AN ABSTRACT OF THE THESIS OF

Sharon E. Smythe for the degree of Master of Science in Wildlife Science presented on February 25, 2015.

Title: Evaluating Tools Used to Estimate and Manage Browse Available to Wintering Moose on the Copper River Delta, Alaska

Abstract approved:

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Ungulates comprise some of the most well researched and intensely managed wildlife populations on earth. As such, they are recognized as ideal study subjects for developing and modifying management tools or theories (Danell et al. 1994, Shipley 2010). An introduced moose (*Alces alces gigas*) population on the Copper River Delta (CRD; Delta) of south-central Alaska functions as a valuable resource for the residents of Cordova and an isolated research population on which to test managerial techniques. Since its introduction (1949–1958), the founding population of 23 moose has grown to over 830 in 2013, divided into two sub-populations. However, in 1964, the largest earthquake recorded in U.S. history (9.2 magnitude) uplifted the Delta by 1.0–4.0 m, initiating delta-wide changes in hydrology, vegetation distributions, and successional processes. The proportion of stands dominated by woody species, especially alder (*Alnus viridis sinuata*) and spruce (*Picea sitchensis*), increased visibly. Furthermore, previous research (1987–89) observed that 90% of the moose on the western region of the Delta wintered within 9–24% of the total land area, possibly restricting their available winter browse. Because moose diets on the CRD are dominated by willows (*Salix* spp.), managers were concerned that the combined effects of a restricted winter range and earthquake-initiated vegetation changes would negatively influence the population. Managers have responded to this concern by 1) supporting work to estimate the nutritional carrying capacity (NCC; i.e., the forage available to a population within a specified area and time) of the Delta, and 2) by exploring the feasibility of mechanical treatment as a means of stimulating browse production for the moose. Thus, the objectives of this thesis were to 1) explore the factors influencing NCC for moose on the west CRD while combining updated digital and field-collected data to estimate NCC, and 2) to assess the effects of mechanical treatment on the production of moose browse across stand types and over time.

We collected field data and evaluated differences in the past (1988–89) and present (2012–13) biomass-predicting regression equations for two willow species (Barclay's and Hooker's willow, *Salix barclayi* and *hookeriana*) used within NCC models to determine 1) whether past and present models of Barclay's willow predicted similarly and 2) whether Hooker's and Barclay's willow differed in average available biomass, nutritional quality, and utilization by moose. The linear coefficients for the current (2013) Barclay's willow, Hooker's willow, and combined equations were 2.2*x*, 1.6*x*, and 1.9*x* larger, respectively, than that derived from the 1988 model for Barclay's willow (which possibly included Hooker's willow data). Thus, willows on the CRD may now be supporting more biomass per stem than predicted by prior models. Hooker's and Barclay's willow did not differ in mean available biomass, nutritional values, or utilization rates. These results suggest a need to evaluate the accuracy of older allometric regressions, though separate identification of the visually-similar Barclay's and Hooker's willow may be unnecessary for future biomass-estimating efforts on the CRD.

To further explore the factors influencing the biomass available to moose and their associated NCC estimates, we compared 5 NCC model types across 4 winter ranges and under 3 winter-severity scenarios for the western CRD moose population. We conducted a sensitivity analysis (*Sx*) of our final model to determine the relative influence of factors affecting NCC estimates. Lastly, we compared current (2012–13) browse available biomass, stand type areas (2011), and NCC results to those obtained by past research (1987–89, MacCracken et al. 1997 and 1959/1986, Stephenson et al. 2006) to determine changes over time, while evaluating the effects of models incorporating satellite-based estimates of stand areas and forage nutritional values on NCC estimates. Because recent aerial survey observations suggest expansion of the moose winter range, our final model estimated NCC between 2,198–3,471 moose depending on winter severity within a winter range encompassing the entire west Delta. These results suggest the current western moose population (approximately 600 in 2013) is below NCC. Model components with the largest and smallest *Sx* were snow depth and tannin- and lignin-caused reductions in forage nutritional quality, respectively. Changes from 1987–2013 in available biomass of forage species ranged from -66–493%, while changes from 1959–2011 in stand type areas ranged from -60–661%. Overall, NCC estimates only declined by 2% from 1959–2013, however inclusion of forage nutritional quality in models reduced NCC estimates by 60%.

Lastly, we assessed the use of hydraulic-axing (i.e., hydro-axing) as tool for increasing the available willow biomass. We evaluated treatment effects on biomass, height, nutritional quality (crude protein, lignin, and tannin levels), utilization, and snow burial of the winter forage species within 3 winter-severity scenarios. Sites were treated in 4 winters (1990–92, 2008, 2010, and 2012) within 5 stand types in 20 locations varying from 0.86–63.40 ha in size. Results indicate few significant differences relative to controls, though treatment significantly increased the ratio of willow to alder. Our results may be limited by sample sizes (*n* = 1–9 per stand type or treatment year) as visual comparison suggests treatment via hydraulic-axing may be an effective method for increasing willow biomass without influencing nutritional quality. However, willows 20–23 years post-treatment are still significantly shorter than untreated willows (*P* = 0.03). Thus, treatment may result in decreased forage available to moose in severe winters.

Management concerns regarding continued earthquake-initiated changes in vegetation distributions and successional processes prompted our investigation. However, studies on the vegetation dynamics of the CRD suggest the vegetation distribution of the Delta may be relatively stable (Boggs 2000, Thilenius 2008). If so, our current estimates of NCC suggest the west Delta can support a larger moose population than is currently present. Hydro-axing may not be necessary to ensure the future of the moose population, though it could be used to counter increases in alder (*Alnus viridis sinuata*) which are likely within certain successional sequences. However, together with earthquakes, the processes determining the future forage available on the CRD include complex, interactive forces such as glaciers, the Copper River, oceanic tides, and zoological- and human-caused influences. These forces and their effects on the vegetation create a dynamic ecosystem for the moose population, are difficult to predict, and may be further complicated by climate change. As a result, application of any managerial tool may be temporary and often difficult. However, this guarantees a constant need for further revision and redevelopment of the tools used to manage the moose population, ensuring that the moose of the CRD will remain an important resource for researching and refining ungulate management worldwide.

Evaluating Tools Used to Estimate and Manage Browse Available to Wintering Moose on the Copper River Delta, Alaska

By

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented February 25, 2015
Commencement June 2015

ACKNOWLEDGEMENTS

I would like to sincerely thank everyone who assisted, supported, or contributed to this thesis at any stage of its development. Many people require thanks by name, including first my advisor, Dr. Dana Sanchez, for her tireless, thorough, and devoted work on this project and my personal development as a scientist. This thesis, significant portions of my education, and hours of story-telling simply would not have occurred without her. My committee members Drs. Clinton Epps, David Hibbs, and Ricardo Mata-Gonzalez generously contributed their time, encouraged rigorous analyses, and greatly improved my thoughts with their wisdom, all while modeling scientific wonder and excellent senses of humor. I would also like to thank Dr. John Van Sickle for his significant statistical assistance, and Dr. Andy Jones for speaking R code. Special thanks goes to the members of the Cordova Ranger Station in the U.S. Forest Service and Alaska Department of Fish and Game for their incredible assistance in funding this project, coordinating field assistants, and donating personal time to slog through the mud and mosquitos: Tim Joyce, Milo Burcham, Erin Cooper, Jason Fode, and all seasonal employees in the Forest Service, along with Charlotte Westing and David Crawley in the Alaska Department of Fish and Game. Gordon Reeves was instrumental in receiving and coordinating funding for this project. Thank you as well to Mr. Lance Westing's 4th, 5th, and 7th grade classes who assisted with sample processing, as well as several Oregon State University undergraduate volunteers. Thank you to Aaron Moffett and other members of the Oregon State University IT staff who responded so promptly and capably to all computer problems. Thanks also to authors James MacCracken and Tom Stephenson for answering my many questions and going out of their way to access files long buried. To all my fellow Fish and Wildlife grad students who have ever offered sympathy or humor when needed, thank you, but especially Jenna Curtis, Kevyn Groot, Tyler Hallman, and Allyson Jackson for their ever-ready ears to my complaints, thoughtful answers to my questions, and solid friendship through it all. And never least, my family. Thank you to my parents for their lifelong example and support, and my brothers for their love and laughter. You all keep me sane.

CONTRIBUTION OF AUTHORS

Dr. Dana Sanchez contributed on every level of this project, from the acquisition and maintenance of funding through study design, data collection, and data analysis to the final stages of writing and review. Dr. Ricardo Mata-Gonzalez assisted extensively with the analysis and writing of Chapters 2 and 4. Dr. David Hibbs offered his wisdom in research design, interpretation of the results in Chapter 3, and especially his understanding of the landscape dynamics influencing the Copper River Delta vegetation described in the Appendix. Dr. Clinton Epps aided greatly with the analyses and comparisons in Chapter 3.

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CHAPTER 1: INTRODUCTION TO THE THESIS

The management of ungulate populations dates back thousands of years, was developed within a variety of cultures and civilizations, and remains one of the most economically, socially, and politically significant tasks of current wildlife managers (Bailey 1983, Leopold 1987, Nowak 1999, Gordon et al. 2004, Festa-Bianchet 2007, Valdez 2013). Considering this history and managers' well-developed understanding of ungulate ecology, it follows that ungulates provide ideal study subjects for developing and modifying management tools (Hudson et al. 1989, Schmitz et al. 2000, Gaillard et al. 2003, Festa-Bianchet 2007).

An introduced moose (*Alces alces gigas*) population on the Copper River Delta (CRD; Delta) of south-central Alaska has developed into a valued resource for the residents of Cordova, Alaska and an advantageous research population on which to test managerial techniques. Though indigenous and distributed across much of Alaska, moose likely were unable to disperse naturally to the CRD due to topographical barriers (MacCracken et al. 1997). Thus, from 1949–1958, 23 moose were released on the Delta to establish a harvestable population, and as of 2013 the population had reached an estimated 830 individuals (C. Westing, 2014, unpublished data). Hunting began in 1960 (25 bulls) and mean harvest has consisted of about 70 moose per year, 26% of which are cows (MacCracken et al. 1997; C. Westing, 2014, personal communication). However, in 1964 the Great Alaskan Earthquake, the largest earthquake recorded in American history (9.2 magnitude), uplifted the Delta by 1.0–4.0 m, initiating changes in land area, hydrology, and soil chemistry (Grantz et al. 1964, Ferrians 1966, Plafker 1969, Stover 1993, Kesti et al. 2007, Thilenius 2008). The resulting effects on the CRD vegetation included increased local geographic distributions (hereafter, distributions) of woody species and an acceleration of succession in some stand types to stages with lower willow (*Salix* spp.) production (Thilenius 1990;2008). Furthermore, as of 1987–89, most (90%) moose on the western region of the Delta wintered within just 9–24% of the total land area, potentially restricting the browse available to the western population during winter (MacCracken et al. 1997). Because moose diets on the CRD are dominated by willows, managers were concerned that the combined effects earthquake-initiated vegetation changes and a restricted winter range could hinder population performance and persistence (MacCracken et al. 1997, Stephenson et al. 2006). Managers have responded to this perceived concern in two ways: 1) by supporting work to estimate the nutritional carrying capacity for moose and 2) by exploring the feasibility of mechanical treatment as a means of stimulating browse production for moose. The objectives of my thesis were to 1) explore the factors influencing nutritional carrying capacity for moose on the west CRD while combining updated remote sensing data and field-collected data to estimate nutritional carrying capacity, and 2) to assess the effects of mechanical treatment on production of moose browse across stand types and over time.

Nutritional carrying capacity (NCC, i.e., ecological carrying capacity) is the largest, stable population of a specified organism in a defined region and time potentially supported by the total available nutrition (Caughley 1979). Nutritional carrying capacity functions as a baseline beyond which further environmental, biological, or managerial factors can be considered in order to understand their potential influences on the population. For ungulates, NCC depends on the interaction between the abundance, availability, nutrition, physiology, and ecology of the forage species and the species-specific physiology and browsing behavior of the ungulate (Caughley 1979, Hobbs and Swift 1985, Jefferies et al. 1994, Hobbs et al. 2003, Pastor and Danell 2003, Windels and Hewitt 2011). Within temperate and arctic zones, ungulate ecology mirrors the cyclical, seasonal changes in browse species availability and nutritional quality. During the winter, dormant browse species decrease in nutritional quality while snow burial limits accessibility, increasing the necessary digestion and foraging time for comparable browse in the summer (Schwartz and Renecker 1997). Because of this, winter was historically considered the limiting period for ungulates and the season in which to calculate NCC (Caughley 1979, Hobbs et al. 1982, MacCracken et al. 1997).

Models of NCC vary in their components and structure, but all require accurate estimates of forage biomass available to the specific ungulate population. In North America, biomass of preferred forage species is commonly estimated with allometric equations, which relate biomass production to plant dimensions, and which should allow for efficient long-term vegetation monitoring (Baskerville 1972, Hytönen et al. 1987, Catchpole and Wheeler 1992). On the CRD, MacCracken and Van Ballenberghe (1993) identified 7 winter browse species and developed basal diameter-mass regression equations with data collected from 1988–89. However, they never developed regression equations for one species, Hooker's willow (*Salix hookeriana*), possibly due to its misidentification as Barclay's willow (*S. barclayi*; J. MacCracken, 2013, personal communication). Furthermore, potential ecosystem-induced changes in available biomass initiated concern about the accuracy of older allometric equations for biomass estimation (Chapin et al. 1995, Klein et al. 2005, Osterkamp 2007). Because of these concerns, equations using recent (2013) samples of Hooker's and Barclay's willow were developed and regression coefficients compared to samples gathered 24–25 years ago. This allowed exploration of two concepts: 1) the potential changes in willow available biomass per stem, and 2) that prior regressions of Barclay's willow were in fact calculated on a combination of Barclay's and Hooker's willow samples. Thus, our objectives in Chapter 2 were to 1) compare regression coefficients and estimates of available biomass produced by MacCracken and Van Ballenberghe's (1993) models for Barclay's willow to those we calculated from recent samples of Barclay's and Hooker's willow to evaluate both concepts, and 2) determine whether average available biomass (g/stem, kg/ha), nutritional quality (crude protein, lignin, tannin, and ash), and utilization (%) by moose differed between the two willow species. These results could have significant implications for regression equation use and NCC estimates.

Prior to this study, winter NCC had been calculated twice on the west CRD. To provide a post-earthquake estimate of NCC, MacCracken et al. (1997) calculated the number of moose supported by the available biomass on his observed winter range under 3 winter scenarios (380–1424 moose). Because of hypothesized decreases in NCC for moose due to earthquake-related vegetation changes and decreased glacial effects, Stephenson et al. (2006) estimated the biomass available to moose within the glacial outwash plains over a 243-year period (1959-2202) to project past and future changes in NCC. He estimated a 31–53% decline in NCC over time, varying with winter severity. However, despite recently experiencing one of the most severe winters recorded on the CRD (2011), the 2013 west CRD moose population (~600) was higher than all severe winter NCC estimates and the management goal of 400-500 moose (C. Westing, 2014, unpublished data). Furthermore, a stable growth rate, little anecdotal evidence of over-use of forage (shrub "brooming"), and high twinning rates (58-65%) indicated that the population was still growing and perhaps under NCC (C. Westing & T. Joyce, 2013, personal communication). This suggests that either 1) earthquake-initiated vegetation changes have not negatively influenced the moose population as expected, 2) moose are accessing more forage on the west CRD, possibly by using a greater proportion of the total area, 3) previous calculations of NCC were conservative, or 4) some combination of these.

