ~3) previous year's growth twigs based on comparison with other, unbrowsed twigs on the same

willow plants. Intensity-adjusted estimates for browse utilization were calculated by multiplying the count of heavily browsed twigs by three to account for the impact of heavy browsing on the count of twigs browsed:

$$\text{Adjusted browse utilization (\% twigs browsed)} = \frac{\text{Browsed twigs} + (\text{Heavily browsed twigs} \times 3)}{\text{Unbrowsed twigs} + \text{Browsed twigs} + (\text{Heavily browsed twigs} \times 3)}$$

This calculation produced a browse utilization response that could range between 0.0 and 1.0 (0% and 100%), the same range as the response without the adjustment, but more accurately reflected the percentage of twigs browsed by accounting for heavy browsing.

Browse Utilization Model Covariates

To examine patterns in browse utilization, I collected data on potentially influential covariates in the field and from remotely sensed data. In the field, I collected data on species, growth form, and height for each sampled willow in each 50 m segment (up to 20 willows). Willow community width was also calculated from data collected in the field. Elevation, distance to conifer cover edge, and distance to willow community edge were estimated from remotely sensed data sets. Field methods and calculations for all of these covariates are detailed below.

Percent Preferred Willow Species. Sampled willows were identified to species in July 2008 to estimate species composition within each segment. Species were initially classified by vegetative separations (i.e. differences in branch and leaf structure as opposed to floral or catkin characteristics) based on the work of Robert Dorn (1997). Additional information was reviewed from various authors regarding the separation of *Salix geyeriana* and *S. lemmonii*, including Hitchcook et al. (1964), Brunsfeld and

Johnson (1985), Joy (1998), Heinze (1994), Fertig and Markow (2001), and Hoag (2005). The vegetative distinctions between Geyer and Lemmon's willow were subtle, but consistent. In June 2009, this species separation was confirmed by examining pistillate catkins from a subsample of willow under a light microscope and in the field with a hand lens. Probable hybrids of these two species were occasionally noted, confirming the observations of hybrids by other researchers where Geyer and Lemmon's willow coexist (Brunsfeld and Johnson 1985, Heinze 1994, Hoag 2005). For this study, willows were classified as one species or the other based on the majority of defining characteristics.

A percent preferred willow species covariate was determined by calculating the percentage of three willow species (planeleaf, Booth's, and Drummond's) sampled within each 50 m segment. Willow species preference was ascertained from publications examining *Salix spp*. palatability to moose and other ungulates in the Northern Rockies/Pacific Northwest (Dorn 1970, Kovalchik et al. 1988, Tyers 2003, Dwire et al. 2006, Baigas 2008). None of these studies included all of the willow species observed and available to moose on the Mount Haggin study area. Thus, it was possible that this covariate would not precisely capture the actual species preference in this study.

Percent Previously Browsed Willow. The growth form was noted for each sampled willow within a 50 m segment for each year that the browse survey was conducted. The growth forms classified in this study were uninterrupted, released, arrested, and retrogressed. These growth forms were adapted from shrub architecture types described by Keigley and Frisina (1998); definitions of the growth forms used in this study can be found in Appendix N. The growth form had the potential to change

annually as willow may be released from or exposed to heavy browsing pressure in any given year. Thus, the percent previously browsed covariate varied annually for any given 50 m segment. The percent of recently heavily browsed willow was calculated from the growth form of the sampled willow within each 50 m segment, with the percentage of arrested and retrogressed types indicating recent heavy browsing. Effectively, this measure provided an estimate of the percent of willow in the segment that had been heavily browsed in either or both of the two winters prior to the survey.

Average Willow Community Height. Concurrent with the summer species identification in July 2008, the height of the sampled willows was measured to establish an average height for the willow community within each segment. Height was measured on all marked willow, whether browse utilization was measured or not (e.g. when all branches on the willow are outside of the browse zone). Average willow height for each segment was calculated as the mean height of all willow (including those too high or too low to be browsed) within the segment.

Willow Community Width. Willow community width was calculated by multiplying the number of segments in each transect by the segment width (50 m). Therefore, all widths were in 50 m increments. Additionally, all segments within a single transect had equal willow community width values. This measurement provided a gross index of the biomass of willow available at that point along the stream course.

Elevation, Distance to Willow Edge and Conifer Edge. Elevation of each segment was estimated from a USGS DEM. Elevation was recorded in meters. Distance to

willow and conifer cover were calculated by taking the point location at the center of each 50 m segment and measuring the distance to the nearest edge in ArcGIS (using the Near tool, ArcGIS 9.3, ESRI, Redlands, CA). Edges were extracted from the Montana Landcover Map layer (MTNHP 2010). Distances to both edges were recorded in meters.

Statistical Analysis

The analysis for this chapter was broken into five sections. The first analysis was an investigation of dependence in the browse sampling structure and how it impacted further analysis. The second analysis examined the distribution of the willow browse utilization and how it related to sampling effort for willow browse monitoring. The third analysis was an a priori model selection exercise to test hypotheses in the form of competing models and to determine which covariates were associated with moose browse utilization in winter. The fourth and fifth analyses were post hoc efforts, comprised of a reformulation of the percent of preferred species covariate to more accurately reflect observed willow browse species selection and an exploratory model selection effort with additional covariates not considered in the a priori models.

Investigation of Dependence. The browse utilization data were examined in the statistical software R version 2.13.1 (R Development Core Team 2011). As the browse utilization response was derived from binary counts of browsed and unbrowsed twigs, a binomial distribution was selected for modeling. An initial examination indicated that the browse utilization response within each year of the study may have been overdispersed, i.e. there was more variability in the data than expected from the binomial distribution.

Each of the three years was examined separately as I expected data from the established survey sites across years to be correlated. For each year, deviance goodness-of-fit tests were conducted on an extra-rich logistic regression model and deviance residual plots were constructed and examined (Ramsey and Shafer 2002). Dispersion parameters for each year were then calculated to quantify the degree of overdispersion in the data.

As a lack of independence between sample units (50 m segments) may have contributed to the observed overdispersion, I tested the degree of dependence of segments using various methods outlined below. The goal of this exercise was to quantify and then appropriately account for any dependence between segments, which if left unaccounted for could bias model selection results and the estimates of variance for model parameters. I expected that the assumption of independence between segments within a transect was likely violated, as two segments within the same transect were more likely to produce similar results then two segments in different transects, even after accounting for available covariates.

To examine the effects of this potential issue on the resulting inference, linked-segment profile plots for browse utilization (the response) were created for each transect and serial and spatial correlation detection techniques were employed to quantify any correlation in the responses (Ramsey and Shafer 2002). All analyses were completed in R version 2.13.1 (R Development Core Team 2011). Linked-segment profile plots are plots that display the browse utilization response (0-100%) of each segment within a transect from one end to the other and allow for an examination of notable drifts from the mean of a transect. Linked-segment profile plots were created with simple code from the

R Book (Crawley 2007). A partial autocorrelation function (PACF) was applied to the longest transects in the study (9-10 segments) to examine serial correlation (one dimensional) using code from the base package of R (R Development Core Team 2011). Spatial correlation (two dimensional) techniques consisted of the construction of variograms and correlograms with code from the *spatial* package (Ripley 2010).

After completing the initial a priori analysis described below, I initiated two additional analyses to further examine the issues of independence and extra-binomial variation. To test the issue of dependence among segments within transects, I completed an analysis at the transect level. For this analysis, variables previously calculated at the segment level were recalculated at the transect level (averaged across all segments within a transect). This method negates any dependence due to cluster effects within a transect as the responses and covariates from all segments were pooled. This requires the assumption that transects were independent, which seemed reasonable as most transects were at least 1 km from the nearest adjacent transect in this study. The richest a priori model was then examined and overdisperion estimated. If overdispersion was greatly reduced, then this would support the hypothesis that segments within a transect were not independent. The second approach to investigating the issue of dependence was a segment level analysis, but with only every other segment included in the analysis (approximately one half) to test for potential non-independence between adjacent segments by excluding adjacent segments. This method removed any dependence between adjacent segments while still retaining a large sample size. Again, the richest a priori model was then examined and overdisperion estimated. If overdispersion was

substantially reduced, then this would support the hypothesis that directly adjacent segments within a transect were not independent.

Sampling Effort. In order for biologists to accurately quantify trends in willow community health or browse utilization, sufficient sample sizes must be employed in monitoring protocols. This may be especially true if a large amount of heterogeneity exists in browse utilization and biologists wish to detect changes in browse utilization from year to year. In order to estimate approximate sample sizes required, I conducted a power analysis with the browse utilization data I collected in the field, under the assumptions that my data were representative of the browse utilization across the study area and that the percent browse utilization measured on each of the 50 m segments in this study would be equivalent to a browse measure at a sample site in a future study. To clarify, the goal of this exercise was not to determine the sample size required for this study, but rather to estimate the sample sizes required in future study or management of willow communities or browse utilization monitoring. No additional covariates were used in this analysis, just the browse utilization measures.

In this case, I sought to determine the sample size necessary to detect a 10% difference in browse utilization from year to year. I decided that a difference of 10% browse utilization would be biologically significant, as it would represent a noticeable increase or decrease in the health of the willow community. This 10% difference in browse utilization has also been noted by other authors as being a change of interest (Dobkin et al. 2002, Singer and Zeigenfuss 2003) and seemed appropriate for the management objectives on my study area. Detecting a smaller percent difference (e.g.

5%) would require an even greater and perhaps unrealistic sampling effort, while when using a larger difference (e.g. 15%), interannual changes may appear to be noise when in reality a signal is occurring (a real, biologically significant difference in browse utilization). Specific to my data, only an increase of 10% browse utilization was tested, as a decrease in 10% browse utilization was not possible for multiple years of data used here (a decrease of 10% would have resulted in browse utilization < 0.0%).

A key assumption of standard sample size or power method is that the distribution of the measure of interest must be normal or normal after a transformation (Cohen 1988). I examined the distribution of browse utilization and determined that an assumption of normality could not be justified, nor could the data be log-transformed to meet the normality assumption. Transforming the data resulted in a bimodal distribution due to the zero-inflated response. Thus, I could not use standard sample size methods. To circumvent this issue, I used non-parametric bootstrapping as it was the only viable method available (Manly 2007). As the question of interest regarded the detection of a 10% change in browse utilization from year to year, ideally two data sets would be used to calculate a sample size necessary to detect a significant difference between years (Manly 2007). I had data from three years, but they all had very similar distributions, both in mean and variance, and the means were not statistically different between any of the years based on overlapping 95% confidence intervals. The data I had collected were not representative of years where browse utilization differed by a biologically important amount either. Therefore, I could not use the two-sample method with my data.

A one-sample method was adapted from techniques for testing sample means

(outlined Efron and Tibshirana 1993 and Manly 2007) and sequential sample size testing demonstrated by Bros and Cowell (1987). For this method, sample sizes ranging from four to 100 were selected, representing possible sample sizes to be used in the field. The largest sample size was less than the minimum number of responses (browse utilization at each 50 m segment) for any given year, and each year was analyzed separately. For each sample size, that number of responses were randomly drawn (with replacement) from the observed responses. This process was repeated 10,000 times to create a bootstrap-t distribution, which could then be compared to the observed t-statistic (t-stat = difference in browse utilization/[standard deviation/√sample size]) for the difference of interest. The observed t-statistic was then compared to the 95% confidence interval created from the bootstrap-t distribution for each sample size to determine at which sample size the detection of an actual difference would become significant with 95% confidence. I also ran this analysis at the 90% confidence interval level, as managers may prefer to use this slightly reduced level of certainty as it yields lower minimum sample sizes. I completed this analysis for each year of data to see what variation was present in sample size estimates based on the distributions of percent browse utilization collected each year.

Browse Utilization Modeling. I developed several a priori hypotheses regarding the relationship between browse utilization and environmental attributes, which took the form of competing models. Initially, I set out to model browse utilization with standard binomial logistic regression (GLMs), since I collected binary count data (browsed or unbrowsed twigs) on 50 m segments (the sampling unit). Due to the overdispersion present in the data, quasi-likelihood methods were required to adequately fit models and

therefore QAIC was used for model selection (Burnham and Anderson 2002). This was an acceptable method for analyzing data for each year independently, but due to replication of sample sites across years it was not a sufficient method to model all years together as the correlation between variables at any sample site across all three years of data could not be properly accounted for with this model structure. While mixed-models (e.g. Zuur et al. 2009) could have been employed with the sample site treated as the random effect, the maximum number of repeated measures at each site was three and the mixed-models approach would have produced complex results and been difficult to interpret accurately as the sample site effect would have been explicitly modeled.

In order to model all three years of data simultaneously while accounting for the cluster effects due to repeat visits to the same sites each year, generalized estimating equations (GEE) were used. With GEE, I could account for site cluster effects by treating the correlation as a nuisance, rather than explicitly modeling site effects with random effects. An added benefit was that GEE also accounted for overdispersion in the data. The downside of using the GEE method was that it does not permit the direct use of AIC or other likelihood based model selection techniques (Pan 2001). Likelihoods for GEEs are not defined since no distribution is assumed.

In order to complete model selection with GEE, Pan (2001) has developed and tested a method to estimate a quasi-likelihood for GEE. This formulation is similar to AIC terms of utilization and interpretation, including an approximate penalty of 2 for additional covariates in the model. Pan named this formulation the “Quasi-likelihood under the Independence model Criterion” or QIC. Analysis was completed in R version

2.13.1 (R Development Core Team 2011). Calculation of QIC was completed with code from the package *geepack* (Yan et al. 2011) and additional code the *ape* package (Paradis 2011). The QIC calculation was also corrected for small sample size (QIC_c). Summary tables were created with code from the package *bbmle* (Bolker 2011) and the package *MuMIn* was used to conduct parameter averaging (Barton 2011).

Prior to developing an a priori model list, all seven covariates were tested for collinearity. Pairwise correlations and VIF (variance inflation factors) were calculated. Any combinations of covariates with correlations > |0.6| would not be included in the same model. Any covariates resulting in VIFs > 5 would also be excluded. Scatterplots of all covariate pairs were also examined for potential nonlinear relationships. Taking into account any collinearity, a model list was developed. These a priori models included four of seven potential covariates: percent preferred willow species, percent of willow previously browsed, willow community width, and elevation. These variables were believed to be the most likely to best account for the variation in browse utilization by moose during the winter season. Average willow community height, distance to willow edge and distance to conifer edge were not included in the a priori models but were explored in a post hoc analysis. The reason for this segregation is explained in the Modeling Predictions section below.

The original model list for single year modeling included all combinations of the four a priori covariates. There were no interactions or quadratic forms, as previous research from other studies and exploratory plots of my data did not demonstrate an obvious need for these functional forms. This resulted in 16 models (Appendix O)

representing the within-year browse utilization hypotheses. In order to test for potential differences among years, this model list was expanded with two year indicator variables that interacted with the intercept and all covariates. The final model list is displayed in Appendix P with 97 models in total.

Using the data from all three years, I fit the candidate models in the final list and used QIC_c model selection to rank the models. For each model, QIC_c model weights were calculated, along with coefficient and standard error estimates. Top models were those with ΔQIC_c scores < 4. However, models with uninformative parameters were removed from the top models (Arnold 2010), which is likely to occur when all possible covariate combinations are included in the candidate model list. Uninformative parameters are those that do not explain enough variation to overcome the 2 AIC per parameter penalty (2 QIC_c in this case) and thus should not be interpreted as having an ecological effect (Arnold 2010). However, this criterion should not be applied without assessing potentially uninformative parameters. Thus, I examined the estimates and uncertainty of the coefficients in each model to ensure that potentially ecologically important parameters and models were not erroneously excluded. If the parameters were deemed to be uninformative upon closer examination, the models were removed to avoid ecological interpretation of parameters that do not have an ecological effect. The covariates of the remaining top models were then averaged (unless interactions prevented averaging) and weighted coefficients (based on model weights) and adjusted standard errors calculated. From these estimates, 95% confidence intervals were calculated to quantify the precision of the model averaged parameter estimates. Changes in the odds

of browse utilization were calculated relative to changes in covariate values (e.g. 20% increase in preferred species) to assess the impact on browse utilization. Predictive plots were also constructed to demonstrate the effect of changing a single covariate (across the observed range of values) on the predicted browse utilization.

Modeling Predictions. I evaluated possible relationships between browse utilization and seven environmental covariates. For four of these covariates, there was strong evidence that they would explain variability in browse utilization. These covariates were percent preferred willow species, the percent of previously browsed willow, willow community width, and elevation. The other three covariates had limited or contradictory evidence in published literature that they would be associated with browse utilization. These covariates were average willow community height, distance to willow edge, and distance to conifer edge.

The species of willow available for browsing may be the greatest single determinant of browse utilization. Preference for certain species of willow has been well documented (Dorn 1970, Stevens 1970, Wilson 1971, Risenhoover 1987, Kovalchik et al. 1988, Tyers 2003, Dwire et al. 2006, Mansson et al. 2007, Baigas 2008) and moose may be especially selective when browse is abundant and highly palatable (Risenhoover 1987). This selection is likely the result of numerous factors, including chemical compounds and willow stature. For instance, different willow species produce different chemicals which make them more or less palatable, as well as hold higher or lower nutritional value (Risenhoover 1989, Renecker and Schwartz 2007). Short-statured willow species may be unavailable during winter as snowpack can often protect shorter

willows from browse pressure (Tyers 2003).

In the northern Rocky Mountains, planeleaf (*Salix planifolia*), Drummond's (*S. drummondiana*), Booth's (*S. boothii*), and Bebb (*S. bebbiana*) willow are typically highly preferred species (Dorn 1970, Kovalchik et al. 1988, Tyers 2003, Dwire et al. 2006, Baigas 2008). Wolf's (*S. wolfii*) willow was noted as intermediately preferred by Stevens (1970) and Tyers (2003), while Geyer (*S. geyeriana*) and Lemmon's (*S. lemmonii*) willow are generally the least preferred. For the purposes of my study, I classified the highly preferred species for my percent preferred species covariate as planeleaf, Drummond's and Booth's willow. Bebb willow would have been included in this category had any been noted in the sampled segments. Thus, I predicted that browse utilization would be associated with the percent of preferred browse species within each segment and that as the percent of preferred species increased, browse utilization would increase.

Moose have the tendency to browse willow plants that have been browsed previously (Molvar et al. 1993, Bowyer and Bowyer 1997, Bowyer and Neville 2003, Stolter 2008). The reason for this preference may vary across willow species. For the tea-leaved willow (*S. phylicifolia*), Stolter (2008) found that new growth from previously browsed willow was more palatable, with "lower concentrations of individual phenolics, a higher biomass, and lower concentrations of nitrogen." Bowyer and Neville (2003) found that nitrogen and tannin content were not reduced in feltleaf willow (*S. alaxensis*) in Alaska, but rather that higher biomass in previously browsed twigs was leading to repeated browsing. Bowyer and Bowyer (1997) found a significant increase in biomass for twigs browsed previously versus those not browsed in grayleaf willow (*S. glauca),*

but did not examine secondary compounds. Others have confirmed the biomass hypothesis in a subspecies of flat-leaved willow (*S. planifolia pulchra*), and found that carbon-based defense compound production had a stronger relationship with the amount of sunlight exposure than with previous browsing (Molvar et al. 1993). Whatever accounts for the increase in palatability, previously browsed willow are preferred over those which have not been browsed in many cases. Thus, I predicted that percent of previously browsed willow and browse utilization would be associated, with increased percent of previously browsed willow yielding increased levels of browse utilization.

Mansson et al. (2007) found that forage availability or the amount of forage present at a site, along with species composition and moose density, explained variability in browse utilization. Others have found that willow canopy cover measures and biomass production estimates (Tyers 2003) have been associated with browse utilization. I did not have the capability to measure forage availability for the large number of sites on the study area and opted instead for a more large-scale covariate. The width of the willow community at the location of the segments would provide an index of the biomass of forage available on a large scale (e.g. within 500 m), with small widths (50 m) representing minimal forage availability compared to large widths (500 m). Thus, I predicted that willow community width would be associated with browse utilization and that as willow community width increased, browse utilization would increase.

Tyers (2003) found that snow depth was a contributing factor in explaining moose presence in willow stands. It is generally accepted that the energetic costs of locomotion increase substantially when snow depths are > 65cm. Additionally, deep snows may

reduce the availability of willow for browsing (Tyers 2003). The snow depth on my study area was highly variable due to changes in topography and drifting, even at a scale smaller than a 50 m segment. There was no way to accurately measure the snow depth, but field observations support noticeable differences in overall snowpack depth from the lowest to the highest elevations. Elevation, therefore, could be treated as a surrogate measure for gross changes in snowpack, with higher elevations accumulating greater snowpack and discouraging moose browse utilization. Thus, I predicted that elevation and browse utilization would be associated, with higher elevations yielding decreased levels of browse utilization.

The distance to conifer cover is occasionally noted as a factor explaining habitat selection of moose (Schwab and Pitt 1991, White et al. 2001, Dussault et al. 2005, Peek 2007, Baigas 2008, Becker 2008). However, I did not find any studies that suggested that distance to conifer cover would be associated to browse utilization. Only one study had quantified how browse availability and conifer edge relate to habitat suitability (Dussault et al. 2006). Based on this work, I expected that willow closer to conifer would receive greater browse utilization. However, this pattern may be limited to periods when snow conditions create more optimal travel conditions in conifer cover or when ambient temperatures require moose to seek thermal cover. In the case of snowpack amelioration, the period of high snowpack may be short or non-existent in some years. Thus, moose may choose to browse willow close to conifers in winter during periods of higher snowpack, but this may not be evident in the browse patterns since moose could browse other willows further from conifer cover during the parts of winter with little snowpack.

In terms of thermal cover, moose may use conifer for thermal cover during warmer times of day (Demarchi 1992) or warmer periods within a season (Schwab and Pitt 1991), although this behavior was notably absent in some populations (Lowe et al. 2010) and may be much more important in summer than in winter (Dussault et al. 2004). It is unknown what impact this may have on browse utilization patterns, but these short-term habitat selection behaviors would be impossible to capture by examining annual browse patterns. Whatever factors may be contributing to moose use of conifer cover (snowpack amelioration and/or thermal cover), browse utilization measures in this study could only quantify the willow use for an entire winter of browsing. Therefore, distance to conifer cover was only examined post hoc as there was not strong support in the literature that this covariate would be associated with browse utilization patterns, especially on an annual basis. However, since limited evidence suggested that a relationship could exist, I did predict that distance to conifer cover would be associated with browse utilization and that as distance to conifer cover increased, browse utilization would decrease.

Like distance to conifer, the distance to willow edge has been noted as a potential covariate explaining moose habitat selection. However, this covariate is generally used to explain use outside of willow habitat types, not within them (Van Dyke et al. 1995, Kufeld and Bowden 1996, Baigas 2008). However, despite the demonstrated relationship between habitat selection and distance to willow, I found no studies suggesting a relationship between browse utilization and distance from willow community edge. Nevertheless, some researchers have hypothesized that willows on the edge of willow communities may be subject to higher browse utilization (Tyers, pers. comm.), due to

increased availability of willows on the edge of willow communities versus those deep within them. This makes intuitive sense, but because of a lack of documentation in the literature, this variable was only tested post hoc. The tentative prediction for this variable was that distance to willow edge and browse utilization would be associated, with greater distances to willow edge yielding decreased levels of browse utilization.

The final covariate examined was average willow community height. Singer and Zeigenfuss (2003) found a weak relationship between willow height and browse utilization, with shorter willows associated with more browse utilization. This could be because browsed willows never achieved taller statures (arrested by browse) rather than shorter willows being subject to greater browse pressure. Conversely, Tyers (2003) found that taller willows received greater browse utilization due to snowpack covering shorter willows. Since this relationship was ambiguous, average willow community height was only examined post hoc. Based on the limited evidence available, my only prediction was that an association might exist between willow height and browse utilization. Neither a positive nor negative association was hypothesized.

I predicted that the variables for the percent of preferred willow species, the percent of previously browsed willow, willow community width, and elevation would be strongly associated with browse utilization. These variables were included in the a priori models. All combinations of these variables were included in the final model list (Appendix P), as no reason could be found to exclude any variable from any specific model. No interactions or quadratic forms were included, as current literature and exploratory plots of my data did not demonstrate an obvious need for these functional

forms. Average willow community height, distance to willow edge and distance to conifer edge were not included in the a priori models but were explored in a post hoc analysis as the support in the literature for these covariates was limited or conflicting.

Post Hoc Preferred Species Covariate. Using methods outlined in Manly et al. (2002) for selection ratios, willow species selection was calculated. Selection ratios show the degree of selection relative to availability and quantify preference or avoidance. For instance, a selection ratio of 2.0 means that a willow species was used at twice the rate that would be expected if that species were selected at the same rate as its availability in the "population" of species. A Type I design framework was employed, as willow use and availability was measured at a population level. Type II or Type III designs would have required data on individual moose willow use and were not applicable to my data. Counts for unbrowsed, browsed and heavily browsed twigs were summed by species at the individual willow level, creating a matrix of used and available willow twigs organized by species. Browsed and heavily browsed twig counts were combined after the heavily browsed twig count was inflated by a factor of three. This was the same method used to create the adjusted browse utilization calculation and was employed in both the used and available counts. R version 2.13.1 (R Development Core Team 2011) was used to calculate the selection ratio with code from the package *adehabitat* (Calenge 2009). Data were analyzed for each year independently and then for all three years combined. Selection ratios were then used to reclassify preferred species and a post hoc percent preferred species covariate was calculated. The final model list was then reanalyzed with the post hoc percent preferred species covariate replacing the original percent preferred

species covariate. Changes in ΔQIC_c values for the top models were examined to determine if models were improved with the post hoc percent preferred species covariate.

It was possible that a post hoc preferred species covariate would be a noticeable improvement over the original covariate, if the local species preference differed from preferences observed elsewhere. The original species preference covariate was based on observations throughout the Northern Rockies on willow preferences of moose and other ungulates. This exercise was not meant to test a specific hypothesis regarding species preference, but to determine the actual species preference on the study area and to see if the species preference observed in this study was notably better or only equal to the original species preference covariate. This method was somewhat circular, in that the post hoc covariate was created from the data and then tested with similar data. However, if the original species preference covariate contained erroneous species preferences, then the inference derived from that covariate may be faulty and could impact management decisions (e.g. species composition isn't strongly associated with browse patterns). Thus, it was critical to determine the actual species preference and to see if it was different from the original species preference (based on changes in QIC_c values). Additionally, it should be noted that the datasets for the two analyses were not identical, as the post hoc species preference was calculated by pooling twig counts for each species across the entire study area, while the preferred species covariate was calculated at the segment scale, based on the species composition of individual willow within each segment. Actual species composition was not employed in the browse utilization modeling, just the percent of preferred species (vs. species that were not preferred).

Post Hoc Browse Utilization Modeling. Using the top models from the post hoc preferred species analysis, I conducted an additional post hoc analysis to see if model fit could be further improved with various functional forms and two-way interactions, as well as testing the 3 covariates not included in the a priori model selection analysis. All three covariates (distance to conifer, distance to willow edge, and willow community height) were added in all possible combinations to the top models. Quadratic forms of the individual covariates (both a priori and post hoc covariates) were tested in all possible combinations and exponential forms were tested in the same manner. The potentially biologically important interactions between percent previously browsed willow and elevation (PREVBRWS×ELEV), percent preferred species and elevation (PREFSPP×ELEV), and percent previously browsed willow and percent preferred species (PREVBRWS×PREFSPP) were tested. The QIC_c scores and ΔQIC_c values for the models with and without the new covariates were examined to determine if the post hoc covariates improved model fit.

Results

Descriptive Results

In the spring of 2008, 35,320 twigs were examined on 108 segments (50 m each) sampled along 39 transects, totaling approximately 5.5 km of surveys. Based on these surveys, the estimated browse utilization averaged across all segments was 11.5% (95% confidence interval of 9.4% to 13.7%; range: 0.0-53.6%). In the spring of 2009, 35,560 twigs were examined on 111 segments along 40 transects. From these data, the estimated

mean of browse utilization was 8.0% (95% confidence interval of 6.2% to 9.8%; range: 0.0-48.1%). In the spring of 2010, 35,320 twigs examined on 111 segments along 40 transects. Based on these surveys, the estimated mean of browse utilization was 8.3% (95% confidence interval of 6.5% to 10.1%; range: 0.0-47.9%). All browse utilization statistics reported here were intensity-adjusted as formulated above.

The browse utilization distribution was heavily skewed in each year of the study (Figure 3.2). Many segments had zero browse utilization: 14, 27, and 23 segments in 2008, 2009, and 2010, respectively. Additionally, the median values were 8.85%, 4.6%, and 4.4% browse utilization for 2008, 2009, and 2010, respectively, well below the means for these distributions. These skewed and zero-inflated distributions presented unique statistical challenges, especially for the sampling effort methods.

A total of 1826 willows were assessed for browse over the course of this study. Of those, 1766, 1778, and 1766 were measured in 2008, 2009, and 2010, respectively. Numbers varied across years due to tag attrition, complete willow loss to beaver, and three segments added in 2009. An additional 84 willow were classified to species but not assessed for browse due to the unavailability of twigs for browsing (mostly below the browse zone). Of 1910 willow classified to species, the number of willows for each species, in descending order, was: 700 Lemmon’s, 459 Geyer, 348 Booth’s, 340 Drummond’s, 35 planeleaf, and 28 Wolf’s willows. Of the 1159 individual willows classified as Geyer and Lemmon's willow, 47 (4.1 %) were potentially hybridized individuals with mixed classification characteristics, of which 16 and 31 were classified as Geyer and Lemmon's, respectively.

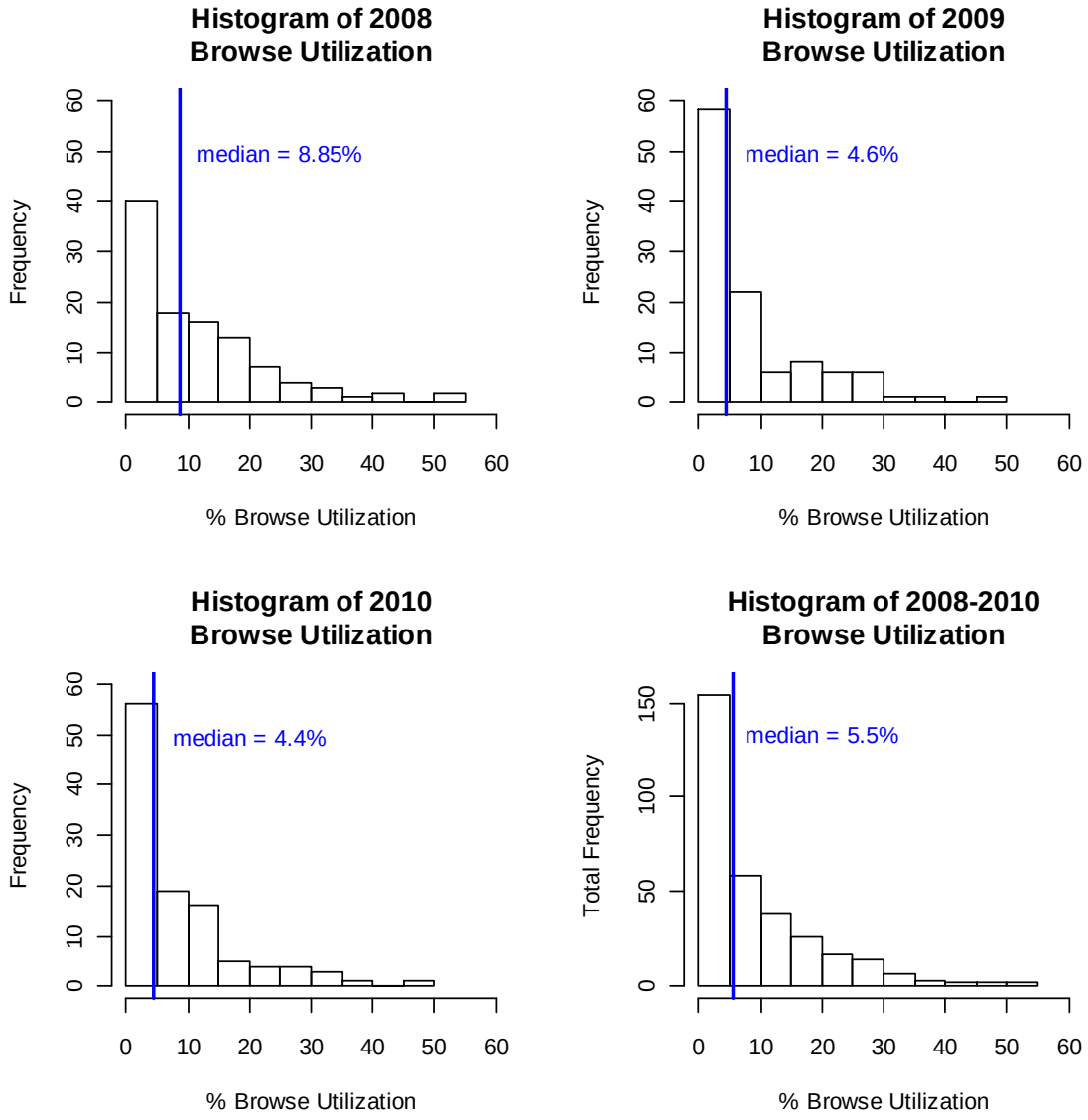

Figure 3.2: Histograms of browse utilization (response) for individual years (2008, 2009, and 2010) and for all 3 years of the study combined. Medians are noted with a blue vertical line and label.

Statistical Results

Investigation of Dependence. The extra-rich model examined for this analysis was comprised of the 4 a priori covariates, all 2-way interactions between them, and quadratic forms for each covariate. The deviance goodness-of-fit test for the extra-rich model (p-value < 0.001) for each individual year of data and a lack of severe outliers in the deviance residual plots suggested that the data were overdispersed, i.e. there was more variability in the data than expected from the binomial distribution. The extra-rich model was examined again using quasi-likelihood methods, resulting in dispersion parameters of 22.21, 15.96, and 19.89 for the 2008, 2009, and 2010 data, respectively.

The linked-segment profile plots were constructed for all transects with > 1 segment, 25 in total. These plots showed a few minor drifts away from the transect means and minimal possible serial correlation, but nothing extreme in any transect that would indicate notable correlation. A sample of these plots for the longer transects can be found in Appendix Q. A partial autocorrelation function (PACF) was constructed for the three longest transects in the study (9-10 segments) and revealed virtually no correlation: the largest lag one serial correlation coefficient (r1) was less than 0.25 and most were around or less than 0.00, indicating minimal serial correlation (Ramsey and Shafer 2002). It should be noted, however, that PACF methods are less likely to detect correlations in short datasets (<50 points). The spatial correlation techniques yielded variograms and correlograms that indicated very minimal spatial correlation for distances (lags) between segments of 50 to 500 m, which represented segments within the same transect. Correlograms for each of the three years of data are displayed in Appendix Q.

