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RESOURCE SELECTION AND CALVING SUCCESS OF MOOSE IN COLORADO

By

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Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Wildlife Biology

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ABSTRACT

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RESOURCE SELECTION AND CALVING SUCCESS OF MOOSE IN COLORADO

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Across much of North America, moose populations (*Alces alces*) are declining due to disease, predation, climate, and anthropogenic pressures. Despite this, populations of moose in Colorado have continued to grow. Studying successful (i.e., persistent or growing) populations of moose can facilitate the continued conservation of the species by identifying habitat features critical for moose persistence.

First, I evaluated calving success of moose in Colorado and the impact of willow habitat quality and nutrition. I then estimated the probability of female moose having a calf using repeated observations in a Bayesian occupancy model. I assigned values for dry matter digestibility, browse intensity, willow height, willow cover, and leaf length based on overlapping sample locations with estimated individual moose homeranges and tested the effect on calf presence. Willow height had the strongest predictive effect on calf presence and was the only covariate with credible intervals not overlapping zero. Dry matter digestibility had no effect, while browse intensity and leaf length were uninformative. Results presented here suggest that the quality (i.e., age and structure) of willow habitat are important for female moose with calves. This work sets the stage for future research on the structure of willow habitat and the incorporation of additional remotely sensed data.

Second, I used a resource selection function to evaluate resource selection by moose in Colorado and the effect of large-scale bark beetle disturbance. Bark beetles have impacted forests across North America, decreasing canopy cover and increasing solar radiation reaching the forest floor. These disturbances lead to an increase in ground forage but have been hypothesized to have a negative impact on thermally sensitive species such as moose. I evaluated resource selection at two scales: a large population scale and finer movement-based scale. The strongest selection by moose was for distance to willow, followed by elevation. Selection for beetle-disturbed habitat was mixed across populations and scales showing little overall effect. The lack of selection for beetle disturbed habitat suggests mixed influences on resource selection by moose. Undisturbed forest had moderately strong positive selection at both scales, illustrating the importance of maintaining undisturbed forest habitat for moose.

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Although a thesis is often written using singular pronouns (as I have done here), it is seldom truly the product of a single person's efforts. I am indebted to many individuals, groups, and organizations that have provided support and contributed to making the project culminating in this thesis a possibility. Here, I have the privilege of recognizing a few of the key people and organizations who have helped me along the way.

I am thankful to Colorado Parks and Wildlife for providing funding for this project, research expertise, field equipment, and logistical support. The incredible level of support by Colorado Parks and Wildlife made the scope and quality of research conducted for this thesis a possibility.

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I view wildlife communities and the world of resource selection. Paul Lukacs had a great impact on my journey, introducing me to the world of Bayesian statistics, and was always happy to lend a hand. Josh Nowak was amazingly generous with his time, eagerly discussing complex models, and taught me a great deal about statistics and the nuances of programming.

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INTRODUCTION: Moose in Colorado

Wildlife populations today are facing diverse and unprecedented pressures including anthropogenic development and dramatic changes in climate. Temperatures during winter are rising more rapidly than any other season, enabling the proliferation of parasites and disease that can have wide reaching impacts to ecological systems. Globally, many species are in decline necessitating deliberate conservation and management efforts to ensure their persistence. Fortunately, an increasingly broad public awareness of the issues facing wildlife has provided landowners, managers, and legislators a mandate for conservation. In the face of unprecedented change, understanding factors driving successful wildlife populations (i.e., stable or increasing) can provide a path for continued conservation.

In this thesis, I examine two populations of moose (*Alces alces*) in Colorado that have been historically successful but face large-scale and increasingly common habitat disturbance. I use innovative techniques and analyses to address shortfalls in our understanding of the ecology of moose. I present results that offer insight into factors that influence population demographics of moose and the importance of undisturbed habitat.

Moose populations across much of the United States have been declining over the last several decades (Murray et al. 2006, Smith and Kilpatrick 2012, DeCesare et al. 2014, DelGiudice 2019). These declines are largely attributed to increases in disease, parasitism, and predation across North America (West 2009). Moose are one of the largest extant ungulates in North America and widely valued by the public. At a time when wildlife managers are challenged to meet growing conservation objectives with fewer resources, filling in knowledge gaps is a key in continuing to meet these objectives. Studying moose in areas at the extremity of their range, such as Colorado, can be especially informative due to the unique challenges faced by these populations.

Moose were an uncommon sight in Colorado prior to the 1970s. Historic records are scant but document the presence of individual moose in the state starting in the 1800s (Bailey 1944). Individual moose observed during the 1800s and early 1900s are thought to have been the result of natural dispersal events from western and northern populations as no reproducing population is known to have existed in Colorado (Olterman et al. 1994). Some biologists have suggested that, given time, moose would have naturally expanded into Colorado as a breeding population (Duvall and Schoonveld 1988); however, anthropogenic sources of mortality would likely have hindered natural dispersal.

Colorado Parks and Wildlife (formerly known as the Colorado Division of Wildlife, henceforth referred to as CPW) translocated 24 moose from Wyoming and Utah to establish a breeding population in North Park Colorado between 1978 and 1979 (Duvall and Schoonveld 1988). Twelve more moose were moved to the Laramie River Valley from Wyoming in 1987. Starting in the 1990s, animals were relocated from North Park to other areas in Colorado to establish additional populations. These relocations were supplemented by additional translocated animals from Utah and Wyoming. Relocation of moose to distribute populations within the state sporadically continued until 2010.

By the early 1990s, Colorado's moose population was growing rapidly as reproduction and survival outpaced mortality. By 1995, the resident moose population in northern Colorado had grown large enough that the state legislature declared Walden, CO the "Moose Viewing Capital of Colorado." Subsequently, the population of moose in Colorado continued to grow and expand into available habitat, reaching an estimated 1,000 individuals in 1991 and 2,400 individuals in 2014 (Timmermann and Rodgers 2017). As of 2019, Colorado's moose population was estimated to be 3,200 individuals (CPW, unpublished data). CPW manages moose populations in 39 game management units and generates revenue from the sale of hunting licenses to

fund research and various management operations.

The state of Colorado lies at the southern extent of the range of moose (Timmermann and Rodgers 2017) and provides a unique assemblage of habitats. Unlike many moose populations in the lower 48 states, populations of moose in Colorado have been relatively robust over the past two decades (Timmermann and Rodgers 2017). In Colorado, predation pressure on moose is minimal and the prevalence of parasites and disease is relatively low. As such, the primary factors limiting moose populations in Colorado are the ability to consume adequate nutrition and survive at southern latitudes in the presence of warming climates (Van Ballenberghe and Ballard 2007).

Two of the oldest moose populations in Colorado, the North Park and Laramie River populations, have been the subject of increased monitoring by Colorado Parks and Wildlife since 2013. Preliminary observations showed differing pregnancy rates between these populations suggesting differences in herd productivity despite geographic proximity and similarities in landscape and climate between population home ranges. The similarity between populations provides a unique opportunity to evaluate differences between these populations and evaluate their effects on population demographics.

Nutrition intake has been extensively linked to productivity in moose and other ungulate species (Heard et al. 1997, Testa and Adams 1998). Due to the geographic and climatic similarities between the North Park and Laramie River populations of moose, a lack of natural predators, and low levels of disease, nutrition intake is a logical explanatory factor to investigate that may explain variation in productivity. In Rocky Mountain National Park, an area geographically proximate to this study area, 90% of moose diet was comprised of willows (Dungan et al. 2005), suggesting that willows are overwhelmingly the most important source of nutrition for moose in this region.

Another key component in understanding populations of moose is habitat use and resource selection relative to rapidly changing forest conditions. Mountain pine beetles have dramatically affected forests across the western United States over the past two decades. A number of studies have discussed hypothetical impacts to ungulates in beetle kill areas, however there are very few published empirical studies examining these impacts (Saab et al. 2014, Ivan et al. 2018). Forage availability, thermal exposure, and navigability have been identified as factors that may influence resource selection in impacted areas (McGregor 1985). Management and conservation efforts of moose in Colorado do not currently consider the impacts of mountain pine beetle epidemics despite widespread landscape level impacts throughout much of the range of moose.

The objectives of this thesis are twofold; in my first chapter, I evaluate calving success as a function of spatial and temporal willow characteristics. With these data, I hope to better understand how willow communities affect moose population demographics by contrasting two spatially proximate populations. In my second chapter, I evaluate moose resource selection at individual and population scales and evaluate the effect of mountain pine beetle impacted habitat along with biotic and geographic variables on resource selection. I believe that this work helps to fill fundamental gaps in our contemporary understanding of what factors are influencing moose populations and may provide valuable guidance for management and conservation efforts.

CHAPTER 1: Willow forage quality impacts on calving success of moose

INTRODUCTION

Reproductive success is one of the most important factors in determining population growth rates. For moose, summer consumption of deciduous leaves is critical to meeting the nutritional requirements that allow for reproduction in the fall (Belovsky 1978). Summer nutrition intake has also been closely linked with calving success (Heard et al. 1997, Testa and Adams 1998). Moose preferentially select for willow (*Salix spp.*) over other forage and are an important component in the diet of moose (Bucher 2007). Dungan et al. (2005) found that 90% of moose diet in Rocky Mountain National Park was comprised of six willow species. These studies suggest that moose in Colorado depend on willow for the majority of their nutrition intake. In conjunction with the well-established link between nutrition intake and calving success of moose, the quality and quantity of willow forage are likely to be key factors in the reproductive success of moose.

Previous work by Colorado Parks and Wildlife (hereafter CPW) found moose pregnancy rates to vary substantially between two spatially segregated, geographically proximate populations of moose (Bergman 2017, unpublished report). Forage quality and quantity remain poorly understood for these two populations and are logical variables to investigate that may explain differences in reproductive success. Furthermore, similarities in landscape composition, habitat availability, and geography may reduce the set of alternative explanatory factors.