Landscape-level evaluations of earthquake-initiated changes in species distributions and succession suggest vegetation composition may now be relatively stable (DeVelice et al. 2001, Thilenius 2008). At present, the post-earthquake availability of shrub biomass seems to have increased on the west Delta relative to that observed before the disturbance, increasing the forage available to the moose (Thilenius 1990, Boggs 2000, Thilenius 2008). However, future changes in vegetation will likely be determined by continued stand aging, successional shifts to climax species, and land form or channel changes due to glacial, river, and tidal effects. These processes are complex, opposing, and difficult to predict (Boggs 2000, Thilenius 2008). Secondly, recent winter aerial surveys suggest the CRD moose population might be expanding beyond the limited winter range previously observed (MacCracken et al. 1997) into areas encompassing most of the west Delta (C. Westing, 2014, unpublished data). If so, this could potentially improve access of the moose population to winter forage. Furthermore, annual mean temperatures across Alaska have risen by 1.7°C since 1949 (ACRC 2014), and our comparisons of models predicting past (1988-89) and current (2013) available willow biomass suggest that willows might now be supporting between 1.9-2.2*x* more biomass per stem. Finally, previous NCC estimates utilized stand area estimates delineated with aerial photography maps, and were calculated with models that did not consider browse nutritional quality. Stand area delineation via aerial maps is subject to lower precision and resolution, and Windels and Hewitt (2011) described significant reductions in NCC due to plant secondary compounds (i.e., tannins). Therefore, we utilized a Satellite Pour l'Observation de la Terre (SPOT version 5 [SPOT5], 2011, Red Castle Resources, Inc.) satellite map of the CRD vegetation to improve the resolution of stand areas estimates (Willhauck et al. 2000, Xie et al. 2008), and included species-specific estimates of nutritional quality (gross energy, tannin, lignin, crude protein, and neutral detergent fiber levels) in our NCC models. Thus, our objectives in chapter 3 were to: 1) estimate utilization of winter browse by moose on the CRD to evaluate anecdotal evidence of minimal browse utilization (< 25%; Singer and Zeigenfuss 2002, Dungan et al. 2010), 2) develop models to estimate NCC with current samples of forage biomass and nutritional estimates while evaluating the effects of model type, winter severity, and winter range extent, 3) perform sensitivity analyses to determine the relative influence of factors within the final model, 4) compare past estimates (MacCracken et al. 1997 & Stephenson et al. 2006) with similarly-configured recalculations to evaluate potential changes in species available biomass, stand areas, and NCC estimates over time, along with potential effects of including browse nutritional quality and satellite-based estimates of stand areas in NCC models. Our results could have significant implications for the management goals for the western CRD moose population and structure of NCC models elsewhere.

To address concerns about potential earthquake-initiated decreases in preferred moose browse, managers (Cordova Ranger District, United States Forest Service) initiated experimental treatment of plots within browse-producing stand types. Mechanical manipulation of forage is a common strategy in the management of ungulate habitat in North America. Because many deer species preferentially browse early-successional forage, habitat management efforts often focus on creating or maintaining stands in early-seral stages (Hundertmark et al. 1990, Renecker and Schwartz 1997, Suring and Sterne 1998). These methods have included mechanical shearing, crushing, and axing of overstory species (Scotter 1980, Thompson and Stewart 1997). Mechanical treatment of moose habitat on the CRD was accomplished through hydraulic-axing (hereafter hydro-axing), or machines which use rotary axes to cut down trees or shrubs up to 15 cm in diameter (Stephenson et al. 1998). First treatments occurred during winters of 1990–1992 (Stephenson et al. 1998), while additional treatment plots were completed in 2008, 2010, and 2012 (M. Burcham & T. Joyce, 2012, personal communication). However, initial analyses of hydro-axing (1990–92; Stephenson et al. 1998) on the CRD were limited in 1) scope (1-3 years post-treatment), 2) species considered (i.e., Hooker's willow was not identified or included), 3) sample sizes for estimates of biomass for some species (i.e., cottonwood, feltleaf willow, and undergreen willow), and 4) data regarding the effects of snow depth on availability of treated browse. Our project included analyses of treatment effects of hydro-axing on forage species 1-23 years post-treatment, on all browse species present in plots, and with winter scenario-specific estimates of reduced browse availability due to snow depths. Thus, our objectives in chapter 4 were to 1) evaluate species-specific and time-since-treatment responses of key winter browse species to mechanical treatment by evaluating available biomass, height, nutritional quality, and utilization and 2) estimate how biomass availability within treated sites might vary with snow depth (i.e., winter severity). Use of heavy hydro-ax equipment in a temperate swamp is a difficult task and managers need data to evaluate the ratio of resource and logistical costs to potential browse production benefits of this habitat management tool. Therefore, our results could have significant implications for continued use of hydro-axing as a moose habitat management tool on the CRD.

Overall, our results will have significant implications for ungulate (specifically moose) management and ecological research. By studying and evaluating the managerial techniques of regression-based biomass estimation, nutritional carrying capacity models, and mechanical treatment of moose habitat, this thesis will refine and provide further tools to aid in the successful management of the CRD moose, a population whose study continues to contribute to the knowledge of ungulate ecology and management worldwide.

CHAPTER 2: PAST AND PRESENT BIOMASS EQUATIONS FOR TWO SIMILAR WILLOWS ON AN ALASKAN DELTA

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ABSTRACT

Estimation of biomass via allometric equations of key forage species is common in ungulate habitat management. Previous research (1988-1989) on the Copper River Delta (CRD; Delta) of Alaska produced regression equations to estimate available winter biomass from basal diameters for browse species sustaining an isolated moose (*Alces alces gigas*) population. However, equations for Hooker's willow (*Salix hookeriana*) were not developed then, either because the species was not present or because it was misidentified as the visually-similar Barclay's willow (*Salix barclayi*). We developed equations and collected field data for both species to determine 1) whether past and present models of biomass production by Barclay's willow predicted similarly and 2) whether Hooker's and Barclay's willow differed in average available biomass, nutritional quality, and utilization by moose. We hypothesized that ecosystem changes on the Delta in recent decades might have influenced shrub growth rates and affected model accuracy. However, because of physical similarities, we did not expect to find significant interspecific differences in available biomass, nutritional values, or utilization. The linear coefficients for the current (2013) Barclay's willow, Hooker's willow, and combined equation were 2.2*x*, 1.6*x*, and 1.9*x* larger, respectively, than that derived from the 1988 model for Barclay's willow, suggesting that willows on the CRD may now be supporting more biomass/stem than predicted by prior models. Average available biomass, nutritional values, and utilization rates did not differ significantly between Hooker's and Barclay's willow. These results suggest a need to verify existing allometric biomass models, and that separate identification of the similar Barclay's and Hooker's willow may not be critical for future biomass estimation efforts.

INTRODUCTION

Accurate identification and biomass estimation of browse available to wild ungulate populations is necessary for their effective management. In North America, biomass of preferred forage species is commonly estimated with allometric equations which should allow for efficient long-term vegetation monitoring (Baskerville 1972, Hytönen et al. 1987, Catchpole and Wheeler 1992). One area to which these methods have been applied is the Copper River Delta (CRD; Delta) of south-central Alaska, the largest continuous wetland on the Pacific Coast of North America (Kesti et al. 2007, [USDA-FS] 2015). Seven winter browse species were identified and basal diameter-mass regression equations were developed to estimate the nutritional carrying capacity (NCC) for the CRD moose (MacCracken and Van Ballenberghe 1993, MacCracken et al. 1997, Christensen et al. 2000). The moose (23 individuals) were first introduced to the CRD in 1949 by state and federal management, having likely been excluded naturally by geography (MacCracken et al. 1997, Klein et al. 2005). The population has grown and as of 2013 over 830 moose were estimated on the Delta (C. Westing, 2014 personal communication). However, in 1964 the largest earthquake recorded in U.S. history (9.2 magnitude) uplifted the Delta by 1-4 m, changing the landscape hydrology, the near-shore soil salinity, and the distribution and successional direction of some vegetation stands (MacCracken et al. 1997, Boggs 2000, Kesti et al. 2007, USGS 2012). In particular, the distribution and abundance of woody species increased notably, including sweetgale (*Myrica gale*), willow (*Salix* spp.), alder (*Alnus viridis sinuata*), spruce (*Picea sitchensis*), and hemlock (*Tsuga heterophylla*) (Thilenius 1990). Five willow species compose 80% of moose winter diets on the CRD along with alder (3%), cottonwood (1%, (*Populus trichocarpa*), and sweetgale (7%) (MacCracken et al. 1997).

To provide ecologically-relevant goals for the moose population in the midst of this change, the NCC was first estimated by MacCracken et al. (1997) on the western side of the CRD (the region more accessible to hunting) using regression equations developed in 1988-89 by MacCracken and Van Ballenberghe (1993). However, prior estimates (MacCracken et al. 1997, Stephenson et al. 2006) did not include models calculating winter biomass of Hooker's willow (*Salix hookeriana*), either because it was not present, was not detected in sampling, or was not differentiated from the visually-similar Barclay's willow (*S. barclayi*) (J. MacCracken, 2013, personal communication). The United States Department of Agriculture's National Resources Conservation Services (USDA-NRCS) first recognized Barclay's willow on the CRD in 1928, but Hooker's willow was not recorded until 2001 ([USDA-NRCS] 2014). Because of this uncertainty, development of basal diameter-mass regression equations for both Barclay's and Hooker's willow with current (2013) samples was warranted.

Potential effects of earthquake-initiated changes in hydrology, stand aging, moose utilization, or climate change on the CRD vegetation provided an additional impetus to recalculate biomass production and NCC. Willows on the CRD increased in distribution and biomass since the uplift (Boggs 2000, Thilenius 2008) and, with aging, have likely continued to increase in mean available biomass and stem diameter. Winter browsing by moose can lead to short-term increases in leader length and biomass, but few studies have evaluated these effects over more than a few years (Bergstrom and Danell 1987, Danell et al. 1994, Bowyer and Neville 2003). Lastly, increased annual temperatures or growing degree days associated with climate change could increase willow growth rates and production (Chapin et al. 1995, Osterkamp 2007). These possible changes in growth rates or structure prompted concern about the long-term accuracy of allometric equations for biomass estimation (Chapin et al. 1995, Klein et al. 2005). Development of equations using recent samples enabled comparison of regression coefficients derived from samples gathered 24–25 years ago. The comparison allowed avenues of exploration, including: 1) potential changes in stem available biomass due to ecological factors, and 2) the possibility that prior estimates of biomass production by Barclay's willow were in fact calculated on a combination of Barclay's and Hooker's willow samples.

Our objectives were twofold. First, we explored whether willow growth rates differed over time by comparing regression coefficients and estimates of available biomass developed by MacCracken and Van Ballenberghe's (1993) Barclay's willow models (1988–89) to those we calculated from recent (2013) samples of Barclay's and Hooker's willows. Next we determined whether species-specific differences existed in average available biomass (g/stem, kg/ha), nutritional quality (crude protein, lignin, tannin, and ash), and utilization (%) by moose. Because of the increased abundance and biomass of woody species since the uplift, increased biomass associated with stand aging, potentially higher shrub biomass among browsed willows, and potential increases in mean daily temperature and growing degree days, we expected biomass estimates derived with our current models to exceed past estimates. Because of similarities in growth form, location, and prevalence, we expected to find no significant interspecific differences between current Barclay's and Hooker's willow.

METHODS

We compiled weather data collected for the CRD from 1934-2013 (ACRC 2014). We calculated mean daily temperature and growing degree days over four 20-year periods (1934-1953, 1954-1973, 1974-1993 and 1994-2013) and over the two research periods (1988-89, 2012-13). We used an analysis of variance (ANOVA) and *t* tests to compare the mean daily temperature and growing degree days of the four 20-year periods and the two research periods, respectively.

We maintained comparability among past and present regression equations (2013 Hooker's, 2013 Barclay's, 2013 combined, 1988 Barclay's) to predict biomass production by following the methodology of MacCracken and Van Ballenberghe (1993). In fall of 2013, we collected basal diameter data (0.01 mm) and samples of available biomass (g/stem) for Hooker's and Barclay's willow. Because the maximum bite diameter recorded on the CRD was 8.3 mm (MacCracken et al. 1997), we clipped all species to that diameter, stored samples fresh frozen from the field, de-leafed, dried at 60°C for 48 hours, and then weighed to the nearest 0.1 g. We measured and sampled a total of 180 Hooker's willows and 163 Barclay's willows. We compared R^2 and slopes of the best-fit transformed and zero-intercept linear models for 2013 samples of each species separately and when combined. We then compared estimates derived from the 2013 models to those produced by the 1988 model (MacCracken and Van Ballenberghe 1993).

To estimate biomass production, nutritional values, and browse utilization of Hooker's and Barclay's willow by moose, we established sampling plots in 7 stand types containing winter browse species. We located those stand types (spruce-hemlock, spruce-cottonwood, cottonwood, alder, alder-willow, willow, and sweetgale) with a Satellite Pour l'Observation de la Terre (SPOT version 5 [SPOT5], 2011, Red Castle Resources, Inc.) map. We generated GIS-randomized points within these stand types and selected 40 total plots. Due to logistical constraints and associated safety concerns, we restricted plots to within 1.5 km of roads. Upon reaching each plot, we verified that the vegetation community matched the SPOT5 classification of the stand type. Plots consisted of three random-start 10 x 1 m belt transects placed 5 m apart running north, north, and west. We measured fall (Sept-Oct 2012, 2013) basal diameters from which we derived estimates of end-of-growing-season biomass, collected fall and spring (Sept-Oct 2012, April-May 2013) forage samples for nutritional analyses, and measured spring (April-May 2013) browse removal by moose (twig bite diameters, or the diameter of the twig at the point of removal by the moose) to calculate over-winter utilization. We measured basal diameters of Hooker's willow in 5 plots, Barclay's willow in 8 plots, and both in 27 plots (Fig 1). Both willows were represented in all stand types except Hooker's willow in spruce-hemlock. At 0.5 m intervals along the transects we measured basal diameters (above the moss layer to the nearest 0.01 mm) on up to three stems. Very large stem basal diameters (> 60.0 mm) increase regression equation heteroskedasticity (MacCracken and Van Ballenberghe 1993). In those cases we measured a branch diameter and estimated how many equivalent branches composed the shrub. We collected 7 late fall and 16 early spring forage samples of Hooker's willow, and 10 late fall and 16 early spring samples of Barclay's willow. Because the maximum bite diameter recorded on the CRD was 8.3 mm (MacCracken et al. 1997), we clipped all species to that diameter, placed samples in paper bags, defoliated them, and stored them fresh-frozen from the field before sending them to Washington State University's Wildlife Habitat and Nutrition Lab (Pullman, WA; MacCracken et al. 1997). We collected measurements of winter use in 19 plots for Hooker's and Barclay's willow. At 0.5 m intervals along each transect, we measured all recent bite diameters (0.1mm). We used *t* tests (95% confidence) to compare the average available biomass (g/stem, kg/ha), crude protein (%), lignin (%), ash (%), tannin (mg/g), and use (%) of Hooker's and Barclay's willow.

RESULTS

The highest mean daily temperatures on the CRD occurred during the period from 1934-1953 (x = 4.7°C; 95% CI: 4.5-4.8°C) but mean daily temperatures have increased over the three most recent 20-year periods (1954-1973: x = 3.2°C [95% CI: 3.0-3.3°C]; 1974-1993: x = 4.2°C [95% CI: 4.0-4.3°C]; 1994-2013: x = 4.2°C [95% CI: x = 4.1-4.4°C]; P: <0.0001). Mean number of annual growing degree days did not vary significantly across the same periods (1934-1953: x = 328 days [95% CI: 226-431]; 1954-1973: x = 313 days [95% CI: 261-365]; 1974-1993: x = 382 days [95% CI: 335-429]; 1994-2013: x = 393 days [95% CI: 328-457]; P = 0.32) (ACRC 2014). Furthermore, the mean daily temperature of the two research periods (1988-89, 2012-13) did not differ significantly (P = 0.4984), and the 2012-13 data period contained 195 fewer total growing degree days than the 1988-89 study period.