For the transect level analysis, large extra-binomial variation was still present and the coefficient values changed when compared to the original segment level analysis. The new coefficient values and 95% CIs suggested that no explanatory covariates were associated with browse utilization at the transect scale. This was possibly due to the large amount of variability in the explanatory covariates within a single transect, which was not accounted for when the covariates were averaged across each transect for this analysis. Regardless, overdispersion was not greatly reduced by modeling the data at the transect scale, indicating that dependence among segments within a transect were not the source of the overdispersion. The second analysis which used only every other segment in the sample did not reduce extra-binomial variation or drastically change the parameter estimates. As overdispersion was not reduced, this analysis also suggested that dependence between adjacent segments was not the source of the overdispersion. Both analyses suggested, as the quantitative methods (e.g. PACF, correlograms, variograms) did above, that there was no evidence that segments within a transect were dependent. Neither of these methods were explored further and the results of these modeling efforts are not presented here.

Through numerous methods, I attempted to detect and quantify any possible dependence between adjacent segments within a transect, but no measures indicated strong correlation. Overdispersion was present, but did not appear to be due to a lack of independence between segments. While these were not the expected results for any of these tests (under the assumption that segments within a transect were not independent), I elected to proceed with the analysis of these data under the assumption that the segments

were functionally independent, as there was little evidence available to suggest otherwise. Potential correlation between segments clustered with a transect was therefore ignored for all other analyses in this chapter.

Sampling Effort. In order to estimate approximate sample sizes required for future browse utilization or willow community health monitoring, I conducted a power analysis using the distribution of the browse data (percent browse utilization) measured on the 50 meter segments in this study. To detect a 10% increase in browse utilization from one year to the next with 95% confidence, 41, 38, and 38 sample sites (e.g. 50 m segments) were required based on the distribution of the data from the years 2008, 2009, and 2010, respectively. With a 90% CI, the number of sample sites required to detect a 10% increase in browse utilization were reduced to 35, 32, and 33 for 2008, 2009, and 2010, respectively. Results differed across years due to the variable browse utilization distributions. Larger sample sizes were required to detect a 10% increase in browse utilization when the mean percent browse utilization for that year was higher (11.5%, 8.0% and 8.3% in 2008, 2009, and 2010, respectively). Although a 10% increase in browse utilization from one year to the next was selected as the level of interest in this study, the sample sizes required to detect other percent changes (e.g. 5%, 15%, 20%) in browse utilization are shown in Table 3.1 for reference.

Browse Utilization Modeling. Collinearity for all 7 covariates was tested prior to running any model selection. No pairs of covariates had correlations > |0.6|. The largest correlation between covariates in the a priori models was 0.400 (between PREFSPP and ELEV). The largest correlation between any covariates was -0.514 (between ELEV and

Table 3.1: A comparison of sample sizes (monitoring sites) needed to detect the percent increase in browse utilization in the first column. As the percent change increased, smaller sample sizes were necessary to detect that change with either 90% or 95% confidence. Results differed across years due to the variable distributions of browse utilization each year. The percent increase (10%) of interest in this study is in bold.

% Increase in Browse Utilization	Data Year	Sample Size Required to Detect the Increase 95% CI	90% CI
5%	2008	72	59
	2009	62	51
	2010	63	51
7.5%	2008	50	42
	2009	46	38
	2010	45	38
10%	**2008**	**41**	**35**
	2009	**38**	**32**
	2010	**38**	**33**
12.5%	2008	36	31
	2009	34	30
	2010	34	30
15%	2008	33	29
	2009	31	28
	2010	32	28
17.5%	2008	31	27
	2009	30	26
	2010	30	26
20%	2008	29	26
	2009	28	25
	2010	29	26
25%	2008	27	24
	2009	27	24
	2010	27	24

DISTCNFR). No covariates had VIFs > 5. The largest VIF was 1.76 (ELEV) followed by 1.72 (DISTCNFR). Scatterplots of all covariate pairs did not reveal any notable nonlinear issues. Therefore, no covariates or covariate pairs were excluded from any models for both the a priori and post hoc analyses.

From the a priori model list of 97 models, twelve models had ΔQIC_c scores < 4 (Table 3.2). However, most of these models contained uninformative parameters (Arnold 2010) and only three models with ΔQIC_c scores < 4 did not include uninformative parameters (models highlighted in gray in Table 3.2). All other models were not well supported by the data (ΔQIC_c scores ≥ 4). As interactions were present in some but not all of the top three models, a weighted average model could not be calculated and inference was independently assessed for each model for parameters with interactions. The coefficients and 95% CIs for the top three models are displayed in Table 3.3. An expanded table with the coefficients for the top 12 models can be found in Appendix R.

Based on a QIC_c model selection analysis of the GEE models (clustered by sample site across years), the covariates for percent of preferred species (PREFSPP), percent of previously browsed willow (PREVBRWS), and willow community width (WIDTH) were all associated with browse utilization. As predicted, the percent of preferred species and the percent of previously browsed willow were positively associated with browse utilization. Willow community width had negative association with browse utilization, counter to my prediction. The covariate for elevation (ELEV) was in two of the three top models along with a YR×ELEV interaction, but was not well supported (aside from YR2010) as its confidence intervals included zero in those two models (Table 3.2), as well as in all the other top models that were excluded from interpretation due to uninformative parameters (Appendix R).

Coefficient estimates from the three top models indicated that the percent of preferred species (PREFSPP) was positively associated with browse utilization after

Table 3.2: Model selection results for browse utilization of willow communities by moose on the Mount Haggin WMA. All models are ranked according to QIC_c and presented along with the number of parameters (k), the ΔQIC_c value (the change in QIC_c value relative to the best model), and the relative model weight (w_i). Abbreviations are: YR (year of browse, 2008, 2009, or 2010), PREFSPP (percent of preferred species willow), PREVBRWS (percent of willow previously browsed, within the last 2 years, based on growth form), WIDTH (total width of the willow community), and ELEV (elevation of the sample site). Models highlighted in gray are those which do not have uninformative parameters (Arnold 2010).

ID	Model Structure	K	QIC_c	ΔQIC_c	w_i
37	YR + PREFSPP + PREVBRWS + WIDTH + WIDTH×YR + ELEV + ELEV×YR	11	402.82	0.000	0.148
40	YR + PREFSPP + PREVBRWS + WIDTH + ELEV + ELEV×YR	9	403.33	0.503	0.115
42	YR + PREFSPP + PREVBRWS + WIDTH	6	403.53	0.708	0.104
13	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH + ELEV + ELEV×YR	11	403.64	0.812	0.099
10	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH + WIDTH×YR + ELEV + ELEV×YR	13	403.78	0.955	0.092
39	YR + PREFSPP + PREVBRWS + WIDTH + WIDTH×YR	8	404.22	1.395	0.074
41	YR + PREFSPP + PREVBRWS + WIDTH + ELEV	7	404.69	1.865	0.058
38	YR + PREFSPP + PREVBRWS + WIDTH + WIDTH×YR + ELEV	9	405.39	2.569	0.041
28	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV + ELEV×YR	13	405.92	3.102	0.031
4	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV + ELEV×YR	13	406.36	3.538	0.025
31	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV + ELEV×YR	11	406.50	3.681	0.024
1	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV + ELEV×YR	15	406.60	3.772	0.023

Table 3.3: Coefficient values (β_i) and 95% confidence intervals (in parentheses) for the covariates in the top three models explaining browse utilization. Abbreviations are the same as those in Table 3.2. Coefficients in bold have confidence intervals that do not span zero.

	Top Models		
Coefficient	37	40	42
Intercept	3.74051	3.94179	**-2.62811**
	(-4.42556, 11.90658)	(-4.0019, 11.88548)	**(-2.98149, -2.27473)**
YR2009	3.57217	2.29239	**-0.36205**
	(-10.58332, 17.72765)	(-11.55769, 16.14246)	**(-0.62105, -0.10306)**
YR2010	**-12.56471**	**-11.69531**	**-0.32233**
	(-22.36465, -2.76478)	**(-20.98888, -2.40174)**	**(-0.56448, -0.08018)**
ELEV	-0.00345	-0.00353	
	(-0.00779, 0.00089)	(-0.00777, 0.00071)	
PREFSPP	**0.55099**	**0.55063**	0.44450
	(0.10683, 0.99515)	**(0.10876, 0.9925)**	(-0.00131, 0.8903)
PREVBRWS	**3.09998**	**3.06522**	**3.12621**
	(2.39296, 3.807)	**(2.36798, 3.76245)**	**(2.43784, 3.81458)**
WIDTH	**-0.00224**	**-0.00243**	**-0.00241**
	(-0.00341, -0.00107)	**(-0.00334, -0.00151)**	**(-0.00333, -0.00148)**
YR2009×ELEV	-0.00197	-0.00142	
	(-0.00943, 0.00548)	(-0.00879, 0.00595)	
YR2009×WIDTH	-0.00157		
	(-0.00355, 0.00042)		
YR2010×ELEV	**0.00647**	**0.00608**	
	(0.00133, 0.01162)	**(0.00113, 0.01102)**	
YR2010×WIDTH	0.00080		
	(-0.00102, 0.00262)		

taking into account all other covariates in the models. The coefficients from the top three models were in strong agreement ($\beta_{PREFSPP}$ = 0.551, 0.550, and 0.445), although the confidence interval in Model 42 barely included zero. The weighted average (based on QIC_c weights) of this covariate was $\beta_{PREFSPP}$ = 0.496 (95% CI = 0.0039, 0.988). From this weighted average, it was estimated that for a 20% increase in preferred species, there was a 1.10 times increase in the odds of browse utilization (95% CI= 1.00, 1.22). Three

plots showing the predicted relationship between percent preferred species and percent browse utilization for each year (based on Model 37) is shown in Figure 3.3. Models 40 and 42 produced nearly identical plots and are not shown here. An absence of YR×PREFSPP in the top models meant that annual differences in predicted browse utilization were due to the yearly indicator (e.g. YR2009) covariates.

Percent of previously browsed willow (PREVBRWS) was also positively associated with browse utilization after taking into account all other covariates in the models. The coefficients from the top three models were in strong agreement ($\beta_{PREVBRWS}$ = 3.100, 3.065, and 3.126). The weighted average (based on QIC_c weights) of this covariate was $\beta_{PREVBRWS}$ = 3.103 (95% CI= 2.400, 3.807). From this weighted average, it was estimated that for a 25% increase in previously browsed willow, there was a 2.17 times increase in the odds of browse utilization (95% CI= 1.82, 2.59). Three plots showing the predicted relationship between percent previously browsed willow and percent browse utilization for each year (based on Model 37) is shown in Figure 3.4. Models 40 and 42 produced nearly identical plots and are not shown here. As the YR×PREVBRWS covariate was not present in the top models, annual differences in predicted browse utilization were due to the yearly indicator covariates.

Willow community width was negatively associated with browse utilization for all years of the study based on the top three models. However, one of the top models (Model 37) included a YR×WIDTH interaction, indicating possible annual variation in this relationship, but the uncertainty was large enough that the interaction coefficients had plausible values that were both positive and negative. The WIDTH coefficients from the

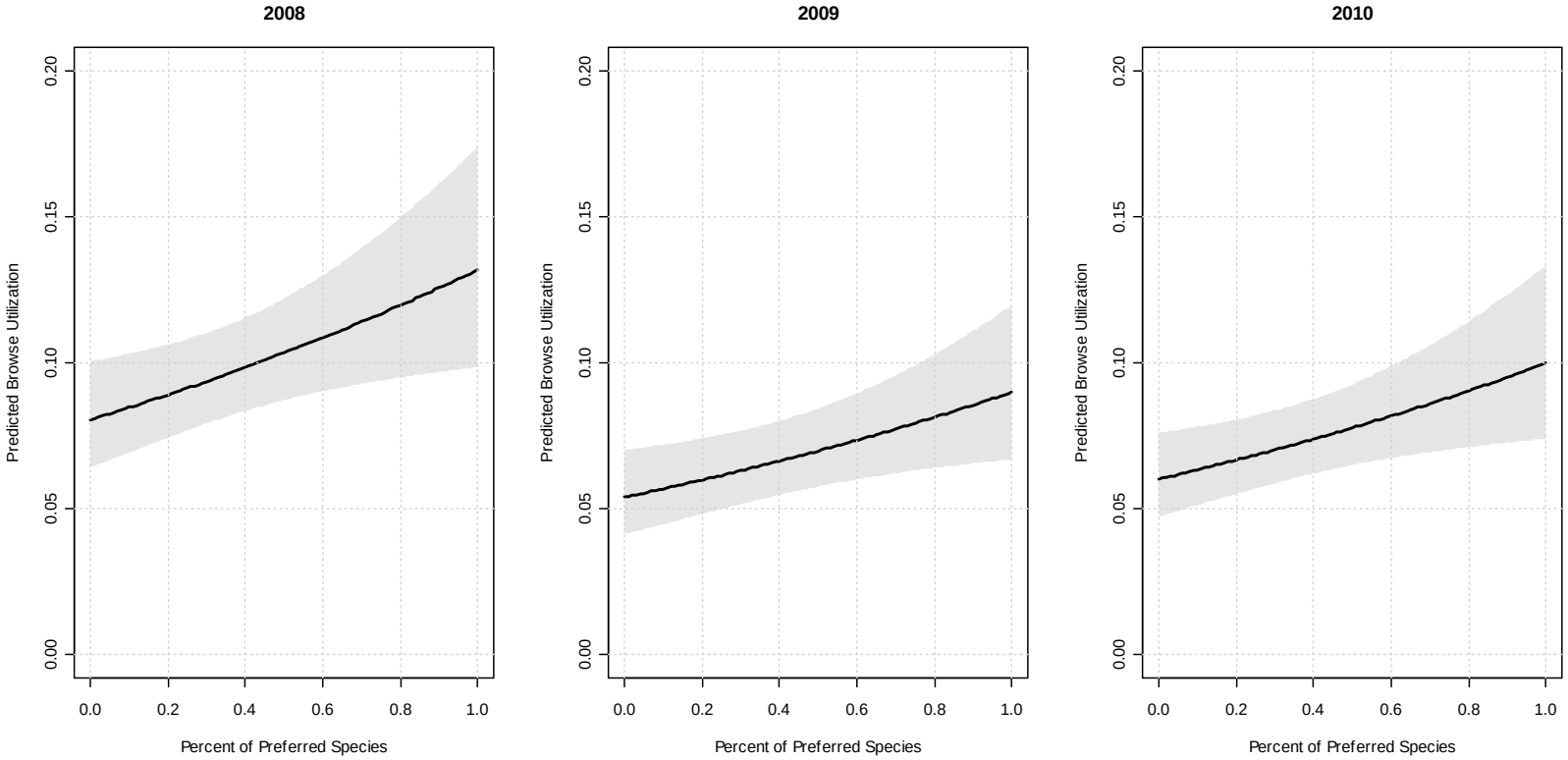

Figure 3.3: A plot showing the predicted relationship between percent preferred species and percent browse utilization for all three years of the study, after accounting for all other covariates in the model. All other covariates were kept at their respective means for this plot. The gray band represents the 95% confidence interval. This plot is based on the coefficients from the top browse utilization model (Model 37), although plots were nearly identical for the other top models.

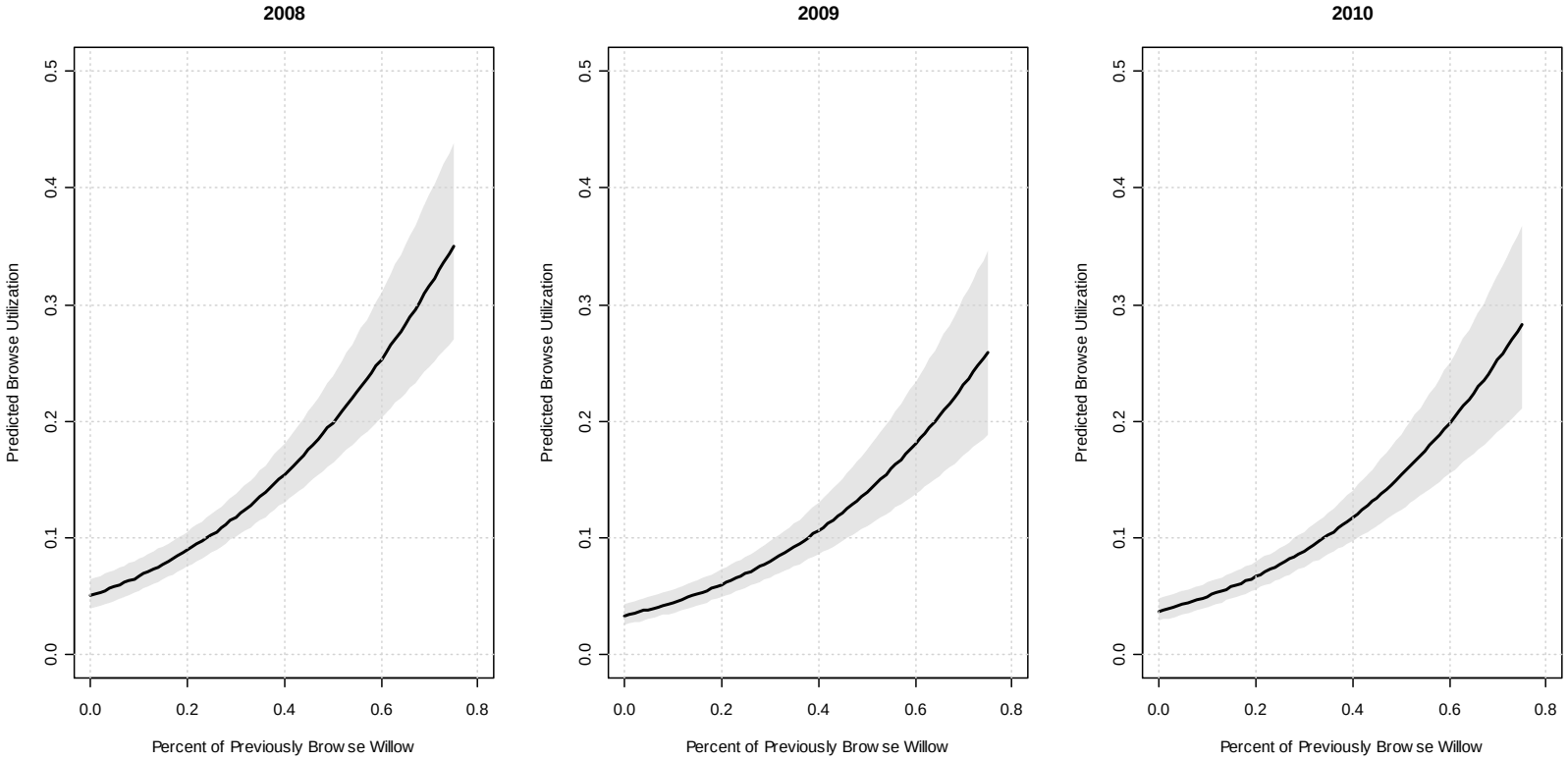

Figure 3.4: A plot showing the predicted relationship between percent previously browsed willow and percent browse utilization for all three years of the study, after accounting for all other covariates in the model. All other covariates were kept at their respective means for this plot. The gray band represents the 95% confidence interval. This plot is based on the coefficients from the top browse utilization model (Model 37), although plots were nearly identical for the other top models.

other two models without interactions were in strong agreement (β_{WIDTH} = -0.00243 and -0.00241). Based on these two coefficients, it was estimated that for a 100 m decrease in willow community width, there was a 1.27 times increase in the odds of browse utilization (95% CI= 1.16, 1.39). Annual plots showing the predicted relationship between willow community width and browse utilization can be found in Appendix S. These plots are based on the model with the interactions (Model 37) and demonstrate the minimal differences between years when the YR×WIDTH interaction accounted for.

There was minimal evidence supporting a negative association between browse utilization and elevation, but this relationship may have been obscured by interannual variation in that relationship, as evidenced by some model selection support for the year and elevation interactions. Two of the top three models included a YR×ELEV interaction and the coefficient for 2010 in those two models suggested a positive association in that year. For each year, however, the plausible coefficient vales for the model averaged estimates of ELEV (and YR×ELEV) could be either positive or negative, suggesting minimal statistical difference between years and no strong association with browse utilization. This is exemplified in the predictive plots showing the relationship between elevation and percent browse utilization, which can be found in Appendix S.

Post Hoc Preferred Species Covariate. Individual browse utilization by species was examined to determine if the a priori hypothesis regarding preferred willow species was correct. Counts for used and available twigs and selection ratios (w_i) for each species (for each year and all years combined) are displayed in Table 3.4. While the literature suggested that Booth's, Drummond's, and planeleaf willow would be highly

Table 3.4: Counts of used and available twigs and selection ratios (W_i) for the species of willow surveyed for browse utilization. Individual years and all years combined data and ratios are presented. Selection ratios > 1 indicate selection for that species, while selection ratios < 1 indicate selection against that species. Selection ratios in bold are significantly different from 1.0 at α=0.05.

	2008			2009		
Species	Used	Available	W_i	Used	Available	W_i
Planeleaf	171	540	**2.61**	204	604	**4.01**
Wolf's	41	182	**1.86**	53	174	**3.61**
Booth's	1267	7376	**1.42**	908	7018	**1.53**
Geyer	1360	9038	**1.24**	936	8780	**1.26**
Drummond's	1090	7088	**1.27**	665	6912	**1.14**
Lemmon's	568	12894	**0.36**	347	13432	**0.31**

	2010			All years		
Species	Used	Available	W_i	Used	Available	W_i
Planeleaf	288	596	**5.70**	663	1740	**3.93**
Wolf's	39	172	**2.67**	133	528	**2.60**
Booth's	951	7072	**1.59**	3126	21466	**1.50**
Geyer	750	8368	1.06	3046	26186	**1.20**
Drummond's	615	6804	1.07	2370	20804	**1.18**
Lemmon's	453	13486	**0.40**	1368	39812	**0.35**

preferred, I found that planeleaf, Wolf's and Booth's willow were the highly preferred species on my study area with selection ratios (w_i) > 1.50. Drummond's and Geyer willow were moderately preferred (1.50 > w_i > 1.00) and Lemmon's willow was strongly selected against on my study area (w_i < 0.50). This pattern existed to varying degrees in all years, although in the winter of 2010 Drummond's and Geyer willow were not selected for or against but rather selected at a frequency equal to their availability.

Due to the discrepancies between the a priori species preference and the observed preferred species, I created a new preferred species variable to determine if it would

improve the fit of the top models or change the coefficient estimates. I reclassified the preferred species to include all species but Lemmon's willow. This covariate was then replaced in the three top models and QIC_c scores compared. The new preferred species covariate (PREFSPP_POST) improved the QIC_c scores of the top 3 models by 13.58-16.49 QIC_c units and increased the weighted average coefficient to $\beta_{PREFSPP} = 0.821$ (95% CI= 0.173, 1.470). Based on this new coefficient value, for a 20% increase in preferred species, there was an estimated 1.18 times increase in the odds of browse utilization (95% CI= 1.035, 1.342). The other coefficient estimates in the top models changed only slightly, but the model selection did significantly change. After substituting the PREFSPP covariate with PREFSPP_POST in all of the a priori models, the QIC_c model selection analysis was rerun. Eight models had ΔQIC_c scores < 4, but only two did not have uninformative parameters. The new top model (Model 15) was actually improved by 22.35 QIC_c units with the PREFSPP_POST covariate. This model actually included a PREFSPP_POST×YR interaction, suggesting possible annual variation in the relationship between percent preferred species and percent browse utilization existed when the preferred species classification was improved (although the interaction coefficients had 95% confidence intervals that included zero). The second top model was Model 42, which was one of the top three models with the original preferred species covariate. The biggest change among the model selection results were that models that included a covariate for elevation (ELEV or YR×ELEV) no longer showed any improvement (i.e. ΔQIC_c scores = 2 for each parameter included) over nested models without the elevation covariate, effectively rendering it an uninformative parameter.

Post Hoc Browse Utilization Modeling. Using the new preferred species covariate (PREFSPP_POST) and the two top models from that model selection (Models 15 and 42), I tested the impacts of adding (in all possible combinations) the three covariates not included in the a priori model selection analysis: distance to conifer cover (DISTCNFR), distance to willow edge (DISTWILL), and average willow community height (HEIGHT). The DISTCNFR and DISTWILL covariates did not improve the models, and HEIGHT only improved models by minimal margins (decreasing 0.063-0.087 QIC_c units), indicating that the addition of the HEIGHT covariate barely explained enough variability to overcome the penalty of 2 QIC_c units. Furthermore, the 95% confidence intervals of the HEIGHT coefficient included zero.

All possible combinations of the quadratic forms of the individual covariates were tested and the combination of $PREVBRWS^2$ and $ELEV^2$ improved the top models greatly (decreasing 32.7-34.6 QIC_c units). Individually, the quadratic forms of $WIDTH^2$, $PREFSPP\_POST^2$, and $HEIGHT^2$ also resulted in moderate improvements (1.93-4.20 QIC_c units). Exponential forms of all covariates were substituted individually and the only covariate that resulted in notable improvement was EXP(WIDTH), which improved the top models by 2.11-2.17 QIC_c units. EXP(HEIGHT) and EXP(DISTCNFR) also produced minor improvements (0.47-1.62 QIC_c units). The potentially important interactions between PREVBRWS×PREFSPP_POST, PREVBRWS×ELEV, and PREFSPP_POST×ELEV were tested independently and in combination. These interactions did not improve model fit and no other interactions were examined.

Discussion

Browse utilization has been measured for decades to quantify the impact of ungulates on various species of shrubs and trees (Stickney 1966, Jensen and Scotter 1977, Wikeem and Pitt 1987, Singer et al. 1994, Romme et al. 1995, Kielland and Bryant 1998, Rooney and Waller 2003, Singer and Zeigenfuss 2003). Recently, monitoring browse condition has been suggested as a potential tool for managing wild ungulate populations (Keigley et al. 2002), including moose. However, for wildlife and habitat managers to effectively use this tool, they need to understand how certain habitat attributes affect moose browse utilization and how much effort is required for effective and meaningful monitoring. They need to know how and where moose impact willow communities and how and where to monitor willow browsing with appropriate sample sizes and placement of monitoring transects to sample areas that are most representative of the entire willow community. Thus, the goal of this research was to improve biologists' understanding of how and where moose browse willow communities in southwestern Montana by evaluating the patterns of browse utilization.

During the course of this study, overall browse utilization was around 10% for each year across the sites monitored on the study area. This was well below the threshold of 20% suggested by a few researchers (Dobkin et al. 2002, Singer and Zeigenfuss 2003) that would indicate possible overutilization of browsed shrubs or result in negative impacts on other species (e.g. avian community diversity). Browse utilization in this study, however, was not universally low, but rather quite heterogeneous, with browse utilization exceeding 40% at some sites each year while others sites had zero utilization.

This pattern is not unique to my study, as many researchers have noted patchy consumption of browse, with some patches preferred over others (Van Dyke et al. 1995, Tyers 2003, Peek 2007, Renecker and Schwartz 2007). Nevertheless, this pattern of heterogeneity suggests that monitoring willow community health or browse utilization could be challenging, as the sample sizes to detect meaningful annual differences may be unrealistically large for biologists or habitat managers to implement.

Fortunately, browse utilization may be somewhat predictable, as demonstrated by the hypotheses tested with QIC_c model selection and coefficients in the top models that were strongly associated with browse utilization. The percent of preferred species and previously browsed willow were both positively associated with browse utilization, as predicted. These associations are not surprising, as many studies have found that moose prefer certain species of willow (Dorn 1970, Stevens 1970, Wilson 1971, Risenhoover 1987, Kovalchik et al. 1988, Tyers 2003, Dwire et al. 2006, Mansson et al. 2007, Baigas 2008) and that moose repeatedly browse willow plants that have been browsed previously (Molvar et al. 1993, Bowyer and Bowyer 1997, Bowyer and Neville 2003, Stolter 2008). The percent of previously browsed willow was a particularly strong predictor in this case, with a 25% increase resulting in a 2.17 times increase in the odds of browse utilization. The original percent of preferred species covariate was not as strongly associated with browse utilization, with a 20% increase resulting in a 1.10 times increase in the odds of browse utilization. The practical application of these numbers demonstrates that across the range of observed values for both covariates, notable changes in the predicted browse utilization occurred, as shown in Figures 3.3 and 3.4.

Contrary to my prediction, browse utilization was negatively associated with willow community width. This covariate was designed to be a surrogate for forage availability, as Mansson et al. (2007) found that forage availability or the amount of forage present at a site was positively associated with browse utilization. Tyers (2003) had a similar finding where moose preferred more productive sites where willow biomass production rates were higher. It makes intuitive sense that patches with greater available browse would be more heavily browsed as moose optimize for greatest input of nutrients at the lowest cost (e.g. optimal foraging theory). Most likely, this surrogate measure did not adequately capture forage availability. Instead, it represented the total volume of willow present at a given point on the stream course and was not specific enough to the browse availability at a local sample site (segment). For instance, if moose browse use was even along stream courses (not effected by volume), then it is possible that the browse impacts at sites with larger volume would be diluted and resulted in lower browse utilization at sites with greater willow community widths. Thus, moose were not selecting for browse where willow communities were less wide, but rather that under the sampling scheme employed in this study, browse was more likely to be captured where willow communities had reduced widths.

Although two of the top three models had elevation and ELEV×YR interaction covariates, there was minimal evidence supporting a negative association between browse utilization and elevation. A negative relationship was expected if elevation was an effective surrogate for snow depth. Although the coefficient for elevation suggested a negative association in 2008 and 2009 and a positive association in 2010, both negative

and positive associations between elevation and browse utilization were plausible in all years. This relationship is shown in the predictive plots in Appendix S. Annual differences in snowpack are one possible reason for these differences. The SWE and snow depth measurements throughout 2008 and 2009 were notably higher than in 2010 (see Figures 2.1 and 2.7). Additionally, it is possible that the negative association between elevation and browse utilization was only present during parts of the winter season when snowpack was greater, which may have been absent in some years (e.g. 2010). This hypothesis is supported by the evidence of cow moose selection for lower elevations when SWE was higher (Chapter 2; Table 2.6 and Appendix J). Since my surveys could only measure browse utilization over the entire winter period, this temporal pattern would have been missed in the browse utilization data. Finally, the minimal range of elevations in the willow communities on the study area may have precluded any notable differences in browse utilization along an elevational/snowpack gradient.

Another notable annual difference was detected in the species preference data. When snow conditions were more severe in 2008 and 2009, five species were browsed at rates significantly greater than their availability. However, during more mild conditions in 2010, the top three species were browsed at slightly higher ratios when compared to 2008 and 2009, while the ratios for the fourth and fifth species declined and were not browsed at rates significantly different from their availability. It is possible that with less severe snow conditions in 2010, moose were able to move more freely around the study area (supported by the home range sizes calculated in Chapter 2; Figure 2.1 and Appendix F) and browse more preferred willow species at higher rates while more easily

avoiding less preferred species.

Post hoc analyses demonstrated that the post hoc percent preferred species covariate resulted in better model fit when compared to the a priori classification. Lemmon's willow was found to be the only willow species that was selected against, while all other species were selected for to varying degrees. Wolf's willow was a surprisingly highly preferred species, but this has been noted to limited degrees in two other studies (Stevens 1970, Tyers 2003). The most unexpected result was the difference in selection for Geyer and Lemmon's willow. These two species are very similar and their classification as unique species (vs. subspecies) has been debated (Brunsfeld and Johnson 1985, Heinze 1994, Hoag 2005). However, moose on my study area selected for Geyer in most years and strongly selected against Lemmon's willow in all years.

Of the additional variables tested post hoc, only average willow community height was supported by the model selection with improvements in QIC_c scores. However, these improvements were negligible (decreasing less than 0.1 QIC_c units) and the coefficient confidence interval included zero, suggesting that average willow community height did not have a strong association with browse utilization after accounting for other covariates in the model. The addition of the covariates for distance to conifer cover or distance to willow edge did not improve the top models. The lack of support for these covariates was not unexpected, as there was only minimal evidence in the literature of their potential associations with browse utilization (Van Dyke et al. 1995, Singer and Zeigenfuss 2003, Tyers 2003, Dussault et al. 2006).

The other post hoc insights were that some alternative functional forms, especially

quadratic forms, improved model fit, while no interactions improved the top models. The quadratic forms for the elevation and percent previously browsed willow covariates yielded the greatest improvement for the top models. Other functional forms only resulted in marginal or no improvements, so the a priori use of strictly linear forms in this study seemed justified.

Issues of Independence and Confounding Factors

In this research, I designed a systematic sampling scheme of willow that was efficient (in terms of time spent in the field) and produced a representative sample of the entire willow community without over- or under-sampling a given stretch of willow along a stream course. However, the design did not produce theoretically independent sample units as many monitoring sites (50 meter segments) were adjacent or close to other sites within each transect. I closely examined this issue with numerous analyses since my data contained obvious extra-binomial variation (overdispersion) and may be indicative of a lack of independence. I could not find a strong or weak spatial autocorrelation between adjacent segments. Effectively, the segments seemed independent, and were treated as such for the other analyses conducted in this chapter. Additionally, I attempted to take into account any transect effect by explicitly modeling browse utilization with transects as the sample unit. At the transect level, I found greatly reduced or non-existent associations between the covariates and browse utilization (compared to the segment level results). This was likely due to substantial heterogeneity in the covariate and browse utilization values within transects, suggesting minimal homogeneity which would lead to a transect effect for each of the transects.

Two other sources could explain the extra-binomial variation noted in this study. First, it was possible that the extra-binomial variation was due to a lack of independence in the binary responses within a segment, as any twig browsed on a given segment (or on an individual willow) would likely accompany more twigs browsed on that segment. This was more or less unavoidable unless only one twig was sampled per willow or per sample site to prevent within willow or within segment dependence. Additionally, there was no way to directly account for this source of non-independence. Second, heterogeneity in probabilities of browse utilization not captured by the covariates examined here was another potential source of overdispersion. Thus, the model structure could have been inadequate, i.e. some important covariates were missing from the model. The most obvious absent covariate was snow depth, as research suggests that this variable may be important for explaining browse patterns on some winter ranges (e.g. Tyers 2003). However, snow depth was nearly impossible to quantify at a 50 m segment scale (and was likely to be variable down to the plant scale). Additionally, snow depth would be highly variable throughout the winter, and it would not be possible to quantify snow depth at the exact time of browse unless moose were backtracked (Tyers 2003) or the established sample sites monitored intensively throughout the winter. I attempted to use elevation as a large-scale surrogate for snow depth, but this covariate was not well supported by the model selection. An accurate and spatially precise snow depth or SWE variable may have greatly reduce the extra-binomial variation found in this study.

Potentially confounding factors in this study were browsing by other ungulates and overall moose density. Other ungulates (elk, cattle) were not present during winter,

but were abundant on the study area in summer and, perhaps most importantly, in fall when elk (Peinette et al. 2001, Brookshire et al. 2002) or cattle (Roath and Krueger 1982, Kauffman et al. 1983) have been known to consume willow. To control this variable, I completed sampling in early spring, before these ungulates were present on the study area. Additionally, I only counted browse from the previous winter, as determined by the color, weathering, and new growth on the browsed twig, reducing the impact of this confounding factor. The other confounding factor was moose density, which probably fluctuated over the course of the study, but did not drastically change. I did attempt to quantify localized moose density (at survey sites) with pellet surveys, but found that most of the sample sites contained no pellet groups and thus were not an effective index of moose abundance or density at that scale. It is important to note that moose densities were moderate to low during the course of this study based on trends in population surveys (MTFWP, unpublished data) and that browse patterns would likely be different or easier to define at higher densities where all or nearly all of the optimal willow patches are occupied and browsed.