Assessing reproductive success of female moose and calf-at-heel status can be time consuming (e.g., ground observations) or expensive (e.g., aerial surveys). Both methods have associated error that, when not corrected for, can lead to bias which reduces the utility of population estimates (White 2005). Bergman et al. (2020) presented a method for correcting for uncertainty in the observation process through

repeated ground observations, which I use here. This method allows for unbiased estimation of calf-at-heel rates but requires rigorous field effort. This effort is not always feasible, necessitating evaluation of less field intensive methods of predicting calving success. One alternative approach is to evaluate whether forage characteristics could be used as an indicator of calving success.

In this chapter I examine the correlation between of forage quality, quantity, and browse intensity on the calving success of Colorado moose by contrasting two spatially separated populations. I use estimates of calving success, gathered through repeated visual observations, and analysis of willow nutrition to investigate the relationship between these variables. I address the following questions: 1) How does willow nutrition, availability, and utilization relate to moose calving success? 2) How does willow nutrition vary relative to the amount of willow available, willow species, browse intensity, and willow height? Finally, I present ways in which the results from this study can be applied to future conservation and management of moose when rigorous demographic monitoring data are not available.

MATERIALS AND METHODS

Study Area

I conducted research in two study areas located in northern Colorado. The first study site, North Park, was located south of the Colorado-Wyoming border 100km west of the Rocky Mountain Front and near the town of Walden. Moose were first translocated to the area during the 1970s and have been there since then. The North Park study area was a wide (14-46km), high elevation valley (2400–2750m) comprised of a mixture of rolling sagebrush (*Artemisia spp.*) hills, irrigated agricultural fields, and riparian corridors dominated by willow (*Salix spp.*). Riparian willow communities were largely comprised of Geyer willow (*S. geyeriana*), mountain willow (*S. monticola*), planeleaf willow (*S. planifolia*), and Booth's willow (*S. boothii*). The hills surrounding North

Park were primarily lodgepole pine (*Pinus contorta*) with Englemann spruce (*Picea engelmannii*) intermixed.

The second study site was along the Laramie River roughly 40km northeast of the North Park study area and was separated by the Rawah Mountains (3200–3840m). Moose were translocated to Laramie River during the early 1980s and have been there since then. The Laramie River Study area was comprised of a narrow valley floor (3.0–8.5km wide) and characterized by riparian willow communities along the river with similar species composition to the North Park study site. Uplands around Laramie River were characterized by rangeland co-dominated by sagebrush and a grass forb mix but occurred with less frequency in comparison to North Park. Larger hills located within the valley were dominated by aspen (*Populus tremuloides*), while slopes to the east and west were dominated by lodgepole pine and Englemann spruce.

Geographic features and climate of both study areas were similar. Elevation of riparian areas ranged from 2,400 to 2,800 m. Temperatures ranged from highs in July of 26.5°C to lows of -15°C in January (USDA-NRCS 2005). North Park tended to have slightly higher maximum temperatures than Laramie River throughout the year by about 2.2°C degrees. Mean low temperatures were more similar although North Park tended to be slightly colder during the winter months. Average annual precipitation was around 40.4 cm for both sites.

Moose in both study areas were managed by CPW. Management actions included limited male and female moose hunting. Predator assemblages were also similar between study sites. Black bears (*Ursus americanus*), mountain lions (*Puma concolor*), and coyotes (*Canus latrans*) were present in both sites whereas wolves (*Canus lupus*) and grizzly bears (*Ursus arctos*) were absent. It was believed that black bears and mountain lions infrequently preyed upon moose resulting in minimal predation pressure (Bergman et al. 2020).

Capture of Moose

Moose were captured by CPW in both the North Park and Laramie River study areas as a part of a broader research initiative from 2015 to 2019. All animal capture, handling, and monitoring was conducted in accordance with approved Institutional Animal Care and Use Committee (IACUC) protocols (University of Montana IACAC file #032-17CBWB-060517 and CPW ACUC #08-2013). Between 20 December and 27 January of each winter (2015–2019), CPW captured adult (≥ 2 years old) female moose via helicopter darting. Moose were sedated using one of three different drug combinations: 1) BAM (54.6 mg of butorphanol, 18.2 mg of azaperone, and 21.8 mg of medetomidine) in combination with ketamine (200 mg), 2) carfentanil (3mg) in combination with xylazine (100mg), or 3) thiafentanil (10mg) in combination with xylazine (25mg). After handling, capture drugs were antagonized with naltrexone (100 mg, antagonist for carfentil and thiafentenil), tolazoline (500mg, antagonist for azaperone and xylazine), or atipamezole (100–150 mg, antagonist for medetomidine and xylazine). Once sedated, moose were blindfolded to minimize stress. Moose received oxygen, via nasal cannula, to minimize risks of adult and fetal hypoxia. Moose were subsequently fitted with satellite and GPS equipped VHF radio- collars (Vectronics Aerospace GmbH, Berlin, Germany model: Vertex Plus, and Advanced Telemetry Systems, Isanti, MN, USA model: G5-2D), as well as uniquely numbered eartags. At the time of capture, blood samples were collected to allow for subsequent determination of pregnancy status via Pregnancy Specific Protein B (PSPB, Wood et al. 1986).

Following the first year of capture, some previously captured moose were recaptured, but only on a random basis. Moose captured in previous years retained satellite collars and remained available for summer field observation. A total of 214 moose were captured between 2015 and 2019. In total, there were 145 unique individuals, 80

from North Park and 65 from Laramie River.

Observation of Moose Calves

Beginning in mid-May of each year, I initiated ground observations of collared moose. Typically, one observer completed ground observations by radio tracking the collared moose to document the presence or absence of a calf. Recent GPS locations of moose expedited ground observations. When a single observer failed to gain an observation after four repeated efforts, a two-observer approach was used. During these scenarios, the second observer was positioned along the exit route that a cow was expected to take, and the first observer radio-tracked the cow moose in the same manner as a single observer approach. An observation was recorded when an identifiable female moose was observed in addition to the surrounding 1-2m area or when a calf was observed in the immediate vicinity of the female.

Repeated observations continued through the end of August. Moose were initially prioritized for observation based on whether or not they had been captured the previous winter (i.e., moose with known pregnancy status were a higher priority for observation). However, once individual moose had been observed at least once, priority was then given to animals based on timing of the most recent observation (i.e., individual moose observed most recently were lowest priority for upcoming observations and animals who had not been recently observed were a higher priority). In addition to observations that occurred as a part of the formal study process, a small number of opportunistic observations by the public ($n = 9$) during autumn months were recorded. Opportunistic observations were only recorded when individual identification of moose (possible due to unique ear tags) was provided.

Willow Surveys

I collected willow samples from both the North Park and Laramie River study sites from 2016 to 2018 during the month of July to assess spatial variation in willow quality, quantity, and utilization. Hereafter, I refer to these samples as ‘spatial samples.’ I used GPS locations from collared moose during the month of June of the same year to represent areas used by moose during summer (June to August). From those, I randomly selected sample points from those classified as willow habitat according to the “Basin Wide Layer Package” (Simpson et al. 2013). For the pilot year, 2016, I randomly selected 40 points from each study area from all points in June after filtering for habitat. For years 2017 and 2018, I selected 60 points from each study area and additionally stratified the random points by individual moose (i.e., either two or three points were selected from the used locations of each moose). By stratifying random locations by moose I avoided biasing observation effort towards moose with more recorded used locations due to collar type or geographic location. I restricted random locations to those $\geq 20\text{m}$ apart. In the event that a point was too close to another location, did not have any willow present within 10m, or was inaccessible (i.e., inaccessible private property), alternative locations were selected sequentially from a list of replacement points (representing approximately 15% of all locations).

At each spatial point I marked the point location and identified the closest willow to the point. I identified each willow to species and collected leaves and twigs from branches. I collected samples from the apical 15–20cm of branches which generally represent the current year’s growth and, depending on the growth stage, previous year’s growth. I sampled the closest branch to the marked point. I collected all samples from branches between 0.5m and 2.5m above ground level which is consistent with observed use in our area (personal observation). The effective browse range of moose reported in literature varies among studies (Stickney 1966, Bergström and

Guillet 2002, Burkholder et al. 2017) but typically falls within a similar range. I collected leaf samples by stripping leaves from branches by hand to simulate moose foraging behavior and clipped twigs from areas where I had stripped leaves. For both leaf and twig samples I collected $\geq 10\text{g}$ (wet weight) from each plant. I randomly selected five leaves from the sample and recorded the length of each. I placed leaf and twig samples in open paper bags and allowed them to air-dry in a low humidity environment for a period of at least two months. Each year, once dry, I transferred samples into sealed plastic bags to prevent further moisture exchange.

I established four 10m transects at each spatial sample location, one in each cardinal direction. I laid a tape reel along each transect and recorded each willow intercepting the tape noting the intercepts, species, and plant height. I did not record willow intercepts outside of the typical browse range of moose (i.e., willow plants shorter than 0.5m or with no leaves below 2.5m).

I measured browse utilization of the willow closest to the spatial point and of the willows closest to 5m and 10m along each transect. For the 5m and 10m samples, I selected the closest willow within 2.5m (to avoid overlapping samples) of the transect for each distance and direction. I followed the sampling protocol developed by Stickney (1966) and modified by Burkholder et al. (2017) for evaluating browse use. In brief, I sampled the closest branch to the sample location within the browse range of moose and evaluated ≥ 20 twigs. Here I use the same definition of twigs as Burkholder et al. (2017), in which twigs are defined as an unbranched portion of a branch with apical or lateral growth consisting of current and previous year's growth. I classified each twig as belonging to one of five categories: 1) unbrowsed (N_{ub}), twigs which do not show any evidence of foraging, 2) browsed (N_b), twigs which have had the apical portion within 15–20cm removed from foraging; 3) leaf stripping (N_s), twigs which have not been browsed but that have leaves stripped off; 4) browsed and leaf stripping

(N_{bs}), twigs that have been browsed and have leaf stripping farther along the branch, and 5) heavily browsed (N_{hb}), twigs that were browsed at a diameter of ≥ 0.5 cm. I expanded upon the the adjusted estimator of browse utilization used by Burkholder et al. (2017) to incorporate additional weighted classifications of browse intensity to reflect increased browse pressure (e.g., N_b receives a weight of 1 and N_{hb} receives a weight of 3). I calculated adjusted browse intensity (B_{adj}) for each plant as:

$$B_{adj} = \frac{N_b + N_s + (N_{bs} * 2) + (N_{hb} * 3)}{N_{ub} + N_b + N_s + (N_{bs} * 2) + (N_{hb} * 3)}$$

In 2017, I selected five willow plants spatially representative of each study site and proximate to vehicle access to enable monitoring of leaf quality as a function of phenology through weekly sampling (hereafter referred to as ‘phenology samples’). For each plant, I collected leaf and twig samples (as described above) every week from May to August of each year (2017 to 2019). I dried phenology samples under the same conditions as the spatial samples.