Basal diameters for Barclay's and Hooker's willow ranged from 2.75–48.32 and 3.07–56.69 mm, respectively, with means of 13.48 and 13.56 mm. Log-log and linear zero-intercept regression models for both willow species individually ($M_{\text{Barclays}} = 0.14[BD]^{1.93}$, $M_{\text{Hookers}} = 0.18[BD]^{1.80}$, $M_{\text{Barclays}} = 3.35[BD]$, and $M_{\text{Hookers}} = 2.43[BD]$ with R^2 = 0.85, 0.84, 0.64, and 0.76, respectively) and a linear model for combined willows ($M_{\text{Both}} = 2.87[BD]$, R^2 = 0.66) sampled in 2013 exceeded model fit achieved by the linear equation for Barclay's willow (possibly including Hooker's; $M_{\text{Barclays}} = 1.51[BD]$, R^2 = 0.44) sampled in 1988. The relationship between basal diameter and biomass of Hooker's and Barclay's willows sampled in 2013 was best fit by log-log regression models. Regression slopes developed with 2013 samples were greater than that derived from the 1988 samples (Fig. 2). The linear coefficients for the 2013 Barclay's willow, Hooker's willow, and combined equations were 2.2 times, 1.6 times, and 1.9 times larger, respectively, than that of the 1988 Barclay's willow model (Fig. 2). However, we were unable to test for significance because we did not have an estimate of the slope variance for the 1988

Barclay's willow. The 2013 linear slope for Barclay's willow was 1.4 times greater than the 2013 Hooker's willow, though the difference was not significant (*P* = 0.94).

Average available biomass (g/stem, kg/ha) did not differ significantly between Hooker's and Barclay's willow (Hooker's: *x* = 13.28 g/stem [95% CI: 8.99-17.56]; Barclay's: *x* = 18.69 g/stem [95% CI: 7.66-29.72]; Hooker's: *x* = 77.94 kg/ha [95% CI: 26.78-129.10]; Barclay's: *x* = 101.57 kg/ha [95% CI: 56.87-146.26]). Nutritional values for both willows significantly differed by season (*P* ranged < 0.0001-0.03), except for lignin (%; Table 1). There were no significant species differences within intraseasonal samples (Table 1). Over-winter utilization by moose reflected this nutritional equivalence and did not differ significantly between the willows (Hooker's: *x* = 7.95% [95% CI: 1.74-14.17]; Barclay's: *x* = 7.95% [95% CI: 4.55-11.35]; *P* = 0.9994).

DISCUSSION

Our understanding of the ecology and factors influencing vegetation growth on the CRD system is still developing, however slopes of all three 2013 linear regression models (Barclay's, Hooker's, combined) were greater than that of the 1988 Barclay's equation, suggesting that ecosystem changes since 1988–89 have increased stem available biomass on the CRD. We lacked the data to determine the causal factor increasing willow stem biomass, but potential factors include earthquake-initiated changes in hydrology, stand aging, moose browsing, increased annual temperatures due to climate change, or some combination. Changes in vegetation distribution and successional processes have likely largely stabilized since the 1964 earthquake (Boggs 2000, Thilenius 2008), but it is possible that remnant effects of increased drainage continued to influence recruitment and growth in Barclay's and Hooker's willows. This would affect the population distribution of basal diameters and associated available biomass. Even without remnant effects of increased drainage, stand ageing would lead to overall increases in basal diameters and available biomass. However, our ranges and maximum basal diameter measurements for both willows were smaller than those observed by MacCracken and Van Ballenberghe (1993) for Barclay's willow (~ 1.0–103.0 mm), suggesting our willow populations may be younger or have lower growth rates. Our utilization rates by moose were also comparable to those observed by MacCracken et al. (1997) for Barclay's willow (mean 7% across stand types), suggesting overall browsing rates have not changed much and are unlikely to be influencing willow growth or structure differently between the two study periods. Lastly, while annual mean temperatures across Alaska have risen by 1.7°C since 1949 (ACRC 2014) and our data showed increases in mean annual temperatures on the CRD since 1954, temperature have not increased significantly since 1974 and we did not detect increases in growing degree days over the same time period. MacCracken et al. (1997) observed mean ages of Barclay's willow across the Delta ranging from 12–33 years. Unless current willows on the CRD are capable of living longer than 40 years (recruiting before 1974), it is unlikely that their growth rates or productivity have been affected by the temperature changes on the CRD. However, for longer-lived species, the increase in mean annual temperatures may be an influential factor.

Overall increase in growth rates confounded our effort to determine whether measurements of Hooker's willow were included in the 1988 sampling and modeling. Potential hybridization between Barclay's and Hooker's willows offers additional complications for current and future investigations. Hybridization might increase the difficulty of species identification in the field, and overlaps in morphological characteristics could explain why we did not detect significant interspecific differences in mean available biomass (Argus 2004). Considering the lack of significant interspecific differences in available biomass, nutritional quality, and use, Hooker's and Barclay's willow appear to be functionally equivalent for some managerial purposes, including calculation of NCC for overwintering moose.

MANAGEMENT IMPLICATIONS

Our results have significant management implications. The regression slopes derived from 2013 samples suggest that willows on the CRD are supporting 1.9-2.2 times more biomass/stem than they did 24–25 years ago, thus increasing over-winter browse availability for moose. Therefore current and future estimates of NCC calculated with the 1988–89 allometric regressions for willow biomass would likely significantly underestimate forage availability for moose. This scenario is likely applicable elsewhere and should be explored for other browse species. Thus, we recommend the cautious use of allometric equations calculated decades ago or within highly variable ecosystems and suggest managers redevelop models using current data. Finally, because we found no interspecific differences between Hooker's and Barclay's willow in the parameters we examined, separate identification of those willows may not be critical for many studies or applications.

TABLES AND FIGURES

Figure 2.1. Satellite vegetation map SPOT5 (2011) of the west Copper River Delta, Alaska, showing roads and locations of 40 plots at which we sampled for biomass, nutritional quality, and moose utilization of Hooker's willow (five plots), Barclay's (eight plots) willows, or both (27 plots) in Fall or Spring 2012-2013.

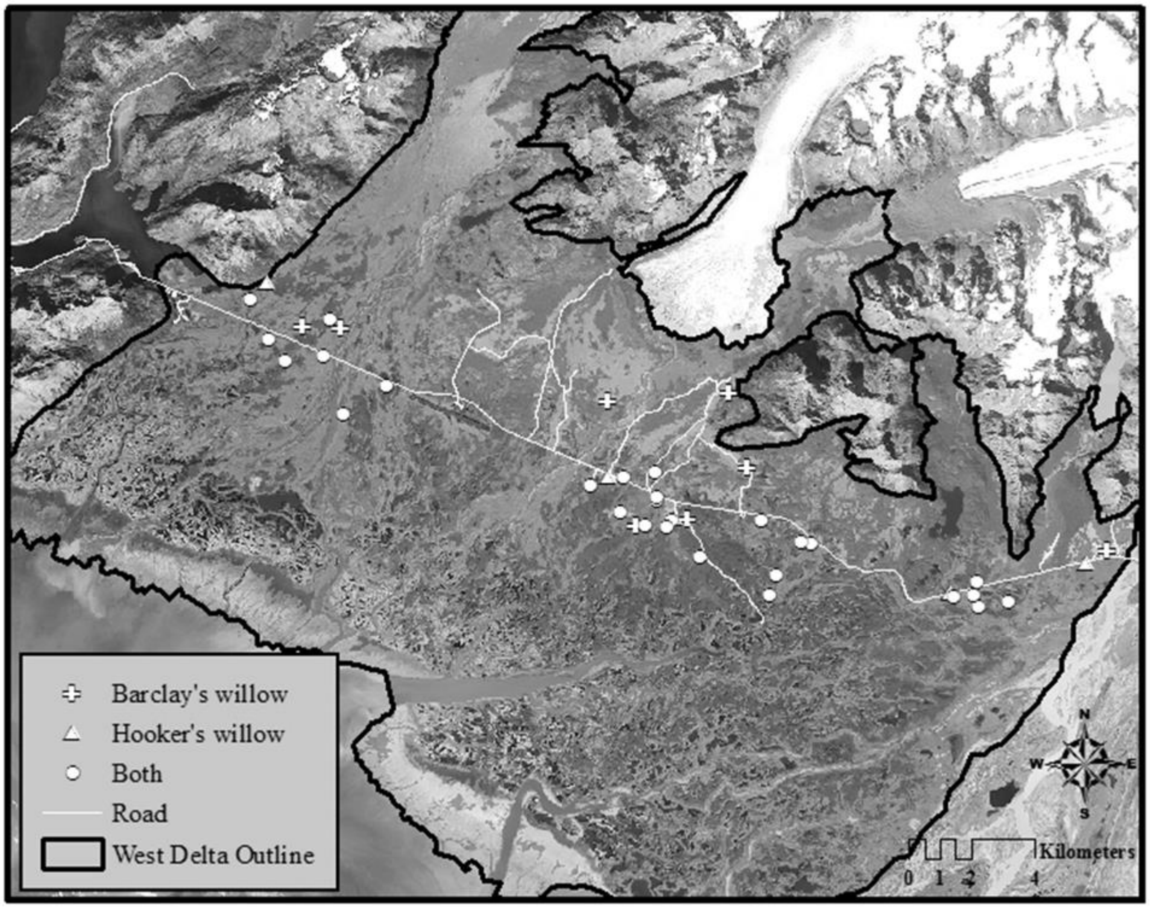

Figure 2.2. Relationship between basal diameter and available winter biomass of Barclay's willow (*Salix barclayi*) and Hooker's willow (*S. hookeriana*) collected (2013) on the western portion of the Copper River Delta of Alaska fitted with best log-log linear (dotted) and best zero-intercept linear (solid) models compared to MacCracken and Van Ballenberghe's (1993) best zero-intercept linear (dashed) model for Barclay's willow collected (1988-89) on the same area.

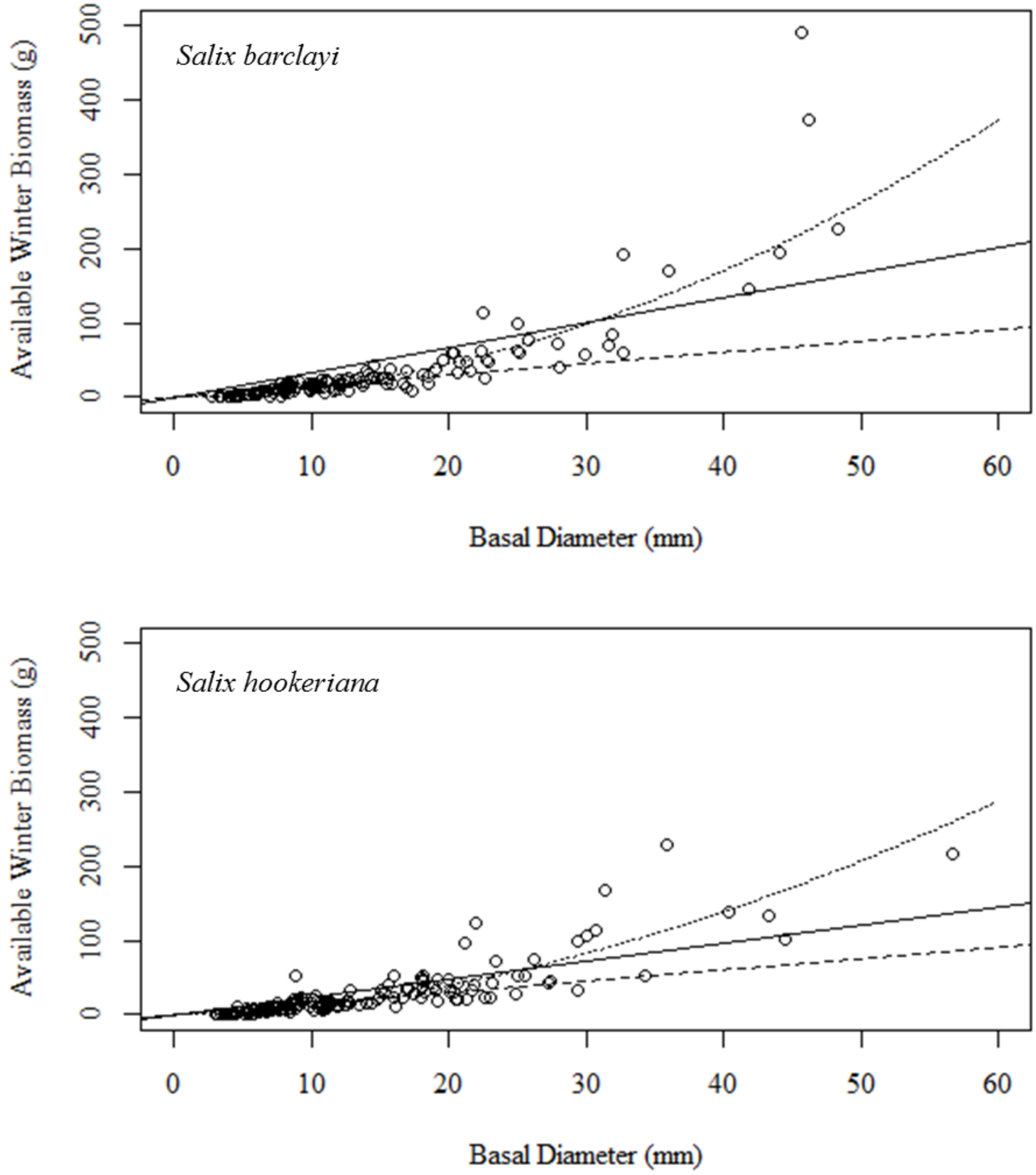

Table 2.1. Comparison of fall and spring crude protein (%), lignin (%), ash (%), and tannin (mg/g) of Hooker's willow (*Salix hookeriana*) and Barclay's willow (*Salix barclayi*) samples collected in 2012-2013 on the Copper River Delta, AK. Significant intraseasonal and interseasonal differences are denoted by * (* < 0.05, ** < 0.005, *** < 0.0005).

	Species or Season	**Protein (%)**	**SD**	**Lignin (%)**	**SD**	**Ash (%)**	**SD**	**Tannin (BSA mg/g)**	**SD**
Seasonal Interspecific Comparison									
Fall									
	Barclay's	6.35	0.48	16.98	2.41	1.91	0.42	9.44	14.2
	Hooker's	6.43	0.52	17.27	3.31	1.82	0.47	9.47	11.09
Spring									
	Barclay's	6.97	0.66	16.1	1.41	2.39	0.48	41.09	32.67
	Hooker's	7.06	1.04	16.15	1.57	2.38	0.42	41.08	13.42
Intraspecific Seasonal Comparison									
Barclay's									
	Fall	6.35	0.48**	16.98	2.41	1.91	0.42*	41.09	32.67***
	Spring	6.97	0.66	16.1	1.41	2.39	0.48	9.44	14.2
Hooker's									
	Fall	6.43	0.52*	17.27	3.31	1.82	0.47*	9.47	11.09***
	Spring	7.06	1.04	16.15	1.57	2.38	0.42	41.08	13.42

CHAPTER 3: EVALUATING MODELS OF NUTRITIONAL CARRYING CAPACITY FOR WINTERING MOOSE ON AN ALASKAN DELTA

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ABSTRACT

Estimates of nutritional carrying capacity (NCC) require careful consideration of ungulate foraging ecology and any limitations to browse availability. Model types used to estimate NCC have historically varied in their incorporation of available biomass and forage selection. We compared 5 NCC models across 4 estimates of winter ranges under 3 winter-severity scenarios for an isolated moose population on the Copper River Delta (CRD; Delta) of south-central Alaska to evaluate the effects of model types and components on NCC estimates. We conducted a sensitivity analysis (*Sx*) of our final model to determine which factors affect NCC estimates most. Lastly, we compared our current (2012–13) forage available biomass, stand type areas, and NCC results (with and without species-specific estimates of forage nutritional quality) to those obtained by past research (1987–89, MacCracken et al. 1997, and 1959–2013, Stephenson et al. 2006) to 1) determine the changes in forage available biomass, stand type areas, and NCC over time and 2) evaluate the effects on NCC estimates of including forage nutritional values in models. Our final model estimated NCC of 2,198–3,471 moose for the entire west Delta depending on winter severity, suggesting the current western moose population (approximately 600 in 2013) is below NCC. Model components with the largest and smallest *Sx* were snow depth and lignin- and tannin-caused reductions in forage nutritional quality, respectively. Changes from 1987–2013 in available biomass (kg/ha) of forage species ranged from -66–493% while changes in stand type total areas (ha) from 1959–2013 ranged from -60–661%. Overall, NCC of the west Delta for moose seems stable relative to past estimates (2% decrease from 1959–2013); however, inclusion of forage nutritional quality in comparable current models reduced NCC estimates by 60% relative to past models.