Management Implications

The heterogeneity of browse utilization observed in this study provides a considerable challenge to biologists interested in monitoring willow community health and the impacts of browse. This was particularly obvious in the sampling effort (power analysis) results, which showed that the absolute minimum sample size for biologists wanting to detect a 10% difference in browse utilization with 90% confidence intervals was 32 sample sites (e.g. 50 m segments), based on the browse patterns on my study area.

There are a number of caveats that biologists need to be aware of prior to employing the sample sizes estimated in this study to a new browse monitoring program. First, the sample sizes were based on the distribution of the browse utilization measured in this study, which was highly skewed and zero inflated. Other measures of browse utilization or willow community condition may produce more normal distributions and may require less effort (smaller sample sizes) for satisfactory monitoring. Second, the samples sizes recommended here were related to the size of the willow browse study area, which was approximately 5,000 hectares. An area 10 times this size is likely to require a larger sample size and may actually record the impacts of multiple moose populations. Finally, a more random or systematic sampling scheme should be employed, as the sampling in this study included some sites that were adjacent to each other. Instead, sample sites should be well distributed in order to obtain a sufficient sample with a minimal chance of having dependence among sample sites. Thus, the sample size recommendations presented here are a good starting point, but optimal sizes are likely to be site-specific and establishing a new browse monitoring program will likely require some experimentation on the part of the managing biologist.

Additionally, it should be noted that the minimum sample sizes recommended in this study may be too low to detect a 10% difference at much higher browse utilization levels (e.g. ~25%) as the necessary sample size in 2008 was larger when the mean percent browse utilization was higher. This was likely due to increased variability in the distribution of browse utilization responses at higher browse utilization levels. This variability may only increase further with higher browse utilization, as some sites could

be more heavily browsed while others may not be browsed at all in some years (although the proportion of unbrowsed sites in the sample may decrease). Conversely, it is possible that browse would become less heterogeneous and easier to monitor as browse utilization reaches substantial levels. Higher densities of moose may distribute the population more evenly across the landscape and result in widespread heavy browsing with little or no light browsing. While this would be easy to monitor in terms of monitoring site sample size, it is likely that less heterogeneous conditions would only exist at levels of heavy browsing that would be unsustainable in terms of willow community health.

Since moose densities on the study area were low to moderate during this study, local biologists may desire and manage for increasing populations. Based on the current percent browse utilization, the willow community can easily support growth in the local moose population. However, as outlined above, the impacts of a larger population may be harder to monitor (unless heavy browsing is widespread) and may present an unrealistic level of effort necessary to capture interannual changes in browse utilization. Nevertheless, there may still be some utility in completing browse surveys at a lower intensity, as patterns will emerge over longer time periods (multiple years or decades), assuming long-term patterns are helpful for the management of the willow communities and moose populations.

The covariates that were strongly associated with browse utilization in this study were the percent of previously browsed willow, the percent of preferred species, and willow community width. Therefore, sites selected in the future should take these factors into account and not be specifically targeted, which could bias the monitoring effort. A

specific example would be the intentional and exclusive placement of browse utilization sampling sites in areas that are already heavily browsed. Heavy browsing is likely to continue at these sites, regardless of changes in browse utilization over a larger area of interest. Browse monitoring sites should therefore be placed in some areas with high utilization and other areas with low utilization, which could be accomplished with random site selection or intentional stratification. Another example of potential bias would be the monitoring of a single species, without regard for the associated species, as the suite of species at a sample site will have an impact on which species are browsed and the degree of browsing pressure. Furthermore, while species preference may not change, use of specific species may vary annually depending on winter conditions, as noted in the species selection data presented here (Table 3.4). Monitoring multiple species would be ideal to capture interannual changes and to account for the impact of browse utilization on the entire willow community. Whether or not multiple species are monitored, the species composition at monitoring sites needs to be considered and appropriately sampled to capture a representative distribution of browse utilization measures in the area of interest. Species will need to be identified and sample sites stratified if substantial heterogeneity in species composition is present.

Knowing that these factors are associated with browse utilization may also be helpful in interpreting results at historical browse sample sites, if these covariates are measured at those sites. Unfortunately, these data must be collected on the ground as they cannot be remotely sensed, requiring additional time and expertise in the field (especially for willow species identification). Interpretation of browse utilization results

without accounting for these factors should be discouraged as bias may skew results and lead to incorrect management decisions.

Although my research demonstrates that it would be preferred to monitor browse across all willow species (or at least taking into account species composition) to capture a holistic picture of browse utilization, some managers may still prefer to monitor a single species of willow as a surrogate for health of the whole community. In this case, it is important for biologists to quantify or at least have solid anecdotal evidence of local species preferences. In my study, the preferred species of willow were different from what was suggested by the literature from nearby areas. Perhaps most importantly, the identification of the species sampled must be straightforward and definitive. For instance, the use of Geyer or Lemmon's willow on my study site would not be recommended, as it would be challenging for an inexperienced biologist to accurately differentiate between these two species with any level of certainty. The classification and differentiation between these two species is notably important in this case, as there is a very significant difference in moose browse selection between these species that could drastically bias results of browse utilization monitoring efforts if these species are used.

The willow species preference data also have interesting implications for habitat restoration. Using less palatable species for riparian restoration and stream bank stabilization is ideal to achieve results, but if a mix of species are used, then the presence of even a few palatable species may result in browsing on nearby, less palatable species. And once individual willow plants are browsed, they are likely to be browsed again. Based on this study, I would not recommend the use of planeleaf, Wolf's and Booth's

willow for riparian restoration. Drummond's and Geyer willow would probably be suitable, but may still attract moose to browse on less desirable species. Lemmon's willow would be an ideal candidate in this area. On the other hand, if habitat restoration is intended to improve habitat for moose use, then the more palatable species, especially the taller statured planeleaf and Booth's willows, would be well-suited to improving winter range for moose.

In conclusion, I have confirmed that browse utilization was not homogeneous on the Mount Haggin Wildlife Management Area moose winter range, a pattern which is likely to be found on many other moose winter ranges in southwestern Montana. Heavily browsed areas are likely to exist even if overall utilization is low and thus areas of heavily browsed willow are probably unavoidable. This may be especially true since there was strong evidence in this study that moose prefer sites with higher percentages of previously browsed willow for current year browsing. Also, potentially predictable patterns exist in willow browse utilization, as it was associated with numerous habitat covariates tested here. The use of these results in coordination with data collected on the ground will allow biologists to improve the placement of willow monitoring transects to sample areas that are more representative of the willow community as a whole.

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CHAPTER 4

SYNTHESIS, MANAGEMENT AND CONSERVATION IMPLICATIONS, AND DIRECTIONS FOR FUTURE RESEARCH

Synthesis

Moose selection for willow communities during the winter season has been well documented in the literature. Recent research has also demonstrated that selection patterns around willow communities have been associated with habitat attributes (e.g. Van Dyke et al. 1995, Poole and Stuart-Smith 2006, Peek 2007, Baigas 2008, Becker 2008). Within willow communities, browse utilization has been shown to be associated with certain attributes as well (e.g. Bowyer and Neville 2003, Dussault et al. 2006, Mansson et al. 2007, Baigas 2008, Stolter 2008). There was general consensus among recent studies about how these factors were typically associated with winter moose habitat selection or browse utilization. The research presented in this thesis confirms hypotheses about the importance of willow communities when they were widely available to moose on winter range and how attributes within and around those communities were associated with habitat selection or browse utilization patterns.

Two approaches were used in this research to gauge how and where moose were using willow communities and habitats surrounding willow communities. The habitat selection analysis (Chapter 2) examined selection by individual moose, averaged over the population of sampled moose, and included selection both within and outside willow communities. Cover type, distance to conifer, distance to willow, elevation, and

interactions with SWE (snow water equivalent) were all associated with habitat selection at both home range and study area scales, while a solar radiation index was only associated with habitat selection at the home range scale. An examination of the resulting resource selection function (RSF) maps showed high probabilities of habitat selection in and directly adjacent to willow communities at lower elevations, with an increasing association with closer distances to conifer cover as SWE increased. A post hoc examination of the association between temperature and habitat selection found that temperature did change the associations between the conifer cover covariates and habitat selection, with moose selecting for conifer cover as temperatures increased.

The browse utilization analysis (Chapter 3) examined population level selection of willows for browsing within willow communities. The percent of previously browsed willow, percent of preferred species, and willow community width covariates were all strongly associated with browse utilization. An association between elevation and browse utilization was only minimally supported and varied from year to year, and the covariates for willow community height, distance to willow edge, and distance to conifer edge were not supported by the data collected in this study.

There were notable and unexpected differences in these two analyses, especially the importance of distance to conifer cover in habitat selection but not in the browse utilization analysis. As demonstrated in the habitat selection analysis, the increased selection for habitats close to conifer cover was restricted to periods with greater levels of SWE and higher temperatures. In fact, there was evidence of selection for further distances to conifer cover when SWE levels were low (Figure 2.5). This selection

behavior probably had the effect of distributing browse utilization across a wide range of distances to conifer cover in any given winter as snow and temperature conditions changed. Since my browse surveys could only measure browse utilization over the entire winter period, this temporal pattern was absent in the browse utilization data.

The other interesting difference was the strong association between elevation and the probability of habitat selection, but a lack of an association between elevation and browse utilization. As with the distance to conifer covariate, this difference could have been an artifact of the temporal changes in habitat selection. Cow moose increased their selection for lower elevations as SWE levels increased, potentially distributing browse utilization across a wide range of elevations as SWE changed. This probably also explains why there was interannual variation in the association between elevation and browse utilization, as different years had different snow conditions. Furthermore, as most of the browse survey locations were at lower elevations compared to the entire winter study area, the association between elevation and browse utilization may have been obscured by the limited range of elevations examined. Had I measured willow browse utilization at higher elevations, a stronger association may have been present in the data.

These discrepancies between the two approaches demonstrated that browse utilization surveys fail to capture important temporal changes in habitat selection and patterns of use within willow communities. Despite these differences, I was interested to see if there was an association between browse utilization and relative probability of habitat selection. I hypothesized that the locations with higher probabilities of habitat selection should have higher browse utilization, and vice versa.

I used data from the browse utilization sample sites to compare values of browse utilization to the probability of habitat selection. New RSF maps were calculated using the average SWE value for the winters prior to browse utilization sampling (2008 = 19.74 cm, 2009 = 17.27 cm, 2010 = 9.86 cm) and the covariates from the top study area scale RSF model, Model 02 (Chapter 2). The browse utilization estimates at the segment level for the three years monitored were then paired with the RSF values at the sample site locations for the respective years. A plot of the data can be seen in Figure 4.1.

Based on this plot, there was only minimal evidence of higher browse utilization at locations with higher habitat selection probabilities. While there certainly were many locations that fit the pattern of low probability of habitat selection/low browse utilization and high probability of habitat selection/high browse utilization, the data had a large amount of noise and data opposing this pattern. For instance, a few locations with low habitat selection probabilities had high browse utilization. These locations could have been browsed during early winter when snowpack was much lower and were only present in the 2008 and 2009 datasets when the snowpack was higher on average (which had a strong relationship with the habitat selection probabilities of sample sites further from conifer cover). On the opposite side of the spectrum, many locations had low browse utilization despite high habitat selection probabilities. These locations were likely left unbrowsed because no moose occupied that location in that year, despite a higher relative probability of habitat selection. If moose population density was higher on the study area during this study, I would have expected the relationship between browse utilization and relative probability of habitat selection to have been stronger.

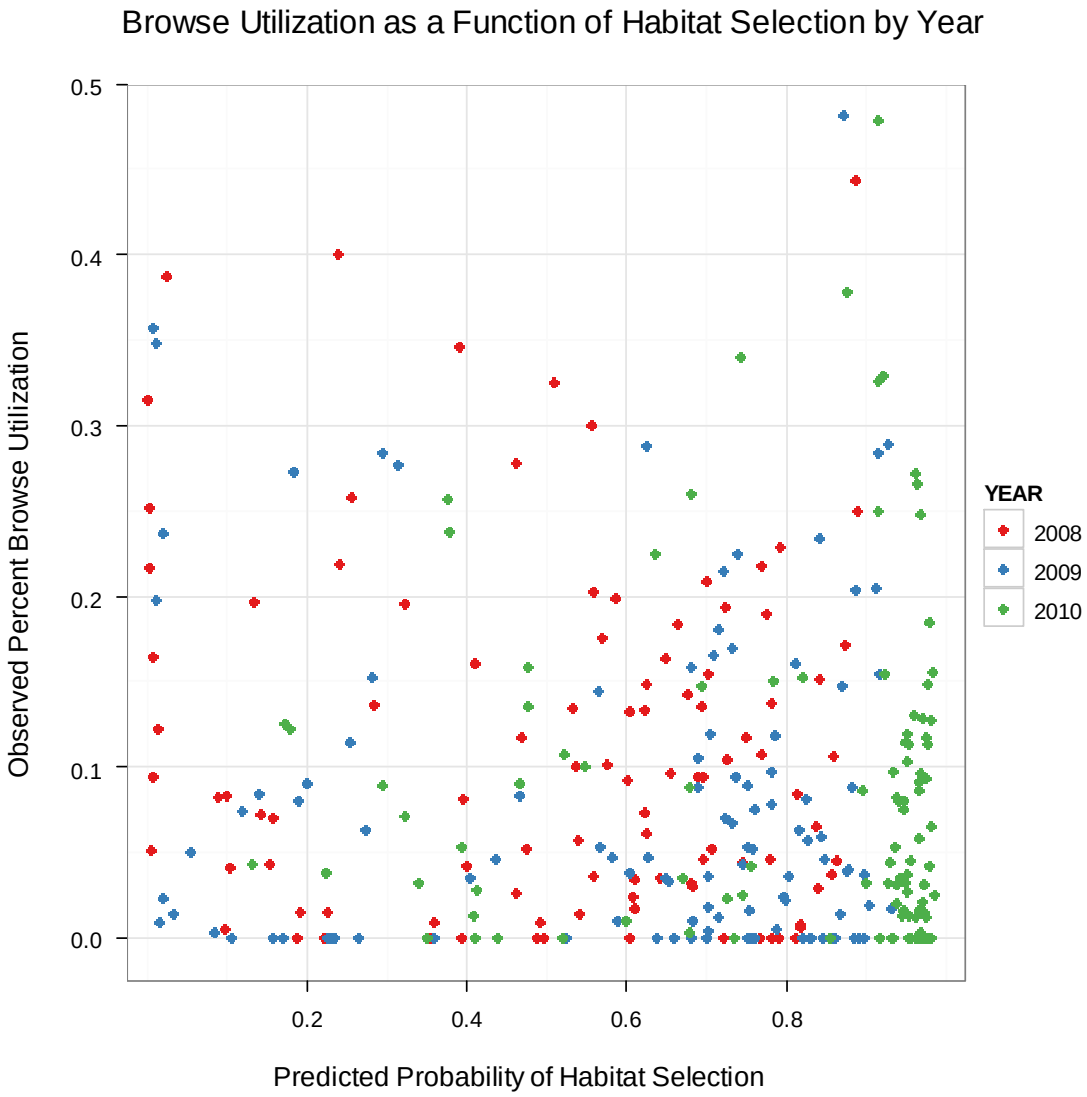

Figure 4.1: A plot showing the relationship between the predicted probability of habitat selection using the top study area scale model and observed browse utilization at the browse survey locations. Data point color represent different years of browse survey and unique RSF models based on average SWE levels for those winters.

Management and Conservation Implications

Willow is an important resource for moose on the Mount Haggin WMA winter range and this is likely true on similar winter ranges in southwestern Montana or other floodplain riparian ranges in the Northern Rockies. Cow moose in this study demonstrated strong selection for willow communities in winter and notable association with this cover type in summer as well (Chapter 2). Home ranges in both seasons were centered on willow stringers along streams and the areas with the highest probability of use based on LoCoH home ranges were almost exclusively in willow communities. Despite this strong selection, the willow communities on the Mount Haggin WMA winter range were browsed at low intensity, with browse utilization less than 15% for all three years in the study and less than 10% for two of those years (Chapter 3). While heavy browsing had been documented with other browse survey methods on my study area less than 10 years prior (Keigley et al. 2002), there was no evidence of widespread heavy browsing during the years studied here (2008-2010). Even with a low overall browse utilization rate on the study area, there were small, localized areas where browse utilization was high, exceeding 40% at a few sites each year. Based on these results, biologists should expect areas of high utilization no matter the density of moose. This may be especially true in areas on winter ranges where a large portion of the moose population is non-migratory, assuming that moose are browsing or leaf-stripping willow in the summer. Additionally, when moose populations are high, the combination of these small areas of high utilization may result in large but patchy areas of willow communities being subject to high browse utilization.

While the impacts of browsing by increasing moose populations was a primary concern when this research was initiated by Montana Fish, Wildlife and Parks in 2006, most moose populations throughout Montana are believed to be stable or decreasing as of 2011 (Smucker et al. 2011) and population declines have been documented in nearby states as well (Tyers 2003, Brimeyer and Thomas 2004, Becker 2008, IDFG 2010). These population declines and their causes are now of much greater interest to wildlife biologists and managers throughout the Northern Rockies. Although predation has been cited by wildlife biologists as a perceived cause of some these declines (Smucker et al. 2011, IDFG 2010), numerous factors may be limiting moose populations in the Northern Rockies.

Sustainable moose populations on the Mount Haggin winter range and elsewhere in the Northern Rockies are likely threatened by multiple factors, including changes to habitat and climate, predation by native carnivores and humans, and the impacts of disease. I found in this research that willow communities and nearby conifer stands are important components of moose habitat. While willow habitats may not be a limiting factor on my study area at this time, other areas in the Upper Big Hole River Valley may be impacted by extensive willow removal on private lands, which will likely impact the populations of moose browsing on those areas. Both willow and conifer habitats may also be impacted by global climate change. For instance, climate change could modify hydrological patterns and in turn change the willow species composition or result in the complete loss of riparian habitat in some locations (Strom et al. 2011). Climatic factors have been associated with willow community health in the Northern Rockies (Beyer et al.

2007), but it has not been determined if climate change will lead to an increase, decrease, or no change in willow community vigor. One study has noted an increase in willow growth due to multiple factors, including wolf and beaver presence in addition to climate changes (Baril et al. 2011). In additional to willow communities, important conifer communities near riparian areas may also be impacted by climate change. Mountain pine beetle infestations (Sambaraju et al. 2011) and increased fire frequency (Westerling et al. 2011) will likely have an increasingly negative impact on conifer communities and conifer canopy cover. Additionally, potential moose forage may have lower nutritional quality in burned habitats than in unburned habitats, resulting in nutritional deficiencies for moose inhabiting burned habitats (Vartanian 2011). This in turn may influence moose populations, especially where moose rely on conifer cover to ameliorate snow conditions during winters of deep snow cover or as thermal refuge during periods of high ambient temperatures. The potential negative impact of forest fires on moose winter range may already be influencing population trends (Tyers 2003, Becker 2008). However, it is possible that moose could temporarily benefit from these changes in areas where forage resources are limited (Ritchie 2008). Mountain pine beetles have already colonized and started to impact the Mount Haggin winter range, although their impact was probably minimal during the period when I collected moose habitat selection and browse utilization data.

Predation by native carnivores may be a greater short-term threat than climate change to moose populations in Montana. Black bears, grizzly bears, and wolves may all prey on moose and moose calves. Predation limits many, but not all moose populations

(Ballard and Van Ballenberghe 2007). In this study, 6 of 13 adult cow moose died while being monitored. Two of these cows were predated upon by wolves or other predators. Predation on calves was not directly monitored in this study as only adults were collared. However, calf survival data from this study can provide a preliminary look at the potential impact of predation. Seven of ten calves survived the summer period (June-Sept) in this study, but only one of six calves survived the winter period (Jan-Apr), which was a particularly poor survival rate. Some of these winter mortalities may be related to difficult snow conditions during a few of the winters in this study (especially 2008), but predation is likely a factor as well and wolf presence on the study area appeared to increase over the period of this study. While the samples sizes were small in this study, it is likely that predation on adult and calf moose does impact population dynamics on the Mount Haggin winter range and may influence other moose populations in Montana where predators are abundant or where predator populations are expanding in extent and size. Further study of moose predation in the Upper Big Hole Valley and in other populations will help wildlife biologists account for predation in order to manage moose populations sustainably and avoid overharvesting.

While not directly addressed in any part of this research, diseases may also threaten the long term viability of moose populations on the Mount Haggin winter range and throughout Montana. Two diseases potentially afflicting moose on the Mount Haggin winter range are winter ticks and the arterial worm *Elaeophora schneideri*. A few ticks were noted on moose on the Mount Haggin winter range, but not at concerning levels. Moose mortalities and hunter harvest early in this study were not examined for *E.*

schneideri, but the last two mortalities (Dec 2009 and Mar 2010) were tested. *E. schneideri* was present in one of these two cow moose, but not at lethal levels. Other diseases, such as Chronic Wasting Disease, could become serious threats if these diseases infect moose populations in Montana.

Directions for Future Research

Future work on moose ecology should focus on impact of changing habitat and climate on habitat selection and population dynamics, the role of predation on populations of moose, and improving aerial or other survey techniques to more accurately monitor moose population trends. Habitat and climate change could include impacts resulting in habitat succession or lack thereof, habitat fragmentation or degradation, or a lack of security from native predators or humans and human development. Research questions may include determining the impact of the mountain pine beetle to modeling future moose habitat or snow conditions under difference climate change scenarios. Mountain pine beetles could reduce critical conifer cover, while climate change could alter willow community extent and vigor as hydrologic patterns shift due to changing winter snowpack accumulations. Climate change could even result in increased competition from other ungulates (both in winter and summer) or increased predation due to apparent competition. A reduction in the severity of winter snow conditions could also create easier access for predators.

While multiple species prey upon moose, new and expanding populations of wolves may have an increasing impact on population dynamics. Both adults and calves

are susceptible to predation by wolves and other predators, so all age and sex classes should be monitored. Calf survival, however, should be a focal area in this long-lived species with low reproductive rates. Although sample sizes in this study were small, summer calf survival was relatively high (70%), but winter calf survival was low (17%). Winter calf survival may be a key element in improving recruitment and sustaining populations, but summer survival should not be ignored as predation during summer seasons can be important in some populations where both bears and wolves are present (Gassaway et al. 1992, Sand et al. 2008). Potential research questions include how different densities of various predators affect survival of adults and calves, if differences in moose survival can be tied to habitat and climatic factors in conjunction with predation, or how indirect effects of predation may limit populations by reducing individual moose fitness or reproductive rates.

Perhaps above all, improved population trend monitoring would provide the biggest improvement to moose management in Montana. Knowledge of more precise population trends would allow for wildlife biologists to monitor for the impacts of hunting, predation pressure, or changes in habitat conditions. While this is likely to be done with aerial surveys, other methods should be investigated, such as hunter interviews. Although I have made suggestions for possible improvements to aerial surveys (primarily timing), more work needs to be done in this area to determine just how variable aerial surveys are and if they can be standardized in some way to better capture trends in moose population sizes on an annual time frame. Specific research questions would include testing various aerial survey methods - potentially even aerial mark and

resight effectiveness, how cover type use changes throughout the winter on different winter range types and affects sightability, and if other techniques such as occupancy modeling from hunter surveys outperform estimates derived from aerial surveys.

Research in these areas will not be easy and will require a large investment of time and financial resources to obtain meaningful results. This is due to the solitary nature of moose during most or all of the year, their low population density in most areas, the fact that they are long-lived and reproduce at low rates, and variability in habitat selection patterns among individuals and between populations of moose. This work will require a dedicated and concerted effort within the state agencies and their collaborators to obtain long-term data sets and data from a range of geographic areas and habitat types.

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APPENDICES

APPENDIX A

CAPTURE DATA

Capture Winter	Cow Moose ID	Capture Date	Collar VHF Freq	Last Successful GPS Location	Total Possible GPS Locations[1]	Acquired Locations	Accurate Locations (DOP<10)	Overall Fix Rate Success[2]	Notes
2007	A	13 Feb 2007	150.030	9 Jun 2007	5581	5319	5136	92.0%	VHF and GPS systems died early
	B	13 Feb 2007	150.040	N/A					VHF and GPS systems died, collar never recovered
	C	13 Feb 2007	150.050	9 Jun 2007	5575	5545	5172	92.8%	VHF and GPS systems died early
	D	13 Feb 2007	150.065	N/A					VHF and GPS systems died, collar never recovered
	5	13 Feb 2007	150.020	15 Jun 2007	5847	5847	5660	96.8%	VHF and GPS systems died early
	6	13 Feb 2007	150.000	14 Jul 2007	7265	6877	6580	90.6%	VHF and GPS systems died early
2008	5[3]	8 Feb 2008	151.385	10 Oct 2008	5870	5870	5825	99.2%	
	6[3]	8 Feb 2008	151.701	10 Oct 2008	5873	5873	5781	98.4%	
	1	8 Feb 2008	150.965	10 Oct 2008	5875	5875	5604	95.4%	Cow spent some time in more rugged terrain
	2	8 Feb 2008	151.180	5 May 2008	2142	2111	2098	97.9%	
	3	8 Feb 2008	151.220	10 Oct 2008	5876	5876	5819	99.0%	
	4	8 Feb 2008	151.355	10 Oct 2008	5875	5875	5762	98.1%	
2009	4[3]	1 Jan 2009	151.180	15 Apr 2010	11249	11249	11134	99.0%	
	7	1 Jan 2009	150.965	28 Sep 2009	6475	6475	6394	98.7%	
	8	1 Jan 2009	151.220	15 Apr 2010	11250	11250	10746	95.5%	Cow spent more time near and in conifer cover
	9	1 Jan 2009	151.355	21 Dec 2009	8441	8441	8314	98.5%	
	10	1 Jan 2009	151.385	7 Mar 2010	10309	10309	10191	98.9%	
	11	1 Jan 2009	151.701	26 Sep 2009	6427	6427	6330	98.5%	

[1] collars in 2007 were scheduled to acquire locations at 0.5 hr intervals, 2008 & 2009 collars at 1.0 hr intervals

[2] fix success = accurate locations/possible locations

[3] indicates moose was recaptured

APPENDIX B

COLLAR ACCURACY DATA

Capture Winter	Cow Moose ID	Left Ear Tag	Right Ear Tag	Capture Date	Collar VHF Freq	Collar Recovery Date	Notes
2007	A	0116M	0121M	13 Feb 2007	150.030	13 Oct 2007	VHF died, collar recovered after hunter mortality
	B	0110M	0122M	13 Feb 2007	150.040	N/A	VHF died, collar never recovered
	C	0114M	0118M	13 Feb 2007	150.050	19 May 2008	VHF died, collar found by shed hunter
	D	0123M	0119M	13 Feb 2007	150.065	N/A	VHF died, collar never recovered
	5	0120M	0125M	13 Feb 2007	150.020	8 Feb 2008[1]	VHF died, 1st collar recovered at recapture
	6	0113M	0124M	13 Feb 2007	150.000	8 Feb 2008[1]	VHF died, 1st collar recovered at recapture
2008	5[2]	0120M	0125M	8 Feb 2008	151.385	10 Oct 2008[1]	
	6[2]	0113M	0124M	8 Feb 2008	151.701	10 Oct 2008[1]	
	1	0107M	0106M	8 Feb 2008	150.965	10 Oct 2008[1]	
	2	0108M	0109M	8 Feb 2008	151.180	5 May 2008	Collar recovered at mortality
	3	0112M	0111M	8 Feb 2008	151.220	10 Oct 2008[1]	
	4	0117M	0115M	8 Feb 2008	151.355	10 Oct 2008[1]	
2009	4[2]	0117M	0115M	1 Jan 2009	151.180	15 Apr 2010[1]	
	7	N/A	0102M	1 Jan 2009	150.965	28 Sep 2009	Collar recovered after hunter mortality
	8	N/A	0104M	1 Jan 2009	151.220	15 Apr 2010[1]	
	9	N/A	0105M	1 Jan 2009	151.355	21 Dec 2009	Collar recovered at mortality
	10	N/A	3413	1 Jan 2009	151.385	7 Mar 2010	Collar recovered at mortality
	11	N/A	3414	1 Jan 2009	151.701	26 Sep 2009	Collar recovered after hunter mortality

[1] indicates collar was recovered at scheduled drop-off or capture

[2] indicates moose was recaptured

APPENDIX C

PARTURITION AND CALF SURVIVAL DATA

Capture Winter	Cow Moose ID	Left Ear Tag	Right Ear Tag	Capture Date	Collar VHF Freq	Calf at Capture	Pregnant at Capture	Spring Calf (Parturition Date)	Winter Calf Notes	Spring Calf Notes
2007	A	0116M	0121M	13 Feb 2007	150.030	Single	Yes	Unk – no localization	Winter calf fate unknown	Spring calf fate unknown, no parturition localization in GPS data
	B	0110M	0122M	13 Feb 2007	150.040	Single	Yes	N/A – collar lost	Winter calf fate unknown	(Possible) spring calf fate unknown
	C	0114M	0118M	13 Feb 2007	150.050	None	Yes	Unk (25 May 2007)		Spring calf fate unknown, parturition localization present in GPS data
	D	0123M	0119M	13 Feb 2007	150.065	None	No	N/A		
	5	0120M	0125M	13 Feb 2007	150.020	None	Yes	Unk (4 Jun 2007)		Spring calf present at Feb 2008 capture
	6	0113M	0124M	13 Feb 2007	150.000	Single	No	N/A	Winter calf fate unknown	
2008	5[1]	0120M	0125M	8 Feb 2008	151.385	Single	Yes	Single (27 May 2008)	Winter calf lost in late Feb 2008	Spring calf lost in early July 2008
	6[1]	0113M	0124M	8 Feb 2008	151.701	None	Yes	Single (17 May 2008)		Spring calf survived summer period (June to mid-Sept 2008)
	1	0107M	0106M	8 Feb 2008	150.965	None	Yes	Single (11 Jun 2008)		Spring calf survived summer period (June to mid-Sept 2008)
	2	0108M	0109M	8 Feb 2008	151.180	None	Yes	N/A – cow mortality		
	3	0112M	0111M	8 Feb 2008	151.220	Single	Yes	Single (31 May 2008)	Winter calf lost in mid-Mar 2008	Spring calf lost in early July 2008
	4	0117M	0115M	8 Feb 2008	151.355	Single	Yes	Single (19 May 2008)	Winter calf lost in late Mar 2008	Spring calf survived summer period (June to mid-Sept 2008)
2009	4[1]	0117M	0115M	1 Jan 2009	150.965	Single	Yes	Single (25 May 2009)	Winter calf survived to calving season (mid-May 2009)	Spring calf survived summer period (June to mid-Sept 2009)
	7	N/A	0102M	1 Jan 2009	150.180	Single	Yes	Single (26 May 2009)	Winter calf lost in Jan 2008	Spring calf lost in early June 2009
	8	N/A	0104M	1 Jan 2009	151.220	None	No	N/A		
	9	N/A	0105M	1 Jan 2009	151.355	None	Yes	Single (18 May 2009)		Spring calf survived summer period (June to mid-Sept 2009)
	10	N/A	3413 (grn)	1 Jan 2009	151.385	None	Yes	Single (22 May 2009)		Spring calf survived summer period (June to mid-Sept 2009)
	11	N/A	3414 (grn)	1 Jan 2009	151.701	None	Yes	Single (22 May 2009)		Spring calf survived summer period (June to mid-Sept 2009)

[1] indicates moose was recaptured

APPENDIX D

MORTALITY REPORTS

May 2008 Collared Moose Mortality Report – revised 15 Jan 2010

Species/Sex – Adult cow moose, radio collared
Frequency – 151.180
Eartag # – 0109M (R), 0108M (L)
Age – 3+ years at capture (Feb 2008), estimated to be ~4 yrs old based on tooth wear

Mortality Location Date – 7 May 2008, 2:30 pm

Mortality Timing – Found dead, estimated 1-4 days old in field, last head live signal on 5 May 2008. Based on GPS data, last major movement was between 8:00-9:00 am MST on 5 May 2008. Stable location until 12:00 am 6 May 2008, then 19 fixes absent from 6 May (struggle? collar upside down?), then stationary and constant locations (same location as before missed fixes) from 9:00pm MST 6 May 2008 on to recovery on 7 May. Estimated time of death from GPS data was 9:00 am MST 5 May 2008, which falls within the window of estimated mortality from physical examination in the field on 7 May.

Location – Mount Haggin WMA, Tenmile Crk
UTM (NAD 83) – 5094351 340000

Health/Observation History – Last located on 4 Apr 2008 in Sevenmile Crk. Did not have visual at that time, cow fled in conifer cover (lodgepole/aspen edge). Solo tracks/beds present indicated cow was alone. Last good visual of this cow was on 7 Mar 2008 in Sevenmile Crk; alone, no indication of compromised physical condition noted at that time.

Mortality Description – Carcass was almost entirely consumed/scavenged when located at 2:30 pm 7 May 2008. Carcass was laying on a dried-up portion of stream bed, partially covered in dirt/grass from nearby bank (caching behavior?). Most of the muscle and all organs except the rumen and a portion of the intestines were gone, but what remain appeared very fresh and not desiccated. Fresh blood was pooled in one spot between the shoulder and ribs (fresh fascia as well). Lower legs still intact, look to be untouched with no obvious bites or wounds. No obvious wounds on what remains of other parts of hide. Only broken bones were a couple of ribs. Nose and tongue consumed, head otherwise intact. No signs of fetus. On what remained of hide, numerous bare patches with broken hair were present and dozens of ticks were present on the underbelly/genital/anal area.

Mortality Site Notes – One wolf (black) and one black bear were flushed from the carcass site. Numerous wolf tracks present in the area on what remained of this winter's snowpack. Moose was gutted and laying next to stream, approximately 35 m from the conifer edge (nearest escape terrain?). There were 6+ fresh blood scats present at the site on 7 May (these were dried-up at the second examination on 8 May). No obvious signs or struggle in the area, but snow was patchy and any struggle in the streambed could've been washed away.

Bone Marrow Condition – A bone marrow sample was collected from a femur on 8 May 2008. Only a field examination was conducted. Marrow was slightly pink, slightly gelatinous (see photos), did not appear out of ordinary for early spring condition (presumably

healthy cow).

Samples Taken – First incisor collected and later lower jaw was retrieved.

Photos Taken – Yes, of mortality site, carcass position, possible hematoma, and bone marrow.

Mortality Conclusions – Cause of death appeared to be potential predation by an unknown predator, but this was difficult to confirm due to the minimal amount of tissue and hide remaining at the mortality site (hematoma not noted) and heavy use of the area by both black bear and wolves. However, the short time frame (<2 days) between death and observation of the carcass seems to favor a predation hypothesis.

December 2009 Collared Moose Mortality Report – revised 15 Jan 2010

Species/Sex – Adult cow moose, radio collared
Frequency – 151.355
Eartag # – 0105M (yellow hex)
Age – 3+ years at capture (Jan 2009), but could be quite old based on missing incisors

Mortality Location Date – 23 Dec 2009, 10:30 am

Mortality Timing – Found dead, estimated 1-4 days old in field, no scavenging yet. Temps cold over the last few days, highs below freezing. GPS location/acquisition data suggests moose was active/moving around until 5:00 am MST 19 Dec 2009. Minimal successful fixes (19) during the next 51 hours, possibly due to struggle/movement and/or GPS antenna submersion. Estimated time of death from GPS data was 8:00 am MST 21 Dec 2009, which falls within the window of estimated mortality from physical examination in the field.