I sent samples to Dairy One Forage Laboratory (Dairy One, Ithaca, NY) for analysis. All samples were analyzed for neutral detergent fiber (NDF), acid detergent fiber (ADF), ash, and acid detergent lignin. For the pilot study year (2017) all spatial samples were analyzed in addition to bi-weekly phenology samples. For years 2018 and 2019, I analyzed average site nutrition for each week by combining phenology samples from each site in equal proportions. I also analyzed all spatial samples separately. I calculate percent dry matter digestibility (DMD) using ash and neutral detergent fiber (NDF) values for each sample as follows (C. Robbins et al. 1987, C. T. Robbins et al. 1987):

$$DMD = (0.9231 * e^{(-0.0451 * \frac{ash}{NDF} * 100)} - 0.03 * (ash * 100)) * NDF + ((-16.03 + 1.02 * (100 - NDF)) - 0)$$

Analytical Methods

Willow nutrition. For each willow samples at each spatial point, I modeled the effect of willow species, browse intensity, leaf length, and willow intercept on DMD. I did not consider the effect of year on nutrition as the intent of this analysis is to explain DMD through the lens of willow characteristics. I used a Bayesian framework for the analysis and evaluated the effect of each covariate based on the credible interval using the following equation:

$$\text{logit}(DMD) = \text{species} + \text{browse_intensity} + \text{leaf_length} + \text{willow_intercept}$$

As nutrition samples were only taken from the closest willow to each spatial point, I only used the species, browse intensity, and leaf lengths from that plant. I limited analysis of species effect on DMD to species with ≥ 10 samples. For leaf length, I averaged the five leaf lengths recorded during collection of the vegetation sample. I averaged the amount of willow intercept (i.e., willow overlapping transects) for each point.

Calf presence and the effect of willow. I estimated the proportion of female moose with a calf for each year using multiple repeated observations of calf presence using an occupancy model as described by Bergman et al. (2020). An occupancy model framework uses a flexible model structure and enables estimation of occupancy (ψ) while accounting for imperfect detection (p). In this case, ψ represents the probability of a female moose having a calf-at-heel. I chose to model ψ varying for each year and site and p varying each month. This structure allowed me to evaluate differences in occupancy between study sites and the effect of additional covariates on ψ for each study site.

To evaluate the effect of spatial willow covariates on ψ I used average values from each point and evaluated which points overlapped with individual moose core home ranges. For each spatial point I calculated the mean value of adjusted browse intensity (B_{adj}), leaf length (L_l), and the proportion of amount of transect intersected by willow. I then calculated the core home range for each moose and year using a 75% Kernel Density Estimate (KDE) using the `adehabitatHR` R package (Calenge 2006). I then intersected spatial samples with each the home range estimate for each individual and year. Last, I assigned covariate values from intersecting points to the respective year and moose. I used a linear model to estimate the effect of individual moose on the covariate of interest as follows:

$$cov = \mu + MooseEffect_i$$

where cov is the covariate of interest (e.g., DMD), $MooseEffect$ varies by individual moose.

I used the estimate ($MooseEffect$) for each individual moose to evaluate the effect of each covariate on ψ . This approach has two key benefits. First, because the core home ranges of moose overlap with differing numbers of spatial samples, the precision of observed covariates varies between individual moose. The linear model accounts for this by varying precision of the estimated effect. Second, this approach allows uncertainty from observed covariates to be correctly propagated in the calf occupancy model.

I used a Bayesian framework for analysis of calf occupancy as it offers the benefit of accurate error propagation across estimated variables and simplifies interpretation of estimated probabilities. I tested the effect of each covariate (DMD, leaf length, willow intercept, browse intensity) on calf occupancy in a univariate model as follows:

$$\psi = (\sin(b_0 + \text{MooseEffect} * \text{covariate_value}) + 1)/2$$

where *MooseEffect* represents the modeled value from the previous equation and *covariate_value* represents the measured value for each covariate (e.g., DMD).

RESULTS

Analysis of spatial samples resulted in 319 measurements of DMD. In 2017, 83 samples (North Park = 42, Laramie River = 41) were collected and analyzed (Table 1.3). In 2018, 120 samples were collected, three samples were censored due to poor drying, yielding 117 measurements of DMD (North Park = 57, Laramie River = 60). In 2019, 119 samples were collected and analyzed for DMD (North Park = 59, Laramie River = 60).

Willow quality did not vary as a function of phenology (i.e., DMD through time) during the survey period (May to August) between sites or across years. A linear model comparing sample week and DMD percent for each study site and year combination found no relationship between week and DMD ($r \leq \pm 0.01$).

Willow covariates (DMD, browse intensity, leaf length, average willow height, willow cover) sampled during July of each year at each spatial point displayed greater variance across both site and year (Figure 1.1). Mean estimates and standard deviations for each combination of site, covariate, and year are provided in Table 1.1. DMD was higher in Laramie River than North Park in 2017 and lower in 2018. In 2019, mean DMD was functionally identical for both study areas. Browse intensity at both sites was highly variable with mean values increasing slightly from 2017 to 2019. Leaf length was similar in both study sites and for all years. Average willow height had high sample variance, was similar across years, and had a higher mean in North Park for all years. Willow cover was also highly variable with a wide distribution and similar

for both sites with slightly lower cover on transects conducted in 2019. A Pearson's pairwise correlation test showed low correlation between all combinations of covariates ($< \pm 0.25$) with the exception of willow height and willow cover which had a positive correlation of 0.47.

Each Bayesian model ran for 100,000 iterations with 50,000 iterations of burn-in on six chains at which point all parameters had reached convergence ($\hat{r} < 1.01$). Analysis of DMD relative to willow browse intensity, height, cover, leaf length, and species revealed few of these factors had a strong influence on DMD with high certainty (Figure 1.2, Table 1.2).

Willow species was largely not a good predictor of DMD with large credible intervals for each species. Whiplash willow (*Salix lasiandra*) had the strongest effect of any species evaluated and was the only species with credible intervals not overlapping zero. Estimates for Geyer willow, mountain willow, and planeleaf willow were similar with a slight positive effect on DMD. Booth willow had a slight negative effect on DMD, however the 50% credible interval overlapped zero.

Browse intensity and willow height both had mean effect estimates that were close to zero and substantially overlapping credible intervals and thus were uninformative. Willow cover had a very slight negative effect on DMD with credible intervals substantially overlapping zero. The effect of leaf length also had a negative effect on DMD and was the only non-species covariate with credible intervals not overlapping zero.

Ground observation efforts resulted in 352 observations of moose (North Park = 148, Laramie River = 204) recorded during the study (Table 1.4). Of those observations, 201 (North Park = 88, Laramie River = 113) had no calf observed, 144 (North Park = 58, Laramie River = 86), had one calf observed, and 7 had twin calves observed (North Park = 2, Laramie River = 5). The observations consisted of 108 unique individuals,

60 and 48 in North Park and Laramie River, respectively.

Mean calf occupancy estimates (ψ) for both study areas were highest in 2015 and 2016 (μ range 0.78—0.93, sd range 0.07—0.11, Figure 1.3). Estimates were most disparate between populations in 2017 with means of $\psi = 0.397$ ($sd = 0.13$) and $\psi = 0.72$ ($sd = 0.138$) for North Park and Laramie River, respectively. In 2018, the ψ estimate was higher for North Park ($\psi = 0.70$, $sd = 0.12$) than for Laramie River ($\psi = 0.59$, $sd = 0.10$). In 2019, ψ was estimated at 0.50 for both populations (sd range 0.11—0.12).

Detection probably (p) was lowest for May, during parturition, with an estimate of 0.48 ($sd = 0.09$, Figure 1.4). Summer months (June, July, and August) had the highest detection probability which increased across that period from 0.77 to 0.90 (sd range 0.06—0.09). Estimated detection of a calf in the fall months decreased ($p = 0.70$, $sd = 0.11$) relative to summer months but remained higher than May detection.

The univariate models testing covariate effects on occupancy showed mixed effects characterized by large credible intervals. The effect of DMD was functionally zero ($\mu = 0.02$) with a wide credible interval (-0.92 — 0.97). The credible interval for the effect of browse intensity substantially overlapped zero ($\mu = -0.59$, credible interval -1.88 — 0.79) and was therefore uninformative. Of the five univariate models, willow cover was the only covariate with a credible interval not overlapping zero (Figure 1.5, Table 1.5). Willow cover showed a moderately strong positive effect on ψ with a mean estimate of 1.32 (credible interval 0.15—1.88). The mean effect of willow height had a mean positive effect on ψ with an estimate of 0.79 (credible interval -0.20 — 1.90) but included a small probability of a negative effect (1.5%). Leaf length substantially overlapped zero with the widest credible interval ($\mu = -0.42$, credible interval -1.93 — 1.75).

DISCUSSION

The lack of trend in willow phenology (i.e., DMD through time) for both study sites supports two of my key assumptions when designing this project. First, nutrition at both study sites is consistent across the survey period. Second, sampling willow nutrition during July provides a representative sample of nutrition throughout the summer months. Evidence that these two assumptions have been met supports the subsequent analyses based on DMD and willow covariates gathered during July of each year.