INTRODUCTION

The concept of carrying capacity has a long and contested history, but is regularly used by wildlife managers as they balance animal populations between what is ecologically sustainable and culturally desirable (Caughley 1979, MacNab 1985, Sayre 2008). Though originally conceived as a static, ideal number for a specific area and single species, more recent applications have recognized the dynamic interactions between a population and its environment, including long-term impacts of succession and climate (Pastor et al. 1997, Van Gils et al. 2004, Beck et al. 2006, Stephenson et al. 2006, McKeon et al. 2009). Furthermore, early models typically focused on maximizing abundance of popular game animals, while more recent efforts have constrained estimates by considering predator-prey interactions, human-caused limitations, and influences of social behavior, or were conducted on non-game species (Decker and Purdy 1988, Hobbs and Hanley 1990, Fritz and Duncan 1994, Berger et al. 1999, Hayward et al. 2007, Wolverton 2008). An alternative, more restricted approach is to estimate the nutritional carrying capacity (NCC, also termed ecological carrying capacity), or the largest, stable population of a specified organism in a defined range supported by the total available nutritional energy (Caughley 1979). Nutritional carrying capacity acts as an idealized baseline to which further environmental, biological, or managerial factors can be added. However, NCC estimation assumes a stable ecosystem. Within highly variable environments, such as within desert ecosystems prone to years of drought followed by shorter periods of abundant forage, balance between an organism and its food base may never be achieved or may fluctuate dramatically, (Caughley et al. 1987, McLeod 1997). Thus, application of NCC estimates require careful consideration of the ecology of the organism and its environment.

For ungulates, NCC is dependent on the species' browsing behavior, which in turn is determined by the abundance, availability, nutrition, physiology, and ecology of the forage species (Caughley 1979, Hobbs and Swift 1985, Jefferies et al. 1994, Hobbs et al. 2003, Pastor and Danell 2003, Windels and Hewitt 2011). Within temperate and arctic ecozones, ungulate ecologies are subject to cyclical seasonal changes in browse species abundance and nutritional quality. Nutritional quality of wintering (dormant) vegetation is relatively low and snow can greatly limit food accessibility. Together, these factors increase the necessary digestion and foraging time for an equivalent quantity of food in the summer (Schwartz and Renecker 1997). Because of this, winter was historically considered the limiting period for ungulates and NCC estimates. However, because ungulates compensate by altering their metabolism and activity during winter, they have lower daily energy requirements and are able to subsist on smaller quantities of food or metabolized fat reserves (McEwan and Whitehead 1970, Mautz 1978b, Hanley 1983, Regelin et al. 1985, Renecker and Hudson 1986). Conversely, the summer months are required to restore body fat and prepare for the energetically-draining behaviors of the fall, winter, and early spring, namely rut, pregnancy, and lactation (Stephenson 1995, Schwartz and Renecker 1997). Thus, more recent studies have recommended estimating the availability of summer forage to calculate NCC (Bobek 1977, Mautz 1978a, Merrill and Boyce 1991, Beck et al. 2006, Dungan et al. 2010). Determining which season is more influential on an ungulate population depends on factors constraining ungulate access to the available forage such as physiology, snow, terrain, or weather.

Consideration of such seasonal factors is required to understand the limitations on the forage available to the moose of the Copper River Delta (CRD; Delta) in south-central Alaska (Fig 1). Moose were introduced (23 individuals) to the CRD from 1949–1958 to develop a resource for the town of Cordova (MacCracken et al. 1997). Though ubiquitous throughout much of Alaska, moose were likely excluded from the CRD by surrounding mountains and glaciers. Since their introduction, the moose population has split into two semi-distinct populations (west and east), growing to an estimated 600 and 230 individuals, respectively (C. Westing, 2014, unpublished data; Fig 2). Hunting began in 1960 and is the largest limitation to adult moose survival (MacCracken et al. 1997). The western population is more heavily harvested and researched because of its size and proximity to Cordova (T. Joyce, 2014, personal communication). While the west Delta encompasses around 54,000 ha, past research (1987–89) by MacCracken et al. (1997) found 90% of the moose wintered within primary and secondary ranges between 4,800-12,900 ha, presumably due to forage availability, snow drifting, and extreme winter winds (-40°C wind chill) from the Copper River Canyon. This restricted winter range likely represents the most severe limitation on available browse for the CRD moose. However, a 9.2 magnitude earthquake (the largest earthquake recorded in American history) in 1964 uplifted the area by 1.0–4.0 m, initiating changes in hydrology, soil salinity, and vegetation while generally increasing the proportion of stands dominated by woody species (Grantz et al. 1964, Ferrians 1966, Plafker 1969, Thilenius 1990, Stover 1993, Thilenius 2008). Because moose on the Delta subsist mainly on willows (61–93% of seasonal diets), the combined effects of a restricted winter range and earthquake-caused vegetation changes may influence population growth (MacCracken et al. 1997, Stephenson et al. 2006).

To provide a post-earthquake estimate of NCC (1987–89), MacCracken et al. (1997) used a forage supply-animal demand model (biomass available relative to biomass consumed over a given time period) to calculate the number of moose supported by the available biomass on the winter range he observed (Fig. 1) under 3 winter scenarios: mild (1,424 moose), moderate (1,347 moose), and severe (380 moose). Because of concerns regarding decreased NCC due to earthquake-related changes in vegetation and decreased glacial effects, Stephenson et al. (2006) predicted changes in stand type areas and available biomass from 1959–2202 within a winter range on the glacial outwash plains using 1959 and 1986 aerial maps (Fig. 1) and a Markov-chain model. They then used a diet-adjusted model (available biomass of forage species reduced according to observed diet ratios) to estimate NCC over that time period. They projected a decline from 453–1,110 moose in 1959 to 211–762 moose in 2202, depending on winter severity (no snow or severe), with 261–950 moose estimated for 2013. However, currently the west CRD moose population (~600) is higher than all severe winter estimates and the current management goal (400–500). Moreover, the current population has a stable growth rate (Fig. 2), with little anecdotal evidence of over-browsing (shrub "brooming"), and high twinning rates (58-65%) (C. Westing & T. Joyce, 2013, personal communication), all despite recently experiencing one of the most severe winters recorded on the CRD (2011/12). These characteristics suggest that 1) earthquake-initiated vegetation changes have not negatively influenced the moose population as expected, 2) moose are accessing more forage on the west CRD, possibly by using a greater proportion of the total area, 3) previous calculations of available biomass, winter severity, or NCC were conservative, or 4) some combination of these.

Landscape-level evaluations of earthquake-initiated changes in stand areas and succession suggest the Delta vegetation might have stabilized since the uplift (DeVelice et al. 2001, Thilenius 2008). Future changes in vegetation will likely be determined by successional processes (stand aging and shifts to later, forested successional stages), channel or land area changes due to glacial, river, or tidal effects, subsidence, or habitat alterations by humans or wildlife such as beavers (*Castor canadensis*) or the moose themselves (Boggs 2000, Cooper 2007, Thilenius 2008). These processes are complex and difficult to predict (Appendix 1). However, currently the effects of the post-earthquake changes on vegetation seem to have largely increased shrub biomass on the west Delta (Thilenius 1990, Boggs 2000, Thilenius 2008).

Recent aerial surveys suggest the CRD moose population might be expanding its winter range beyond the bounds observed by MacCracken et al. (1997) and moving into areas encompassing most of the west Delta, thereby potentially increasing the amount of available winter forage. However these same surveys suggest that the highest moose densities might still occur within the primary region of the range previously observed (MacCracken et al. 1997, C. Westing, 2014, personal communication).

Annual mean temperatures across Alaska have risen by 1.7°C since 1949 (ACRC 2014), and comparisons between regression equations developed in 1988–89 and 2013 to predict biomass production by willow species on the CRD suggest willows might currently be supporting between 1.9–2.2*x* more biomass/stem than previously estimated (Chapter 2). Effects of winter severity on available biomass (e.g., levels of snow drifting) might also be lessened. Furthermore, previous NCC models used estimates of stand areas (i.e., stand type, location, and size) produced through photographic aerial maps and estimates of forage biomass unconstrained by nutritional quality. Estimation of vegetation with aerial photography is subject to lower precision and resolution (Willhauck et al. 2000, Xie et al. 2008), and plant secondary compounds (i.e., tannins) have been shown to reduce NCC estimates considerably (Windels and Hewitt 2011). We utilized a Satellite Pour l'Observation de la Terre (SPOT version 5 [SPOT5], 2011, RedCastle Resources, Inc., Salt Lake City, UT) satellite map of the CRD vegetation to enable more detailed estimates of the stand areas and included species-specific estimates of nutritional quality (e.g., gross, energy, tannin, lignin, crude protein, and neutral detergent fiber levels) in our NCC models.

Our objectives were to: 1) estimate utilization of winter browse by moose on the CRD to establish current utilization of browse and evaluate anecdotal evidence that recent browse use has been low (< 25%; Singer and Zeigenfuss 2002), 2) develop models to estimate NCC with current samples of forage biomass and nutritional estimates while evaluating the effects of model type, winter severity, and winter range extent, 3) perform sensitivity analyses to determine the relative influence of factors within the final model, and 4) compare past estimates (MacCracken et al. 1997 & Stephenson et al. 2006) with similarly-configured recalculations to evaluate potential changes in species available biomass, stand areas, and NCC estimates over time, along with potential effects of including browse nutritional quality and satellite-based estimates of stand areas in NCC models. We hypothesized 1) that due to potentially higher population densities of moose in the observed winter range (per MacCracken et al. 1997), the winter forage species would show some signs of over-browsing (>25% use) in that range, but little signs of over-browsing external to that region, 2) that our NCC estimates would differ by model type, winter scenario, and winter range, but all would estimate NCC above the current moose population (600), while winter scenario would have the greatest effect on NCC estimates, 3) that nutritional quality of forage and snow depth would be the most influential factors (i.e., high proportional sensitivity) in NCC models, and 4) that a) current estimates of available forage biomass, non-forested stand type areas, and comparable NCC estimates would all be higher relative to past estimates, b) models incorporating forage nutritional quality would predict lower NCC relative to biomass-only models, and c) models constructed with satellite-based estimates of stand areas would produce considerably different NCC estimates than those constructed with aerial maps.

METHODS

Study Area

The CRD is the largest continuous wetland (over 283,000 ha) in the Pacific Northwest (USDA-FS, Kesti et al. 2007). The west Delta (0–300 m in elevation) is surrounded by the Pacific Ocean to the southwest, 3 glaciers (Scott, Sheridan, and Sherman) and the Chugach Mountain Range (over 2000 m in elevation) to the north and northeast, and the Copper River to the east (Kesti et al. 2007). The Copper River is almost 20 km across at its mouth and channels winter winds that produce gusts of 193 km/h through the Copper River Canyon. Soil types include deposits of aeolian sands, alluvial sands and gravels, and marine glacial silts with very fine sands (Davidson and Harnish 1978). Mean annual precipitation and temperature from 1909–2014 at the Merle K. “Mudhole” Smith Airport weather station on the west Delta were 230 cm and 4.0 °C, respectively, with mean monthly temperatures ranging from -8.9–16.3 °C ([WRCC] 2015). Hydrological dynamics and continuous channel changes due to glacial, river, and tidal effects determine the vegetation structure and overall maintain an abundance of wetland species (MacCracken 1992, Boggs 2000). Woody browse important to moose ecology in the winter includes 5 willow species, including feltleaf willow, Barclays willow, undergreen willow, Hookers willow, and Sitka willow (*Salix alexensis, S. barclayi, S. commutata, S. hookeriana,* and *S. sitchensis,* respectively), as well as Sitka alder (*Alnus viridis sinuata*), black cottonwood (*Populus trichocarpa*), and sweetgale (*Myrica gale*) (MacCracken et al. 1997). These 8 forage species are found in 7 stand types identified on the SPOT5 (2011) map: spruce-hemlock, spruce-cottonwood, cottonwood, alder, alder-willow, willow, and sweetgale. The earthquake and associated uplift likely changed the hydrological dynamics (draining and desalinating the soil), shifting the Delta from an herbaceous-dominated ecosystem to a shrub- and forest-dominated ecosystem, while accelerating succession in some stand types from herbaceous-, sweetgale- and willow-dominated stands to stands dominated by alder, cottonwood, Sitka spruce (*Picea sitchensis*) or western hemlock (*Tsuga heterophylla*) (Boggs 2000, Thilenius 2008).

Estimation of Biomass Availability and Utilization

To estimate the biomass available to moose within NCC models and forage utilization by moose, we generated GIS-randomized points within the 7 stand types and selected 53 total plots (7–9 per stand type). Due to logistical constraints and associated safety concerns, we restricted selection of those plots to within 1.5 km of roads (Fig. 1). Upon reaching each plot, we verified the vegetation community matched the SPOT5 classification of the stand type (Viereck 1992). Plots consisted of three random-start 10 x 1 m belt transects (running north, north, and west) placed 5 m apart. To capture maximal forage growth, we collected fall (Sept–Oct 2012–13) basal diameters, stem density, and stem height of the 8 browse species within the transects. To capture over-winter utilization by moose and forage nutrition, we collected late-winter (April–May 2013) bite diameters and browse samples of the 8 browse species.

We measured basal diameters (0.01 mm) above the moss layer on the 3 closest stems every 0.5 m along the transects and estimated available biomass (g/stem) with regression equations (MacCracken and Van Ballenberghe 1993, Stephenson et al. 2008, Chapter 2). Very large stem basal diameters (> 60.0 mm) increased heteroskedasticity of biomass estimates produced by regression equations (MacCracken and Van Ballenberghe 1993). Thus, in those cases we measured a branch diameter, estimated the number of equivalent branches on the stem, and summed the biomass available on the branches. We counted the number of stems (stem density, *n*/30 m^2) of each forage species present within the belt areas. We measured the total height (m) on up to 3 stems per species within each transect and, to allow for changes in available biomass with increasing snow depth, we visually estimated the biomass (%) present in 1 m increments from 0–6 m (the range of moose browsing within mild to severe winter snow depths). We calculated the species-specific mean available biomass (stem biomass x stem density, kg/ha, and incrementally, %), and height (m) within each stand type.

On the stem closest to every 0.5 m, we measured bite diameters (0.01 mm) of every browsed twig. We calculated browse removal (use; g/twig) with regression equations (MacCracken and Van Ballenberghe 1993) and then summed the total biomass consumed per stem (g/stem). We used analyses of variances (ANOVAs) to compare the average utilization (%) of the 8 forage species in the 7 stand types and within different winter ranges. We collected samples of available biomass of every species recorded in a plot for nutritional analyses of gross energy (cal/g), crude protein (%), lignin (%), tannin levels (mg/g), and neutral detergent fiber

(NDF, %). Because the maximum bite diameter recorded on the Delta was 8.3 mm (MacCracken et al. 1997), we clipped all species to that diameter, placed samples in paper bags, defoliated them, and stored them fresh-frozen from the field before sending them to Washington State University's Wildlife Habitat and Nutrition Lab for analysis (Pullman, WA; MacCracken et al. 1997). We calculated the mean species-specific gross energy, crude protein, lignin, and tannin within each stand type.