Location – Mount Haggin WMA, NE tributary of Seymour Crk
UTM (NAD 83) – 334458 5088203

Health/Observation History – Last located on 5 Dec 2009 in same drainage as mortality. Did not have visual due to cow fleeing in conifer cover. Tracks/beds present indicated cow/calf pair, but snow was unconsolidated and I could not definitively identify the second tracks as calf tracks; bed was almost assuredly a calf bed (short, small). Last visual of this cow/calf on 25 Sept 2009 in LaMarche Crk with a young bull; she appeared healthy and calf at that time looked to be male.

Mortality Description – Cow was half submerged in a pond (front half exposed), nearly completely covered in mud that had frozen. See photos for exact posture of body. At first examination it appeared as though she had frozen completely, but this was just due to the frozen coat of mud encasing her body. After cutting through the hide to remove the head, is

was found that the muscle tissue around neck was not frozen, despite constant freezing temps and single digit lows, but rather well refrigerated. Minimal decomposition odor, mainly from esophagus. The humerous was also extracted for a bone marrow sample and minimal freezing was noted in the tissue in the right front leg.

Mortality Site Notes – Pond had an opening of 13 ft by 7 ft, iced over ¾" to 1½" thick. Most of pond is over 5 ft deep, including next to cow, and exceeded 6 ft deep in a few spots. Pond was filled with a semi-viscous mixture of water and mud. Mud appeared to be splashed up on all sides of pond and even on nearby willows, most likely due to the cow's attempt to escape. It appeared as though the pond was the remains of a 30-50 year-old (?) beaver pond which had nearly filled in with sediment and had been (mostly) covered by a mat of grasses, which would explain why there was a sudden drop-off at the edges of the open water (not a gradual slope). Well-established willows covered the most of the bottom of the drainage, including over the old pond.

Lots of sign of the calf in area, with calf bed/tracks (150 m north of mort. site) as recent as <12 hours prior based on snowfall from the previous night. Moose beds (presumably calf) found adjacent to and near the mortality site.

Bone Marrow Condition – A bone marrow sample was collected from right humerous as the femurs were inaccessible. Marrow was pink, opaque, solid (see photos). Dr. Ramsey confirmed field assessment that cow was not in a weakened state due to malnutrition (bone marrow normal, healthy).

Samples Taken – Yes, head/bone marrow sample taken to lab and examined by Dr. Ramsey. Head was examined for parasites and 3 arterial worms were found in both the left and right carotid arteries. No meningeal worms or ear mites detected. Presence of arterial worms in this number has been documented in other moose sampled this fall in Montana and Dr. Ramsey did not think this low number of worms would be a "heavy enough burden to cause her significant adverse effects" and "likely did not contribute" to the mortality. CWD test was negative.

Photos Taken – Yes, of mortality site, carcass position, and bone marrow.

Mortality Conclusions – Cause of death appeared to be accidental entrapment in near freezing water and viscous mud, leading to hypothermia.

March 2010 Collared Moose Mortality Report – revised 9 Apr 2010

Species/Sex – Adult cow moose, radio collared
Frequency – 151.385
Eartag # – 3413 (green circle)
Age – 3+ years at capture (Jan 2009), didn't examine teeth before submitting head to lab, jaw not returned

Mortality Location Date – 7 Mar 2010, 11:15 am

Mortality Timing – Found dead, estimated 12-36 hours old in field, scavenging had begun. Temps mild the night prior, lows in the upper teens (°F). GPS location/acquisition data indicates moose was active/moving around until 2:00 am MST 7 Mar 2010. Estimated time of death from GPS data was 2:00 am MST 7 Mar 2010, corresponds with estimated mortality time from examination in the field.

Location – Mount Haggin WMA, E. Fork of Sullivan Creek
UTM (NAD 83) – 337277 5091433 (337280 5091435 according to GPS collar)

Health/Observation History – Last located on 6 Feb 2010 in Lower Deep Creek. Good visual as she fled with calf, both looked in good condition and the calf at that time looked to be female. Last heard her signal on 28 Feb 2010. It sounded like she was in the French Creek Canyon, but GPS data had her at E. Fork Sullivan/Deep Crk confluence at that time.

Mortality Description – Cow was lying on her left side on top of the snow (legs in the snow). Predators/scavengers had opened up three areas: upper throat, the right side of the abdominal cavity, and her rump/posterior, but only minimal consumption had occurred. I did not look for other openings or blood on the left side of the body. Blood and intestines were scattered within a 2 meter radius of the body. Body was still quite warm, no sign of freezing/cooling despite temperatures the night prior (upper teens, °F). Hair was ripped off in many spots and claw marks were readily apparent on the right side of her thoracic cavity (rib cage). No winter ticks were noted. Overall body condition looked very good, including condition of the hide/fur.

Mortality Site Notes – As I approached the site (from the south), I noticed multiple wolf tracks within 50-100 m of the carcass. Coyote tracks were also seen. Magpies and crows could be seen in the willows above the site and a golden eagle flushed from the carcass as well. A coyote was spotted about 50 m to the west, fleeing away from the carcass area. The moose was located in the middle of a thicket of willows, inside a small opening (2x5 m). Snow packed down within 2m of the carcass, presumably by wolves and other scavengers. Snow depth (uncompacted) in the willows was ~45 cm. No blood scats were seen in the immediate area.

I backtracked the cow moose tracks and pursuing wolf tracks for more than 300 meters before losing the tracks in other fresh moose and wolf tracks. After 100 m back, there were no more signs of blood. At 200 m back I was still seeing tufts of hair on the ground (pulled off by wolves?) and occasionally on willow branches. Tracks were in hoar frost/skiff of snow from the last few nights. The wolves were able to stay on top of the crusted snow during the pursuit, while the moose was punching through 30-45 cm of snow. There were 3 wolves in pursuit based on the tracks, and the pack was probably ~ 5 wolves in total (based on tracks entering and leaving the general area). The edges of the moose tracks were clean and crisp, indicating the chase happened during the cooler evening/pre-dawn hours after the crust had re-frozen (confirmed by GPS collar). There was no sign of the calf at the mortality site or during the backtrack.

I do not know if the wolves had left the immediate area before or during my arrival. There were 3 snowmobilers that had passed within 400 m of the site less than one hour prior. Presence of other scavengers may indicate that the wolves had left before I would have disrupted them.

Bone Marrow Condition – Excellent for this time of year, light pink and hard.

Samples Taken – Head taken to lab, but had been somewhat consumed on ventral side (tongue missing). Tested negative for CWD. No report on arterial or meningeal worms (areas potentially consumed by wolves).

Photos Taken – Yes, of carcass, site, bone marrow, and wolf tracks.

Mortality Conclusions – Cause of death was a predation event by a pack of wolves.

APPENDIX E

WINTER AND SUMMER SEASON DATES

Year	Cow Moose ID	Collar VHF Freq	Winter Dates and Locations			Summer Dates and Locations			Notes
			Start Date	End Date	Accurate Locations[1]	Start Date	End Date	Accurate Locations[1]	
2007	A	150.030	13 Feb 2007	10 Apr 2007	2579	24 Apr 2007	9 Jun 2007[3]	2076	Summer data are limited, collar died early in summer period
	C	150.050	13 Feb 2007	10 Apr 2007	2511	24 Apr 2007	9 Jun 2007[3]	1969	Summer data are limited, collar died early in summer period
	5[2]	150.020	13 Feb 2007	10 Apr 2007	2632	24 Apr 2007	15 Jun 2007[3]	2425	Summer data are limited, collar died early in summer period
	6[2]	150.000	13 Feb 2007	10 Apr 2007	2565	24 Apr 2007	14 Jul 2007[3]	3414	Summer data are limited, collar died early in summer period
2008	5[2]	151.385	8 Feb 2008	30 Apr 2008	1957	10 May 2008	10 Oct 2008[3]	3659	Collar dropped off at summer end date
	6[2]	151.701	8 Feb 2008	30 Apr 2008	1943	10 May 2008	10 Oct 2008[3]	3631	Collar dropped off at summer end date
	1	150.965	8 Feb 2008	30 Apr 2008	1888	10 May 2008	3 Sept 2008	2690	Moose at made range shift at summer end date
	2	151.180	8 Feb 2008	30 Apr 2008	1956				Moose died on 5 May 2008, no summer data
	3	151.220	8 Feb 2008	30 Apr 2008	1887	10 May 2008	10 Oct 2008[3]	3659	Collar dropped off at summer end date
	4[2]	151.355	8 Feb 2008	30 Apr 2008	1944	10 May 2008	10 Oct 2008[3]	3612	Collar dropped off at summer end date
2009	4[2]	151.180	1 Jan 2009	30 Apr 2009	2841	10 May 2009	10 Nov 2009	4380	
	7	150.965	1 Jan 2009	30 Apr 2009	2854	10 May 2009	28 Sept 2009[3]	3345	Moose harvested on summer end date
	8[2]	151.220	1 Jan 2009	30 Apr 2009	2784	10 May 2009	10 Nov 2009	4105	
	9	151.355	1 Jan 2009	30 Apr 2009	2834	10 May 2009	10 Nov 2009	4356	
	10[2]	151.385	10 Jan 2009	30 Apr 2009	2612	10 May 2009	10 Nov 2009	4389	Moose didn't localize before 10 Jan 2009
	11	151.701	12 Jan 2009	20 Apr 2009	2297	10 May 2009	26 Sept 2009[3]	3299	Moose migrated for winter, harvested on summer end date
2010	4[2]	151.180	1 Jan 2010	15 Apr 2010[3]	2481				Collar dropped off at winter end date, no summer data
	8[2]	151.220	1 Jan 2010	15 Apr 2010[3]	2449				Collar dropped off at winter end date, no summer data
	10[2]	151.385	1 Jan 2010	7 Mar 2010[3]	1558				Moose died on winter end date, no summer data
Mean (Total)					2345.89 (44572)			3400.60 (51009)	If summer 2007 data are excluded (due to limited period of data collection), means are 22.4427 and 2.9795, respectively

[1] accurate locations are those with DOP<10, see Appendix X for fix interval and fix rate success

[2] indicates moose was recaptured or monitored for multiple winters

[3] end of period determined by end of data collection (collar drop, mortality, etc.)

APPENDIX F

HOME RANGE ESTIMATES

Year	Cow Moose ID	Collar VHF Freq	Winter Home Range Size Estimates		Summer Home Range Size Estimates		Notes
			Fixed Kernel[1]	aLoCoH[2]	Fixed Kernel[1]	aLoCoH[2]	
2007	A	150.030	2.6499	0.3162	9.7308	1.3299	Summer data are limited, collar died early in summer period
	C	150.050	6.6298	0.6303	25.2368	2.7041	Summer data are limited, collar died early in summer period
	5[3]	150.020	23.8354	4.0595	21.9909	3.0501	Summer data are limited, collar died early in summer period
	6[3]	150.000	15.0684	1.7369	12.8872	2.2089	Summer data are limited, collar died early in summer period
2008	5[3]	151.385	12.5872	2.3322	18.4023	3.3056	
	6[3]	151.701	6.1266	0.8281	16.1877	1.7090	
	1	150.965	2.4359	0.2021	37.2748	3.9436	
	2	151.180	3.2136	0.3815			Moose died before any summer data were collected
	3	151.220	3.2779	0.3442	9.0450	1.3609	
	4[3]	151.355	4.8308	0.3429	20.5555	1.9820	
2009	4[3]	151.180	6.3606	0.7860	21.3937	2.0296	
	7	150.965	4.3882	0.7301	13.8525	0.9961	
	8[3]	151.220	12.3884	1.0927	26.3367	7.2676	
	9	151.355	15.1299	1.2317	51.8242	5.8875	
	10[3]	151.385	6.0456	0.7430	19.5578	3.1066	
	11	151.701	8.2299	0.5291	12.4395	1.1860	
2010	4[3]	151.180	11.4536	0.7482			Collar dropped off at end of winter, no summer data
	8[3]	151.220	12.0065	1.2168			Collar dropped off at end of winter, no summer data
	10[3]	151.385	28.1342	3.9847			Collar dropped off at end of winter, no summer data
Mean			9.7259	1.1703	21.1144	2.8045	If summer 2007 data are excluded (due to limited period of data collection), means are 22.4427 and 2.9795, respectively

[1] area within the 95% contour of a fixed kernel home range in km^2

[2] area within the 90% isopleth of an adaptive local convex hull home range in km^2

[3] indicates moose was monitored for multiple winters

APPENDIX G

ORIGINAL LOCATIONS AND SEASONAL HOME RANGE FIGURES

The following appendix contains figure clusters for all individual moose collared over the course of this study. Each cluster contains 4 panels, each at the same scale and encompassing the same geographical area. The extent of the area covered is indicated on the center map which shows the study area polygon for reference. The scale bar refers to the scale of the four panels, not the center map. The moose and year noted at the bottom of each figure cluster.

The top two panels display data for the winter season. In the upper left panel, the 95% contour of the fixed kernel home range estimate is displayed, along with all of the location points collected during the winter period. In the upper right panel, the LoCoH (local convex hull) home range estimate is displayed, along with the fixed kernel home range for reference.

The bottom two panels display data for the summer season, assuming the individual moose was still collared in that summer of that year. In the lower left panel, the 95% contour of the fixed kernel home range estimate is displayed, along with all of the location points collected during the summer period. In the lower right panel, the LoCoH home range estimate is displayed, along with the fixed kernel home range for reference.

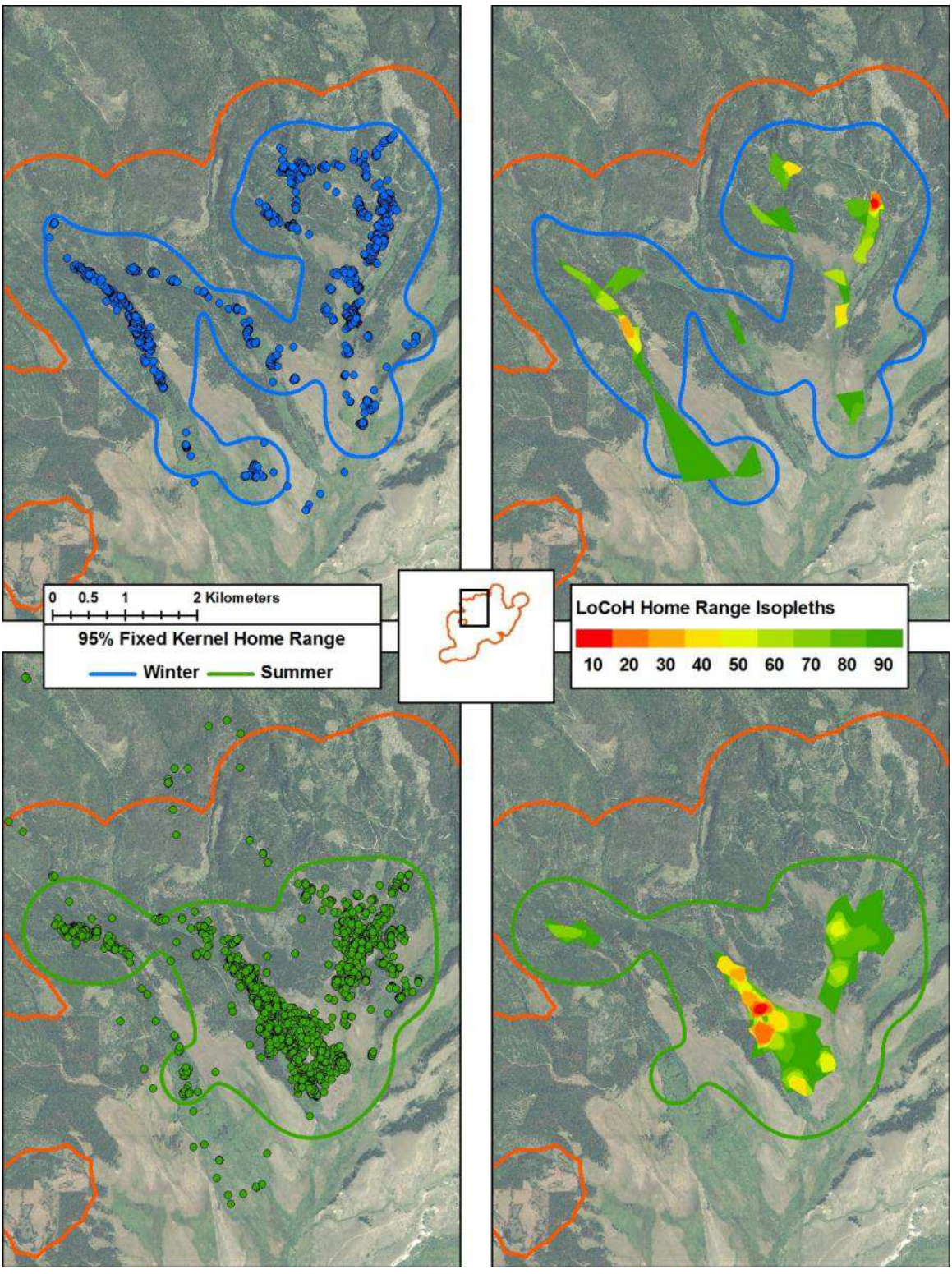


Figure G.1: The panels above show the seasonal locations and home range estimates for cow moose 6 in 2007. Data in these panels are as described at the start of Appendix G.

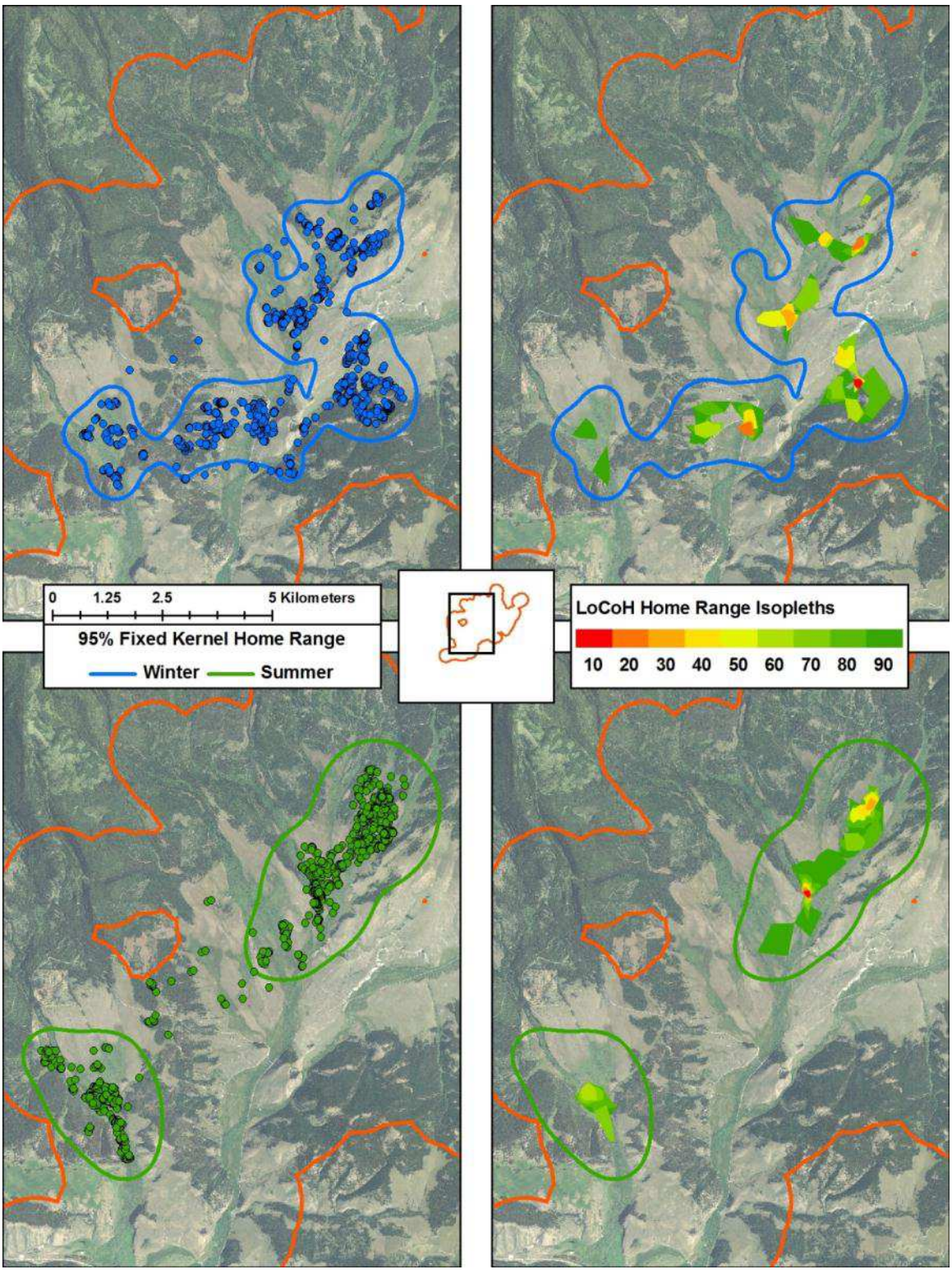


Figure G.2: The panels above show the seasonal locations and home range estimates for cow moose 5 in 2007. Data in these panels are as described at the start of Appendix G.

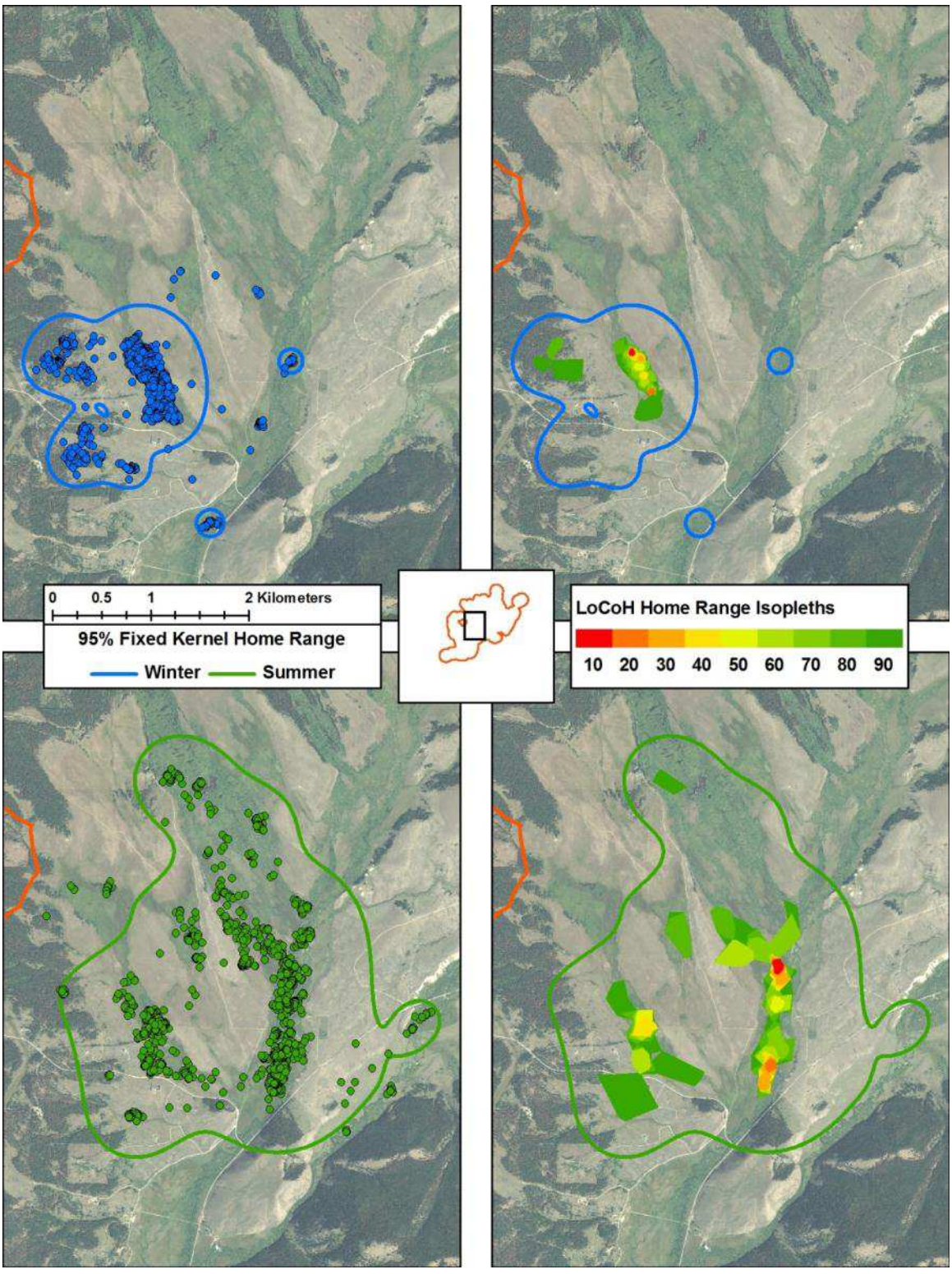


Figure G.3: The panels above show the seasonal locations and home range estimates for cow moose A in 2007. Data in these panels are as described at the start of Appendix G.

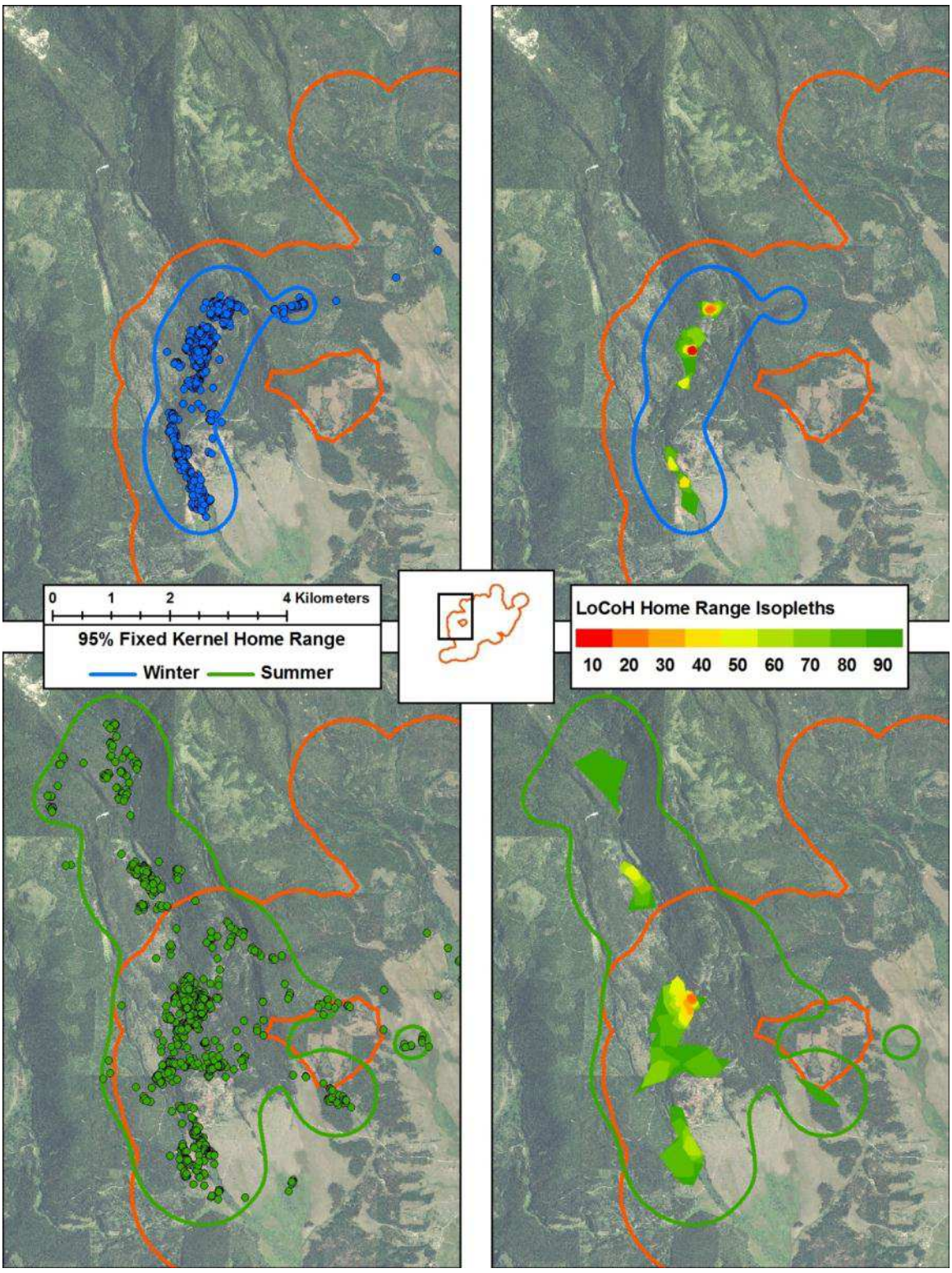


Figure G.4: The panels above show the seasonal locations and home range estimates for cow moose C in 2007. Data in these panels are as described at the start of Appendix G.

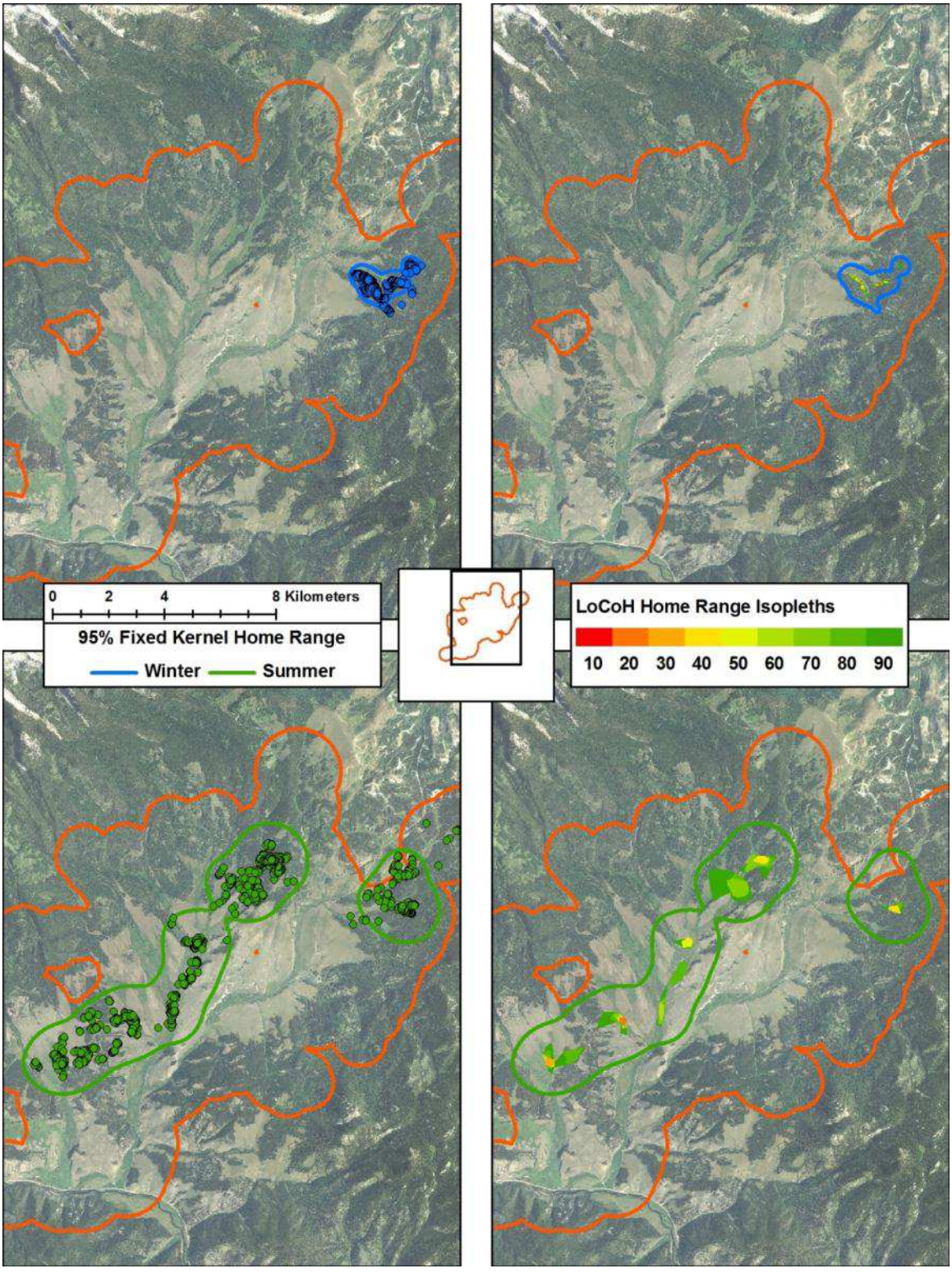


Figure G.5: The panels above show the seasonal locations and home range estimates for cow moose 1 in 2008. Data in these panels are as described at the start of Appendix G.

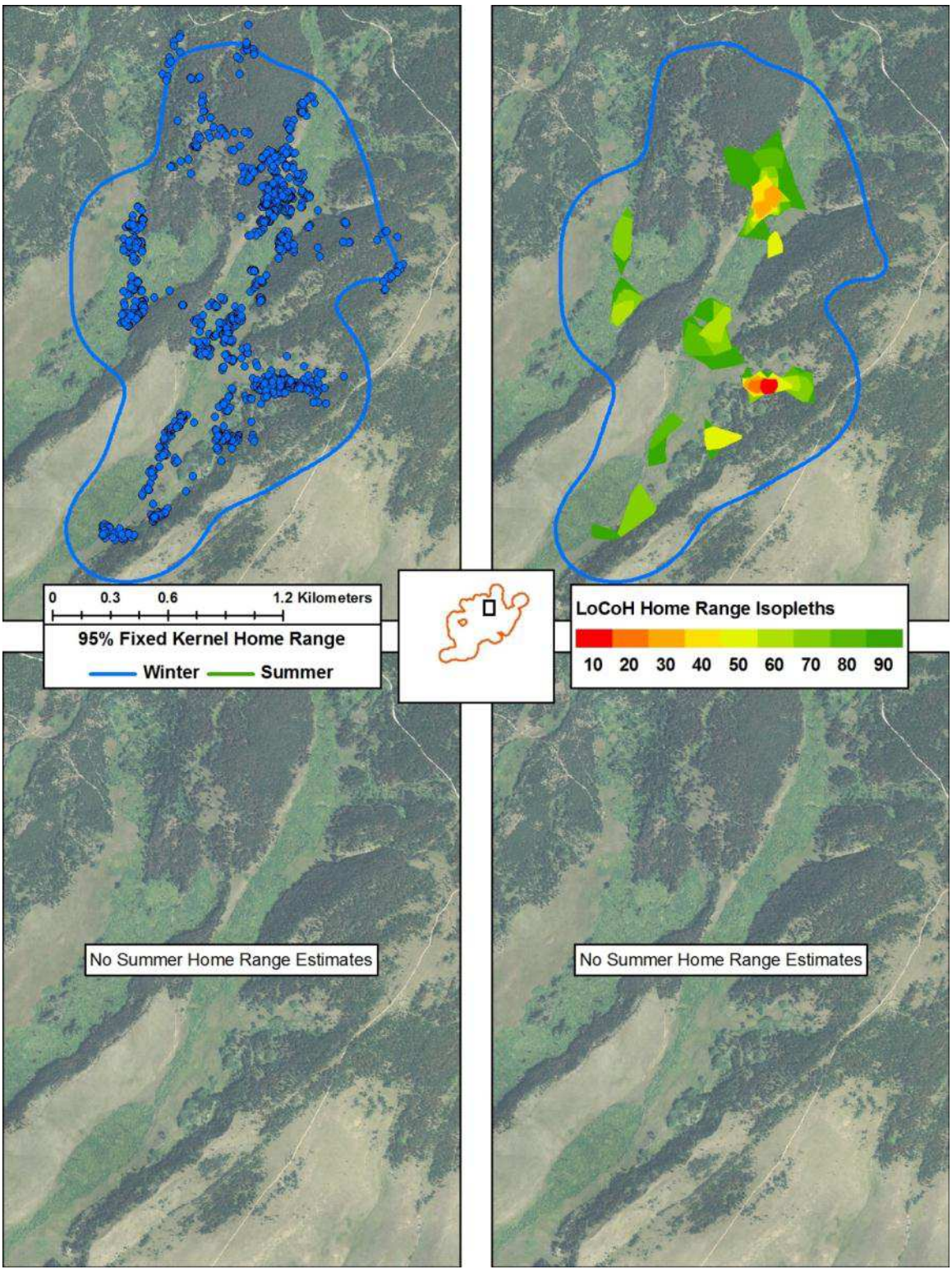


Figure G.6: The panels above show the seasonal locations and home range estimates for cow moose 2 in 2008. Data in these panels are as described at the start of Appendix G.