Site level DMD varied substantively site and year without a consistent pattern during the study period (Figure 1.1, Table 1.1). Of particular interest, mean DMD was higher in Laramie River than North Park in 2017, lower in 2018, and practically equal in 2019. These measurements of DMD closely track estimates of ψ for 2017, 2018, and 2019 in which Laramie River had higher then lower then equal estimates of ψ in comparison to North Park, respectively.

Credible intervals overlapping zero for most covariates in the analysis of DMD relative to willow characteristics (Figure 1.5, Table 1.2) suggests that the covariates considered in this study are not sufficient to accurately predict DMD. Prior research has identified differences in nutrition based on willow species (Stolter et al. 2005, Stumph and Wright 2007); however, these differences may be overshadowed by temporal, geographic or morphological characteristics (Stumph and Wright 2007). If the objectives of future survey efforts are to assess the relative nutrition quality of willow, simply monitoring the covariates used here is not sufficient. That said, these data can still provide valuable information when used to evaluate the probability of female moose having a calf-at-heel. The general trends in ψ (Figure 1.3) align closely with Bergman et al. (2020). Of note, when compared to previously reported estimates of ψ the decrease in 2017 can largely be ascribed to a single population (North Park)

rather than a decrease in ψ across both populations. Additionally, ψ appears to be more variable between sites through time than previously thought. Estimates for 2015 to 2017 support observations by CPW biologists that a higher proportion of female moose in Laramie River had calves each year than in North Park. However, this pattern does not hold for 2018 and 2019 in which Laramie River had first lower ψ estimates and then functionally identical estimates to North Park. It is important to note that, for each year, 95% credible intervals for both populations overlap one another. Thus, the results presented here do not allow for certainty that ψ differs between these populations for the years evaluated.

The greatest advantage of employing a Bayesian framework in these analyses was the ability to use an integrated model evaluating the effect of each covariate on ψ with appropriate error propagation. In this model, the uncertainty in calf occupancy for each individual moose was carried into the estimate of covariate effects on ψ . Although this results in broader credible intervals for estimates, it provides a more truthful assessment of covariate uncertainty. This uncertainty is readily apparent in the estimate of covariate effects on calf occupancy (Figure 1.2). Although credible intervals of all but one estimate ended up overlapping zero these estimates can still provide biologically relevant trends and information.

The high probability of a positive effect of willow height and the positive effect of willow cover suggest that these covariates result in an increase in ψ . Overall, female moose were more likely to have a calf when they had access to large (i.e., tall), high density (i.e., high ratio of willow cover) willow. Although a substantial body of work has documented moose preference for willow habitat and forage (Dorn 1970, Stevens 1970, Dungan et al. 2005, Bucher 2007), this provides evidence that high density, mature willow habitat is even more important for female moose with calves.

The high degree of uncertainty in the effect of browse intensity is likely due to

high variance in the raw parameter estimates (Figure 1.2, Figure 1.1). The estimates trended negative (0.88 probability) but are inconclusive. Two possible biological explanations of a negative effect are that female moose are more likely to have a calf either in areas with lower densities of moose or in areas with sufficiently dense willow that it results in lower browse intensity. The first explanation is supported by literature which has documented female moose to calve in areas that are less frequently used by solitary moose (Dussault et al. 2005). Some evidence suggests that individual moose exhibit different strategies (Poole et al. 2007), explain the uncertainty in this estimate. Because of the lack of a clear relationship between browse intensity and DMD (Figure 1.5) it is unlikely that this effect is being driven by selection for more nutritious plants.

Leaf length was the least informative of the covariates considered with widest credible interval (Figure 1.2). This is likely due to relatively low variation in the parameter between site, year, and individual sample (Figure 1.1). These results indicate that leaf length is not a useful parameter for explaining moose calf occupancy.

The novel approach I employed, evaluating spatial samples based on the overlap with individual home ranges, proved to be a useful technique to evaluate sparse measures of nutrition and vegetation quality at landscape scales. In using this method, I was able to leverage available spatial use data from individual moose to provide estimates for each individual rather than distilling all analyses to the site level. This approach enables a much more robust analysis of effects than solely looking at effects at the site level. Despite this, limitations in the amount of fine resolution data available led to reduction in the precision of estimates.

Collecting and analyzing DMD at the scale required to estimate individual nutrition without spatial averaging is likely not feasible. This supports further application of the methodology I used given similar objectives. Future studies addressing this

question may wish to analyze composite samples consisting of multiple willow plants to reduce sampling variability.

At a site level, DMD closely tracked with estimates of ψ suggesting that variation in willow DMD is biologically significant to moose. That said, the predictive utility of this relationship is likely limited due to sampling variability and model uncertainty in ψ . A comparison of site level covariates would be useful with large differences in ψ between populations or years. When comparing similar estimates of ψ (e.g., study populations in 2015, 2016, 2019) the variance in DMD measurements will likely be greater than the difference in occupancy, thereby reducing the utility of the covariate.

Looking forward, the results from this study provide valuable information to guide the conservation and management of moose. Similarities between the two study sites allowed me to analyze the effect of willow characteristics on moose calf occupancy that can facilitate future management. Monitoring of calf-at-heel rates is notoriously expensive and, in many instances, cost prohibitive for long-term studies. Here, I provide evidence that an assessment of willow maturity and density may serve as a good indicator of spatial areas that support higher levels of calving success. In practice, this may be applied as a coarse measure of suitability when making conservation or management decisions. This study also provides the foundation for further investigation of this relationship and draws to light the possibility of incorporating remote sensed vegetation surveys (e.g., vegetation height from lidar) to evaluate habitat quality for reproducing female moose.

FIGURES

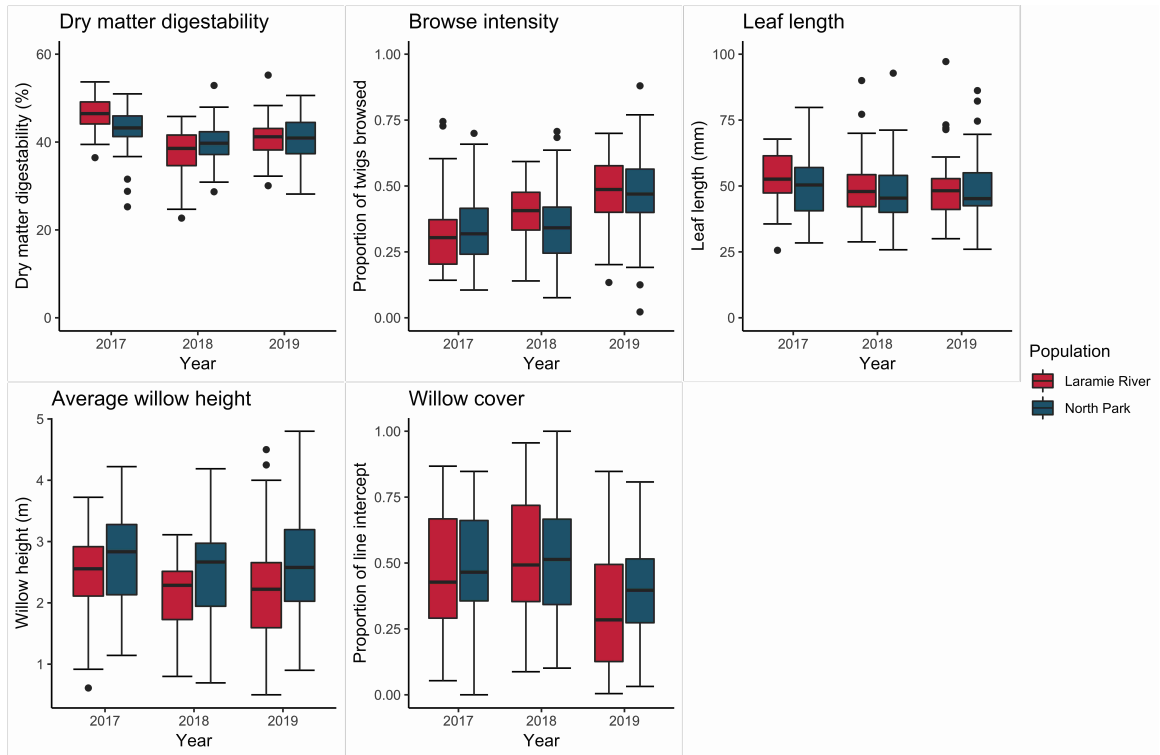


Figure 1.1. Measurements of willow dry matter digestibility (DMD), browse intensity, leaf length, average height, and cover from willow samples at spatial points within two moose population homeranges, Laramie River and North Park CO from 2017 to 2019.

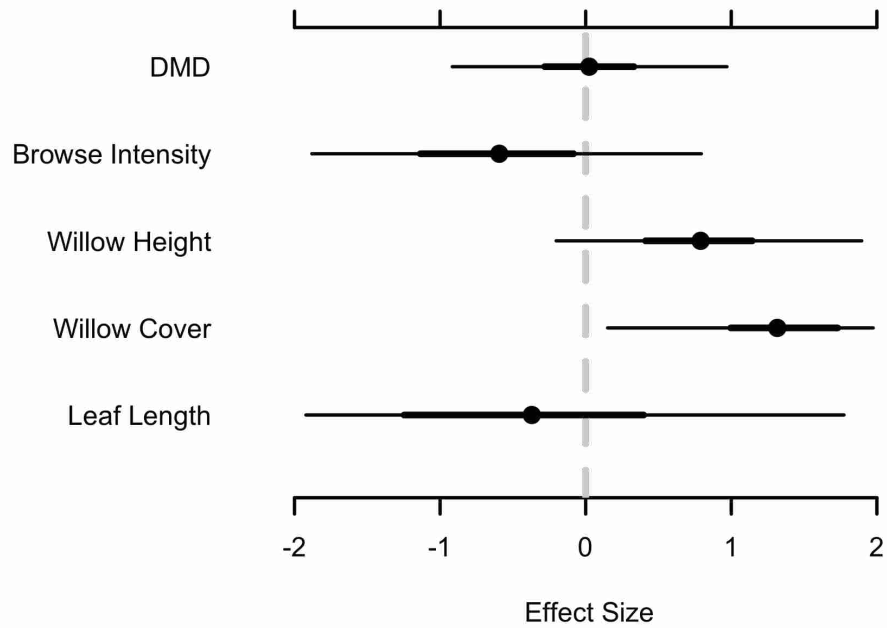


Figure 1.2. Effect of willow dry matter digestibility (DMD), leaf length, and willow cover on moose calf occupancy. Points represent the mean estimate for each covariate. Bold lines and thin lines represent 50% and 95% credible intervals, respectively.