Modeling Nutritional Carrying Capacity

Development of winter scenarios.– We developed winter scenarios (mild, moderate, and severe) by visually identifying and then summarizing data on mean winter snow depth (cm) and length (days from first snowfall to last) collected from 1917–2012 by the Alaska Climate Research Center (ACRC 2014) weather station at Cordova's "Mudhole Smith" Airport. We used ANOVAs to test for significant differences in mean snow depth, winter length, and temperature (°C) among scenarios. We then adjusted model components of available biomass and winter length by the mean snow depth and number of days for each scenario.

Delineation of winter ranges and estimation of stand type areas.–We initially defined 3 ranges relevant to the wintering moose population (Fig. 1): 1) an aggregate of the primary and secondary ranges (hereafter "observed range") as determined by movements of radio-collared moose from 1987–89 when approximately 200 were present (MacCracken et al. 1997), 2) the entire west Delta, to incorporate evidence from recent aerial surveys showing range expansion of the current moose population beyond the observed range (C. Westing, 2014, unpublished data), and 3) an inference range restricted by the maximum distance (1.5 km) of sampling plots from the roads. After investigating effects of road distance (m) on available biomass (kg/ha) using generalized linear, log-log, and log-linear models, we developed a 4th range definition (road bias-adjusted range), which adjusted the estimates of available biomass in cottonwood, alder-willow, willow, and sweetgale stand types. Other stand types did not differ significantly with increasing plot distance from roads. The road bias-adjusted range summed adjusted estimates of available biomass outside the inference range and unadjusted estimates of biomass within the inference range to re-calculate the total biomass across the west Delta range (Fig. 1).

Stand type areas (ha) within each winter range were determined by the SPOT5 (2011) vegetation map. Area estimates of the SPOT5 map were corrected according to the error matrix developed by Red Castle Resources, Inc. (Salt Lake City, UT) through spot-proofing. We could not account for the inherent error in the spot-proofing process.

Development of NCC models.–We developed 5 models of NCC using modifications of the models developed by MacCracken et al. (1997; forage supply-animal demand), Stephenson et al. (2006; diet-adjusted, 2 variations), and the historically-relevant Hobbs and Swift (1985; diet-restricted, 2 variations; Fig. 3). All 5 models incorporated species- and stand type-specific estimates of nutritional quality (gross energy, available protein reductions due to tannin levels, digestible dry matter reductions due to lignin amounts, and percentage of NDF) and available biomass (kg/ha) to calculate the digestible energy (kcal/ha) available within the 7 stand types (Fig. 3). We adjusted estimates of available biomass within stand types according to the mean snow depths (m) in winter scenarios. We averaged species-specific values of available biomass and nutrition, but used a Monte Carlo simulation to bootstrap stand type-specific digestible energies (amplifying our small sample sizes, *n* = 7–9), produce sampling distributions for each stand type, and provide estimates of stand variability. We then multiplied the sampling distribution of the stand type digestible energies by range-specific estimates of stand type areas (ha), calculated the total median stand type digestible energies, summed the total median digestible energies, and compared the total calculated winter scenario- and range-specific digestible energy to the total energy required by an average adult female moose (500 kg) across a scenario-specific winter length (number of days) to determine the total number of moose supported within a specified range (Fig. 3).

The 5 models differed in their approach to available biomass. In the open-diet model (a modification of the forage supply-animal demand model; MacCracken et al. 1997), we assumed equal selection probability for all forage species (i.e., did not consider forages “preferred” or “non-preferred”), and reduced the available biomass of forage species to 25% (i.e., utilization is 25%) to simulate sustainable browsing of forage species (Singer and Zeigenfuss 2002, Dungan et al. 2010). However, because moose do selectively browse certain species over others, we reduced the available biomass in the diet-adjusted model (Stephenson et al. 2006) of all non-willow browse (cottonwood, alder, and sweetgale) by the observed rates of occurrence in fecal analyses to account for diet selection and gut mixing: cottonwood to 1.0%, alder to 3.0%, and sweetgale to 7.0 % (MacCracken et al. 1997). However, because the diet-adjusted model assumes 100% use of available willow biomass, which is potentially unsustainable, we ran a third model which reduced available willow biomass in the diet-adjusted model to 25% (diet-adjusted, 25% use model). Because preferred forages might ultimately restrict NCC, the diet-restricted model (Hobbs and Swift 1985) constrains the available biomass by the most limiting preferred forage as determined by the browse species' proportions observed in diet analyses. The fecal analysis of MacCracken et al (1997) determined willows were most abundant in the CRD moose diet but could not differentiate among willow species, so we used the total available biomass of willows as the limiting forage. Because the diet-restricted model also assumes 100% use of willow biomass, we developed a fifth model which limits willow available biomass to 25% (diet-restricted, 25% use model).

Sensitivity Analysis

We conducted a sensitivity analysis to assist managers in determining which factors within the final NCC model influence the estimate most, thereby being most ecologically or managerially important. We increased 9 independent factors (protein reduction due to tannins, lignin content, gross energy, stem biomass, stem density, snow depth, stand type area, winter length, and the energy needed by wintering moose) by 5% and calculated the percent change in NCC and the proportional sensitivity (*Sx*).

Comparing to Past Nutritional Carrying Capacity Estimates

We could not replicate the NCC model (forage supply-animal demand) structure used by MacCracken et al. (1997) because we lacked estimates of stand type areas in the observed winter range during his study period (1987–89). As a proxy for NCC change, we evaluated differences in past (1987–89) and present (2012–13) estimates of species available biomass in winter by calculating the difference (%) in available biomass (kg/ha) between the two data collection periods for the 8 winter forage species. Because Hooker's willow was probably sampled collectively with Barclay's willow in the 1987–89 sampling (J. MacCracken, 2012, personal communication, Chapter 2), the willows were combined for this analysis.

We were able to replicate the NCC model structure (diet-adjusted) used by Stephenson et al. (2006). Thus, in order to compare changes in NCC over time (1959, 1986, and 2013), evaluate the accuracy of the 2013 projected estimate relative to recent biomass data (2012–13) and stand areas estimates (SPOT5, 2011), and determine the effect of including forage nutritional quality on current NCC model estimates, we matched model type (biomass only, diet-adjusted), moose intake rates (52.1 kg/BW$^{0.75}$/day; MacCracken et al. 1997), winter range area (glacial outwash plains range; Fig. 1), stand type areas, winter length (181 days), and snow effects (45% reduction in available biomass in tall stand types and 85% reduction in short stand types in severe winter scenario). Stand type areas were calculated for 1959 and 1986 and projected for 2013 by Stephenson et al. (2006). Because the maps by Stephenson et al. (2006) differed in stand type classification relative to our map, we reclassified his stand types to match those categorized by the SPOT5 map (Table 1) and then recalculated his stand type areas. Stephenson et al. (2006) estimated the change in vegetation and NCC from 1959 to 1986 within a winter range on the glacial outwash plains using aerial maps and then used a Markov-chain model of vegetation change to project the changes in stand type areas and NCC for 2013. We compared the difference (%) between his projected 2013 estimate, our NCC estimate with current biomass data, and our NCC estimate with both current biomass and stand type area data. Then we compared an energy-based NCC estimate (incorporating nutritional quality of forage) with a biomass-based NCC estimate for 2013 and calculated the difference (%). Lastly, we evaluated the changes (%) in stand type areas (ha) within a larger section of the Delta (including the glacial outwash plains and a portion of the Delta marsh uplifted during the 1964 earthquake) across the three maps (1959, 1986, and 2011; Stephenson et al. 2006).

RESULTS

Though located near the Scott Glacier and Copper River, feltleaf willow never occurred within our randomized plots and was subsequently removed from our analyses. The 7 remaining forage species in the 7 stand types varied in mean available biomass (kg/ha), gross energy (cal/g), crude protein (%), lignin (%), tannin (mg/g), and NDF (%) levels (Tables 2 and 3).

Mean utilization (%) of total available biomass (kg/ha; all species) and willow species did not differ between plots sampled on the west Delta (7.7% [± 4.4%] and 6.1% [± 2.9%], respectively) and those in the primary observed range (7.3% [± 6.2%] and 10.0 % [± 6.8%], respectively), with the potentially highest moose population densities. Mean utilization of total available biomass across stand types ranged from 0.0–19.1 % and differed significantly (*P* = 0.02), while mean utilization of total willow available biomass across stand types ranged from 0.0–12.7 % and did not differ significantly (Table 3). Mean species-specific utilization included cottonwood (1.6%), alder (3.8%), Sitka willow (6.7%), Barclay’s willow (7.9%), Hooker’s willow (8.0%), undergreen willow (0.7%), and sweetgale (13.8%).

Winter length in mild, moderate, and severe winter scenarios of models averaged 147 (± 7), 163 (± 8), and 178 (± 22) days, respectively, and differed significantly (*P* = <0.001). Snow depths averaged 11.40 (± 1.52), 25.81 (± 2.40), and 63.89 (±16.51) cm, respectively, and differed significantly (*P* = <0.001). Temperatures averaged -1.34 (± -0.81), -2.77 (± -0.70), and -3.09 (± -0.72) °C, respectively, and differed significantly (*P* = 0.01). Between 1917–2012 mild, moderate, and severe winter scenarios occurred 49, 29, and 11 times, respectively, while 6 winters were unclassifiable due to incomplete data.

Winter ranges defined for our models ranged 4,811–53,945 ha and varied in stand type composition (Table 4). As plot distance from the roads increased, significantly different estimates of biomass in cottonwood, alder-willow, willow, and sweetgale stands were best explained by log-log, linear, log-log, and log(x) models, respectively (*P* = 0.002-0.04; R^2 = 0.43-0.85). The regression models predicted reductions in available biomass (kg/ha) by 99.7%, 91% and 95% in cottonwood, alder-willow and willow stands, and increases in available biomass by 208% in sweetgale stands over 1.5 km from the roads.

Estimates of NCC across all models, ranges, and scenarios ranged from 195–5,228 moose, generating moose densities from 0.01–0.13 moose/ha. Mean estimates of NCC in the 4 ranges (entire west Delta, road bias-adjusted, plot inference, and MacCracken et al. observed) across all winter scenarios and models were 2,356, 2,535, 824, and 849, respectively (Fig. 4). Thus, NCC estimates using the road bias-adjusted range were 7.6% higher than the unadjusted west Delta range, while estimates using the inference range and total observed range were 65.0% and 63.9% lower, respectively, relative to the west Delta range. However, the highest moose densities were predicted in the total observed range. Mean NCC estimates using diet-adjusted and diet-restricted (100% use) models across all ranges and winter scenarios were 22.6% and 17.8% higher, respectively, than estimates using the open-diet model. The diet-adjusted (100% use) model produced estimates 5.9% higher than the diet-restricted (100% use) model, but model estimates reduced by 70.3% and 75.0%, respectively, when available biomass was reduced to 25%. Estimates of NCC decreased by 20.3% and 34.2% as winter severity increased.

The open-diet model in a severe winter scenario was chosen as our final model because of its conservative approach to forage availability and allowance for diet flexibility. Because of the possibility of winter range expansion, we chose to run the final model within the west Delta range. Percent changes in NCC from the sensitivity analysis on this model and range varied from -1.00–9.64% (Table 5). Proportional sensitivity (*Sx*) ranged from -0.20–1.93, with the lowest and highest *Sx* attributed to protein reduction due to tannins and snow depth, respectively.

Changes in species-specific available biomass (kg/ha) between 1987–89 and 2012–13 sampling periods ranged from -66–493% (Table 6), in which cottonwood biomass increased the most, sweetgale decreased the most, and Sitka and undergreen willow changed the least (-9 and 9%, respectively). Stephenson et al. (2006) estimated NCC in mild (no snow) winter scenarios increased from 1959 to 1986 by 1% and would decrease by 16% in 2013 (A, B, and C in Fig. 5). Our matched model (using our updated biomass data and the stand type areas predicted by Stephenson et al. [2006], D in Fig. 5) also found NCC would decrease by a comparable 20% in 2013. However, when we used our SPOT5 (2011) stand type areas, NCC only decreased by 3% (E in Fig. 5). Our energy-based model (incorporating nutritional values for forage species; F in Fig. 5) produced NCC estimates 60% lower than our biomass-based model (E in Fig. 5). The changes in stand areas (ha) for the 7 stand types ranged from -30.3–660.7% between the 1959 and 1986 maps, and -74.4–203.7% for between the 1986 and 2011 maps (Table 7).

DISCUSSION

Overall, we saw no evidence of over-browsing (>25% forage utilization) by moose on the CRD, suggesting current herbivory by moose is not negatively impacting the winter forage base. This further supports evidence from anecdotal observations of forage species condition, high twinning rates, and rump fat levels, suggesting the current west CRD moose population is accessing sufficient nutrition during winter and is below NCC. However the most conservative models (diet-adjusted and diet-restricted with 25% use within smaller winter ranges and severe winter scenarios) estimated that the current moose population might be above NCC. A severe winter in 1970–71 did reduce the population of almost 200 moose by 15–20%, supporting more conservative estimates and suggesting the Delta may not be able to support a substantial moose population during severe winters. However, the current moose population survived another severe winter in 2011 with minimal losses (estimated 601 moose in 2011 and 609 moose in 2013; Fig.2), suggesting the CRD moose have improved their access to winter browse, perhaps by expanding winter range use or diet selection, and the most conservative models are underestimating NCC.

Conceivably, the moose population wintering in 1970–71 could have subsisted within a smaller winter range (as suggested by later observations by MacCracken et al. 1997). If so, this may have reduced their access to available forage and contributed to their decline. Recent aerial surveys suggest the current moose population is using range beyond the 1987–89 winter range observed by MacCracken et al. (1997) and, thus, increasing their access to winter forage. This larger range potentially buffered them against the effects of the 2011 severe winter, and suggests that the smaller definitions of winter range extents might now be inappropriate. If the CRD moose have in fact expanded their winter spatial distribution, we expect that any models within either the plot inference or past observed winter ranges might be limited in applicability. Even if observations from the recent aerial surveys are spurious, without further detailed data on space use and resource selection by the moose, models using smaller winter ranges may underestimate the browse available to the moose and the associated NCC. Furthermore, moose diets are not as inflexible as the diet-adjusted and diet-restricted models would imply, or may have changed since 1970–71. Hobbs and Hanley (1990) cautioned against assuming herbivores are limited to the diets observed during a specific study period. Density-dependent factors in both the herbivores and their forage may influence browsing behavior and diets over time or in different regions (Vivas and Saether 1987). No free-choice or in-field diet analyses have been conducted on the current moose population to determine the extent to which the CRD moose might adjust their diets. However, the high use of sweetgale in our analyses suggests the limited diet assumed by the diet-adjusted and diet-restricted models may be too conservative. Similarly, our estimates of the biomass available in the road bias-adjusted range may be inaccurate. Our sample sizes for detecting changes in available biomass in plots with increasing distance from the roads were small (n = 7–9) and limited in scope (≤ 1.5 km), and it is possible these factors limited our ability to detect a significant difference in available biomass within spruce-hemlock, spruce-cottonwood, and alder stand types. Furthermore, the significant differences we did detect in cottonwood, alder-willow, willow, and sweetgale stand types may have been over- or under-predicted. The 208% increase in available biomass within sweetgale stands seems counter-intuitive, while the reduction of available biomass in cottonwood stands by 99.7% defies personal observation.

Thus, we selected our final model, the open-diet (25% use) model in the west Delta range, because of its diet, which allows for density-dependent dietary adjustments and forage recovery from herbivory, and the choice of winter range relying on the fewest problematic assumptions. Our final model predicted moose densities of 0.04-0.06 moose/ha, depending on the winter scenario. These densities are comparable to those found in surrounding game management units (0.003-0.09 moose/ha; P. Harper, 2010, unpublished data) in Alaska.