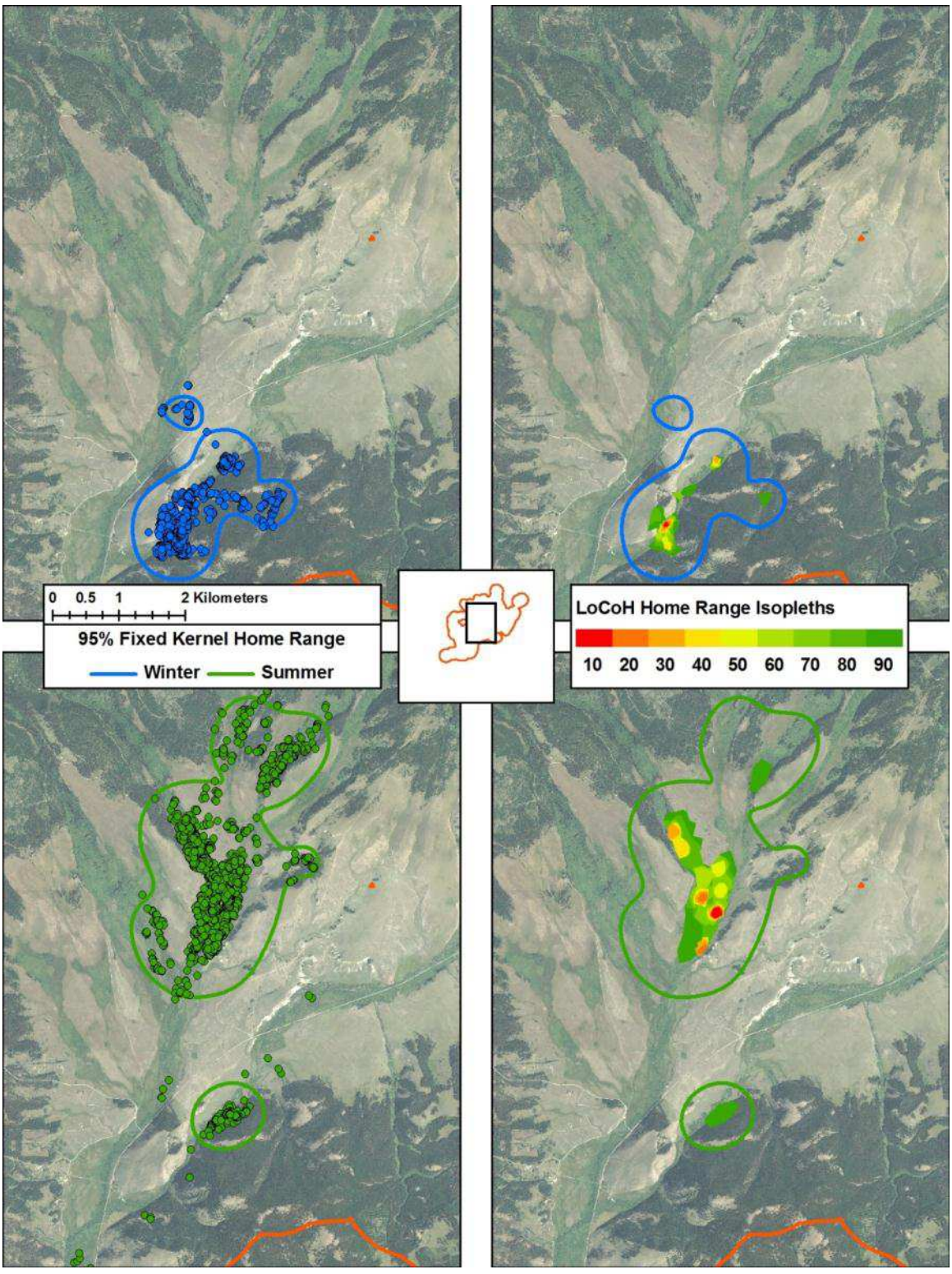


Figure G.7: The panels above show the seasonal locations and home range estimates for cow moose 3 in 2008. Data in these panels are as described at the start of Appendix G.

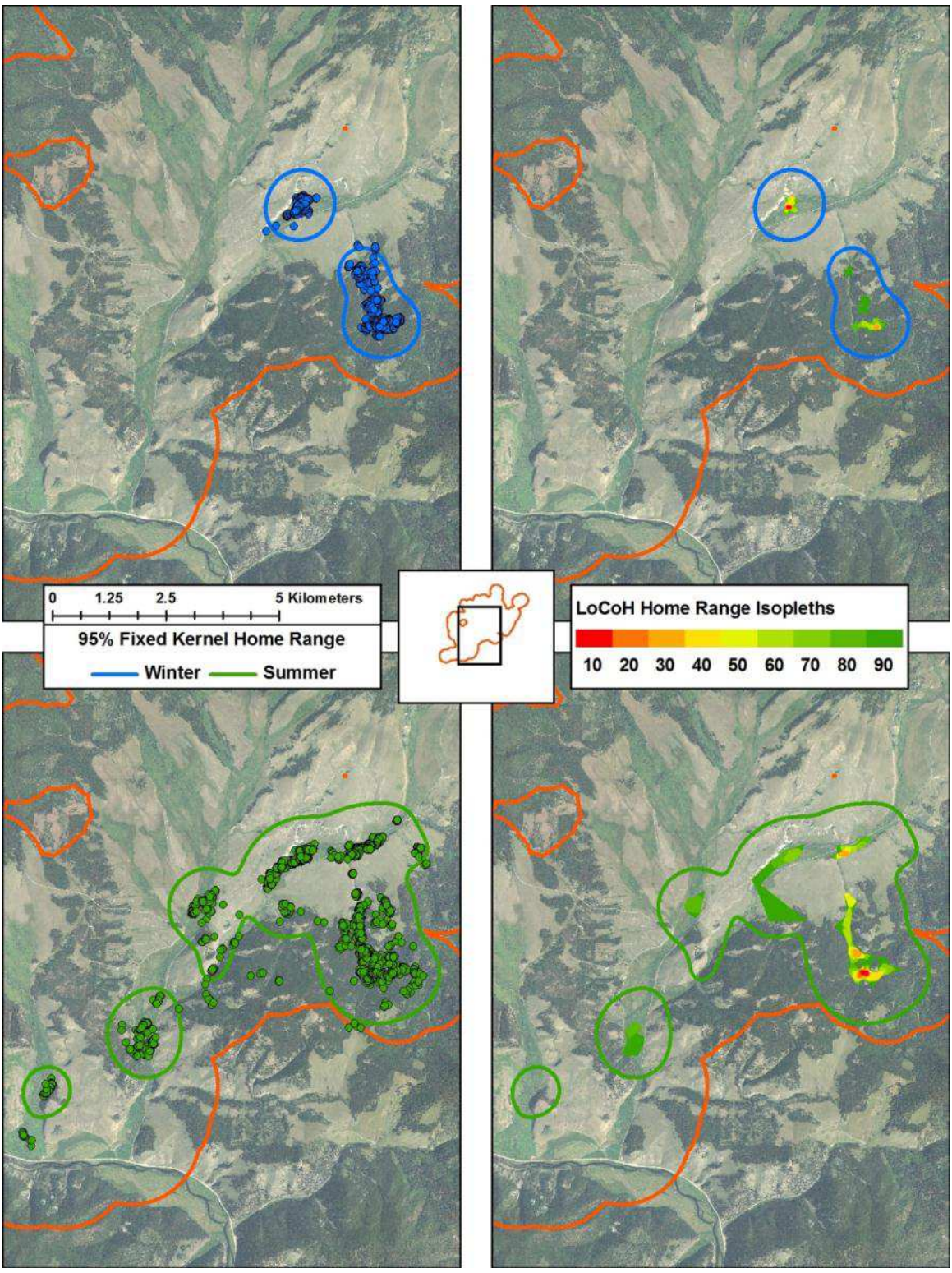


Figure G.8: The panels above show the seasonal locations and home range estimates for cow moose 4 in 2008. Data in these panels are as described at the start of Appendix G.

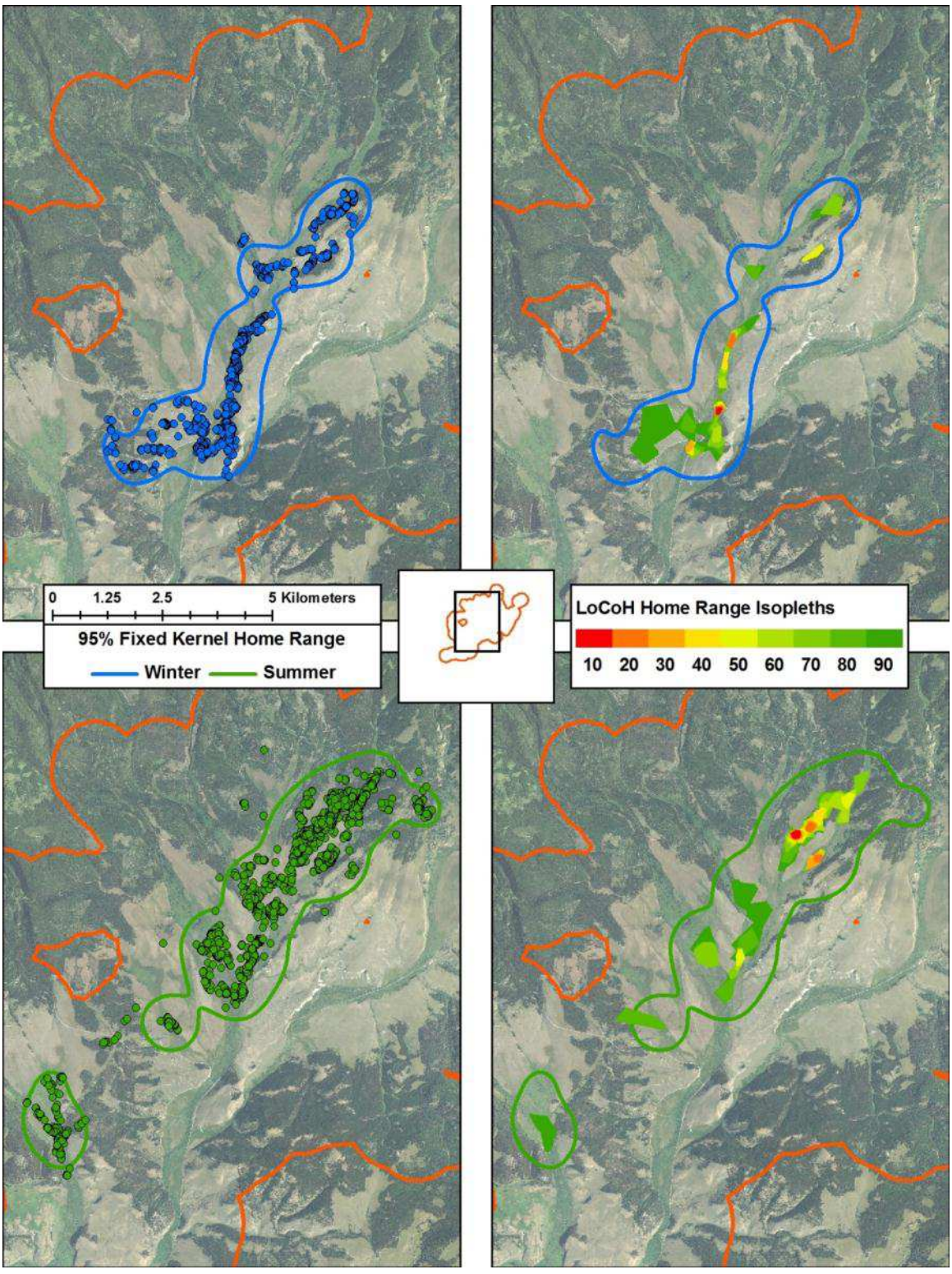


Figure G.9: The panels above show the seasonal locations and home range estimates for cow moose 5 in 2008. Data in these panels are as described at the start of Appendix G.

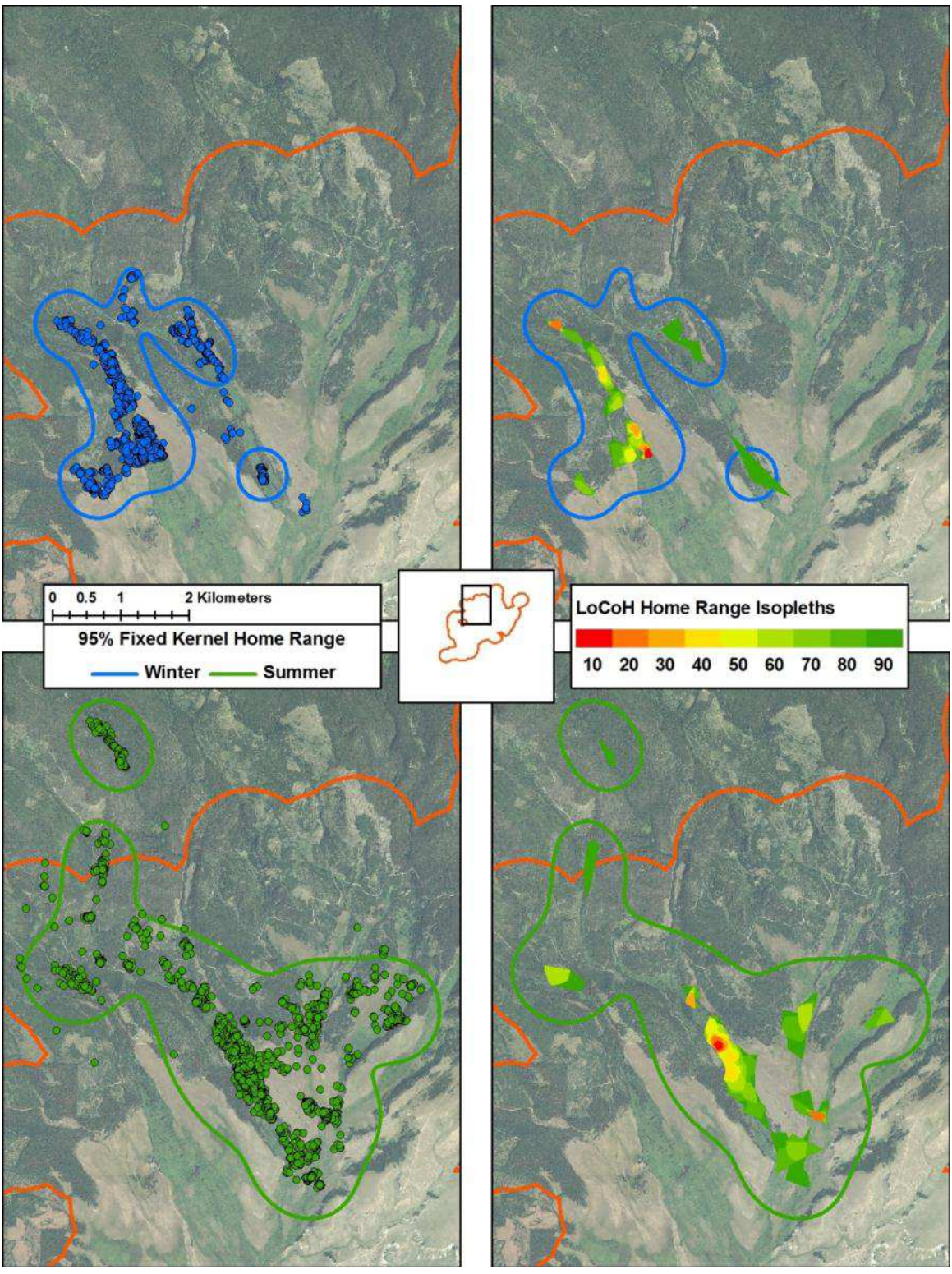


Figure G.10: The panels above show the seasonal locations and home range estimates for cow moose 6 in 2008. Data in these panels are as described at the start of Appendix G.

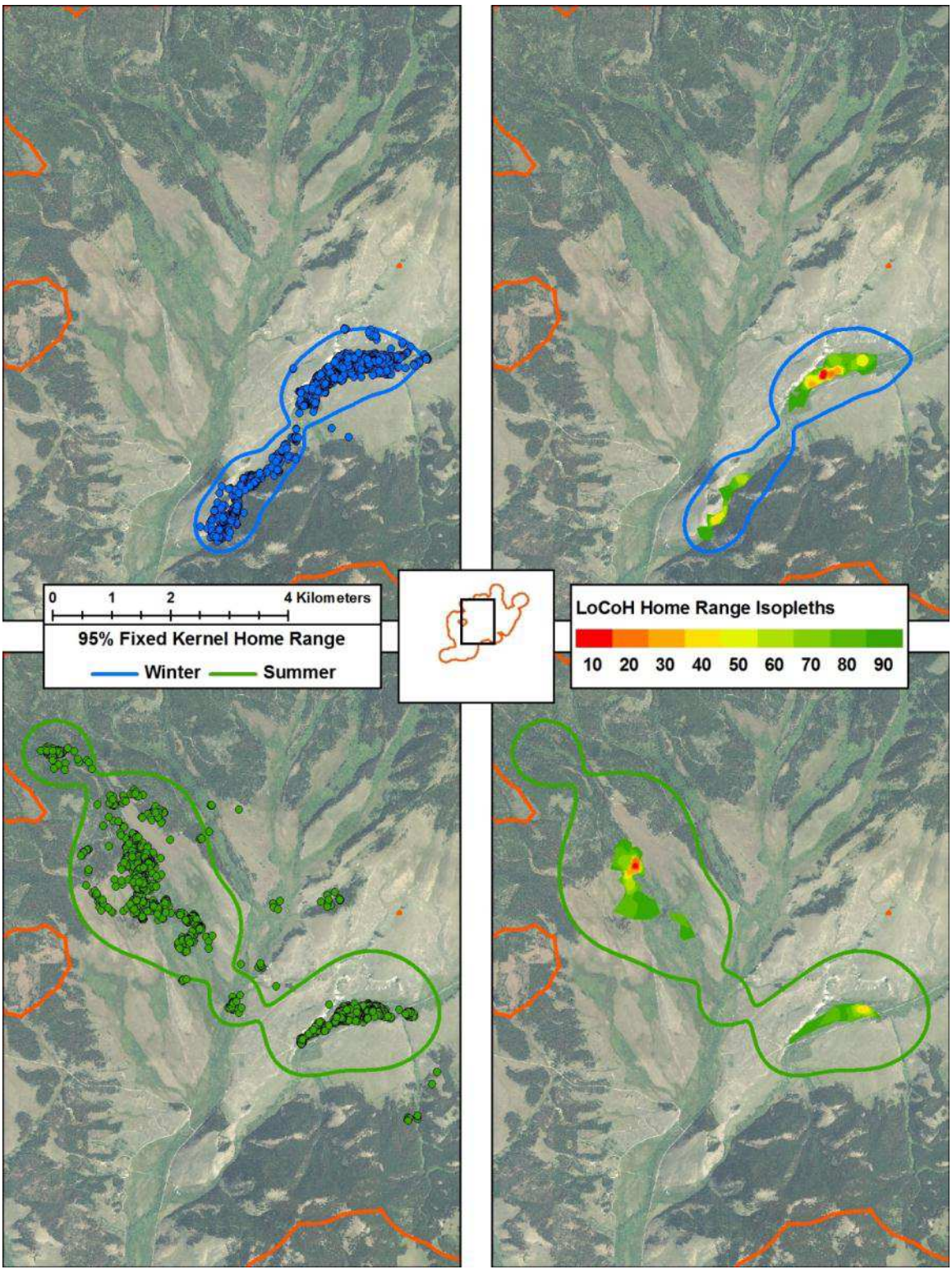


Figure G.11: The panels above show the seasonal locations and home range estimates for cow moose 7 in 2009. Data in these panels are as described at the start of Appendix G.

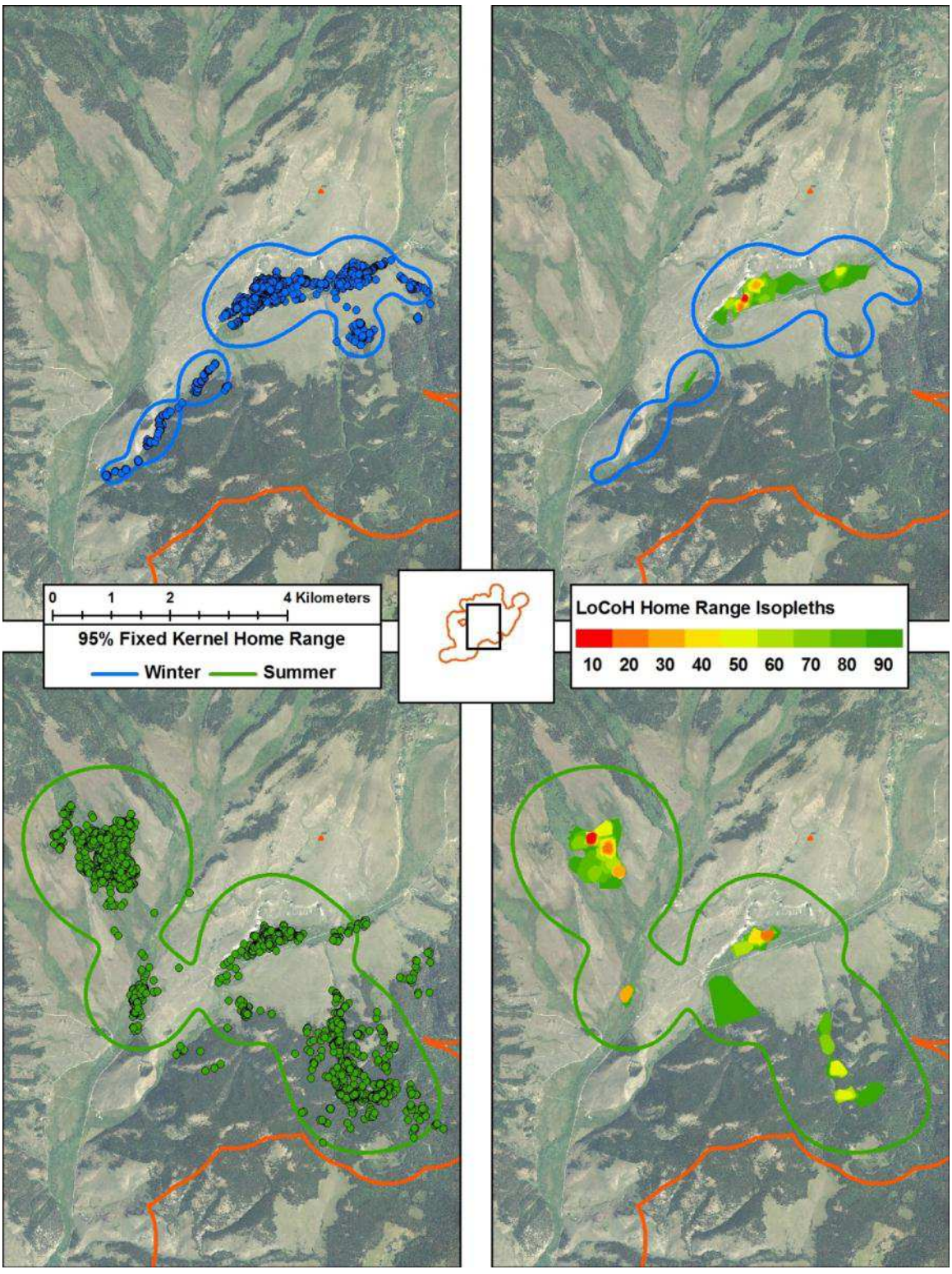


Figure G.12: The panels above show the seasonal locations and home range estimates for cow moose 4 in 2009. Data in these panels are as described at the start of Appendix G.

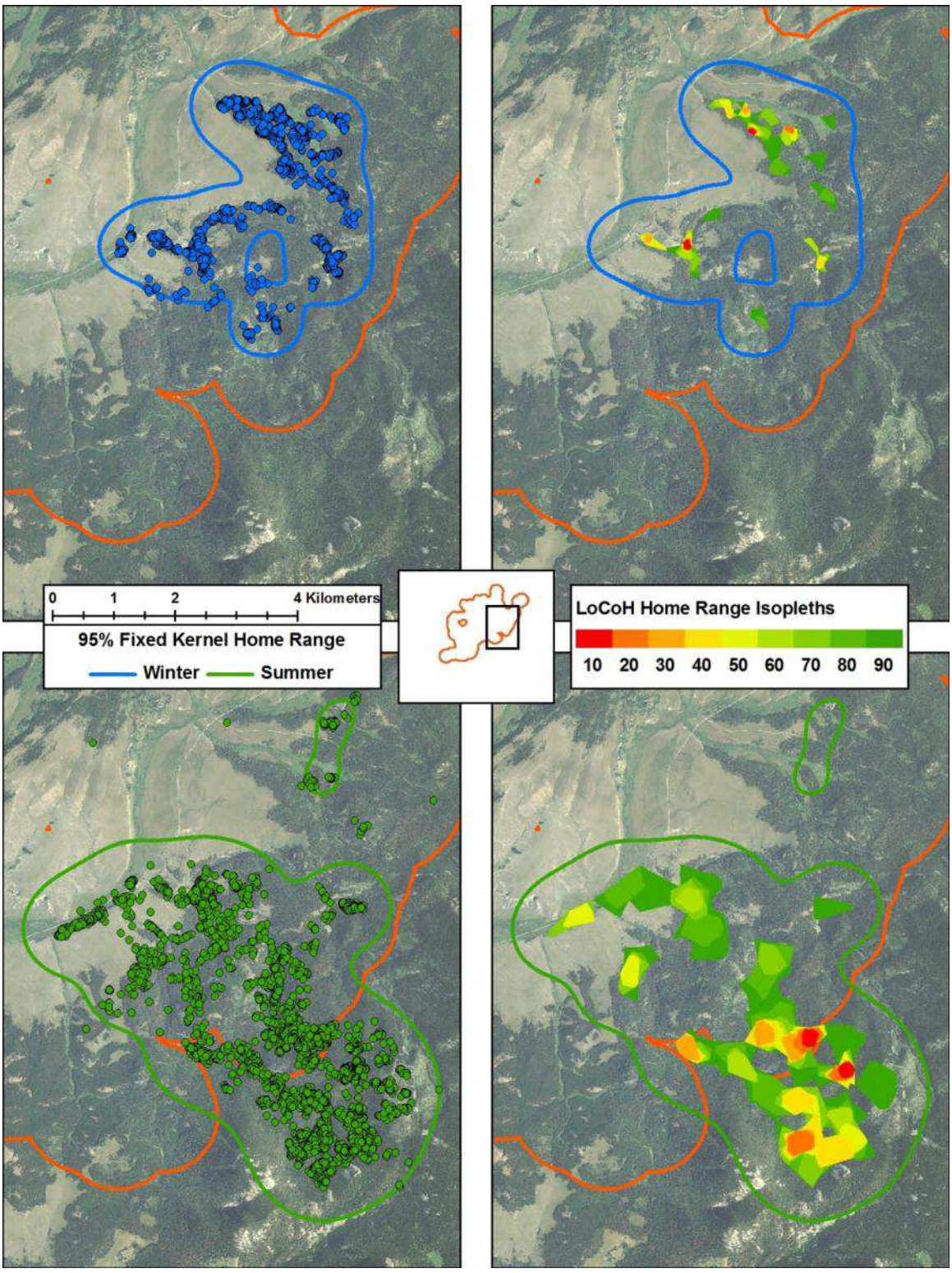


Figure G.13: The panels above show the seasonal locations and home range estimates for cow moose 8 in 2009. Data in these panels are as described at the start of Appendix G.

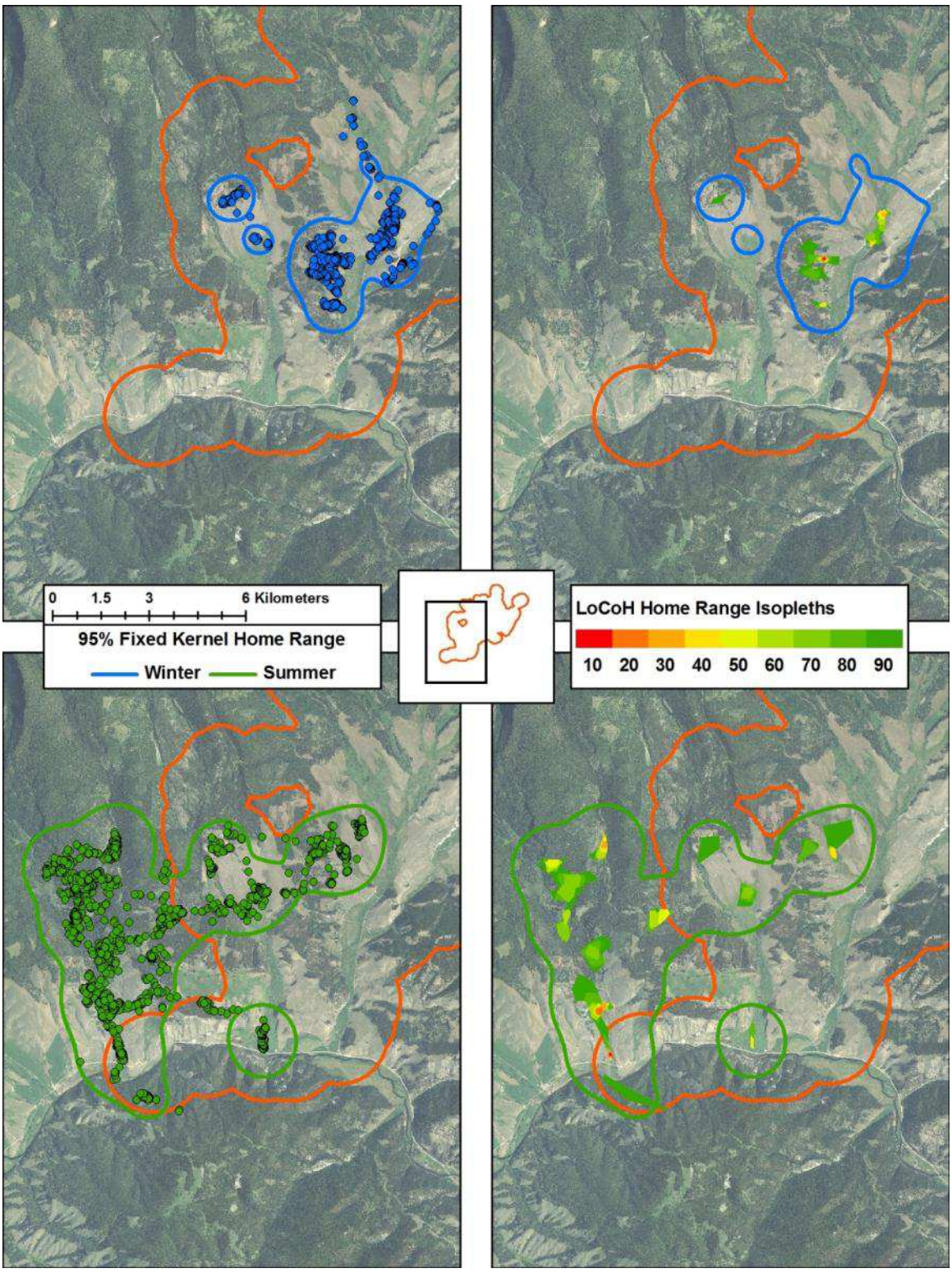


Figure G.14: The panels above show the seasonal locations and home range estimates for cow moose 9 in 2009. Data in these panels are as described at the start of Appendix G.