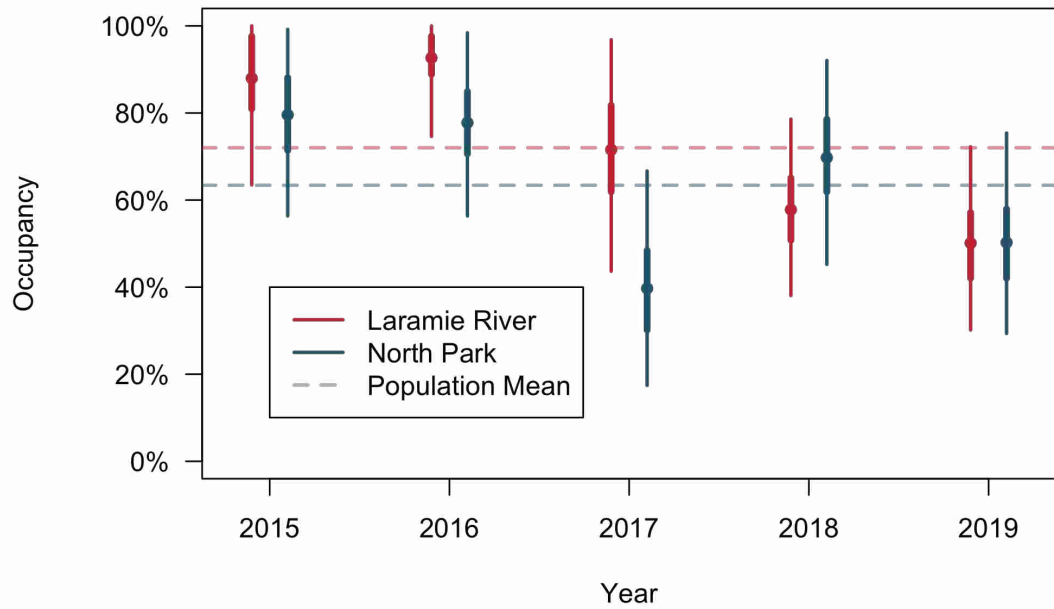


Figure 1.3. The probability of a female moose having at least one calf in North Park and Laramie River populations for years 2015 to 2019. The center point represents the mean estimate. Bold and thin vertical lines represent 50% and 95% credible intervals, respectively. Dashed horizontal lines represent the mean probability of calf occupancy for each population for all years.

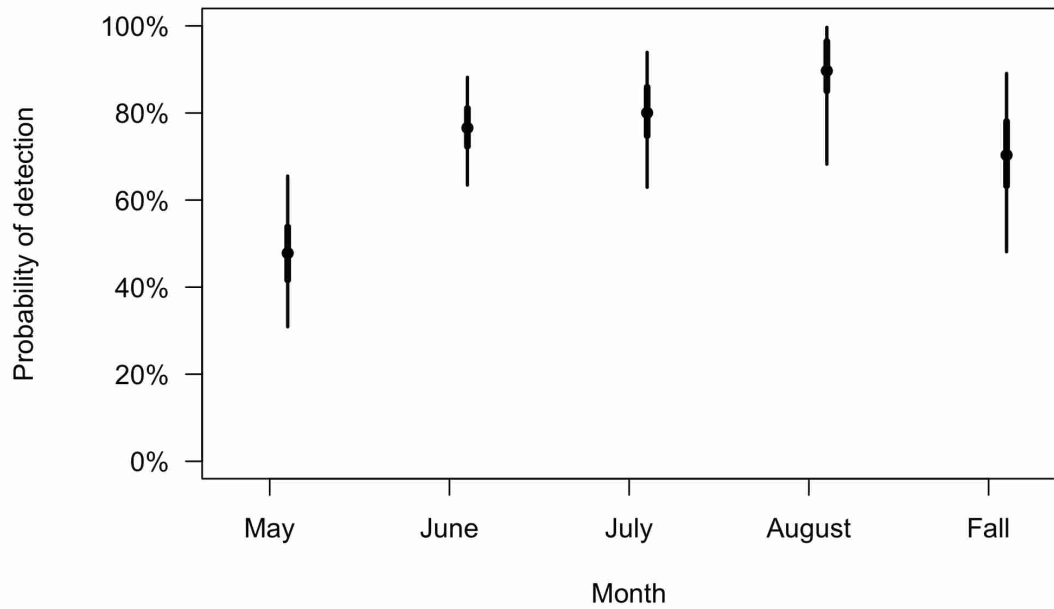


Figure 1.4. The probability of observing a calf with a uniquely identifiable female moose for each survey period: May, June, July, August, Fall. The center point represents the mean estimate. Bold and thin vertical lines represent 50% and 95% credible intervals, respectively.

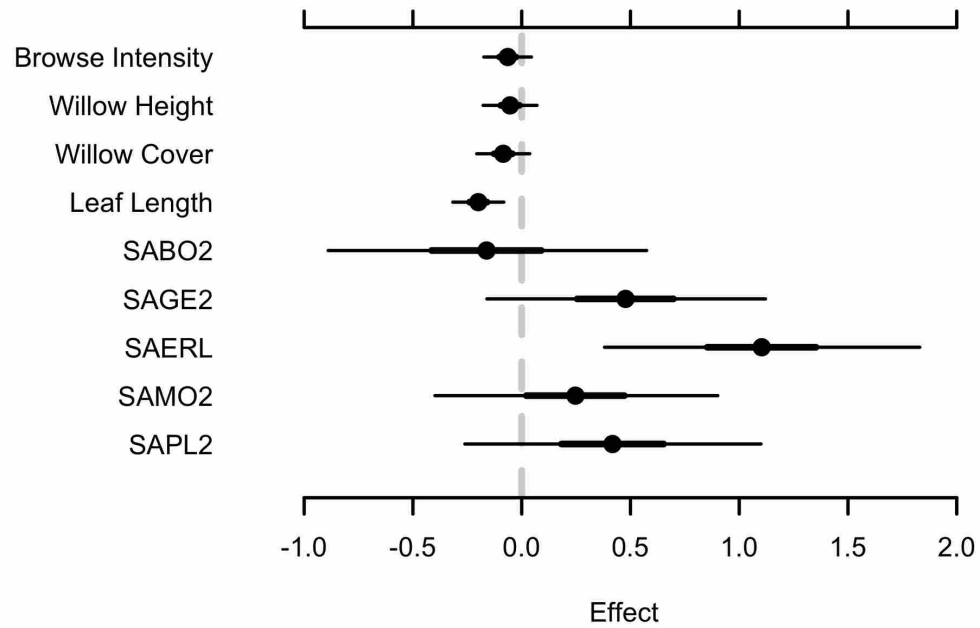


Figure 1.5. Effect of willow browse intensity, height, cover, and leaf length and species (*Salix spp.*) on percent dry matter digestibility. Willow species analyzed are Booth's willow (*S. boothii*, SABO2), Geyer willow (*S. geyeriana*, SAGE2), Strapleaf willow (*S. ligulifolia*, SAERL), Mountain willow (*S. monticola*, SAMO2), and Planeleaf willow (*S. planifolia*, SAPL2). Bold lines and thin lines represent 50% and 95% credible intervals, respectively.

TABLES

Table 1.1. Mean and standard deviation values of willow, browse intensity (proportion browsed), dry matter digestibility (DMD, %), leaf length (mm), average willow height (m), and willow cover (proportion of transect covered) for each site (Laramie River and North Park) and year (2017 to 2019).

Site	Covariate	2017		2018		2019	
		Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
Laramie River	Browse Intensity	0.32	0.15	0.40	0.12	0.48	0.13
North Park	Browse Intensity	0.35	0.15	0.34	0.13	0.47	0.15
Laramie River	DMD	46.52	3.68	37.53	5.35	41.50	6.30
North Park	DMD	42.76	5.25	39.58	4.60	40.98	5.52
Laramie River	Leaf Length	53.16	10.50	51.39	16.34	48.55	11.53
North Park	Leaf Length	50.13	11.90	47.45	11.72	48.64	12.16
Laramie River	Willow Height	2.53	0.68	2.21	0.76	2.20	0.95
North Park	Willow Height	2.99	1.19	2.48	0.78	2.67	0.88
Laramie River	Willow Cover	0.46	0.22	0.53	0.23	0.32	0.22
North Park	Willow Cover	0.47	0.25	0.51	0.21	0.39	0.17

Table 1.2. Effect of spatial willow covariates on dry percent dry matter digestibility (DMD). Willow species analyzed are Booth’s willow (*S. boothii*, SABO2), Geyer willow (*S. geyeriana*, SAGE2), Strapleaf willow (*S. ligulifolia*, SAERL), Mountain willow (*S. monticola*, SAMO2), and Planeleaf willow (*S. planifolia*, SAPL2). The 2.5% and 97.5% columns represent the lower and upper credible interval of the estimate, respectively.