However, it was difficult to determine a reliable estimate of NCC for the west CRD moose. First, as already discussed, we lacked the data to determine an accurate wintering moose range. The range estimated with radio-collared moose by MacCracken et al. (1997) was likely too conservative for current conditions considering recent observations during aerial surveys. However, it is also unlikely the moose are using the entire west Delta range, as we did calculate higher moose densities within the total observed range, suggesting some areas provide more suitable moose habitat than others. The current population spread may also be in flux. Forage use estimated by MacCracken et al. (1997) in 1987–89 (≤ 15%) in their observed range was similar to our current estimates across the inference range. This suggests the potentially dispersing moose are responding to browsing or social pressures, though without further data we cannot determine the causal factor. Thus, the most accurate NCC estimate for the current CRD moose is likely somewhere between the entire west Delta range and the past observed range estimates, but that may continue to change as the moose population does. We recommend further research to determine the current moose range and factors driving their winter range choice.

Secondly, the browsing tolerance of the CRD forage species has not yet been determined. Studies in Denali and interior Alaska found winter use of forage by moose varied from 0.9–31.2% to 1–46%, respectively, and reported some short-term chemical effects, but neither study evaluated the long term effects of high forage use on forage biomass production (MacCracken and Viereck 1990, Miquelle et al. 1992). However, a review by Augustine and McNaughton (1998) found that intermittent herbivory (e.g., due to migration or non-herding) and nutrient-rich ecosystems were key factors in supporting the regrowth capacity of palatable species. A later study by Persson et al. (2007) confirmed that regrowth ability varied along a habitat productivity gradient and found birch (*Betula pubescens* and *B. pendula*) could tolerate 25–40% use in productive sites. Considering the influx of nutrients tidally, glacially, and through actinorhizal species on the Delta, preferred forages (e.g., willows) may be able to support high levels (> 25%) of consumption by moose. We recommend further research to determine the tolerance level of CRD forages.

Thirdly, the dynamic nature of the forces governing the CRD vegetation make all estimates of NCC temporary and non-ideal to some degree. The hydrology, soil quality, land area and form of the Delta are dictated by several landscape-level forces including: 1) glacial growth and retreat, 2) glacial or lake stream flooding, sedimentation, erosion, and channel cutting, 3) river flooding, sedimentation, and erosion, 4) tidal flooding, soil and water salification, sedimentation, and erosion, and 5) periodic earthquake-initiated cycles of uplift and subsidence (Boggs 2000). These geological factors may interact with zoological factors, such as beaver (*Castor canadensis*) or moose plant feedback-cycles, or human factors, including logging, mechanical treatment of habitat (Chapter 4), and road development (Maurer and Ray 1992, Danell et al. 1994, MacCracken et al. 1997, Christensen et al. 2000, Wright et al. 2002, Stephenson et al. 2006, Cooper 2007). A review of these complex, interactive forces and their potential effects on the availability of forage for the moose population is provided in Appendix 1. However, comparison of past (1987–89, MacCracken et al. [1997]) and present (2012–13) species available biomass suggests most current forage species may have less available biomass (kg/ha), with the exception of undergreen willow (+9%) and cottonwood (+493%). The notable increase in cottonwood is likely over-estimated due to methodological differences (i.e., the classification of a “stem” versus a “tree”), as personal observations did not record the level of recruitment required to make such an increase in biomass likely for cottonwood. These reductions in species biomass would suggest effects due to landscape-level factors, resulting in decreased forage biomass available to the moose. The changes in stand type areas within a subsection of the west CRD from 1959–2011 present a more complex scenario, but also suggest decreases in preferred forage available to moose. From 1959–86 and 1986–2011, forested stand types areas (spruce-hemlock, spruce-cottonwood, and cottonwood) increased by 51.9% and 7.6%, respectively, while willow-based stand types (alder-willow and willow) decreased by 6.0% and 70.2%, respectively. However, alder and sweetgale stand areas increased by 338.7% and 172.1% from 1959–86 and by 135.0% and 128.0% from 1986–2011, respectively. Comparison of comparable NCC estimates (A, B, and E in Fig. 5) within the glacial outwash plain over time suggests the Delta NCC has remained stable or decreased only slightly. This could be explained by diet flexibility of the moose, or because stands dominated by non-preferred forages still contain willow components. Thus, increases in non-willow stands may simultaneously decrease and increase the willow biomass available to moose. The degree to which these stand changes continue will ultimately determine the NCC of the Delta for the moose.

Finally, it is very likely climate change will influence many, if not all, factors included within our NCC models. We found evidence of increased willow growth relative to 1988–89 data (Chapter 2) and it is unknown if other species are responding similarly. The occurrence of severe winters on the CRD has diminished from 4 in the 20 year period from 1917-1936, 3 in 1937-1956, 2 in 1957-1976, 1 in 1977-1996, and 1 so far in 1997-2014. Rates and patterns of succession, nutritional quality of forage species, and moose dietary needs may all be affected by these changes. In all, the dynamics between the forces governing delta hydrology and vegetation, shifting moose ranges, and climate change determine the incredible variability inherent to this system. McLoud (1997) questioned the validity of calculating carrying capacity within non-equilibrium ecosystems. For the moose of the CRD that may be a valid question. Alternatively, our current NCC estimates represent a “snapshot” in time as hydrological, successional, climatic, zoological, and cultural influences continue to drive vegetation change.

MANAGEMENT IMPLICATIONS

The diversity of our model estimates provide flexibility for managers to evaluate and test the major factors driving NCC estimates on the CRD or adjust their management goals as the ecology of the moose changes. For the current conditions, our final NCC model estimates (2,198–3,471) suggest the CRD moose population can be increased at this time. Past authors have recommended using estimates from severe winter scenarios for developing management goals, and our sensitivity analysis suggests snow depth is the most influential factor in NCC for the CRD moose. There are valid reasons for choosing a conservative approach (Stephenson 1995, MacCracken et al. 1997, Stephenson et al. 2006), but the severe scenario and its associated snow depths may no longer be biologically relevant if reductions in severe winters persist. Thus, management goals designed around moderate winter scenarios may be more appropriate. However, because we lack detailed data on daily snow depths, drift formation, melt rates, and compaction on the CRD, we used snowfall data collected at the Mudhole-Smith Airport. We are therefore cautious in weighting that factor beyond the quality of the data, and recommend concerted efforts be invested in learning the variable extent to which this factor determines browse availability. Furthermore, because increasing harvest opportunities is a primary motive in growing this moose population, we recommend managers create management goals around the maximum sustained yield of a population, or half of NCC (Caughley 1976). However, we caution managers as substantial literature suggests managing for total maximum sustained yield without consideration for the limitations in population estimates or within a highly variable environment can lead to delayed recognition of over- or under-harvest, population instability, and ecosystem damage (Larkin 1977, Lande et al. 1997). Thus, we ultimately recommend management goals that are less than half of NCC.

Overall, results from the sensitivity analyses suggest that of the factors included and capable of being managerially manipulated, managing for higher stem densities or larger areas with preferred forage may most efficiently use limited management resources. This supports use of mechanical treatment (e.g., hydraulic-axing) to increase willow biomass on the Delta (Stephenson et al. 1998) (Chapter 2).

Despite the surprisingly minimal *Sx* of tannins and lignin in our sensitivity analysis, inclusion of nutritional quality and use of an energy-based model had a dramatic effect on our NCC estimates relative to the estimates by Stephenson et al. (2006). These results are similar to those recorded by Windels and Hewitt (2011) which found varying concentrations of digestible protein and digestible energy reduced carrying capacity estimates by 4–47% and 0–50%, respectively. We recommend that all future models of NCC incorporate species-specific nutritional values. Furthermore, we suggest that use of models that allow for 100% forage use produce inherently risky management goals relative to forage browsing tolerance. Thus, we recommend restraining available biomass within NCC models to levels of utilization which allow for forage recovery (Singer and Zeigenfuss 2002). We also recommend consideration of summer-based NCC estimates as 1) considerable research suggests ungulate reproductive success may be determined by fat reserves gained during spring and summer foraging rather than reserves lost during the nutritionally-limited winter period, and 2) the forage available to the CRD moose may no longer be limited by a restricting winter range (Bobek 1977, Mautz 1978a, Merrill and Boyce 1991, Cook et al. 2001, Cook et al. 2004, Beck et al. 2006, Dungan et al. 2010). Finally, estimates of NCC may need to be obtained fairly frequently (perhaps on a decadal scale) to modify management goals relative to climatic and hydrological changes. Alternatively, research could be performed on the interactions between vegetation and climate change on the Delta in order to better understand the complex mechanisms driving such interlaced processes.

TABLES AND FIGURES

Figure 3.1: The west Copper River Delta, AK road structure, sampling plots used to estimate winter available forage and utilization by moose (2012–13), and moose wintering ranges used in estimation of current and historic moose nutritional carrying capacity, including the entire west Delta, a sampling plot inference range (buffered 1.5 km from the roads), past observed ranges from 1987-89 collar data (primary and secondary; MacCracken et al. 1997), and a past range in the glacial outwash plains (Stephenson et al. 2006).

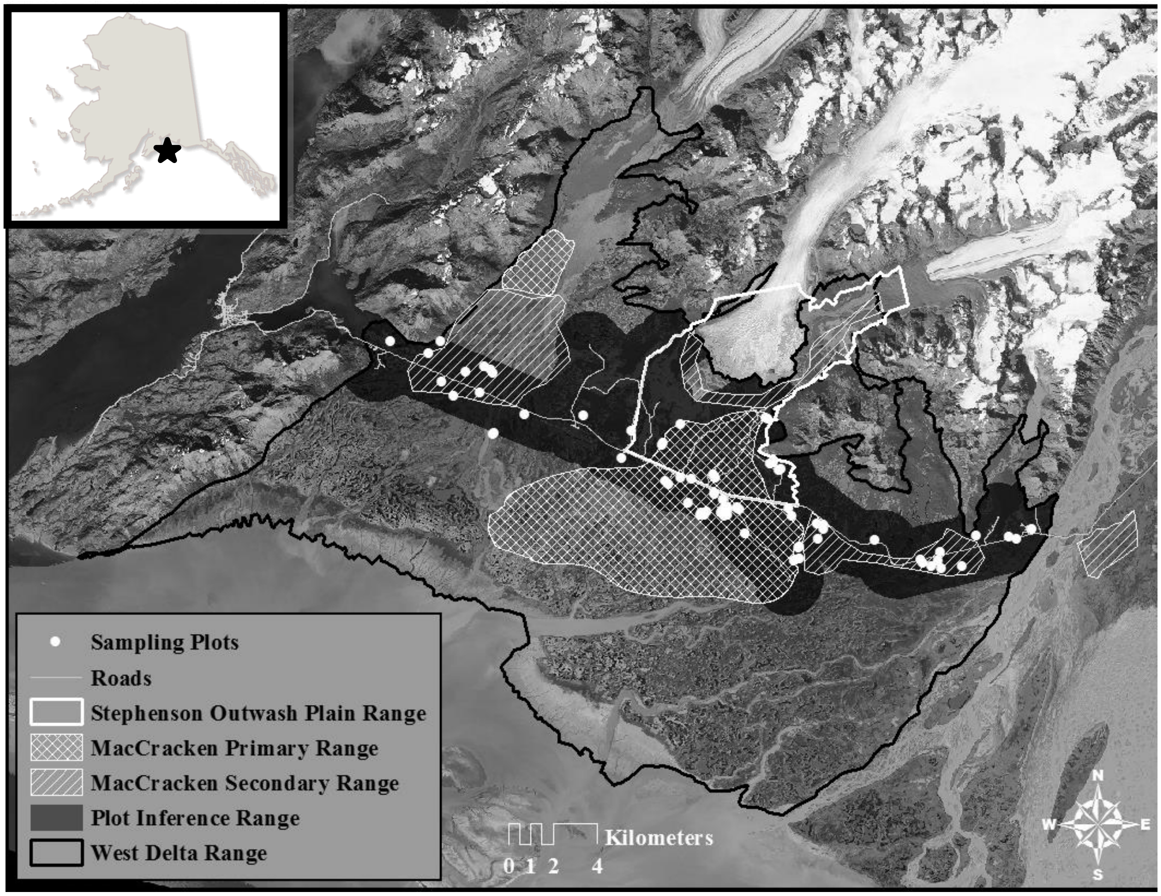


Figure 3.2: Single (dot) and loess moving average (line) estimates of the moose population on the west Copper River Delta, AK since their introduction from 1949–59 (light grey). Moose counts (1963–2013) were conducted via winter aerial surveys and annual totals were estimated using minimum counts (black) or Gassaway surveys (grey; C. Westing, personal communication).

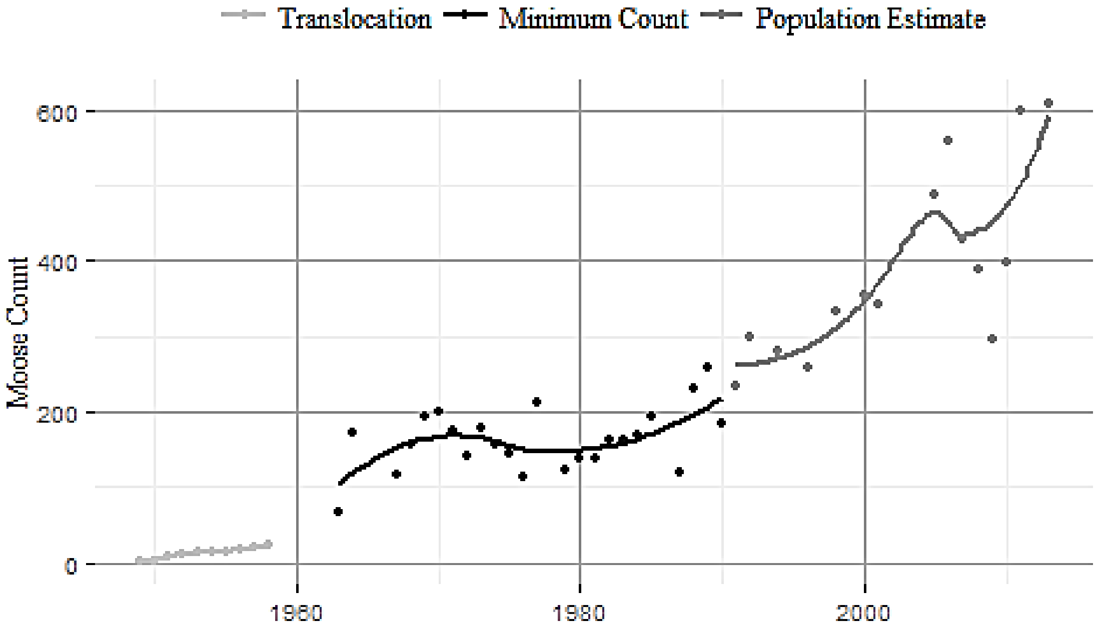
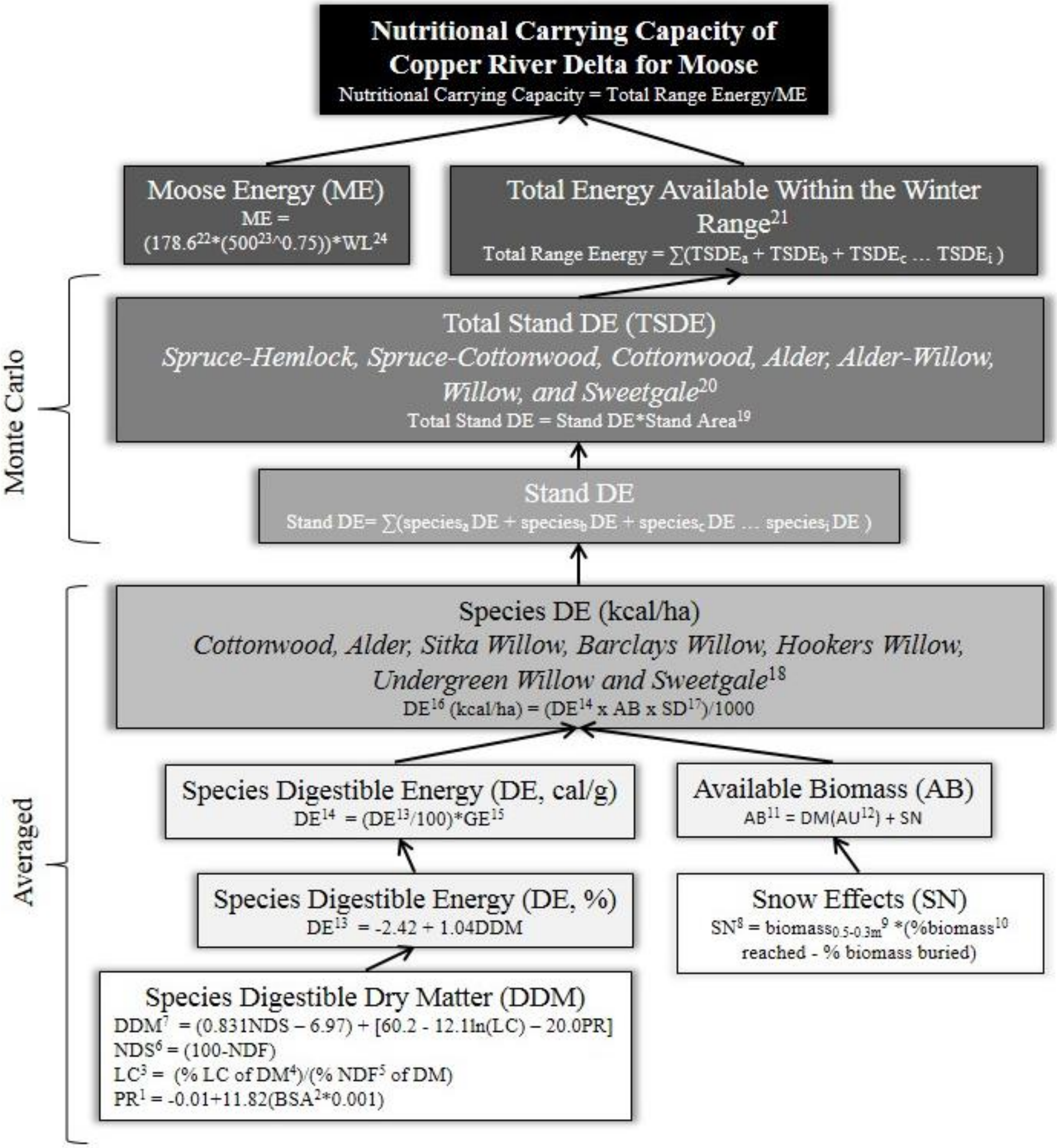