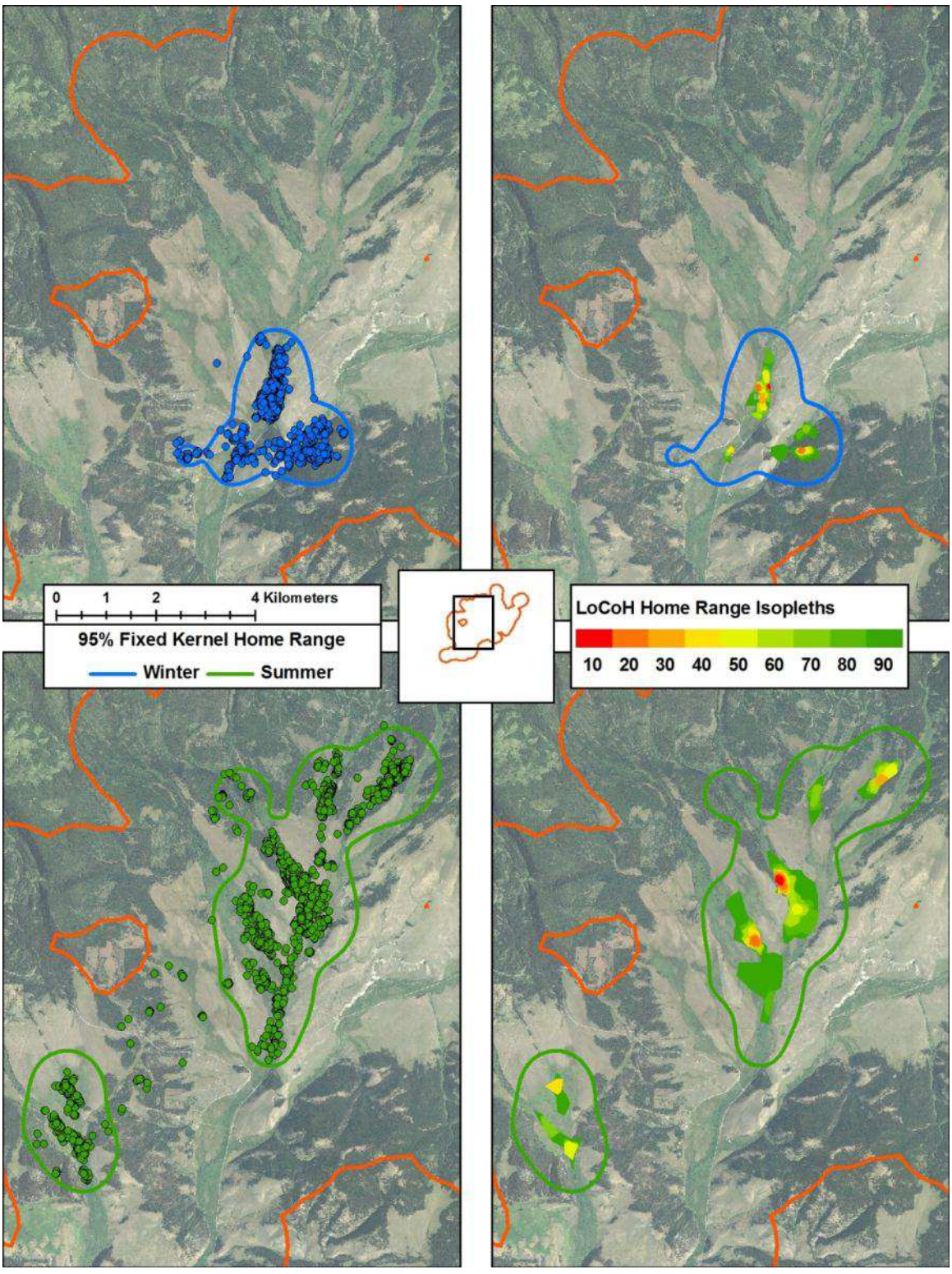


Figure G.15: The panels above show the seasonal locations and home range estimates for cow moose 10 in 2009. Data in these panels are as described at the start of Appendix G.

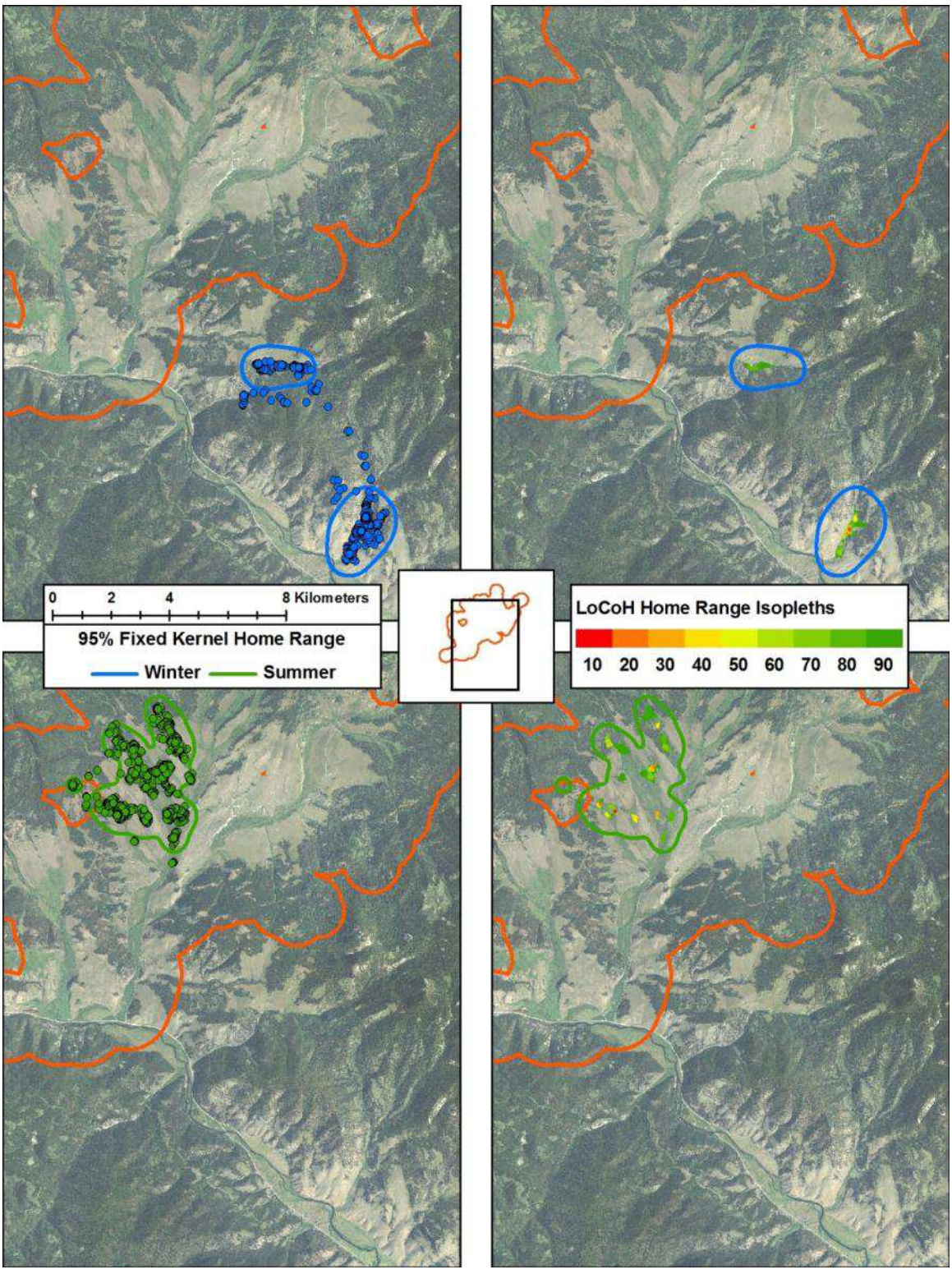


Figure G.16: The panels above show the seasonal locations and home range estimates for cow moose 11 in 2009. Data in these panels are as described at the start of Appendix G.

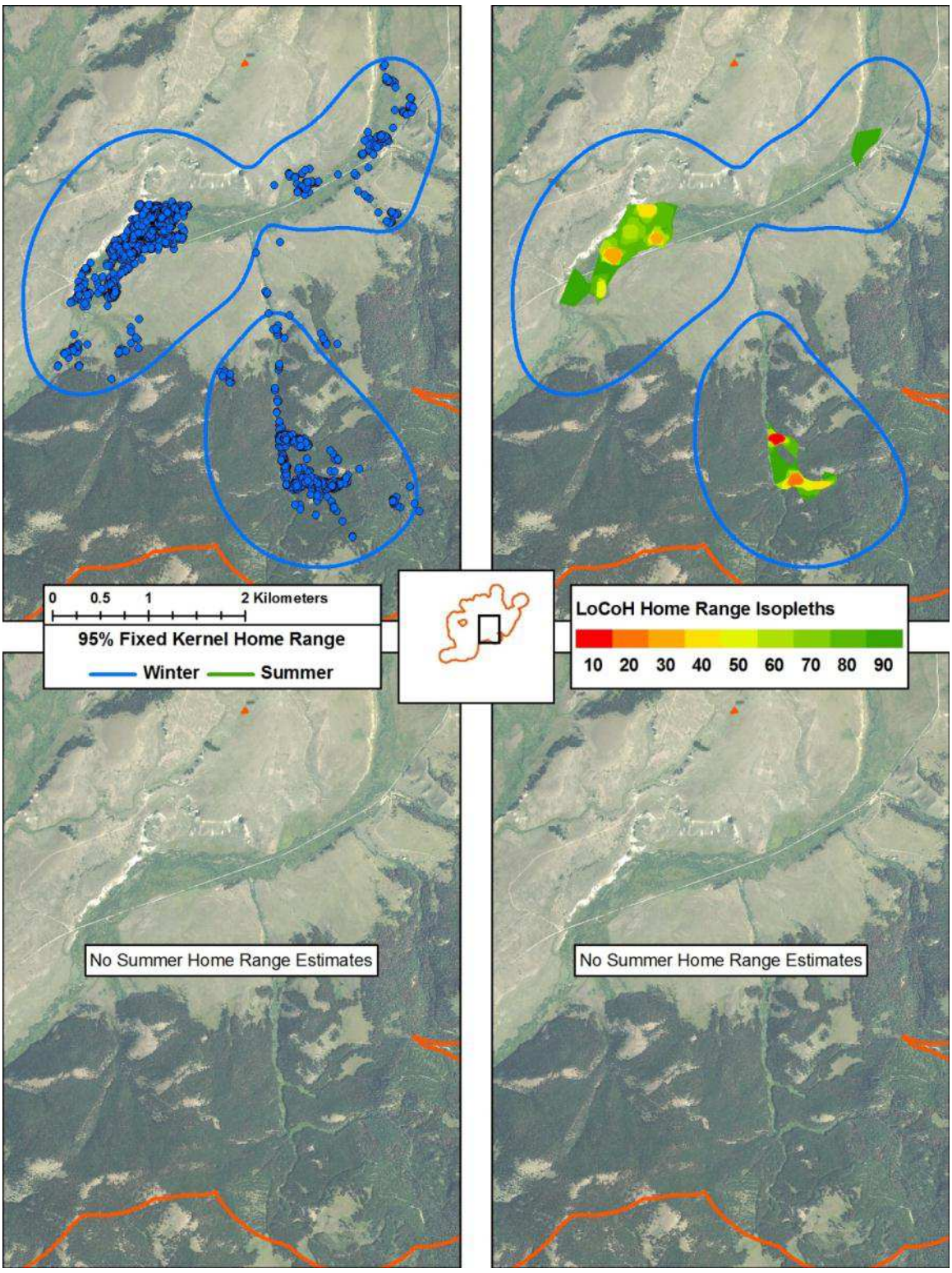


Figure G.17: The panels above show the seasonal locations and home range estimates for cow moose 4 in 2010. Data in these panels are as described at the start of Appendix G.

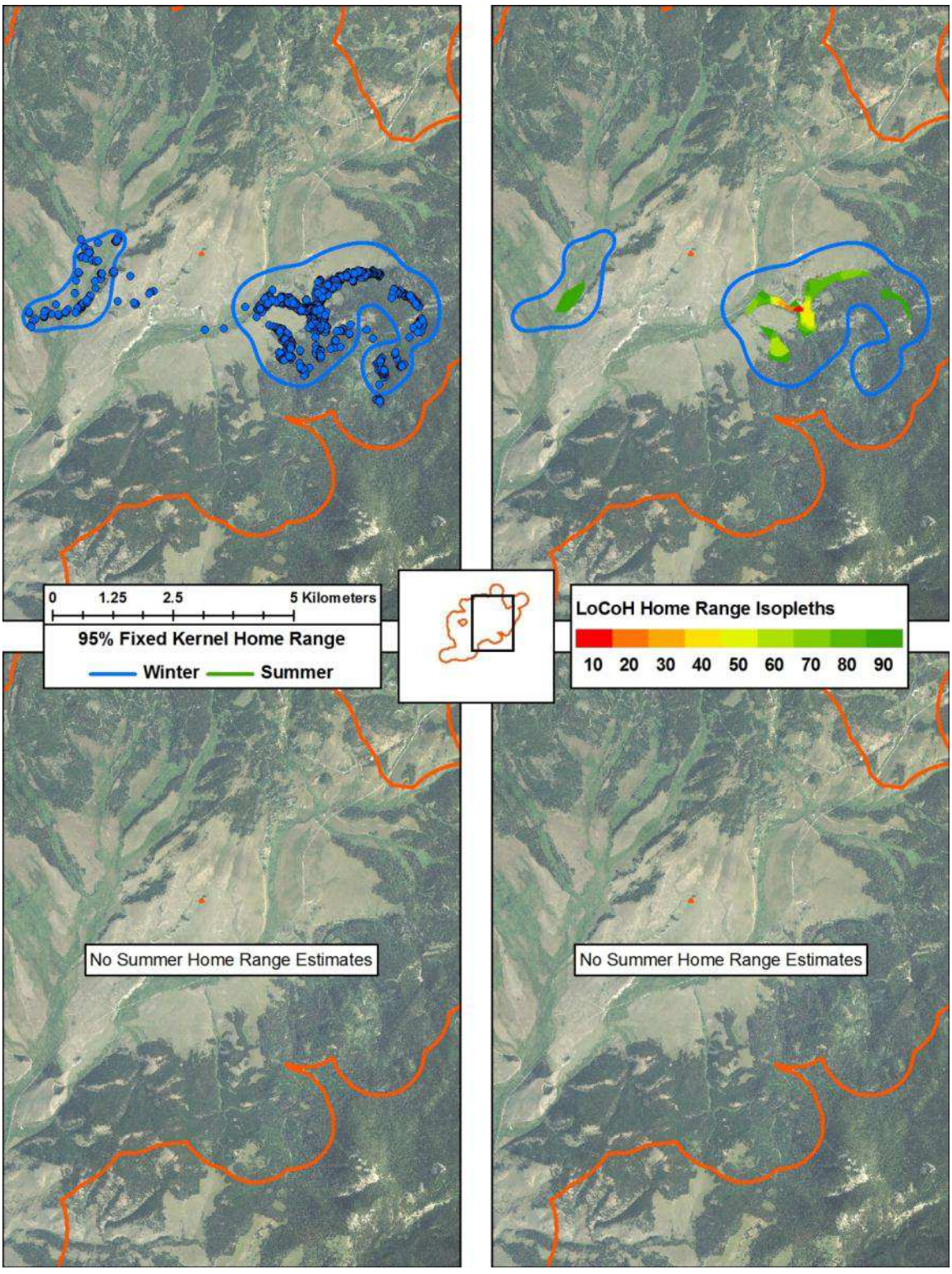


Figure G.18: The panels above show the seasonal locations and home range estimates for cow moose 8 in 2010. Data in these panels are as described at the start of Appendix G.

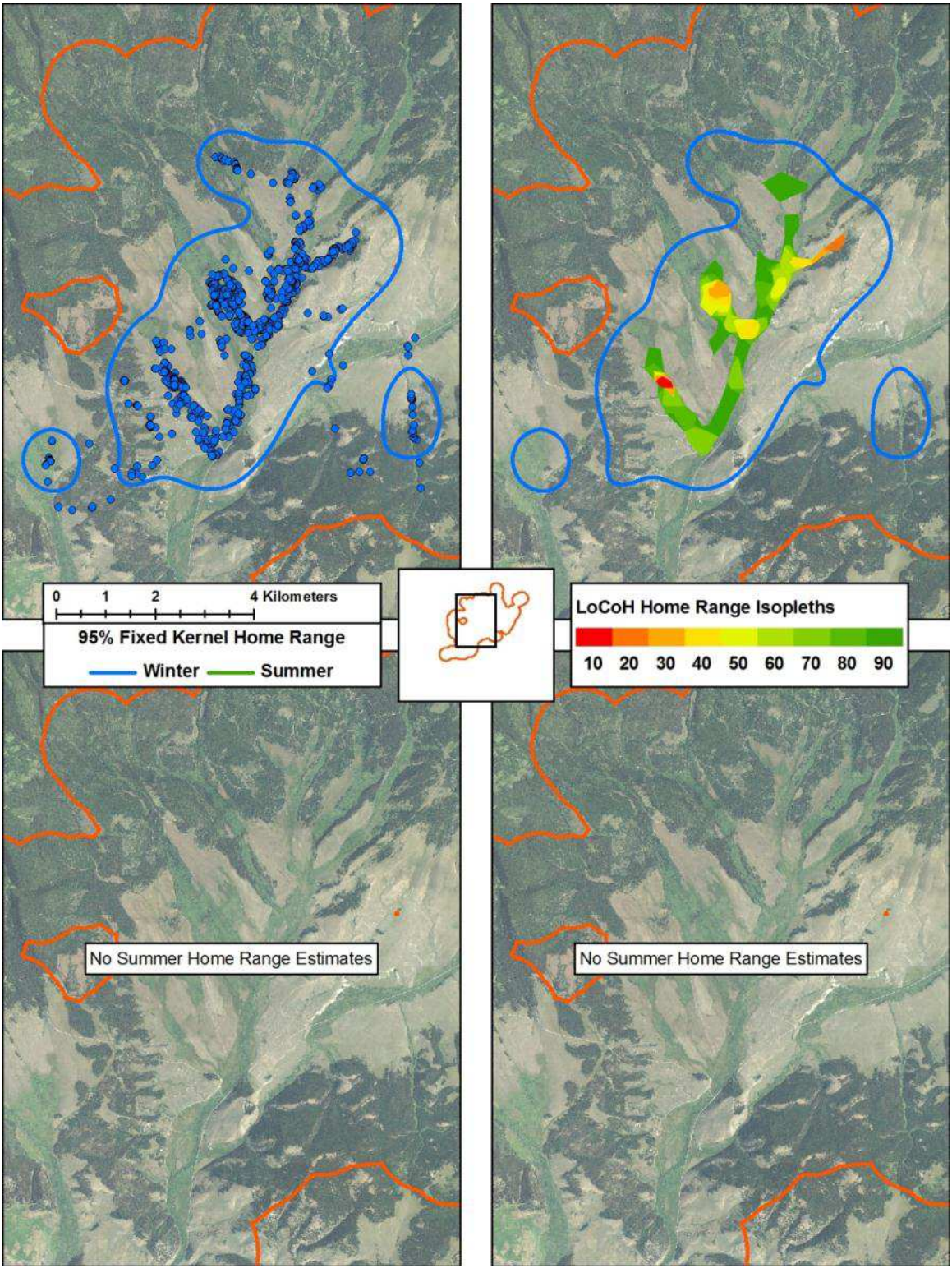


Figure G.19: The panels above show the seasonal locations and home range estimates for cow moose 10 in 2010. Data in these panels are as described at the start of Appendix G.

APPENDIX H

USED AND AVAILABLE LOCATIONS

The following appendix contains figures displaying the locations of used and available locations for the home range scale winter resource selection function (RSF) modeling for each individual moose. Used locations are a subsample of all used locations (all locations were displayed in Appendix G), systematically selected at 5 hour intervals as explained in Chapter 2. Available locations were randomly selected from within the 95% contour of the fixed kernel winter home ranges at a ratio of 5:1 to used locations. Winter 95% fixed kernel home ranges are displayed for reference.

Each figure contains 4 panels, one for each individual moose for every winter that moose was monitored. The figure title indicates which moose (by Moose ID) locations are displayed (in order of upper left, upper right, lower left, lower right) and the year(s) for those moose. Refer to the figures in Appendix G to determine where in the study area each winter home range is located.

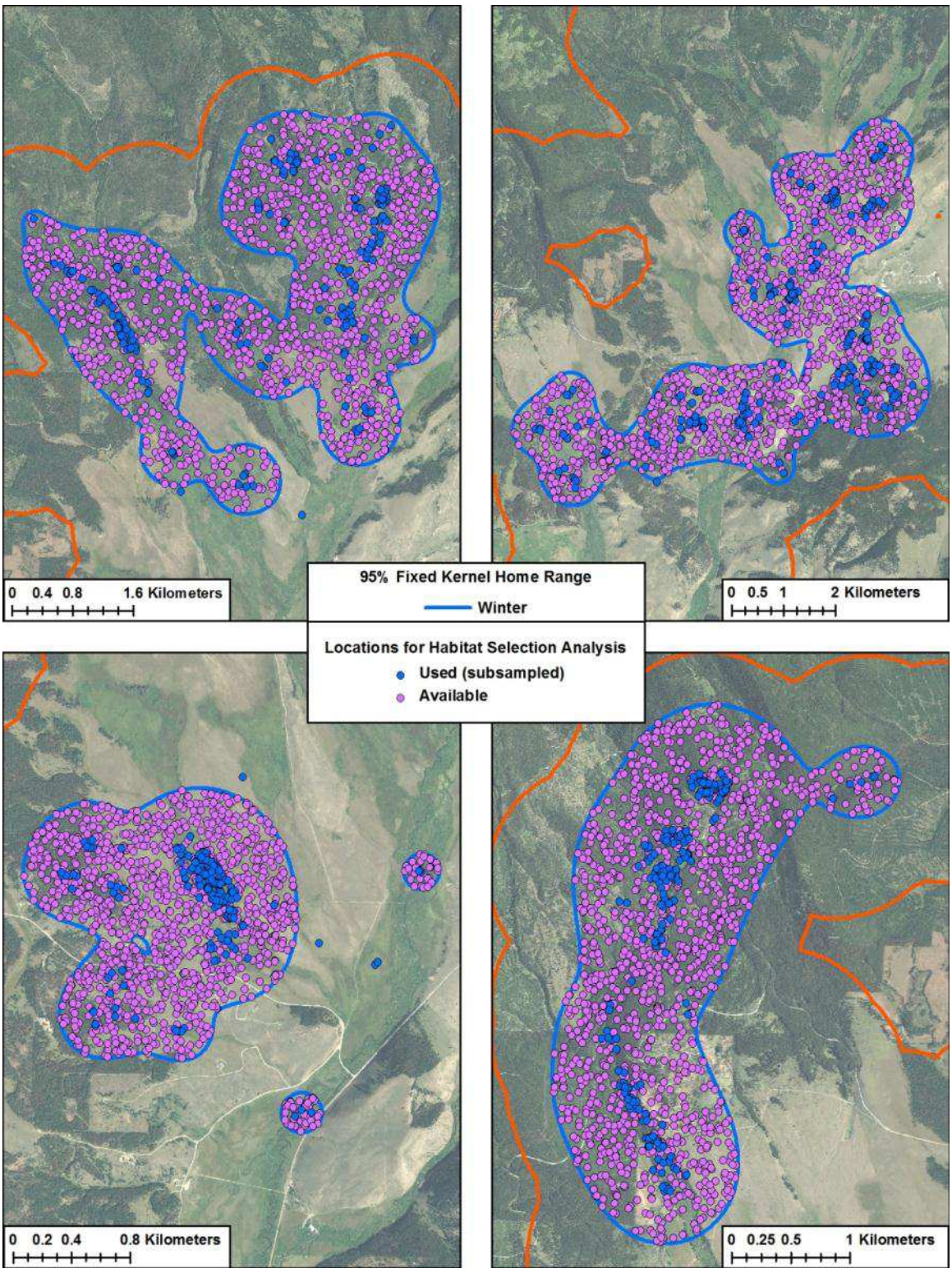


Figure H.1: Used and available points for home range scale winter RSF analysis. These data are from moose 6, 5, A, and C in 2007.

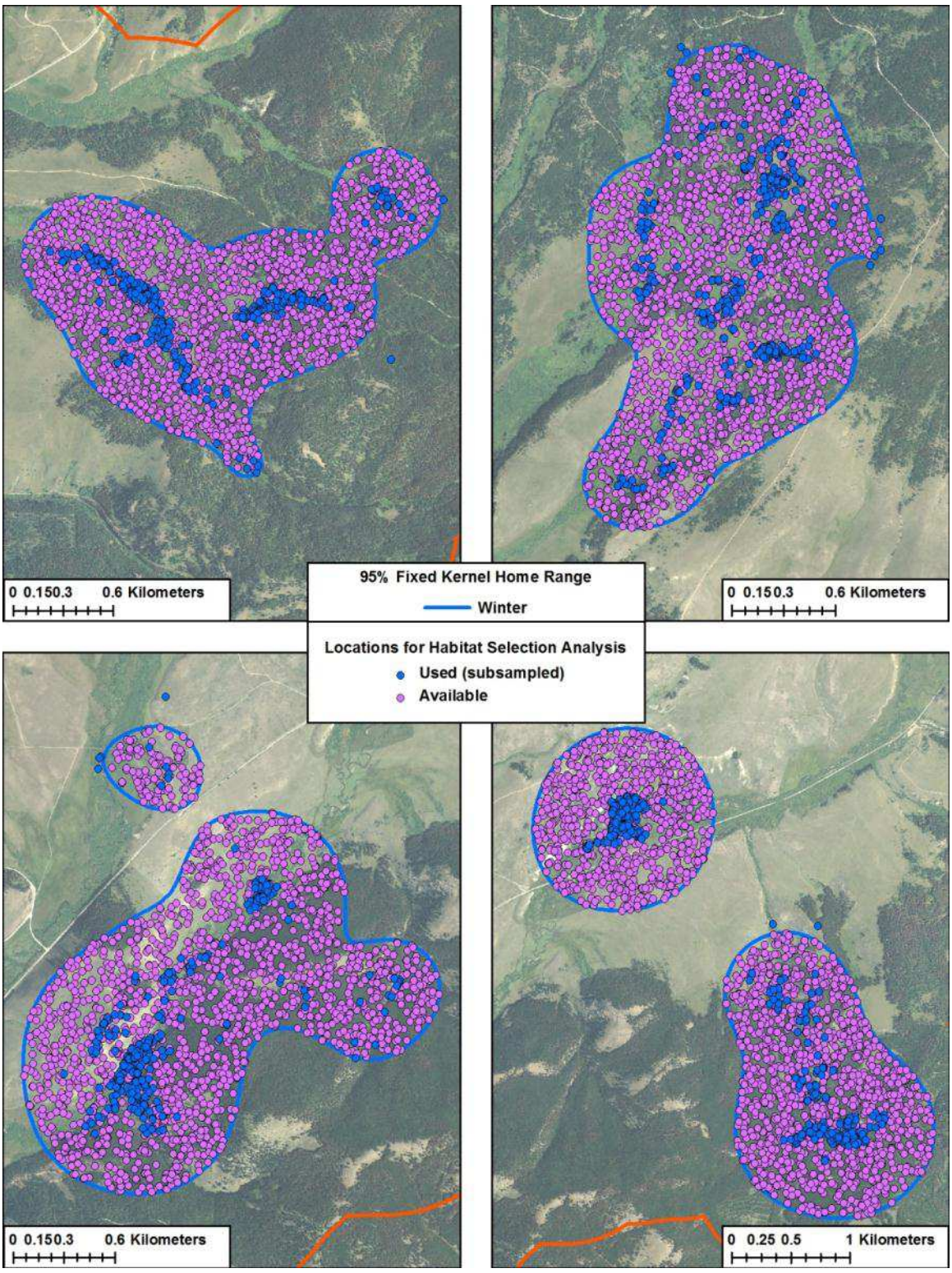


Figure H.2: Used and available points for home range scale winter RSF analysis. These data are from moose 1, 2, 3, and 4 in 2008.

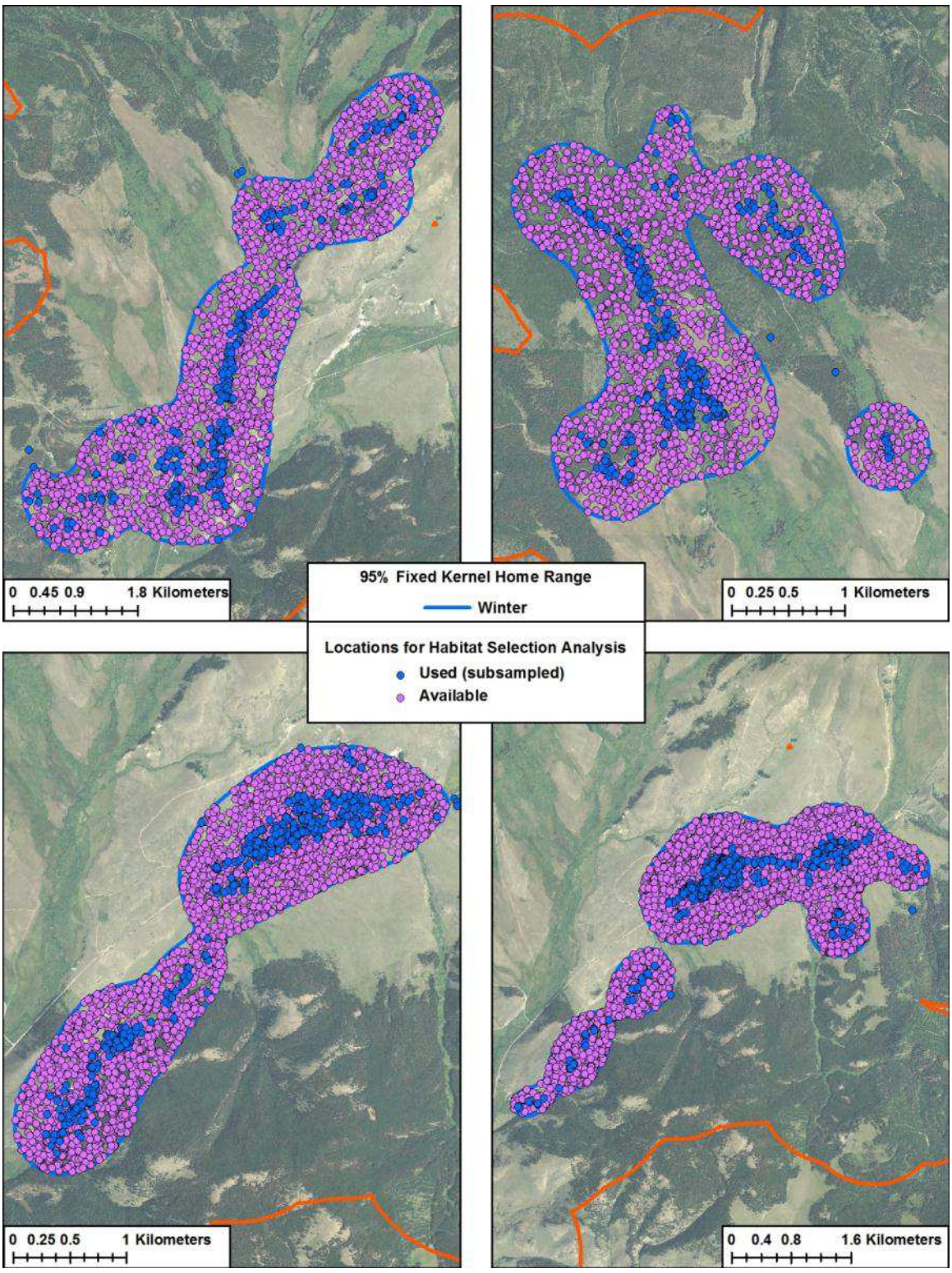


Figure H.3: Used and available points for home range scale winter RSF analysis. These data are from moose 5 and 6 in 2008, and moose 7 and 4 in 2009.

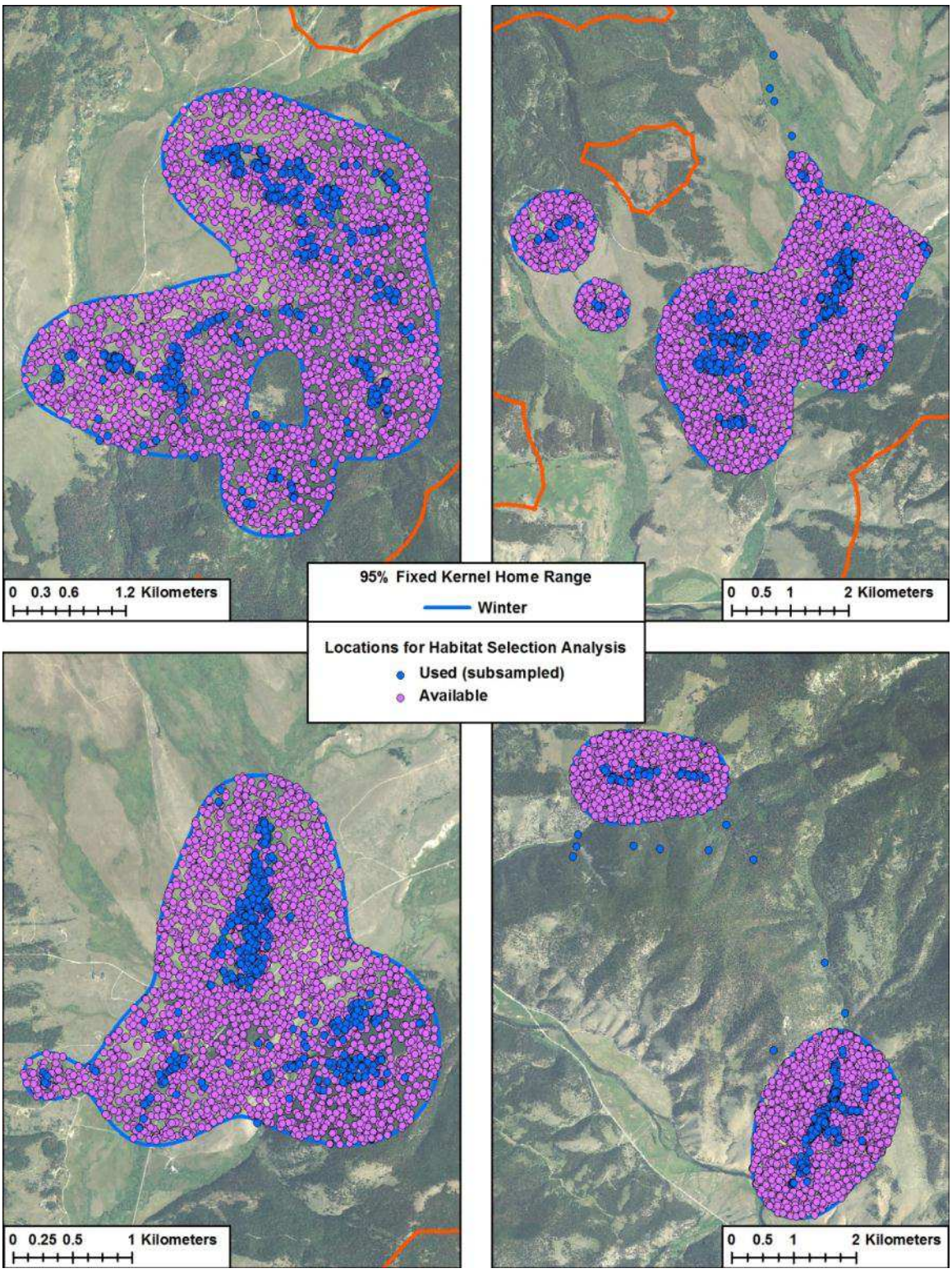


Figure H.4: Used and available points for home range scale winter RSF analysis. These data are from moose 8, 9, 10, and 11 in 2009.