	Mean	Std Dev	2.5%	97.5%
Browse Intensity	-0.06	0.06	-0.17	0.04
Willow Height	-0.05	0.06	-0.18	0.07
Willow Cover	-0.09	0.06	-0.21	0.04
Leaf Length	-0.20	0.06	-0.32	-0.08
SABO2	-0.16	0.37	-0.89	0.57
SAGE2	0.48	0.33	-0.16	1.12
SAERL	1.10	0.37	0.38	1.83
SAMO2	0.25	0.33	-0.40	0.90
SAPL2	0.42	0.35	-0.26	1.10

Table 1.3. Numeric summary of spatial willow samples by willow species for years 2017 through 2019. Willow species (*Salix spp.*) are Bebb willow (*S. bebbiana*, SABE2), Booth’s willow (*S. boothii*, SABO2), Drummond willow (*S. drummondiana*, SADR), Strapleaf willow (*S. ligulifolia*, SAERL), Geyer willow (*S. geyeriana*, SAGE2), Strapleaf willow (*S. lasiandra*, SALAC), Mountain Willow (*S. monticola*, SAMO2), and Planeleaf willow (*S. planifolia*, SAPL2)

Year	SABE2	SABO2	SADR	SAERL	SAGE2	SALAC	SAMO2	SAPL2	Total
2017	0	7	0	1	52	0	22	1	83
2018	2	8	1	7	56	4	29	10	117
2019	1	8	0	16	53	3	16	22	119
Total	3	23	1	24	161	7	67	33	319

Table 1.4. Numeric summary of observations of female moose in Colorado during the study between 2015 and 2019. Categorized by month and year, these observations were used to model detection probability (p) and calf presence (ψ). Fall observations were generally opportunistic and include all observations from September to December of the calendar year.

	Summer				Fall	Total
	May	June	July	August		
2015	19	40	19	6	1	85
2016	20	20	8	11	13	72
2017	12	18	8	12	2	52
2018	18	19	13	17	7	74
2019	2	49	8	5	5	69
Total	71	146	56	51	28	352

Table 1.5. Effect of spatial willow dry matter digestibility (DMD), browse intensity, height, cover, and leaf length on calf occupancy ψ evaluated in univariate occupancy models. The 2.5% and 97.5% columns represent the lower and upper credible interval of the estimate, respectively.

	Mean	Std Dev	2.5%	97.5%
DMD	0.02	0.48	-0.92	0.97
Browse Intensity	-0.59	0.72	-1.88	0.79
Willow Height	0.79	0.54	-0.20	1.90
Willow Cover	1.32	0.51	0.15	1.97
Leaf Length	-0.37	1.05	-1.92	1.77

CHAPTER 2: Effects of large-scale disturbance on resource selection by moose

INTRODUCTION

Understanding moose (*Alces alces*) habitat use and selection (defined below) in the context of large-scale disturbances is fundamental to conservation of the species. Increased thermal exposure as a result of large-scale disturbances has been identified as a problem for moose due to a loss of canopy cover (McGregor 1985). Because Colorado is at the southern extent of the range of moose (Timmermann and Rodgers 2017), thermal stress may be of greater importance to moose in the region and merits additional consideration. Moose occur across a broad range of habitats, but the ability for moose to adapt to large-scale changes in habitat structure remains poorly understood.

I broadly define habitat as a region in environmental space that is composed of multiple dimensions, each representing a biotic or abiotic environmental variable that can be associated with the use of a location by an animal (Beyer et al. 2010). Habitat use refers to the frequency of an animal's locations that are associated with a given habitat. I define resource selection as habitat use disproportionate to the availability at the sampled scale (Manly et al. 2007).

Moose are highly adapted to cold climates making avoidance of thermal stress an important factor in resource selection (Renecker and Hudson 1986). Furthermore, the energetic costs to moose of reducing body temperature is greater than for other large ungulates as moose pant rather than sweat when their upper critical temperature is exceeded (Schwab and Pitt 1991). (Renecker and Hudson 1986) documented moose panting at relatively low ambient temperatures in summer and winter (20°C and -2.2°C, respectively). Moose may also mitigate thermal exposure through use of the environment features by seeking cover under foliage or submersing themselves in water

(Belovsky 1978, Schwab and Pitt 1991). Additional research has found that very fine scale selection by moose may alleviate thermal stress when their critical threshold is exceeded (Olson et al. 2014, 2017)

Bark beetle epidemics resulting in large-scale tree mortality are responsible for changes in the availability of understory forage and thermal cover, two key resources for moose (McGregor 1985). In the short term, due to bark beetle epidemics, forage availability for ungulates in impacted areas of coniferous forests is expected to increase due to a more open canopy (Stone and Wolfe 1996, Williston and Haeussler 2006). Longer-term canopy cover will be reduced as impacted trees begin to lose their needles. Reduced canopy cover may result in increased thermal stress or reduced habitat availability for thermally sensitive species (McGregor 1985, Ritchie 2008).

Mountain pine beetles (*Dendroctonus ponderosae*) have been studied since the early 1900s when they were first labeled as a pest by the timber industry (McGregor 1985). Populations of mountain pine beetle are classified into four phases: endemic, incipient-epidemic, epidemic, and post-epidemic (Safranyik and Carroll 2006). In the endemic phase beetle densities are very low and are insufficient to cause tree mortality (Amman 1984). The phases are defined by increasing annual tree mortality up to the epidemic phase and a decline in mortality in the post-epidemic phase (Cole 1981). The most recent epidemic in Colorado peaked around 2008, characterized by mass tree mortality, and pine beetle populations currently persist in the endemic stage (Colorado Forest Service 2017).

A mountain pine beetle epidemic has severely affected forests across British Columbia and the western United States over the past two decades. In the United States, an estimated 5.4 Mha of trees perished between 1997 and 2010 (Meddens et al. 2012). Bark beetle populations in the United States have since declined from epidemic levels but their legacy continues to have large-scale impacts on forest structure and

wildlife communities.

Despite the breadth of knowledge on mountain pine beetles and landscape-level impacts, little is known about their effect on habitat use by wildlife. A review of ecological consequences of mountain pine beetle by Saab et al. (2014) found only a single study (Stone 1995) that provided empirical evidence of impacts for a number of species including moose. Recent work by Ivan et al. (2018) found moose selected for forest impacted 4-7 years previously but had high model uncertainty. Additional work studying elk *Cervus canadensis* has shown avoidance of beetle-impacted areas and highlighted potential tradeoffs between forage, locomotion, and thermoregulation (Lamont et al. 2019).

In this chapter I examine moose resource selection in a landscape characterized by large-scale mountain pine beetle disturbances. I evaluate key drivers of resource selection by moose in Colorado including habitat and landscape covariates. I additionally focus on how moose select for habitat that has been impacted by mountain pine beetles. Finally, because of the high prevalence of disturbed forest, I evaluate resource selection by moose for forest that has not been disturbed bark beetles.

MATERIALS AND METHODS

Study Area

I studied populations of moose in two spatially separated study areas located in northern Colorado. The first study site, North Park, was located south of the Colorado-Wyoming border 100km west of the Rocky Mountain Front and near the town of Walden. Moose were first translocated to the area during the 1970s and have occupied the area since then. The North Park study area was a wide (14-46km), high elevation valley (2400–2750m) comprised of a mixture of rolling sagebrush (*Artemisia spp.*) hills, irrigated agricultural fields, and riparian corridors dominated by willow

(*Salix spp.*). Riparian willow communities were largely comprised of Geyer willow (*S. geyeriana*), mountain willow (*S. monticola*), planeleaf willow (*S. planifolia*), and Booth's willow (*S. boothii*). The hills surrounding North Park were primarily lodgepole pine (*Pinus contorta*) with Englemann spruce (*Picea engelmannii*) intermixed.

The second study site was along the Laramie River roughly 40km northeast of the North Park study area and was separated by the Rawah Mountains (3200–3840m). Moose were translocated to Laramie River during the early 1980s and have constantly occupied the study area since then. The Laramie River Study area was comprised of a narrow valley floor (3.0–8.5km wide) and characterized by riparian willow communities along the river with similar species composition to the North Park study site. Uplands around Laramie River were characterized by rangeland co-dominated by sagebrush and a grass forb mix but occurred with less frequency in comparison to North Park. Larger hills located within the valley were dominated by aspen (*Populus tremuloides*), while slopes to the east and west are dominated by lodgepole pine and Englemann spruce.

Geographic features and climate of both study areas were similar. Elevation of riparian areas ranged from 2,400m to 2,800m. Temperatures ranged from highs in July of 26.5°C to lows of -15°C in January (USDA-NRCS 2005). North Park tended to have slightly higher maximum temperatures than Laramie River throughout the year by about 2.2°C degrees. Mean low temperatures were more similar although North Park tended to be slightly colder during the winter months. Average annual precipitation was around 40.4 cm for both sites.

Moose in both study areas were managed by CPW. Management actions included limited male and female moose hunting. Predator assemblages were also similar between study sites. Black bears (*Ursus americanus*), mountain lions (*Puma concolor*), and coyotes (*Canus latrans*) were present in both sites whereas wolves (*Canus lupus*)

and grizzly bears (*Ursus arctos*) were absent. It was believed that black bears and mountain lions infrequently preyed upon moose resulting in minimal predation pressure (Bergman et al. 2020).

Capture of Moose

Moose were captured by Colorado Parks and Wildlife (henceforth CPW) in both the North Park and Laramie River study areas as a part of a broader research initiative from 2015 to 2019. All animal capture, handling, and monitoring was conducted in accordance with approved Institutional Animal Care and Use Committee (IACUC) protocols (University of Montana IACUC file #032-17CBWB-060517 and CPW ACUC #08-2013). Between 20 December and 27 January of each winter (2015–2019), CPW captured adult (≥ 2 years old) female moose via helicopter darting. Moose were sedated using one of three different drug combinations: 1) BAM (54.6 mg of butorphanol, 18.2 mg of azaperone, and 21.8 mg of medetomidine) in combination with ketamine (200 mg), 2) carfentanil (3mg) in combination with xylazine (100mg), or 3) thiafentanil (10mg) in combination with xylazine (25mg). After handling, capture drugs were antagonized with naltrexone (100 mg, antagonist for carfentil and thiafentetil), tolazoline (500mg, antagonist for azaperone and xylazine), or atipamezole (100–150 mg, antagonist for medetomidine and xylazine). Once sedated, moose were blindfolded to minimize stress. Moose received oxygen, via nasal cannula, to minimize risks of adult and fetal hypoxia. Moose were subsequently fitted with satellite and GPS equipped VHF radio- collars (Vectronics Aerospace GmbH, Berlin, Germany model: Vertex Plus, and Advanced Telemetry Systems, Isanti, MN, USA model: G5-2D), as well as uniquely numbered eartags. Satellite GPS collars were set record locations at either 3, 4, or 8 hour intervals dependent on collar type and time of year to balance the resolution of data gathered with the duration of collection.