Figure 3.3: General model structure used to estimate nutritional carrying capacity of the Copper River Delta, AK for moose wintering in 2012–13. Species-specific values of biomass and nutrition within stand types were averaged, but stand type-level values of energy were analyzed using a Monte-Carlo simulation to get estimates of variability and amplify small sample sizes (*n* = 7–9).



[1] PR = protein reduction (g of protein lost/100 g protein); Spalinger et al. (2010)
[2] BSA = bovine serum albumin (mg/g DM); Spalinger et al. (2010)
[3] LC = lignin-cutin concentration (g/100 g NDF); Spalinger et al. (2010)
[4] DM = dry matter estimated from regression equations (g/stem); MacCracken et al (1997), Stephenson et al. (2006), and Chapter 2
[5] NDF = neutral detergent fiber (% of DM)

[6] NDS = neutral detergent solubles (g/100 g DM); Spalinger et al. (2010)
[7] DDM = digestible dry matter (g/100 g DM); Spalinger et al. (2010)
[8] SN = snow effects (g DM/stem)
[9] $\text{biomass}_{0.5\text{-}3.0m}$ = biomass within moose browsing reach without effects of snow depth (g DM/stem)
[10] %biomass = percent of total stem biomass newly reached or buried by snow
[11] AB = available biomass (g DM/stem)
[12] AU = adjusted use (%) according to model type (25% of all forage species in total available forage; 1.0-7.0% for non-preferred species and 25 or 100% for willow species in diet-adjusted; and 0% for non-preferred species and 25 or 100% for willow species in diet-restricted)
[13] DE = digestible energy (%); Schwartz and Renecker (1997)
[14] DE = digestible energy (cal/g); Schwartz and Renecker (1997)
[15] GE = gross energy (cal/g)
[16] DE = digestible energy (kcal/ha)
[17] SD = stem density (N/ha)
[18] Browse species for wintering moose on the Copper River Delta
[19] Area (ha) as determined by SPOT5 (2011) satellite vegetation map
[20] Stand types relevant to wintering moose ecology on the Copper River Delta
[21] Either full west Delta range, road bias adjusted west Delta range, plot inference range, or the past observed ranges (MacCracken et al. 1997)
[22] Resting metabolic need (148.6) + 20% due to activity; Schwartz et al. (1988) & Parker et al. (1984)
[23] Weight (kg) of average adult female moose; Miquelle et al. (1992)
[24] WL = winter length (days) adjusted according to winter scenario (mild, moderate, or severe)

Table 3.1: Stand types categorized by a Satellite Pour l'Observation de la Terre (SPOT version 5 [SPOT5], 2011, Red Castle Resources, Inc.) satellite map of the Copper River Delta, AK relative to stand types categorized by Stephenson et al. (2006).

SPOT5 Stand Types	**Stephenson et al. (2006) Stand Types**
Spruce-Hemlock	Woodland Spruce, Closed Spruce, Open Spruce
Spruce-Cottonwood	Open Mixed Spruce Cottonwood, Woodland Mixed Spruce Cottonwood
Cottonwood	Woodland Cottonwood, Open Cottonwood
Alder	Tall Closed Alder Willow
Alder-Willow	Tall Open Alder Willow
Willow	Low Willow Sweetgale
Sweetgale	Low Willow Graminoid, Low Sweetgale
Other	Emergent Aquatics, Graminoid Forbs, Gravel, Pond, Glacial or Tidal Waters, Mud, Rock, Bog, Mud or Sedge, Glacier

Table 3.2. Stand type- and species-specific values of mean gross energy (cal/g), crude protein (%), lignin (%), tannin (mg/g BSA), and neutral detergent fiber (%) for the 7 winter forage species (Barclays willow, undergreen willow, Hookers willow, and Sitka willow [*Salix barclayi, S. commutata, S. hookeriana,* and *S. sitchensis*], Sitka alder [*Alnus viridis sinuata*], black cottonwood [*Populus trichocarpa*], and sweetgale [*Myrica gale*]) found in the 7 stand types (spruce-hemlock, spruce-cottonwood, cottonwood, alder, alder-willow, willow, and sweetgale) important to wintering moose ecology and sampled late winter(April–May) of 2012–13 on the west Copper River Delta, AK.

Stand Type	**Browse Species**	**Gross Energy (cal/g)**	**± CI**	**Crude Protein (%)**	**± CI**	**Lignin (%)**	**± CI**	**Tannin (mg/g)**	**± CI**	**NDF (%)**	**± CI**
Spruce-Hemlock	Cottonwood	5,240	--	4.74	--	18.22	--	0.0	--	78.92	--
	Alder	5,566	--	7.64	--	14.69	--	31.6	--	56.62	--
	Sitka Willow	4,999	--	6.04	--	15.60	--	0.0	--	62.68	--
	Barclay's Willow	5,232	--	6.86	--	18.69	--	0.0	--	53.71	--
	Hooker's Willow	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Undergreen Willow	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Sweetgale	5,359	--	7.04	--	22.31	--	88.3	--	64.81	--
Spruce-Cottonwood	Cottonwood	5,296	10	5.71	0.20	13.27	0.01	0.0	0.0	44.78	2.38
	Alder	5,566	--	7.64	--	14.69	--	31.6	--	56.62	--
	Sitka Willow	4,836	64	6.63	0.99	13.03	0.47	45.3	0.4	58.38	1.71
	Barclay's Willow	5,393	--	6.97	--	16.44	--	40.8	--	51.27	--
	Hooker's Willow	5,373	--	7.10	--	16.01	--	42.0	--	54.32	--
	Undergreen Willow	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Sweetgale	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--

Table 3.2. Continued…

Stand Type	**Browse Species**	**Gross Energy (cal/g)**	**± CI**	**Crude Protein (%)**	**± CI**	**Lignin (%)**	**± CI**	**Tannin (mg/g)**	**± CI**	**NDF (%)**	**± CI**
Cottonwood	Cottonwood	5,367	88	7.10	1.27	17.06	1.33	0.0	0.0	52.33	5.39
	Alder	5,566	[b]--	7.64	[b]--	14.69	[b]--	31.6	[b]--	56.62	[b]--
	Sitka Willow	5,028	135	5.69	0.46	16.63	2.54	24.5	21.6	65.12	6.91
	Barclay's Willow	5,378	[b]--	8.13	[b]--	15.28	[b]--	42.7	[b]--	44.81	[b]--
	Hooker's Willow	5,373	[b]--	7.10	[b]--	16.01	[b]--	42.0	[b]--	54.32	[b]--
	Undergreen Willow	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Sweetgale	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
Alder	Cottonwood	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Alder	5,566	[b]--	7.64	[b]--	14.69	[b]--	31.6	[b]--	56.62	[b]--
	Sitka Willow	5,280	25	7.04	1.02	14.37	1.20	11.9	11.7	56.68	3.74
	Barclay's Willow	5,392	65	7.29	0.90	16.13	1.14	7.8	8.1	57.19	5.53
	Hooker's Willow	5,416	61	7.83	0.89	14.26	1.44	36.0	7.4	55.42	1.29
	Undergreen Willow	5,380	[b]--	6.78	[b]--	17.48	[b]--	70.8	[b]--	57.77	[b]--
	Sweetgale	5,359	[b]--	7.04	[b]--	22.31	[b]--	88.3	[b]--	64.81	[b]--
Alder-Willow	Cottonwood	5,309	[b]--	5.98	[b]--	14.67	[b]--	0.0	[b]--	49.51	[b]--
	Alder	5,566	[b]--	7.64	[b]--	14.69	[b]--	31.6	[b]--	56.62	[b]--
	Sitka Willow	5,317	28	8.01	0.48	15.07	0.98	35.2	9.4	62.07	2.29
	Barclay's Willow	5,526	15	6.65	0.04	15.90	0.26	40.3	2.0	48.76	1.92

Table 3.2. Continued…

Stand Type	Browse Species	Gross Energy (cal/g)	± CI	Crude Protein (%)	± CI	Lignin (%)	± CI	Tannin (mg/g)	± CI	NDF (%)	± CI
	Hooker's Willow	5,304	11	5.68	0.13	16.93	0.25	46.6	6.4	64.61	0.60
	Undergreen Willow	5,380	[b]--	6.78	[b]--	17.48	[b]--	70.8	[b]--	57.77	[b]--
	Sweetgale	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
Willow	Cottonwood	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Alder	5,566	[b]--	7.64	[b]--	14.69	[b]--	31.6	[b]--	56.68	[b]--
	Sitka Willow	5,242	63	7.90	0.42	13.00	0.17	52.5	6.2	54.91	1.34
	Barclay's Willow	5,159	113	6.54	0.23	14.94	0.30	36.0	19.2	54.07	5.75
	Hooker's Willow	5,297	7	7.37	0.48	17.26	1.38	32.9	9.1	56.92	1.58
	Undergreen Willow	5,380	[b]--	6.78	[b]--	17.48	[b]--	70.8	[b]--	57.77	[b]--
	Sweetgale	5,186	[b]--	7.60	[b]--	21.42	[b]--	56.5	[b]--	64.76	[b]--
Sweetgale	Cottonwood	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Alder	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--	[a]--
	Sitka Willow	5,311	[b]--	6.69	[b]--	14.23	[b]--	55.8	[b]--	56.45	[b]--
	Barclay's Willow	5,510	35	6.87	0.44	16.41	1.41	84.7	17.5	47.10	2.30
	Hooker's Willow	5,446	40	7.42	0.72	16.15	1.07	52.3	8.5	49.04	2.01
	Undergreen Willow	5,380	3	6.78	0.03	17.48	0.26	70.8	3.7	57.77	1.10
	Sweetgale	5,416	[b]--	6.85	[b]--	22.61	[b]--	98.9	[b]--	64.82	[b]--

[a] Browse species did not occur in stand type.
[b] Replicates were combined before processing or sample sizes were too small to allow estimation of variability.

Table 3.3. Stand type- and species-specific estimates of mean available biomass (kg/ha) and consumption (use, %) by moose for the 7 winter forage species (Barclays willow, undergreen willow, Hookers willow, and Sitka willow [*Salix barclayi, S. commutata, S. hookeriana,* and *S. sitchensis*], Sitka alder [*Alnus viridis sinuata*], black cottonwood [*Populus trichocarpa*], and sweetgale [*Myrica gale*]) found in the 7 stand types (spruce-hemlock, spruce-cottonwood, cottonwood, alder, alder-willow, willow, and sweetgale) relevant to moose winter ecology and sampled August–September 2012–13 (biomass) and April–May 2013 (use) on the west Copper River Delta, AK.

Stand Type	**Species**	**Available Biomass (kg/ha)**	**± CI**	**Use (%)**	**± CI**
Spruce-Hemlock	Cottonwood	1.91	4.68	11.00	[b]--
	Alder	39.93	48.77	0.00	[b]--
	Sitka Willow	60.20	100.00	6.00	[b]--
	Barclay's Willow	37.97	44.06	5.00	[b]--
	Hooker's Willow	[a]--	[a]--	[a]--	[a]--
	Undergreen Willow	[a]--	[a]--	[a]--	[a]--
	Sweetgale	0.72	1.77	82.00	[b]--
	Total	140.74	146.70	2.33	10.04
Spruce-Cottonwood	Cottonwood	9,232.08	8,755.42	0.00	0.00
	Alder	198.70	122.32	0.00	0.00
	Sitka Willow	135.55	163.73	0.00	0.00
	Barclay's Willow	26.54	52.28	0.00	0.00
	Hooker's Willow	0.95	2.25	0.00	0.00
	Undergreen Willow	[a]--	[a]--	[a]--	[a]--
	Sweetgale	[a]--	[a]--	[a]--	[a]--
	Total	9,593.81	8,596.51	0.00	0.00

Table 3.3. Continued…

Stand Type	Species	Available Biomass (kg/ha)	± CI	Use (%)	± CI
Cottonwood	Cottonwood	22,945.35	13,512.84	0.00	0.00
	Alder	335.20	307.93	0.67	2.86
	Sitka Willow	14.02	18.62	1.00	12.71
	Barclay's Willow	4.13	6.54	0.00	0.00
	Hooker's Willow	7.56	11.29	0.00	0.00
	Undergreen Willow	[a]--	[a]--	[a]--	[a]--
	Sweetgale	[a]--	[a]--	[a]--	[a]--
	Total	23,306.26	13,461.58	0.00	0.00
Alder	Cottonwood	0	0	[c]--	[c]--
	Alder	868.81	697.63	0.2	0.56
	Sitka Willow	73.18	62.57	10	16.12
	Barclay's Willow	48.1	38.83	6.2	4.6
	Hooker's Willow	72.21	125.03	5.25	16.71
	Undergreen Willow	2.27	3.61	0	[b]--
	Sweetgale	0.02	1841.4	[c]--	[c]--
	Total	1,064.59	776.83	3.60	1.53
Alder-Willow	Cottonwood	19.57	47.90	[c]--	[c]--
	Alder	411.54	103.81	2.67	9.40
	Sitka Willow	288.60	319.52	2.00	25.41
	Barclay's Willow	90.17	95.45	3.33	8.73
	Hooker's Willow	53.23	57.22	3.00	38.11
	Undergreen Willow	5.51	12.14	0.00	[b]--
	Sweetgale	[a]--	[a]--	[a]--	[a]--
	Total	868.64	245.54	3.33	3.80

Table 3.3. Continued…

Stand Type	Species	Available Biomass (kg/ha)	± CI	Use (%)	± CI
Willow	Cottonwood	[a]--	[a]--	[a]--	[a]--
	Alder	61.46	65.99	18.00	41.49
	Sitka Willow	179.79	208.81	9.67	29.63
	Barclay's Willow	277.87	177.12	13.00	88.94
	Hooker's Willow	210.40	348.47	23.00	49.62
	Undergreen Willow	21.47	22.51	0.00	0.00
	Sweetgale	63.44	89.47	7.50	95.30
	Total	814.44	311.67	12.67	20.23
Sweetgale	Cottonwood	[a]--	[a]--	[a]--	[a]--
	Alder	[a]--	[a]--	[a]--	[a]--
	Sitka Willow	13.87	30.29	13.00	165.18
	Barclay's Willow	187.25	184.64	10.14	8.18
	Hooker's Willow	167.11	86.55	8.00	11.59
	Undergreen Willow	18.38	15.35	1.17	3.00
	Sweetgale	273.07	97.88	15.57	17.80
	Total	659.67	209.13	19.14	14.68

[a] Browse species did not occur in stand type.