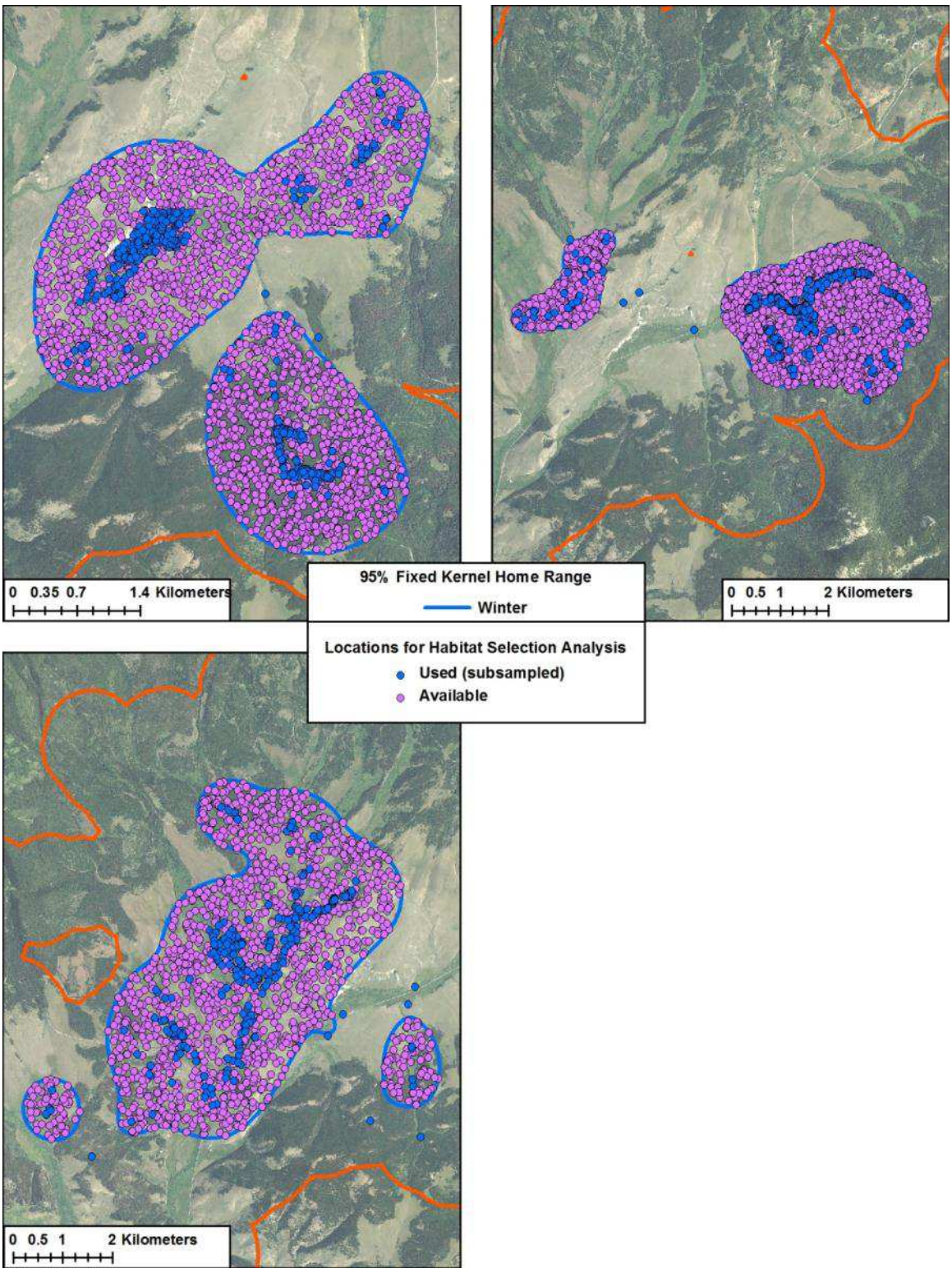


Figure H.5: Used and available points for home range scale winter RSF analysis. These data are from moose 4, 8 and 10 in 2010.

APPENDIX I

A PRIORI MODEL LIST FOR RSF MODEL SELECTION

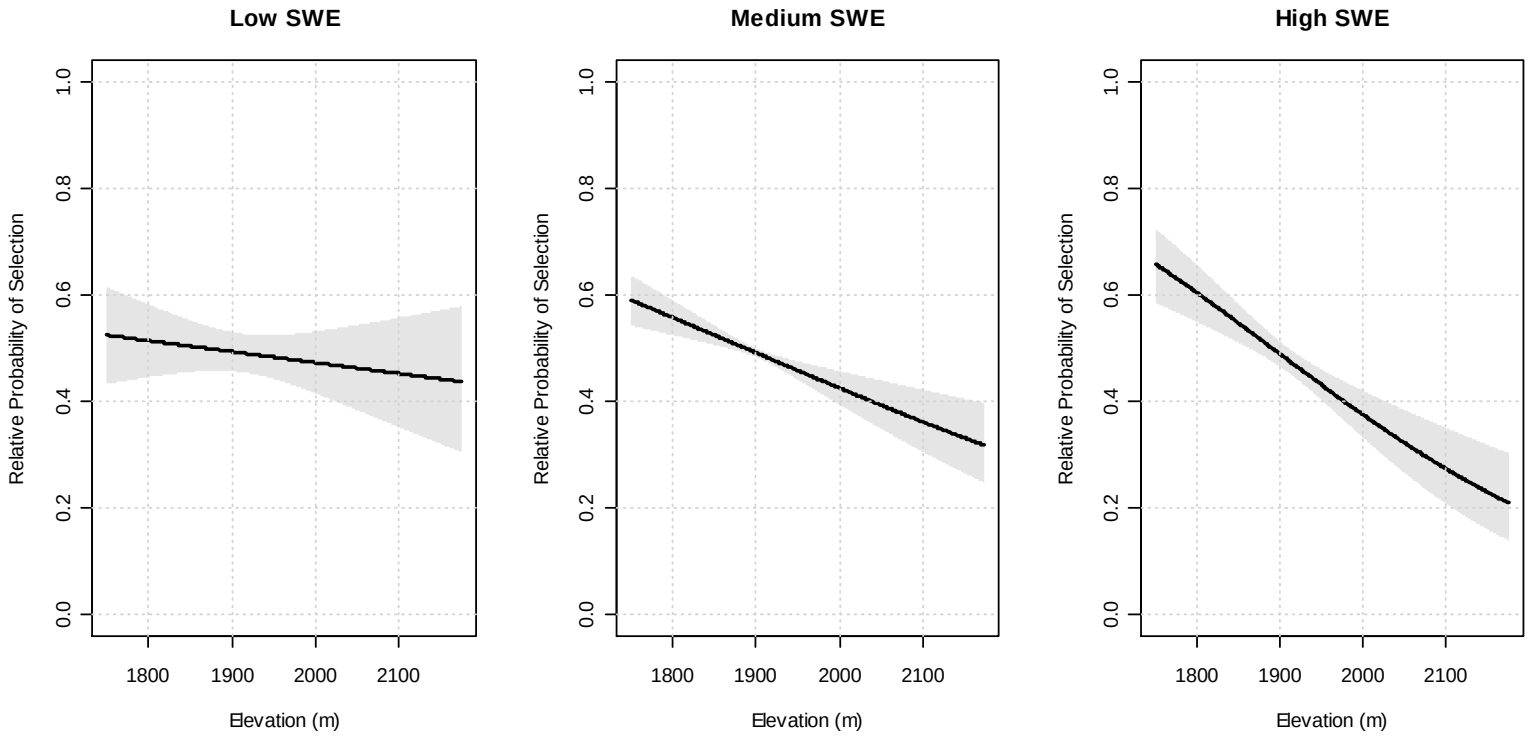
The following table is an a priori model list used in the generalized linear regression analysis to evaluate factors influencing habitat use by cow moose on the Mount Haggin WMA for the winters of 2007 through 2010. Abbreviations are: COVERTYPE (either WILLOW & ASPEN, CONIFER, or GRASSLAND & OTHER), DIST_CON (distance to conifer cover edge, in meters), DIST_WIL (distance to willow cover edge, in meters), ELEV (elevation in meters), SRI (solar radiation index summed across the winter season, in megawatt hours per meter squared), and SWE (snow water equivalent).

Model ID	Model structure
1	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI
2	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE
3	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV
4	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + SRI
5	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + SRI
6	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE
7	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV + ELEV×SWE + SRI
8	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV + ELEV×SWE
9	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV
10	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV + SRI
11	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL + SRI
12	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_CON×SWE + DIST_WIL
13	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI
14	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE
15	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV
16	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV + SRI
17	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + DIST_WIL×SWE + SRI
18	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + DIST_WIL×SWE
19	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + ELEV + ELEV×SWE + SRI
20	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + ELEV + ELEV×SWE
21	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + ELEV
22	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL + SRI
23	COVERTYPE + COVERTYPE×SWE + DIST_CON + DIST_WIL
24	COVERTYPE + COVERTYPE×SWE + DIST_CON + ELEV
25	COVERTYPE + COVERTYPE×SWE + DIST_CON + ELEV + SRI
26	COVERTYPE + COVERTYPE×SWE + DIST_CON + SRI
27	COVERTYPE + COVERTYPE×SWE + DIST_CON
28	COVERTYPE + COVERTYPE×SWE + DIST_WIL+ ELEV

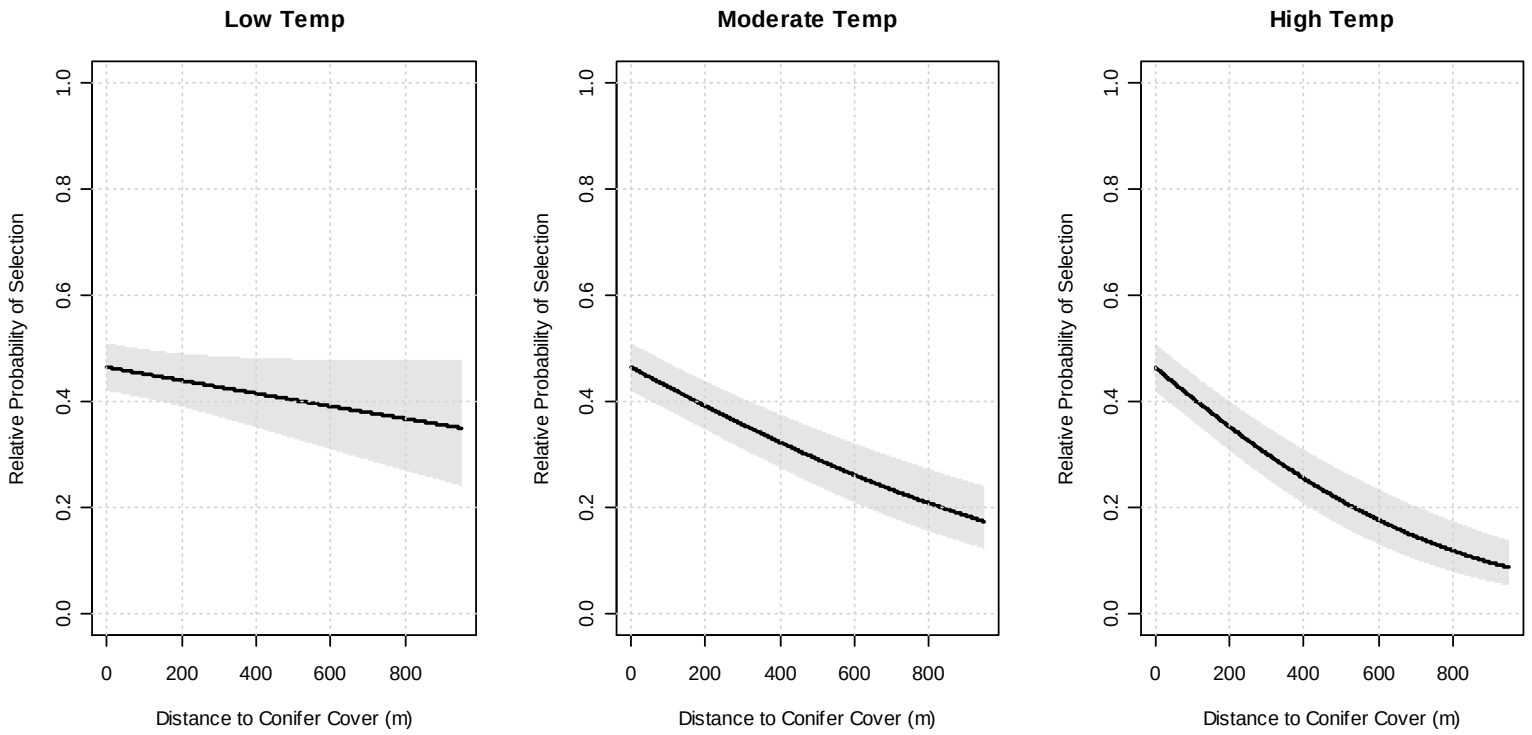
Model ID	Model structure
29	COVERTYPE + COVERTYPE×SWE + DIST_WIL + ELEV + SRI
30	COVERTYPE + COVERTYPE×SWE + DIST_WIL + SRI
31	COVERTYPE + COVERTYPE×SWE + DIST_WIL
32	COVERTYPE + COVERTYPE×SWE + ELEV + ELEV×SWE + SRI
33	COVERTYPE + COVERTYPE×SWE + ELEV + ELEV×SWE
34	COVERTYPE + COVERTYPE×SWE + ELEV
35	COVERTYPE + COVERTYPE×SWE + ELEV + SRI
36	COVERTYPE + COVERTYPE×SWE + SRI
37	COVERTYPE + COVERTYPE×SWE
38	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI
39	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE
40	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV
41	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + ELEV + SRI
42	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE + SRI
43	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + DIST_WIL×SWE
44	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV + ELEV×SWE + SRI
45	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV + ELEV×SWE
46	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV
47	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + ELEV + SRI
48	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL + SRI
49	COVERTYPE + DIST_CON + DIST_CON×SWE + DIST_WIL
50	COVERTYPE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE + SRI
51	COVERTYPE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV + ELEV×SWE
52	COVERTYPE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV
53	COVERTYPE + DIST_CON + DIST_WIL + DIST_WIL×SWE + ELEV + SRI
54	COVERTYPE + DIST_CON + DIST_WIL + DIST_WIL×SWE + SRI
55	COVERTYPE + DIST_CON + DIST_WIL + DIST_WIL×SWE
56	COVERTYPE + DIST_CON + DIST_WIL + ELEV + ELEV×SWE + SRI
57	COVERTYPE + DIST_CON + DIST_WIL + ELEV + ELEV×SWE
58	COVERTYPE + DIST_CON + DIST_WIL + ELEV
59	COVERTYPE + DIST_CON + DIST_WIL + SRI
60	COVERTYPE + DIST_CON + DIST_WIL
61	COVERTYPE + DIST_CON + ELEV
62	COVERTYPE + DIST_CON + ELEV + SRI
63	COVERTYPE + DIST_CON + SRI
64	COVERTYPE + DIST_CON
65	COVERTYPE + DIST_WIL+ ELEV
66	COVERTYPE + DIST_WIL + ELEV + SRI
67	COVERTYPE + DIST_WIL + SRI
68	COVERTYPE + DIST_WIL
69	COVERTYPE + ELEV + ELEV×SWE + SRI
70	COVERTYPE + ELEV + ELEV×SWE
71	COVERTYPE + ELEV
72	COVERTYPE + ELEV + SRI
73	COVERTYPE + SRI
74	COVERTYPE
75	ELEV + ELEV×SWE + SRI
76	ELEV + ELEV×SWE
77	ELEV
78	ELEV + SRI
79	SRI

APPENDIX J

ADDITIONAL PREDICTIVE PLOTS



A plot showing the interactive effect of SWE on the predicted relationship between elevation and relative selection by cow moose, after accounting for all other covariates in the model. The gray band represents the 95% confidence interval. This plot is based on the original coefficients from the top home range selection model (Model 38), although the plots for the top study area models were nearly identical. All other covariates were held at their respective means for this plot, excluding SWE which was plotted at SWE = 8.96, 15.66, and 23.00 cm to represent low, moderate, and high levels of SWE.



A plot showing the interactive effect of temperature on the predicted relationship between distance to conifer cover and relative selection by cow moose, after accounting for all other covariates in the model. The gray band represents the 95% confidence interval. This plot is based on the coefficients from the top home range selection model (Model 38) with the addition of a TEMP×DIST_CONIFER interaction. All other covariates were held at their respective means for this plot, while temperature was plotted at TEMP = -9.89, -2.40, and 3.89 °C to represent low, moderate, and high temperatures.

APPENDIX K

RSF MODEL VALIDATION TABLE

This table contains the frequency distributions, percentage, and cumulative percentage of moose locations within equal-area RSF intervals summed over the 3 SWE levels modeled. If the model were no better than a random model, then approximately 5% of moose locations would occur in each RSF interval. The greater the cumulative percentage of locations in the higher bins (e.g. >75%), the better the model performs. If the model were no better than a random model, then the cumulative percentage at >50% would be 50%.

	HR Level Selection – Model 38			SA Level Selection – Model 02			SA Level Selection – Model 39		
RSF interval	Number of locations	Percent of locations	Cumulative percent	Number of locations	Percent of locations	Cumulative percent	Number of locations	Percent of locations	Cumulative percent
95 – 100%	71	21.8%	21.8%	75	25.0%	25.0%	81	27.0%	27.0%
90 – 95%	59	18.2%	40.0%	70	23.3%	48.3%	64	21.3%	48.3%
85 – 90%	32	9.8%	49.8%	43	14.3%	62.7%	46	15.3%	63.7%
80 – 85%	29	8.9%	58.8%	27	9.0%	71.7%	20	6.7%	70.3%
75 – 80%	17	5.2%	64.0%	11	3.7%	75.3%	11	3.7%	74.0%
70 – 75%	21	6.5%	70.5%	10	3.3%	78.7%	8	2.7%	76.7%
65 – 70%	18	5.5%	76.0%	6	2.0%	80.7%	14	4.7%	81.3%
60 – 65%	14	4.3%	80.3%	11	3.7%	84.3%	9	3.0%	84.3%
55 – 60%	22	6.8%	87.1%	10	3.3%	87.7%	3	1.0%	85.3%
50 – 55%	11	3.4%	90.5%	2	0.7%	88.3%	9	3.0%	88.3%
45 – 50%	2	0.6%	91.1%	5	1.7%	90.0%	8	2.7%	91.0%
40 – 45%	7	2.2%	93.2%	8	2.7%	92.7%	5	1.7%	92.7%
35 – 40%	7	2.2%	95.4%	5	1.7%	94.3%	5	1.7%	94.3%
30 – 35%	3	0.9%	96.3%	4	1.3%	95.7%	6	2.0%	96.3%
25 – 30%	6	1.8%	98.2%	4	1.3%	97.0%	5	1.7%	98.0%
20 – 25%	1	0.3%	98.5%	3	1.0%	98.0%	1	0.3%	98.3%
15 – 20%	2	0.6%	99.1%	3	1.0%	99.0%	1	0.3%	98.7%
10 – 15%	2	0.6%	99.7%	2	0.7%	99.7%	1	0.3%	99.0%
5 – 10%	1	0.3%	100.0%	0	0.0%	99.7%	2	0.7%	99.7%
0 – 5%	0	0.0%	100.0%	1	0.3%	100.0%	1	0.3%	100.0%
Total	325	100.0%	NA	300	100.0%	NA	300	100.0%	NA

APPENDIX L

ADDITIONAL RSF MAPS

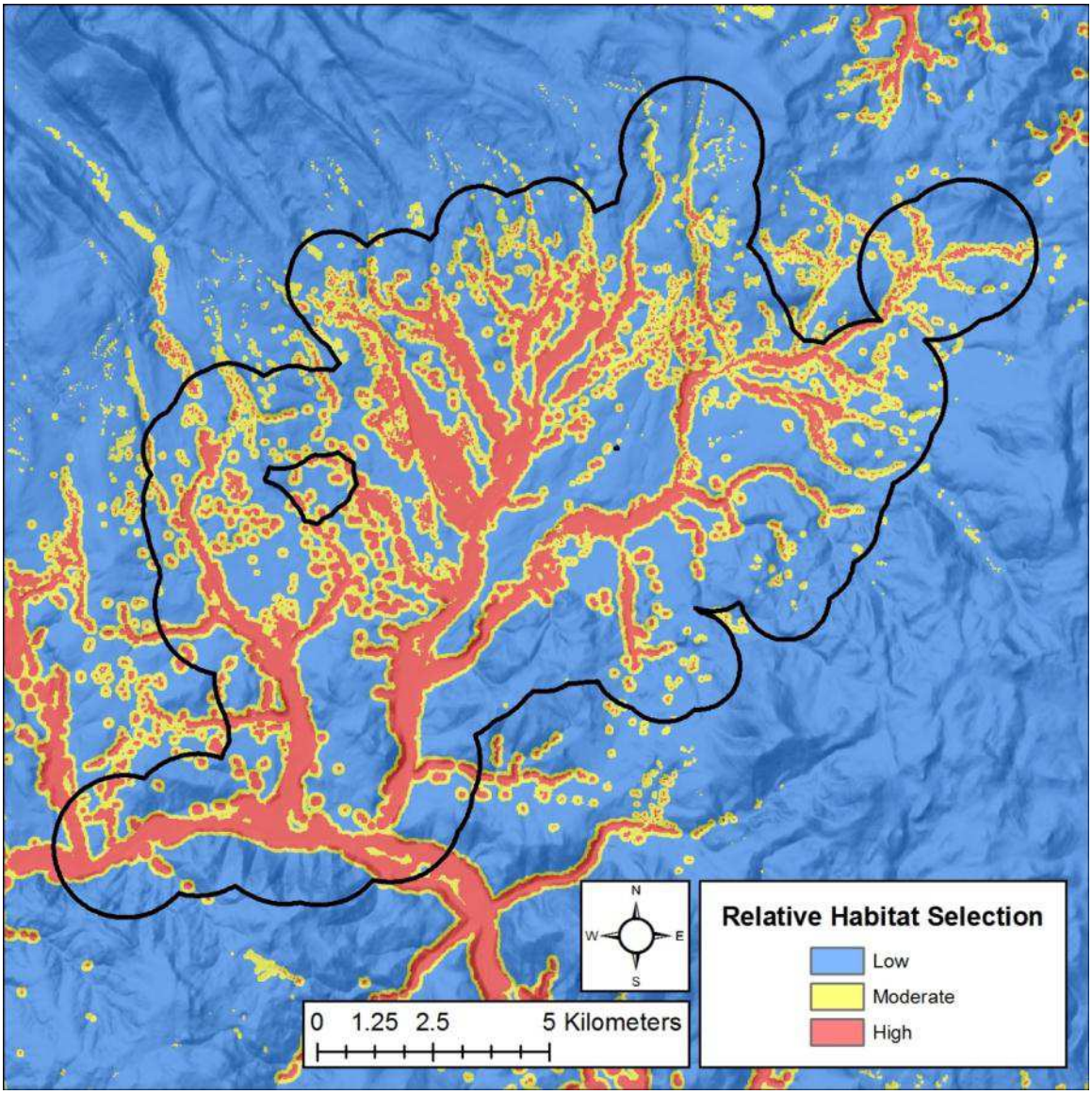


Figure J.1: This map shows the relative habitat selection across the study area and surrounding area by cow moose during periods of low snowpack (SWE = 8.96 cm). Model 39 from the study area scale analysis was used to create this map. The RSF values were grouped into 3 bins: low probability (0-50%), moderate probability (50-75%), and high probability (75-100%).

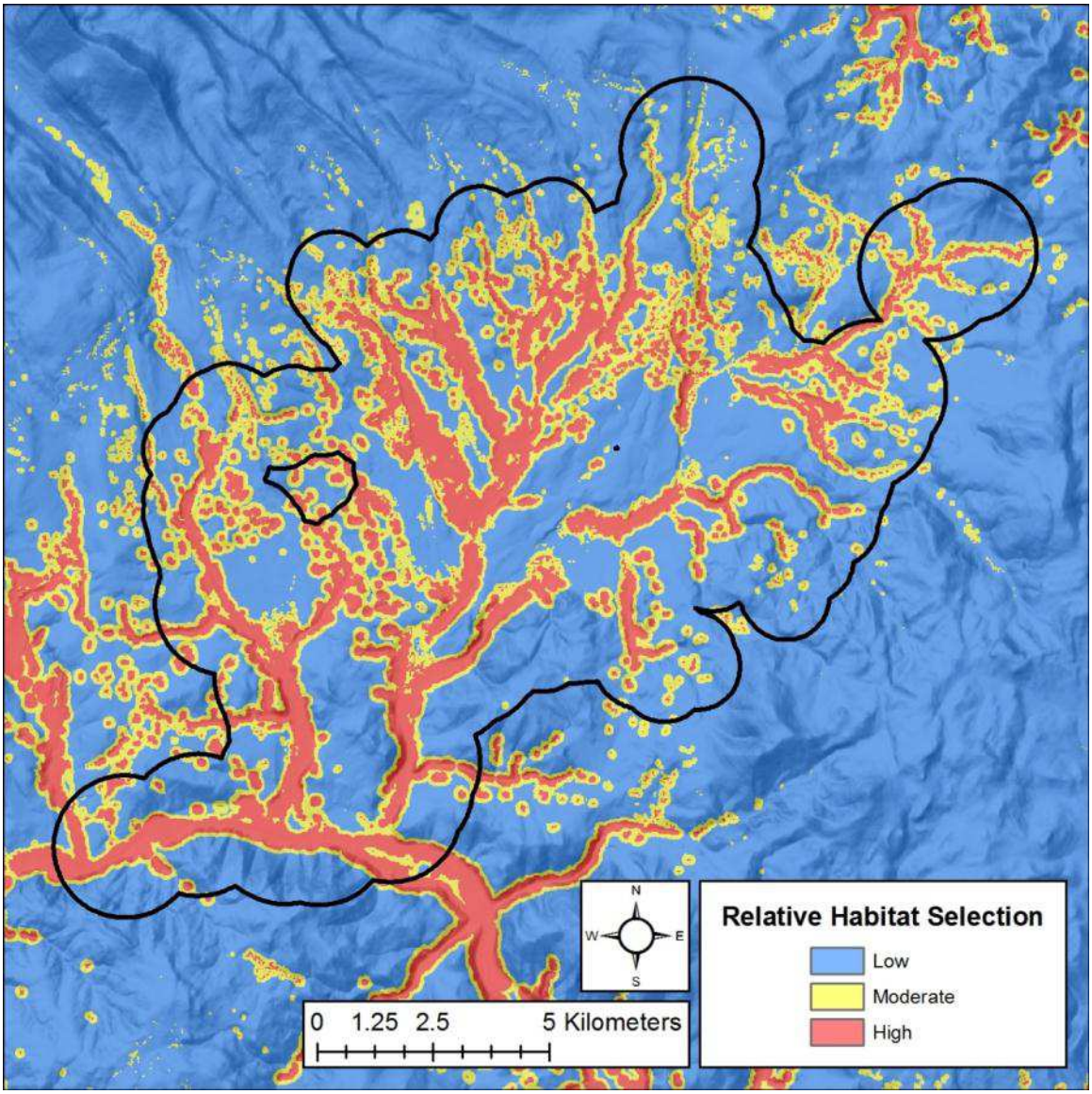


Figure J.2: This map shows the relative habitat selection across the study area and surrounding area by cow moose during periods of moderate snowpack (SWE = 15.66 cm). Model 39 from the study area scale analysis was used to create this map. The RSF values were grouped into 3 bins: low probability (0-50%), moderate probability (50-75%), and high probability (75-100%).

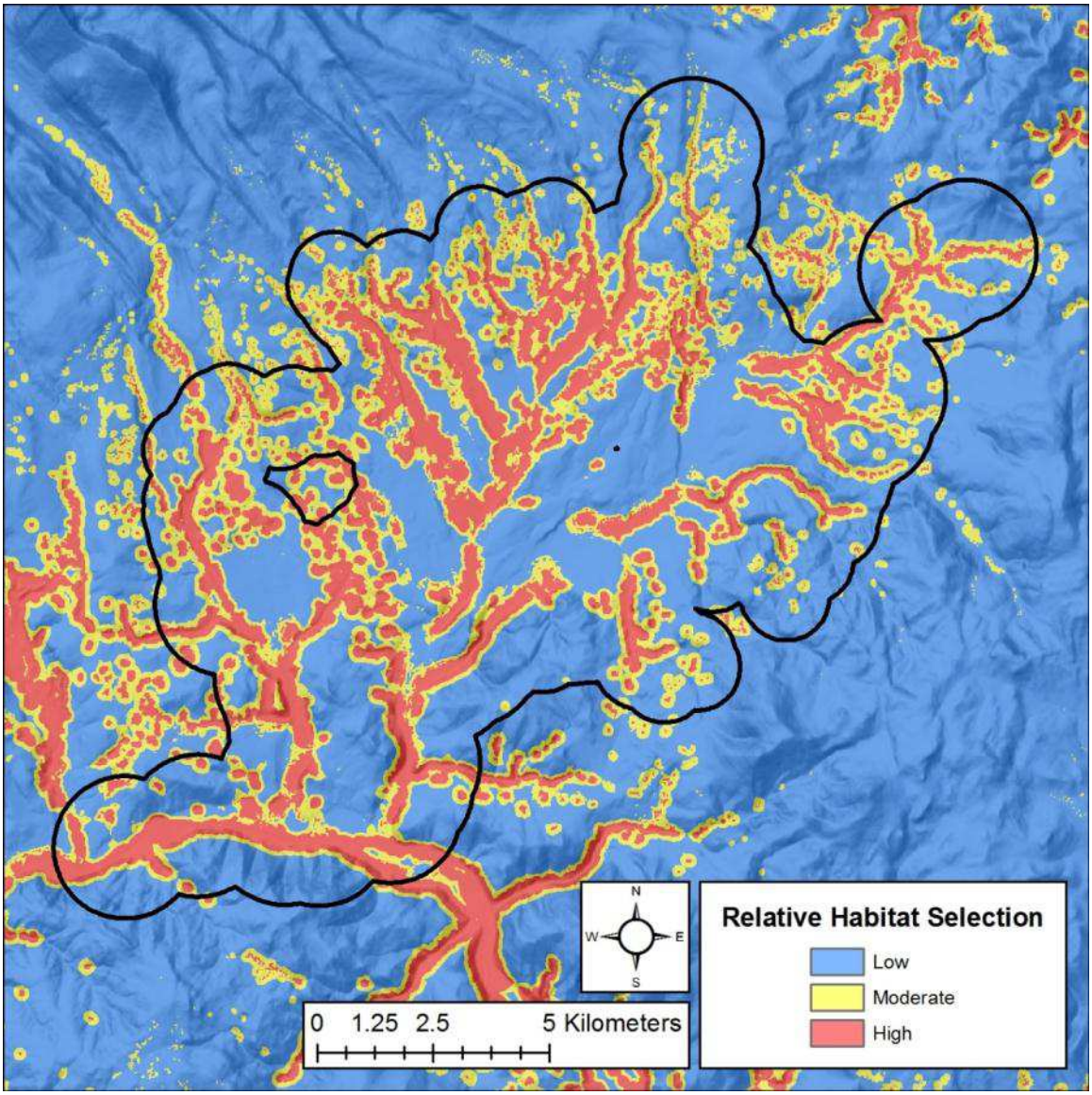


Figure J.3: This map shows the relative habitat selection across the study area and surrounding area by cow moose during periods of high snowpack (SWE = 23.00 cm). Model 39 from the study area scale analysis was used to create this map. The RSF values were grouped into 3 bins: low probability (0-50%), moderate probability (50-75%), and high probability (75-100%).

APPENDIX M

BROWSE SURVEY METHODOLOGY

Definitions:

Willow plant-
a group of branches of the same species emerging from the same general location of ground (a common root system); usually less than 1 m^2, unless the willow is older (and well established); if there is a clean break between willows branches (>25 cm) that appear to have different source points for the branches, then there are multiple willows

Willow branch-
a section of a willow plant that can be traced back to a single beam at no more than 25 cm above the ground, often emerging from the ground as a single beam, expanding into smaller branches and twigs; selected branches must be intact, not broken and have at least 5 twigs or browsed twigs if used for browse measurements

Willow twig-
the smallest unit of a branch where apical or lateral growth is occurring, consisting of current year's growth and often previous year's growth as well; for a twig to be counted as unbrowsed or browsed in this browse survey, it must be at least 3cm in length; selected twigs must be intact, not broken

Willow leader-
a twig at the tip of a branch, at its tallest, most distal point; leaders are always twigs, but twigs are only leaders if they are the tallest twigs; leaders are most easily found by following up the largest diameter portion of the branch from the base to the tip, usually in a linear, straight progression unless the branch was previously browsed; if the willow splits evenly (in diameter) at one point, then the straightest portion is followed

CYG-
current year's growth; generally the twigs or twig tips of the more distal portions of a branch that grew during the most recent growing season (e.g. if willow are monitored in spring, then CYG is actually from the last summer)

PYG-
previous year's growth, any part of the branch which is not current year's new growth; generally older, larger parts of twigs and branches

Secondary stem-
a twig that is derived from growth lower on a willow branch, below the leader

Browse zone-
a range in vertical height extending from 75 cm to 200 cm above the ground; willow is 100% available in this range during all times of the year as snow depth does not generally exceed 75 cm; if any part of the leader is within this zone (base to tip), the branch is available, even if other twigs counted are just outside of the browse zone

Unbrowsed twig-
a twig with all current growth and buds intact; note that unbrowsed twigs can have evidence of browsing from previous years (previously browsed twigs), but not the most recent year (winter) since CYG must be intact and not browsed

Browsed twig-
a twig that has been bitten off within the current year's growth in the last year (winter), but browsing did not extend to previous year's growth

Heavily browsed twig-
a twig that has been bitten off down to any previous year's growth, where more than just the current year's growth was consumed in the last year (winter)

Previously browsed twig-
a browsed twig that was browsed prior to the last year, twig tip is usually gray and weathered and bark around bite may be necrotic (blackened) and dead; occasionally twigs browsed early in winter or late in fall may appear to be previously browsed, but close observation of growth from the previous year (e.g. Did the browsed point start to send out shoots?) can usually be used to clear these ambiguous cases.

Mechanically protected-
leaders and secondary stems are unavailable to moose browsing due to either dead branches (often hedged) or a combination of dead and live branches (often too tall).

Protocol key from a sample point	Recorded result or action
1. Selecting a plant:	
a. No willows within 2.5 m radius of point	Mark "NW" (no willows)
b. Only willow within 2.5 m has already been sampled	Mark "SW" (sampled willow)
c. Nearest (or next nearest if nearest has already been sampled) willow within 2.5 m has not been sampled	Continue on to 2.
2. Selecting 4 branches:	
a. The leaders of the nearest four branches are either outside the browse zone or are mechanically protected	Continue on to 3.
b. The leaders of the nearest four branches are within browse zone and are not mechanically protected	Continue on to 7.
3. Nearest 4 branches are unavailable	
a. Four branches within 1 m are available, use these four as opposed to nearest four	Continue on to 7.
b. Four available branches cannot be found within 1 m	Continue on to 4.

4. Branches are unavailable

a. The leaders of branches are below the browse zone	Mark "TL" (too low)
b. The leaders of branches are above the browse zone	Continue on to 5.
c. The leaders of branches are mechanically protected	Continue on to 6.

5. Leaders are above browse zone

a. Secondary stems are available on four branches	Continue to 7, but start classifying at 2 m and note "SS" (secondary stems)
b. Secondary stems are unavailable, usually protected	Mark "TH" (too high)

6. All leaders are mechanically protected

a. By a thicket of willow (live and dead)	Mark "PT" (protected-thicket)
b. By dead willow (browsed or unbrowsed)	Mark "PD" (protected-dead)

7. Classify twigs on 4 branches

a. None are recently browsed	Mark "UB" (unbrowsed)
b. Some are recently browsed	Classify top 5 twigs (starting at their base) as either unbrowsed, browsed, or heavily browsed. Ignore previously browsed twigs.

Notes on classifying the twigs:

The most distal 5 twigs on 4 branches are measured. The top 5 are defined as the twigs for which the *base* (of CYG) of the twig is the closest to the leader (tallest point of the branch).