Following the first year of capture, some previously captured moose were recap-

tured, but only on a random basis. Between 2014 and 2020, 108 (North park = 55, Laramie River = 48) unique female moose were captured and fitted with GPS collars. Unique combinations of individual moose and study year provided 339 GPS monitoring years.

Data sources

I used vegetation classifications of habitat in Colorado (Simpson et al. 2013) and collapsed all habitats dominated by willows into a single willow classification. I then created a raster layer with the distance from willow habitat for the entirety of both study areas at a 30m resolution. I additionally collapsed all habitats dominated by trees to a single habitat layer termed forest. I used elevation data from the USGS National Elevation Dataset (USGS 2005) and derived slope and aspect from the elevation later using the `raster` R package (Hijmans 2019). Beetle kill disturbance, identified by tree canopy mortality, was surveyed yearly by the USFS Forest Health Monitoring program between 1994 and 2016. These data were adapted by CPW and converted into a single layer reflecting the year of initial impact (Ivan et al. 2018).

Analytical methods

I used a Bayesian hierarchical multi-scale model to evaluate resource selection for each population at two scales. In this model, I evaluated each scale independently using a hierarchical model with a hyperprior for the metapopulation consisting of both North Park and Laramie River. I then created a hyperprior for use of habitat classifications (e.g., beetle kill, undisturbed forest) for each population drawn from the distribution of the metapopulation. Finally, for each population, I created individual priors for each covariate, with the effect of habitat type drawn from a normal distribution. This structure enables sharing of information between covariates observations and populations while allowing for estimation of individual covariates. I derived conditional selection (i.e., covariate estimates based on selection occurring at both spatial scales)

for both populations of moose by taking the product of individual estimates for each scale.

To generate used and available data for the home range scale, I created a 95% kernel density estimate of population home range using the `sp` R package. Within each population home range, I randomly selected one available point for each recorded GPS location. To represent fine-scale resource selection I used a step selection process to generate used and available data. First, I created 8-hour steps from recorded locations using a minimum of three consecutive steps and a tolerance of 90 minutes (i.e., sequential locations recorded within 8 hours \pm minutes of the last recorded location) for each individual moose using the (`amt`) R package (Signer et al. 2019). I then generated one available location for each step based on a random step length and turning angle drawn from the distribution of observed values. For each of the used and available locations, I extracted values for distance to willow, elevation, slope, aspect, year of beetle kill (if present), and forest. I then used aspect to create a measure of northness by taking the cosine of aspect in radians. To derive undisturbed forest (i.e., forest not impacted by pine beetles), I identified points classified as forest habitat that did not have a year of initial beetle impact.

I limited evaluation of slope to values $\geq 5^\circ$ to remove the effect of small, potentially population wide, geographic slopes. For aspect, as my primary interest is related to thermal exposure, I limited evaluation of the covariate to locations used during daytime hours as determined by GPS location and sunrise and sunset times. To maintain consistency with available locations, I assigned available points a date and time from either the used step location or in the same sequence as used points at the home range scale. Last, I centered and scaled ($\mu = 0$, $sd = 1$) all continuous covariate values prior to analysis.

RESULTS

During the study, I recorded 453,194 (North Park = 233,850, Laramie River = 219,344) locations of moose using GPS collars. Using 8-hour sequential steps, the number of points was reduced to 202,812 (North Park = 104,618, Laramie River = 98,194) used locations. To ensure equal model weight of each scale and population, I randomly selected used and available observations from each population and scale equal to the population and scale with the fewest number of observations. I ran the model for 1,000 iterations with 500 iterations of burn-in on three chains at which all parameters had reached convergence ($\hat{r} < 1.01$).

For all covariates, the effect on resource selection was stronger at the home range scale than the step selection scale (Figure 2.1, Table 2.1). Distance to willow habitat had the strongest effect on resource selection by moose in both the Laramie River and North Park populations. The effect of distance to willow was stronger for North Park than Laramie River at the home range scale and weaker at the step selection scale.

The effect of elevation was mixed for population and scale. Both populations avoided higher elevation at the home range scale, and this was stronger for the Laramie River population. At the step selection scale, moose in Laramie River showed a small negative selection for elevation, while moose in North Park showed a slight positive selection for higher elevation locations.

Northness had a small, consistently negative, influence on selection for both populations and spatial scales. Moose in North Park displayed the strongest effect at the home range scale of either population. Selection for northness by moose in Laramie River was similar between both spatial scales and was in between the two scale estimates for North Park.

Selection for forest habitat impacted by pine beetles showed mixed effects based

on population and spatial scale. Both populations showed positive selection for beetle disturbed forest at the home range scale with a much stronger effect for North Park. At the step selection scale, North Park showed an avoidance of areas disturbed by pine beetles while there was functionally no effect for Laramie River.

Undisturbed forest habitat was positively selected for by both populations at both spatial scales. Positive selection was strongest at the home range scale in Laramie River. The smallest effect was for Laramie River at the step selection scale. Estimates for North Park were between those of the Laramie River population with higher selection at the home range scale and weaker selection at the step selection scale, respectively.

Selection conditional on both spatial scales showed very similar estimates for the two populations of moose with high similarity in credible intervals (Figure 2.2, Table 2.2). The size of the conditional effect represents a measure of the relative strength of an effect and does not indicate the direction of the effect on selection. The effect of beetle kill was excluded from the conditional selection analysis because of the lack of a consistent impact on selection at the two spatial scales. The strongest conditional effect on selection was distance to willow, followed by slope and undisturbed forest. Northness had the smallest consistent effect for both populations. The effect of elevation was variable between populations due to differing and inconsistent directions of selection at the home range and spatial scales.

DISCUSSION

The fact that selection was stronger at the home range scale than the step selection scale across all covariates aligns with literature demonstrating that the strength of selection decreases with increasingly fine measures of availability (Beyer et al. 2010). The strongest predictive factor for both populations of moose was proximity to willow (Figure 2.1, Table 2.1). This result is consistent with the high importance of willow

for moose in Colorado (Dungan et al. 2005, Chapter 1).

The estimates of conditional selection are of particular interest as they provide a measure of covariate importance that is less dependent on the scale at which availability is determined. This allows for more meaningful comparisons of selection between populations. For distance to willow, although effect estimates were variable between population and scale, conditional selection was very similar between the two populations. This suggests that the two scales at which availability of resources was surveyed adequately accounts for differences in resource availability at different scales for the two populations surveyed.

Avoidance of elevation (i.e., selection for lower elevations) by moose is consistent with established literature. During winter months in mountainous regions, moose tend to select for lower elevations likely due to lower snow depths (Poole and Stuart-Smith 2006). For moose in Colorado, selection for elevation is likely influenced by availability of willow forage, which is most common in lower elevation riparian corridors. Strong selection against high elevation locations at the home range scale suggest that, within population home ranges, moose are much more likely to use low elevation areas. While selection was mixed at the step selection scale both estimates were very small and close to zero (μ range: -0.05-0.03) suggesting minimal selection is occurring at the fine scale.

The avoidance of northness (i.e., selection for South slopes) challenges the notion that moose at the southern extent of their range are constantly avoiding high exposure areas to limit thermal stress. This is consistent with moose behavior at more northern latitudes (e.g., Montana, British Columbia) at which moose demonstrate selection for southern slopes in winter months (Matchett 1985, Langley 1993, Poole and Stuart-Smith 2006). Although the relative strength of the northness effect is weak (Figure 2.1, Table 2.1), these results suggest that moose are not showing different selection

behavior for north aspects in southern populations. The fact that estimates of the effect of northness are similar for both populations when conditional selection is evaluated (Figure 2.2, Table 2.2) suggests that the scales evaluated are adequately capturing differences in resource availability across scales of both populations.

I did not observe avoidance of thermal exposure, but it is possible that moose were avoiding thermal exposure either only a small portion of the time or at a finer scale than I was able to evaluate. Future studies should consider fine-scale measurement or modeling of temperature to evaluate resource selection only during times the thermal threshold of moose was exceeded. That said, moose may still be using landscapes at such a fine scale (e.g., clearing litter from a bed site, Olson et al. 2017) that GPS locations and habitat classifications are unable to capture differences in resources.

To this point, the covariates largely serve to characterize typical resource selection by moose. In general, these results align closely with behavior of moose in similar habitats been documented in the literature (Dorn 1970, Stevens 1970). Establishment of this baseline enables me to further evaluate additional covariates of interest and test for their effects.

Simultaneously evaluating selection by moose for disturbed and undisturbed forest habitat provides a much more complete evaluation of the impacts of large-scale disturbances. Selection at the home range scale by both populations of moose for habitat impacted by mountain pine beetles showed varying effects (Figure 2.1, Table 2.1). The differing sign of the effect and substantially larger effect size for the North Park population is likely a product of resource availability. The North Park population home range contains a much higher proportion of sagebrush uplands thereby increasing the strength of selection for forest habitat. The Laramie River population has much higher proportional availability of forest habitat and therefore shows a smaller selection effect.

In both study areas, most coniferous forest habitat has been impacted by mountain pine beetles at some point in the last 20 years. The effect of selection for habitat disturbed by mountain pine beetles exhibited by the Laramie River population of moose was very small at the home range scale and did not occur at the more fine scale. Although moose in North Park showed moderately strong selection at the home range scale, the effect at the fine scale had the opposite sign (i.e., positive effect at the home range scale and negative effect at the step selection scale). This suggests that, although moose in North Park were documented using more disturbed habitat than is available at the population scale, the combined effect is likely negligible. Rather than indicating no selection, this result may indicate a mixture of selection pressures. Moose may be concurrently selecting for increased forage (McGregor 1985) and avoiding increased thermal exposure (Renecker and Hudson 1986) resulting in little overall effect. The high availability of willow, the preferred forage of moose in this region (Dungan et al. 2005), also likely reduces the value of increased ground forage. If only one of these factors was influencing selection, moose would be much more likely to display selection or avoidance of beetle-impacted forests.

Selection by moose for undisturbed forest (i.e., forest not impacted by pine beetles) had a strong effect when compared to beetle-disturbed forest. Consistency in the sign of the effect between all combinations of population provides evidence for uniformity of the effect between populations. Evaluation of conditional selection for undisturbed forest, which showed similar effect sizes for both populations, further supports this conclusion. A disproportionately small amount of undisturbed habitat was available to both populations, resulting in wider credible intervals for the estimate. Overall, the size of the effect of undisturbed forest was similar to slope and second in size only to distance to willow.

The results presented here show limited selection or avoidance of disturbed habitat

but highlight the importance of access to undisturbed habitat. Notably, this analysis does not rule out the possibility that beetle epidemics reduce habitat suitability for moose. Forest disturbance was so widespread in both study areas that moose were functionally unable to avoid use of disturbed habitat. This suggests that evaluation of undisturbed habitat may provide a better measure of habitat quality for moose than measuring disturbance directly. Looking forward, management and conservation efforts may benefit from focusing on availability of high quality or undisturbed habitat patches when faced with large-scale disturbances.

FIGURES

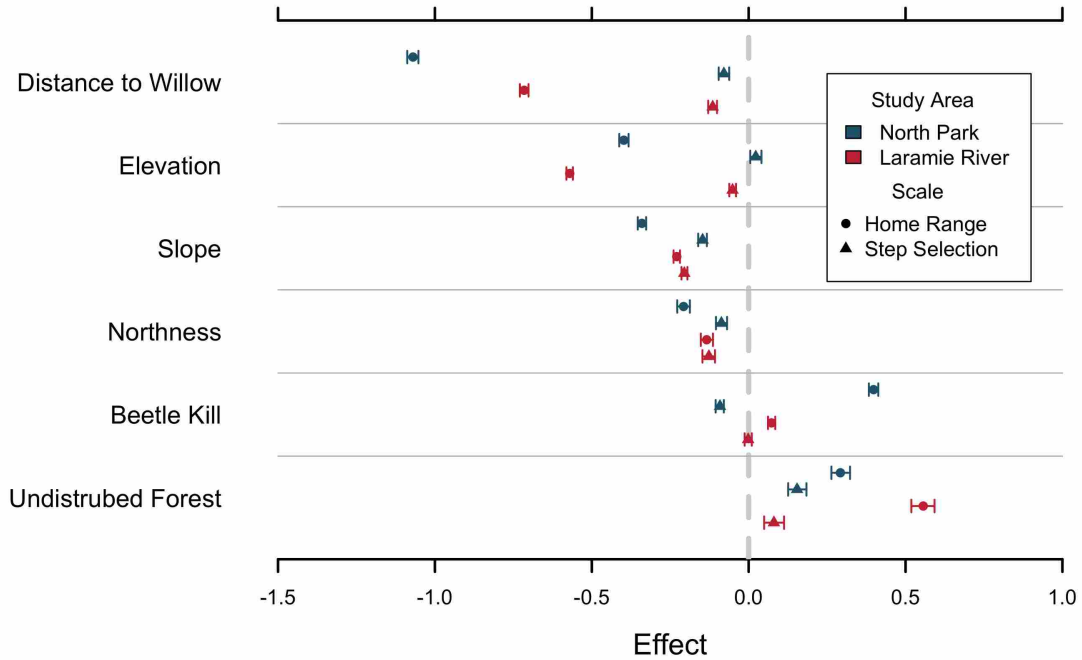


Figure 2.1. The effect of distance to willow, elevation, slope, northness, habitat impacted by beetles (beetle kill), and habitat undisturbed by beetles (undisturbed forest) on resource selection by two spatially segregated populations of moose at two spatial scales from 2015 to 2020. Whiskers represent 95% credible intervals.

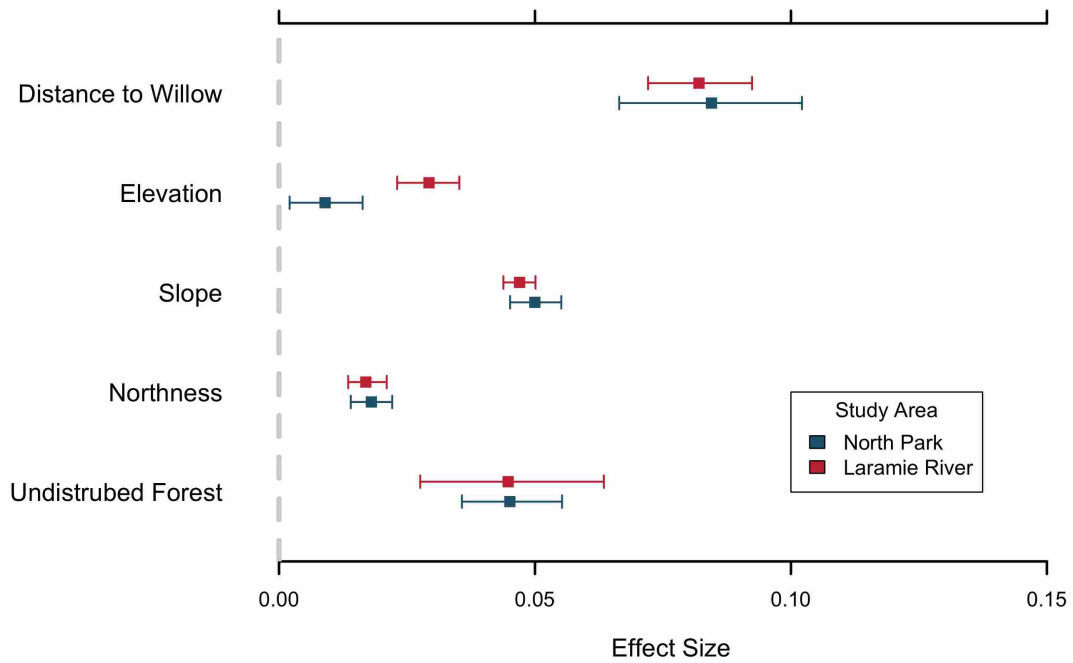


Figure 2.2. The effect of of distance to willow, elevation, slope, northness, habitat impacted by beetles (beetle kill), and habitat undisturbed by beetles (undisturbed forest) on resource selection by two spatially segregated populations of moose conditional on selection at both the home range and step selection spatial scales. Data are from 2015 to 2020. Whiskers represent 95% credible intervals.

TABLES

Table 2.1. Numeric summary of the effect of of distance to willow, elevation, slope, northness, habitat impacted by beetles (beetle kill), and habitat undisturbed by beetles (undisturbed forest) on selection by two spatially segregated populations of moose at two spatial scales from 2015 to 2020.

Covariate	Scale	Population	Mean	Lower CI	Upper CI
Distance to willow	HR	North Park	-1.07	-1.09	-1.05
Distance to willow	SSF	North Park	-0.08	-0.10	-0.06
Distance to willow	HR	Laramie River	-0.72	-0.73	-0.70
Distance to willow	SSF	Laramie River	-0.11	-0.13	-0.10
Elevation	HR	North Park	-0.40	-0.41	-0.38
Elevation	SSF	North Park	0.02	0.01	0.04
Elevation	HR	Laramie River	-0.57	-0.58	-0.56
Elevation	SSF	Laramie River	-0.05	-0.06	-0.04
Northness	HR	North Park	-0.21	-0.23	-0.19
Northness	SSF	North Park	-0.09	-0.10	-0.07
Northness	HR	Laramie River	-0.13	-0.15	-0.11
Northness	SSF	Laramie River	-0.13	-0.15	-0.11
Slope	HR	North Park	-0.34	-0.35	-0.33
Slope	SSF	North Park	-0.15	-0.16	-0.13
Slope	HR	Laramie River	-0.23	-0.24	-0.22
Slope	SSF	Laramie River	-0.21	-0.21	-0.20
Beetle Impact	HR	North Park	0.40	0.38	0.41
Beetle Impact	SSF	North Park	-0.09	-0.11	-0.08
Beetle Impact	HR	Laramie River	0.07	0.06	0.08
Beetle Impact	SSF	Laramie River	0.00	-0.01	0.01
Undisturbed Forest	HR	North Park	0.29	0.26	0.32
Undisturbed Forest	SSF	North Park	0.15	0.13	0.18
Undisturbed Forest	HR	Laramie River	0.56	0.52	0.59
Undisturbed Forest	SSF	Laramie River	0.08	0.05	0.11

Table 2.2. Numeric summary of effect of of distance to willow, elevation, slope, northness, habitat impacted by beetles (beetle kill), and habitat undisturbed by beetles (undisturbed forest) on resource selection by two spatially segregated populations of moose conditional on selection at both the home range and step selection spatial scales. Data are from 2015 to 2020.

Covariate	Population	Mean	Lower CI	Upper CI
Distance to willow	North Park	0.08	0.07	0.10
Distance to willow	Laramie River	0.08	0.07	0.09
Elevation	North Park	0.01	0.00	0.02
Elevation	Laramie River	0.03	0.02	0.04
Northness	North Park	0.02	0.01	0.02
Northness	Laramie River	0.02	0.01	0.02
Slope	North Park	0.05	0.05	0.06
Slope	Laramie River	0.05	0.04	0.05
Beetle Impact	North Park	0.04	0.03	0.04
Beetle Impact	Laramie River	0.00	0.00	0.00
Undisturbed Forest	North Park	0.05	0.04	0.06
Undisturbed Forest	Laramie River	0.04	0.03	0.06

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