Mark closest branch with a labeled aluminum tag at 125 cm above ground level or 20 cm below top of the branch if the branch does not exceed 140 cm in height.

APPENDIX N

SHRUB ARCHITECTURE TYPES

Arrested (AR) – intensely browsed plant, growth capped below 100 cm, browse level usually uniform; indicates constant intense browse since establishment

Retrogressed (RT) – intensely browsed plant, growth capped above 100 cm, may have various levels of browse; indicates previous light-to-moderate browse and current intense browse pressure

Released (RLS) – >2 year light-to moderate or unbrowsed growth above arrested or retrogressed level; does not require that branches have exceeded the browse zone; indicates previous intense browse and current light-to-moderate browse (if plant is below browse zone)

Uninterrupted (UN) – no intensely browsed branches, branches may or may not have escaped the browse zone; indicates no previous intense browse

Note: these classifications apply to a **majority** of the branches, not just **any** single branch
Adapted from Keigley et al. (1998, 2003) to reflect recent browse pressure

APPENDIX O

INITIAL A PRIORI MODEL LIST FOR BROWSE UTILIZATION

The following table is an initial model list used in the generalized linear regression analysis to evaluate factors influencing browse utilization of willow communities by moose on the Mount Haggin WMA for the winters of 2007-08 through 2009-10. Abbreviations are: PREFSPP (percent of preferred species willow), PREVBRWS (percent of willow previously browsed, within the last 2 years, based on growth form), WIDTH (total width of the willow community), and ELEV (elevation of the sample site).

Model ID	Model structure
1	PREFSPP + PREVBRWS + WIDTH + ELEV
2	PREFSPP + PREVBRWS + WIDTH
3	PREFSPP + PREVBRWS + ELEV
4	PREFSPP + PREVBRWS
5	PREFSPP + WIDTH + ELEV
6	PREFSPP + WIDTH
7	PREFSPP + ELEV
8	PREFSPP
9	PREVBRWS + WIDTH + ELEV
10	PREVBRWS + WIDTH
11	PREVBRWS + ELEV
12	PREVBRWS
13	WIDTH + ELEV
14	WIDTH
15	ELEV
16	NULL

APPENDIX P

EXPANDED A PRIORI MODEL LIST FOR BROWSE UTILIZATION

The following table is an expanded model list used to evaluate factors influencing browse utilization of willow communities by moose on the Mount Haggin WMA for the winters of 2007-08 through 2009-10. Abbreviations are the same as Appendix N, with the addition of: YR (year indicator variable, 2008, 2009, 2010).

Model ID	Model structure
1	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV + ELEV×YR
2	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV
3	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR
4	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV + ELEV×YR
5	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV
6	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + WIDTH
7	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + ELEV + ELEV×YR
8	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR + ELEV
9	YR + PREFSPP + PREFSPP×YR + PREVBRWS + PREVBRWS×YR
10	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH + WIDTH×YR + ELEV + ELEV×YR
11	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH + WIDTH×YR + ELEV
12	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH + WIDTH×YR
13	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH + ELEV + ELEV×YR
14	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH + ELEV
15	YR + PREFSPP + PREFSPP×YR + PREVBRWS + WIDTH
16	YR + PREFSPP + PREFSPP×YR + PREVBRWS + ELEV + ELEV×YR
17	YR + PREFSPP + PREFSPP×YR + PREVBRWS + ELEV
18	YR + PREFSPP + PREFSPP×YR + PREVBRWS
19	YR + PREFSPP + PREFSPP×YR + WIDTH + WIDTH×YR + ELEV + ELEV×YR
20	YR + PREFSPP + PREFSPP×YR + WIDTH + WIDTH×YR + ELEV
21	YR + PREFSPP + PREFSPP×YR + WIDTH + WIDTH×YR
22	YR + PREFSPP + PREFSPP×YR + WIDTH + ELEV + ELEV×YR
23	YR + PREFSPP + PREFSPP×YR + WIDTH + ELEV
24	YR + PREFSPP + PREFSPP×YR + WIDTH
25	YR + PREFSPP + PREFSPP×YR + ELEV + ELEV×YR
26	YR + PREFSPP + PREFSPP×YR + ELEV
27	YR + PREFSPP + PREFSPP×YR
28	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV + ELEV×YR
29	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV
30	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR
31	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV + ELEV×YR
32	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV
33	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + WIDTH
34	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + ELEV + ELEV×YR
35	YR + PREFSPP + PREVBRWS + PREVBRWS×YR + ELEV
36	YR + PREFSPP + PREVBRWS + PREVBRWS×YR
37	YR + PREFSPP + PREVBRWS + WIDTH + WIDTH×YR + ELEV + ELEV×YR
38	YR + PREFSPP + PREVBRWS + WIDTH + WIDTH×YR + ELEV
39	YR + PREFSPP + PREVBRWS + WIDTH + WIDTH×YR
40	YR + PREFSPP + PREVBRWS + WIDTH + ELEV + ELEV×YR
41	YR + PREFSPP + PREVBRWS + WIDTH + ELEV
42	YR + PREFSPP + PREVBRWS + WIDTH
43	YR + PREFSPP + PREVBRWS + ELEV + ELEV×YR

Model ID	Model structure
44	YR + PREFSPP + PREVBRWS + ELEV
45	YR + PREFSPP + PREVBRWS
46	YR + PREFSPP + WIDTH + WIDTH×YR + ELEV + ELEV×YR
47	YR + PREFSPP + WIDTH + WIDTH×YR + ELEV
48	YR + PREFSPP + WIDTH + WIDTH×YR
49	YR + PREFSPP + WIDTH + ELEV + ELEV×YR
50	YR + PREFSPP + WIDTH + ELEV
51	YR + PREFSPP + WIDTH
52	YR + PREFSPP + ELEV + ELEV×YR
53	YR + PREFSPP + ELEV
54	YR + PREFSPP
55	YR + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV + ELEV×YR
56	YR + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR + ELEV
57	YR + PREVBRWS + PREVBRWS×YR + WIDTH + WIDTH×YR
58	YR + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV + ELEV×YR
59	YR + PREVBRWS + PREVBRWS×YR + WIDTH + ELEV
60	YR + PREVBRWS + PREVBRWS×YR + WIDTH
61	YR + PREVBRWS + PREVBRWS×YR + ELEV + ELEV×YR
62	YR + PREVBRWS + PREVBRWS×YR + ELEV
63	YR + PREVBRWS + PREVBRWS×YR
64	YR + PREVBRWS + WIDTH + WIDTH×YR + ELEV + ELEV×YR
65	YR + PREVBRWS + WIDTH + WIDTH×YR + ELEV
66	YR + PREVBRWS + WIDTH + WIDTH×YR
67	YR + PREVBRWS + WIDTH + ELEV + ELEV×YR
68	YR + PREVBRWS + WIDTH + ELEV
69	YR + PREVBRWS + WIDTH
70	YR + PREVBRWS + ELEV + ELEV×YR
71	YR + PREVBRWS + ELEV
72	YR + PREVBRWS
73	YR + WIDTH + WIDTH×YR + ELEV + ELEV×YR
74	YR + WIDTH + WIDTH×YR + ELEV
75	YR + WIDTH + WIDTH×YR
76	YR + WIDTH + ELEV + ELEV×YR
77	YR + WIDTH + ELEV
78	YR + WIDTH
79	YR + ELEV + ELEV×YR
80	YR + ELEV
81	YR
82	PREFSPP + PREVBRWS + WIDTH + ELEV
83	PREFSPP + PREVBRWS + WIDTH
84	PREFSPP + PREVBRWS + ELEV
85	PREFSPP + PREVBRWS
86	PREFSPP + WIDTH + ELEV
87	PREFSPP + WIDTH
88	PREFSPP + ELEV
89	PREFSPP
90	PREVBRWS + WIDTH + ELEV
91	PREVBRWS + WIDTH
92	PREVBRWS + ELEV
93	PREVBRWS
94	WIDTH + ELEV
95	WIDTH
96	ELEV
97	NULL

APPENDIX Q

PLOTS FROM THE INVESTIGATION OF INDEPENDENCE

The first three figures of this appendix are the linked-segment profile plots for the longest transects surveyed for browse utilization. Each plot represents one transect and the browse utilization (%) on consecutive segments (1-X) within that transect. One set of plots was constructed for each year, as labeled below and the same transects are displayed for each year for comparison. These plots showed a few minor drifts away from the transect means and minimal possible serial correlation. Consecutive segments rarely persisted at low or high percent browse utilization and bounced around the mean for each transect (the horizontal line).

The last figure contains the correlogram plots for the three years of browse utilization data, which display the correlation between segments at varying lag intervals (in meters) based on the two- dimensional location of each segment site. Values of 0.0 indicate no autocorrelation, while a value 1.0 would indicate strong autocorrelation. The first point on each plot is the autocorrelation at 0 meters of lag and displays strong autocorrelation as expected. Subsequent values almost immediately drop to 0.0 in each year, indicating minimal autocorrelation at distances greater than 0 meters.

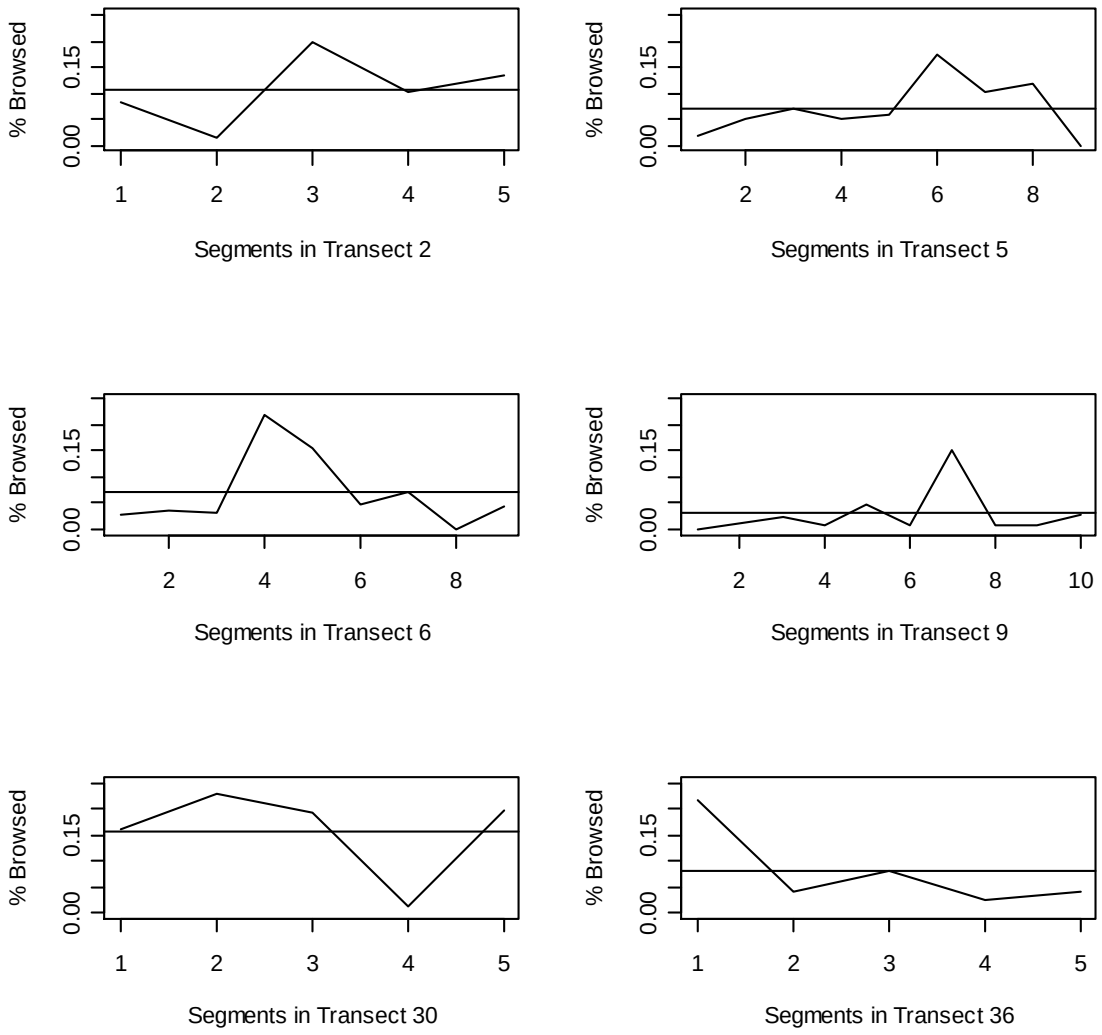


Figure P.1: Linked-segment profile plots for 2008.

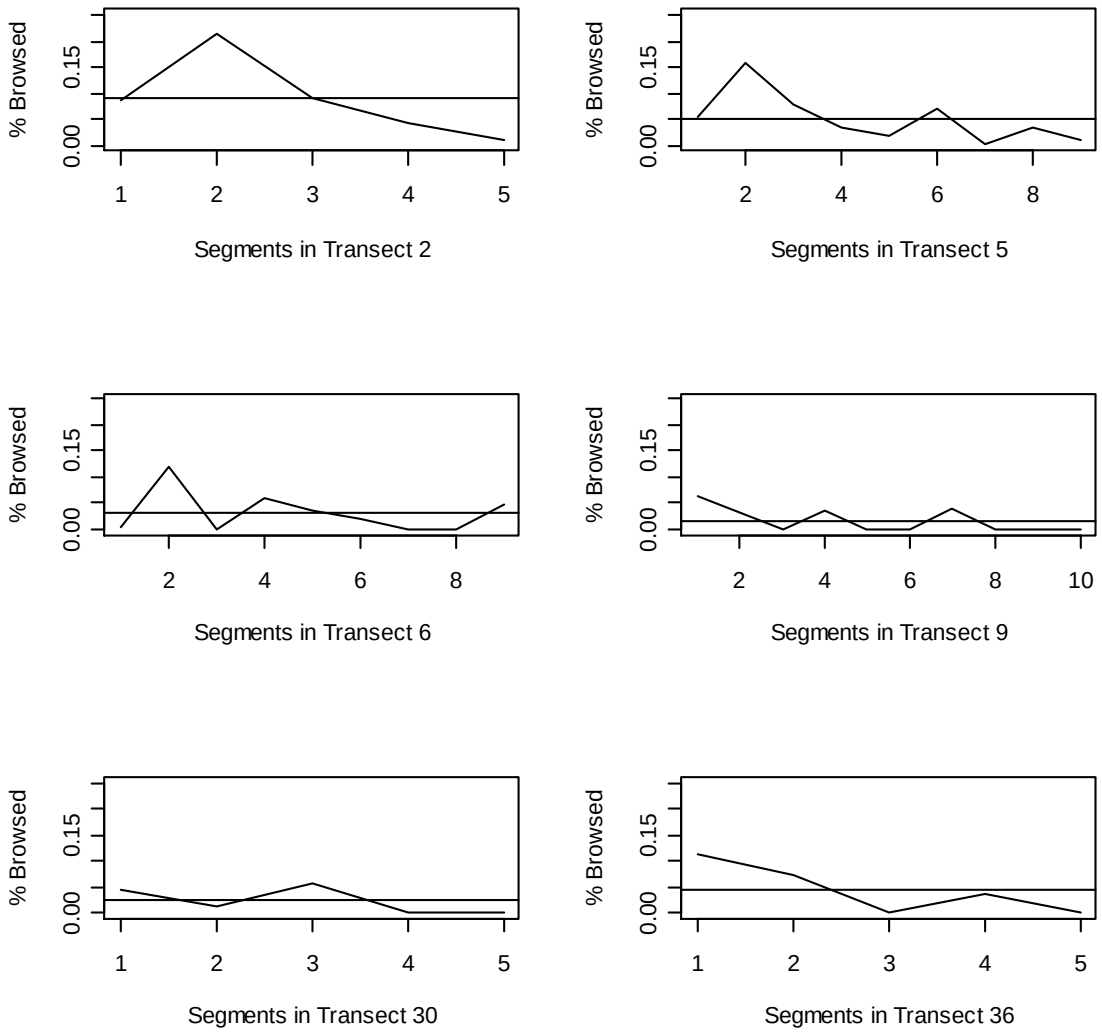


Figure P.2: Linked-segment profile plots for 2009.

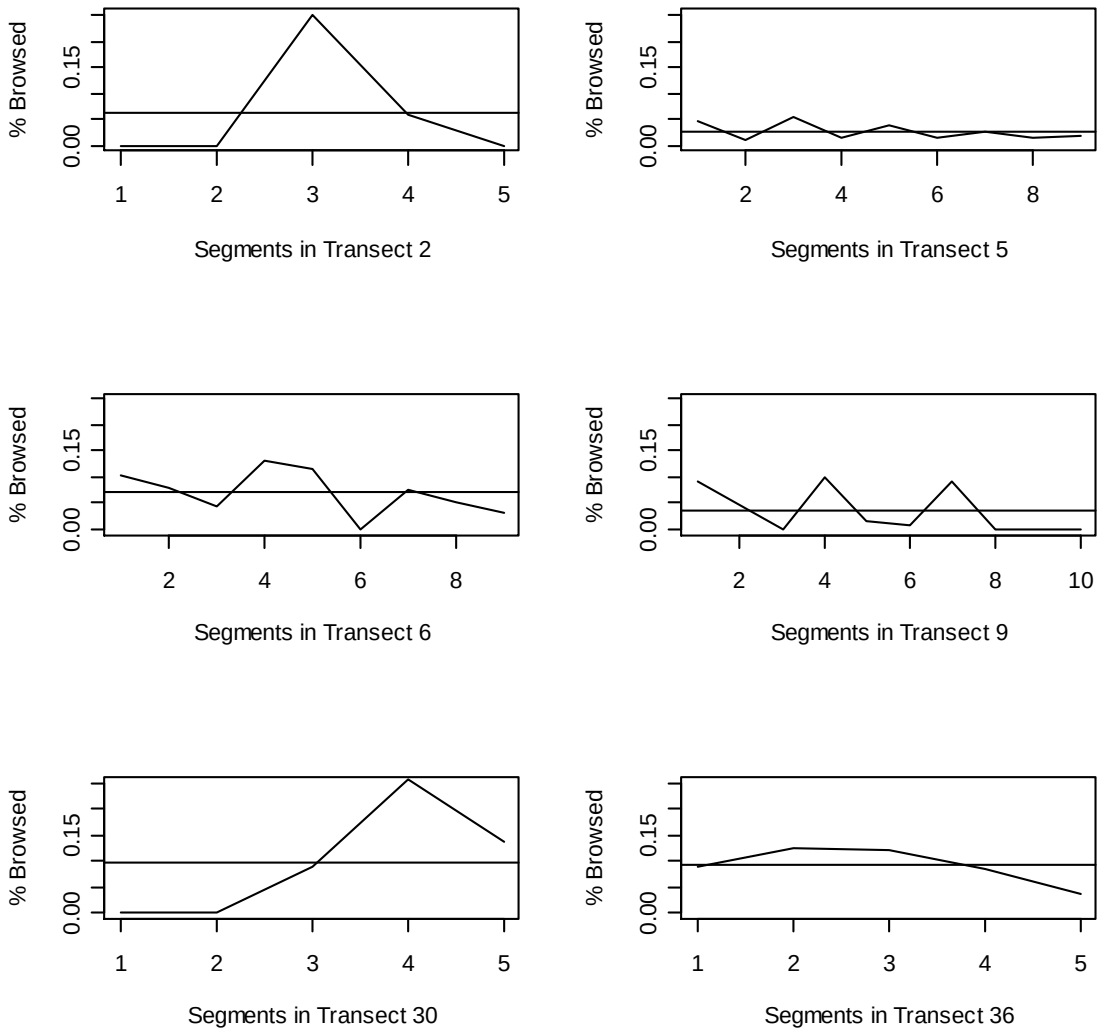


Figure P.3: Linked-segment profile plots for 2010.

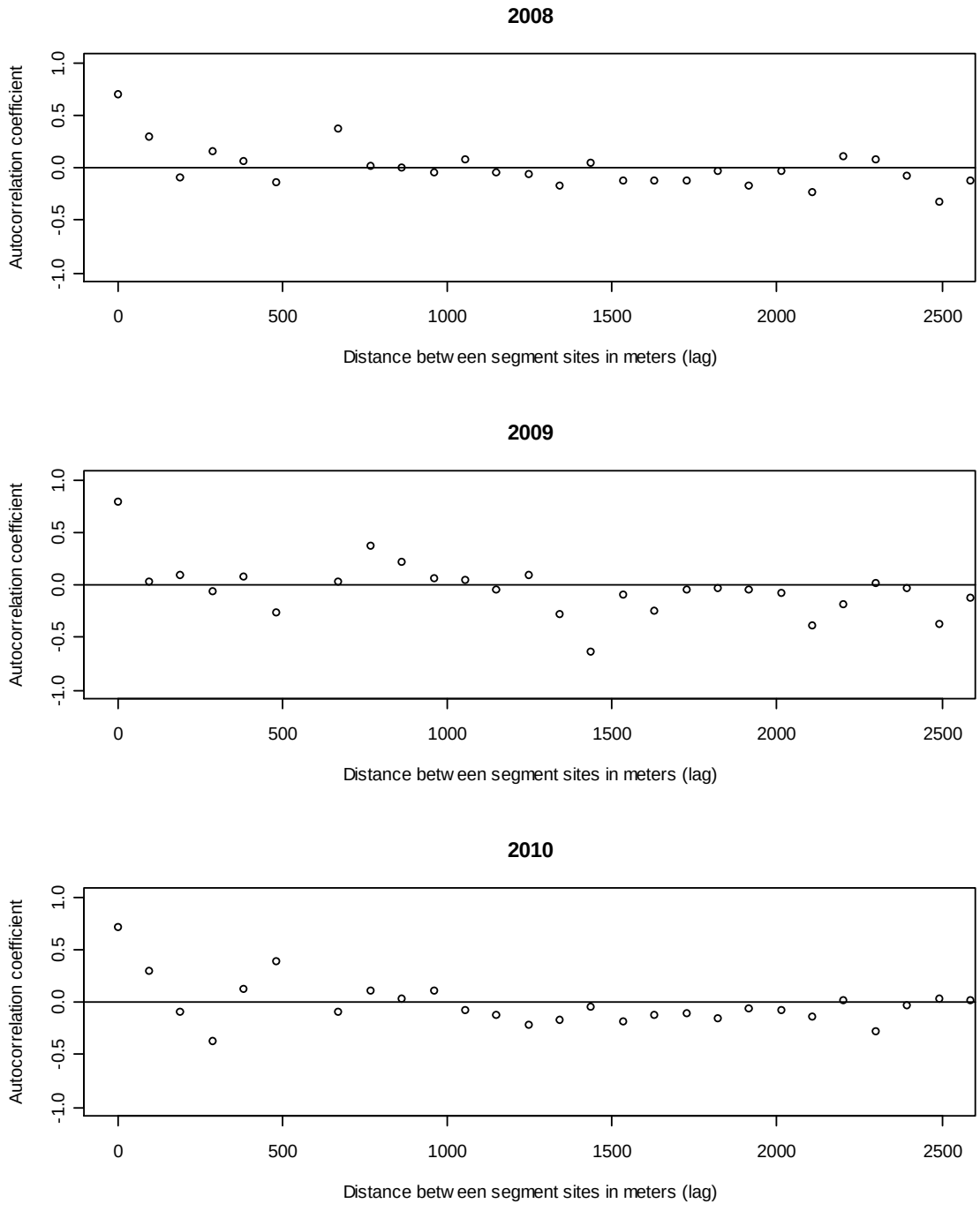


Figure P.4: Correlograms for the three years of browse utilization data.

APPENDIX R

COEFFICIENT VALUES FOR BROWSE UTILIZATION MODELS

This table contains the coefficient estimates (βs) from the top twelve models of the browse utilization analysis. Models 37, 40, and 42 were deemed informative, while the other nine models all had uninformative parameters (Arnold 2010). Coefficients in bold had 95% confidence intervals that did not include zero.

Models	Intercept	YR2009	YR2010	ELEV	PREFSPP	PREVBRWS	WIDTH
Model 37	3.741	3.572	**-12.565**	-0.00345	**0.551**	**3.100**	**-0.00224**
Model 40	3.942	2.292	**-11.695**	-0.00353	**0.551**	**3.065**	**-0.00243**
Model 42	**-2.628**	**-0.362**	**-0.322**	NA	0.444	**3.126**	**-0.00241**
Model 13	5.292	1.419	**-16.343**	-0.00434	**0.822**	**3.161**	**-0.00243**
Model 10	5.176	2.133	**-16.575**	-0.00432	**0.854**	**3.176**	**-0.00208**
Model 39	**-2.673**	-0.153	-0.374	NA	0.444	**3.138**	**-0.00217**
Model 41	0.981	**-0.362**	**-0.321**	-0.00194	**0.553**	**3.072**	**-0.00244**
Model 38	0.960	-0.144	-0.364	-0.00196	**0.553**	**3.082**	**-0.00218**
Model 28	3.794	3.511	**-12.898**	-0.00345	**0.544**	**2.957**	**-0.00222**
Model 4	5.424	1.467	**-17.240**	-0.00438	**0.826**	**2.958**	**-0.00239**
Model 31	3.982	2.212	**-11.877**	-0.00353	**0.546**	**2.960**	**-0.00242**
Model 1	5.328	2.125	**-17.582**	-0.00436	**0.859**	**2.941**	**-0.00204**

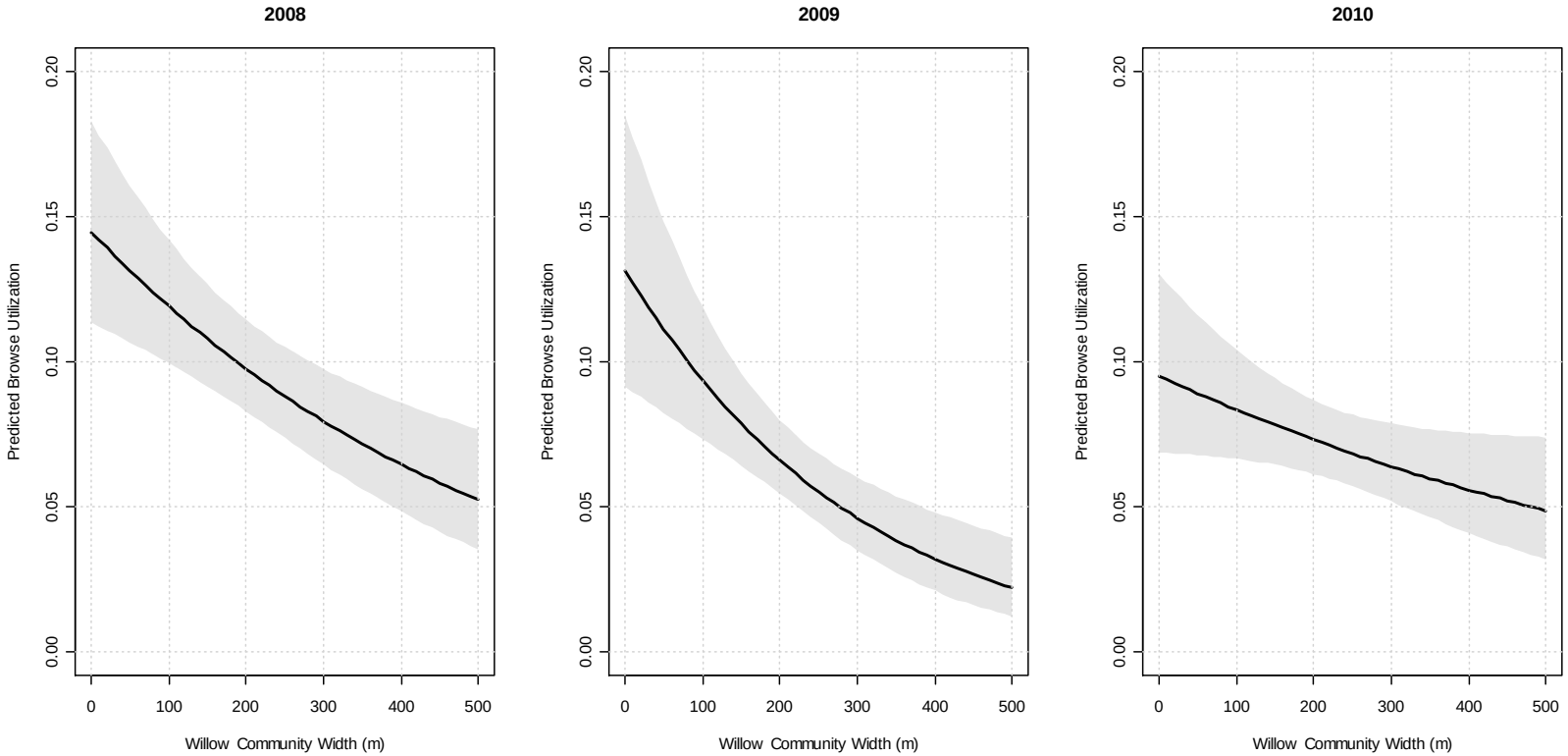
Models	YR2009×ELEV	YR2009×PREFSPP	YR2009×PREVBRWS	YR2009×WIDTH	YR2010×ELEV	YR2010×PREFSPP	YR2010×PREVBRWS	YR2010×WIDTH
Model 37	-0.00197	NA	NA	-0.00157	**0.00647**	NA	NA	0.000803
Model 40	-0.00142	NA	NA	NA	**0.00608**	NA	NA	NA
Model 42	NA	NA	NA	NA	NA	NA	NA	NA
Model 13	-0.00091	-0.168	NA	NA	**0.00876**	**-0.809**	NA	NA
Model 10	-0.00111	-0.301	NA	-0.00175	**0.00886**	**-0.792**	NA	0.000278
Model 39	NA	NA	NA	-0.00130	NA	NA	NA	0.000346
Model 41	NA	NA	NA	NA	NA	NA	NA	NA
Model 38	NA	NA	NA	-0.00135	NA	NA	NA	0.000296
Model 28	-0.00196	NA	0.1074	-0.00158	**0.00659**	NA	0.320	0.000856
Model 4	-0.00095	-0.158	0.0790	NA	**0.00917**	**-0.883**	0.517	NA
Model 31	-0.00140	NA	0.1014	NA	**0.00614**	NA	0.216	NA
Model 1	-0.00113	-0.294	0.1281	-0.00177	**0.00932**	**-0.868**	0.573	0.000318

APPENDIX S

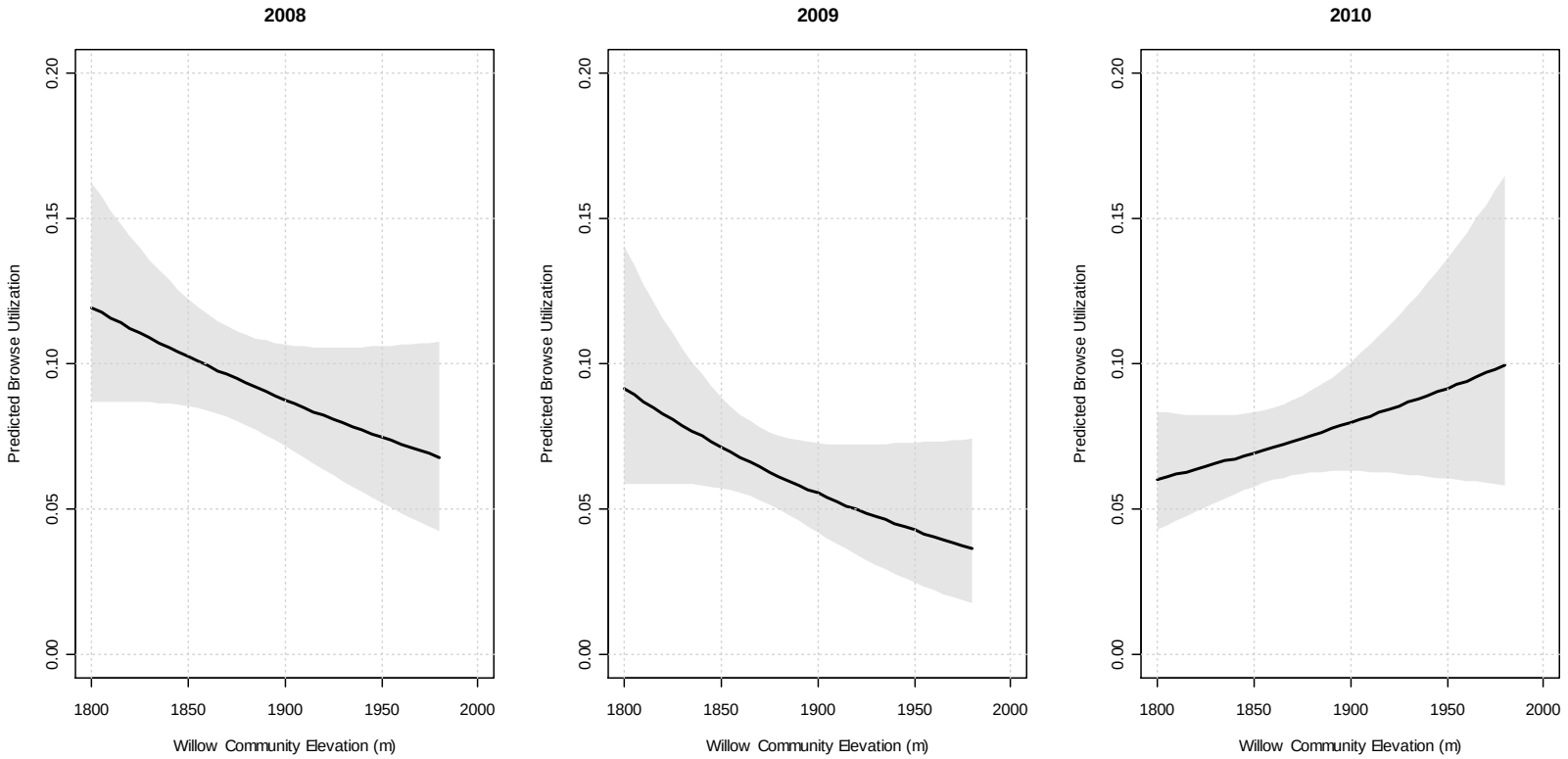
ADDITIONAL PREDICTIVE PLOTS

The following two figures show plots of the predicted relationship between two environmental covariates (willow community width and elevation) and percent browse utilization for all three years of the study, after accounting for all other covariates in the model. All other covariates were kept at their respective means for these plots. The black line indicated the point estimate with the gray area delineating the 95% Confidence Intervals (CIs).

These plots were based on the coefficients from the top browse utilization model (Model 37). The plots for width and elevation did vary across the top models, due to the inclusion or exclusion of WIDTH×YR and ELEV×YR interactions. The plots for elevation were drastically different but all showed high levels of variance based on wide 95% CIs which included a slope of zero.



A figure of the predicted relationship between willow community width and percent browse utilization for all three years of the study, after accounting for all other covariates in the model. Modest differences between years were due to the WIDTH×YR interaction in the model (Model 37) used to construct these plots.



A figure of the predicted relationship between elevation and percent browse utilization for all three years of the study, after accounting for all other covariates in the model. The model used to construct these plots was Model 37, which had an ELEV×YR interaction that resulted in different (but not significantly different) predicted relationships between the winters of 2008-2009 and 2010.