[b] Sample sizes were too small to allow estimation of variability.

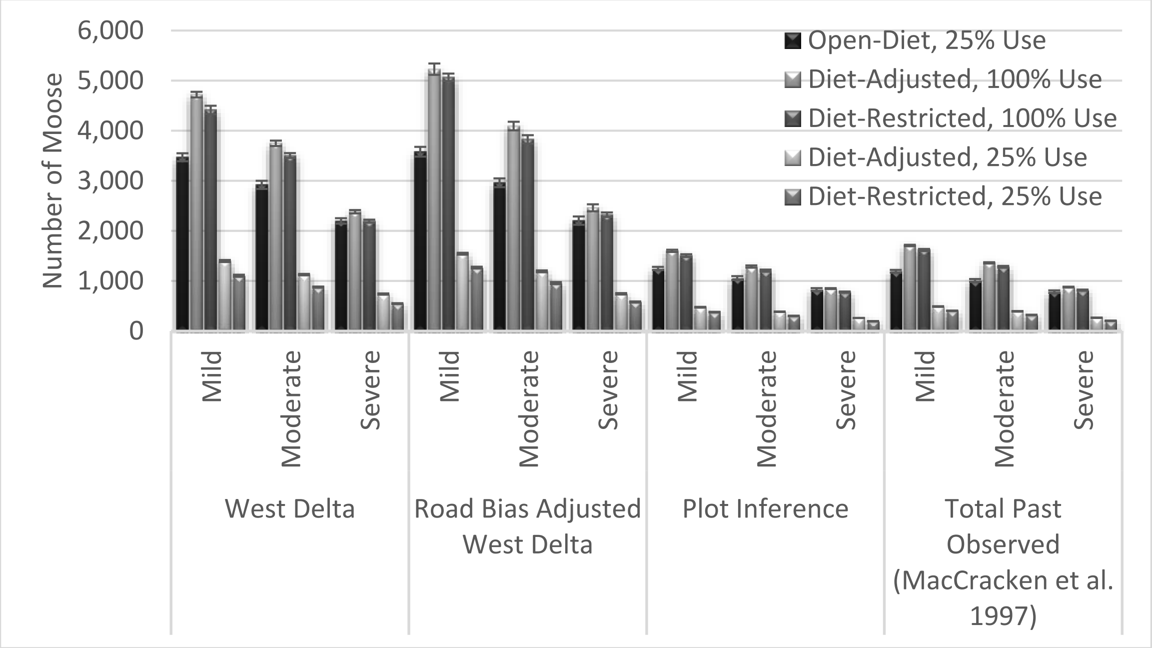
[c] Browse species was not sampled.

Table 3.4: Summary of total and stand type-specific areas (ha) of winter ranges used to calculate the nutritional carrying capacity of moose on the Copper River Delta, AK in 2012-13. The west Delta range encompasses the entire study area. The road bias-adjusted range includes estimates of stand areas beyond the plot inference range where stand biomass is influenced by road effects. The plot inference range is restricted to the maximum plot distance from roads (1.5 km). The primary, secondary, and total (summed) observed ranges represent winter ranges used by collared moose in 1987–89 (MacCracken et al. 1997).

Range	**Total Area**	**Spruce-Hemlock**	**Spruce-Cottonwood**	**Cottonwood**	**Alder**	**Alder-Willow**	**Willow**	**Sweetgale**
West Delta	53945	6808	4381	448	9684	3696	3648	6949
Road Bias-Adjusted West Delta	38358	2841	2167	315	6777	2557	2575	5215
Plot Inference Range	15588	3967	2214	133	2907	1139	1073	1734
Primary Observed Range	8184	571	783	61	1663	782	928	1864
Secondary Observed Range	4811	275	548	32	1522	410	415	534
Total Observed Range	12995	846	1331	93	3185	1192	1343	2398

Figure 3.4: Estimates of nutritional carrying capacity (number of moose, ± CI) and moose densities (moose/ha) on the Copper River Delta, AK in 2012–13 using 5 models (open-diet/25% use, diet-adjusted/100% use, diet-restricted/100% use, diet-adjusted/25% use, and diet-restricted/25% use), across 4 ranges (west Delta, road bias-adjusted, plot inference, and past observed), and under 3 winter scenarios (mild, moderate, and severe). The open-diet model allowed equal utilization of the 7 winter forage species, while the diet-adjusted models restricted forage biomass according to diet ratios, and diet-restricted models limited forage biomass to willows. Percent use restricted biomass availability to allow forage recovery (25% use) or complete consumption (100% use). The winter ranges decreased in area (left to right) and consisted of the entire study area (west Delta), the west Delta with estimates of available forage biomass adjusted according to road effects (road bias-adjusted), a range restricted by our plot spatial distribution (≤ 1.5 km from the roads; plot inference), and a range determined by a previous study (MacCracken et al. 1997).

Figure 3.4. Continued…



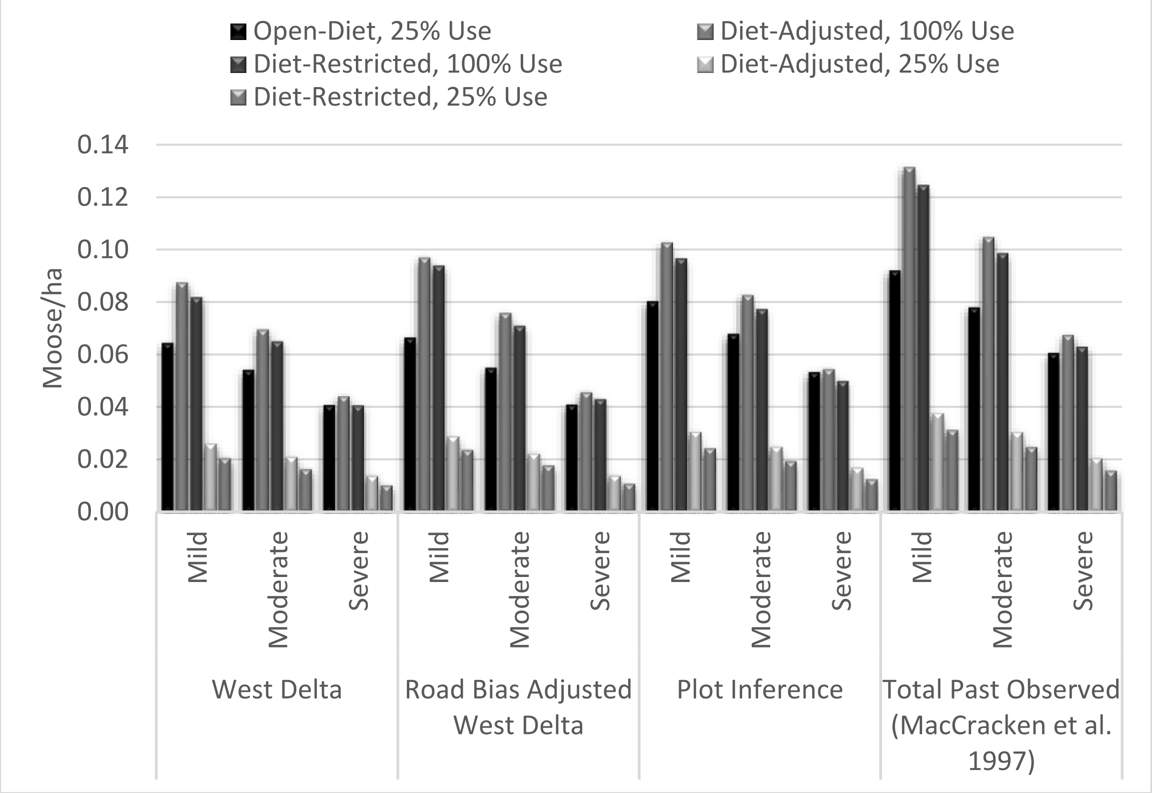


Table 3.5: **C**hanges (%) and proportional sensitivities (*Sx*) of the independent components in an open-diet (25% use of all forage species) model used to estimate nutritional carrying capacity for moose within the west Delta winter range in a severe winter on the Copper River Delta, AK.

Model Variable	**% Adjusted**	**Full Delta NCC**	**± CI**	**% Change**	**Proportional Sensitivity (Sx)**
No Change	0	2,198	54	--	
Protein Reduction	+5%	2,169	75	-1.33	-0.27
Lignin	+5%	2,176	64	-1.00	-0.20
Gross Energy	+5%	2,292	75	4.28	0.86
Stem Biomass	+5%	2,284	87	3.90	0.78
Stem Density	+5%	2,314	87	5.27	1.05
Snow Depth	+5%	2,410	94	9.64	1.93
Area	+5%	2,316	52	5.35	1.07
Winter Length	+5%	2,093	51	-4.76	-0.95
Moose Energy	+5%	2,093	51	-4.76	-0.95

Table 3.6: Past (1987–89; MacCracken et al. 1997) and present (2012–13) estimations and differences (%) of biomass (kg/ha) of the 8 forage species available to wintering moose on the western region of the Copper River Delta, Alaska.

Browse Species	**1987–89 Biomass, kg/ha (SD)**[a]	**2012–13 Biomass, kg/ha (SD)**	**Change 1987–89 to 2012–13, %**
Cottonwood (*Populus trichocarpa*)	17.50 (27.45)	103.77 (205.92)	493
Alder (*Alnus viridis sinuata*)	415.75 (378.78)	283.88 (332.44)	-32
Sitka Willow (*Salix sitchensis*)	102.75 (117.97)	93.29 (93.63)	-9
Barclay's Willow (*S. barclayi*)	269.00 (114.04)	107.58 (91.08)	-26[d]
Hooker's Willow (*S. hookeriana*)	NA[b]	92.53 (71.45)	NA[d]
Undergreen Willow (*S. commutata*)	7.50 (5.26)	8.15 (9.21)	9
Feltleaf Willow (*S. alexensis*)	155.75 (180.15)	NA[c]	NA
Sweetgale (*Myrica gale*)	226.75 (259.05)	76.20 (132.09)	-66

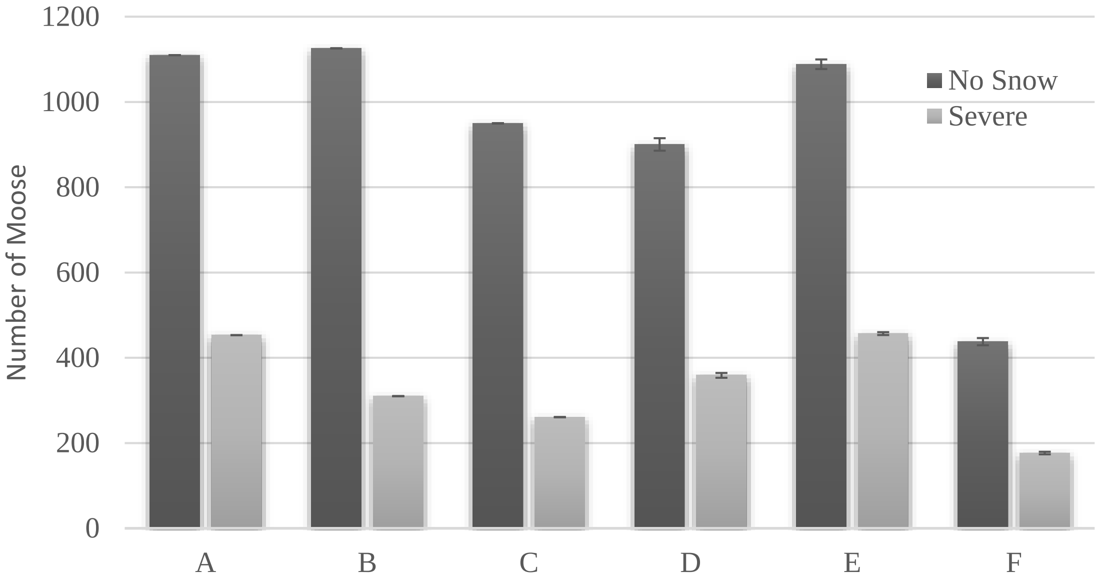
[a] MacCracken et al. (1997)

[b] Not sampled; possibly combined with Barclay's willow.

[c] Did not occur in sampling plots.

[d] Combined biomass of 2012–13 Barclay's and Hooker's willow before calculating % change.

Figure 3.5: Nutritional carrying capacity estimates (numbers of moose) on a subsection of the glacial outwash plains (Stephenson et al. 2006) of the western Copper River Delta, AK using different map years (1959, 1986, or 2011), map types (aerial, projected, or satellite), data collection periods (1990–93 or 2012–13) used to estimate biomass of forage species, and model types (biomass-based or energy-based) within 2 winter scenarios (no snow and severe). Confidence intervals are provided where available. Projected map estimates of stand areas were calculated using a Markov-Chain model of vegetation change (Stephenson et al. 2006). Energy-based models include nutritional quality estimates of forage species.



		A	B	C	D	E	F
Map Used for Stand Area (ha) Estimate	1959 Aerial Map[a]	X					
	1986 Aerial Map[a]		X				
	2013 Markov-Chain Projected Map[a]			X	X		
	2011 SPOT5 Satellite Map					X	X
Forage Species Biomass Collection Period	1990–93[a]	X	X	X			
	2012–13				X	X	X
Model Type	Biomass-based (kg/ha)	X	X	X	X	X	
	Energy-based (kcal/ha)[b]						X

[a] Stephenson et al. 2006

[b] Energy-based estimates incorporate species-specific values of nutritional quality.

Table 3.7: Total areas (ha) and between-year changes (%) of the 7 stand types relevant to moose winter ecology and all others combined (other) classified with 1959 and 1986 aerial maps (Stephenson et al. 2006) and a 2011 Satellite Pour l'Observation de la Terre (SPOT version 5 [SPOT5] satellite map within a subsection of the glacial outwash plains and uplifted marsh (delineated by Stephenson et al. 2006) on the west Copper River Delta, AK.

Stand Type	**1959 Areas**	**1986 Areas**	**2011 Areas**	**% Change 1959–1986**	**% Change 1986–2011**
Spruce-Hemlock	1,511	2,043	1,600	35.2	-21.7
Spruce-Cottonwood	56	426	1,170	660.7	174.7
Cottonwood	176	178	78	1.1	-56.2
Alder	331	1,452	3,412	338.7	135.0
Alder-Willow	1,254	874	349	-30.3	-60.1
Willow	1,937	2,127	544	9.8	-74.4
Sweetgale	567	1,543	3,519	172.1	128.0
Other	11,967	9,151	7,168	-23.5	-21.7

CHAPTER 4: IMMEDIATE AND CONTINUING EFFECTS OF MECHANICAL TREATMENT ON WINTER MOOSE BROWSE

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ABSTRACT

Sites containing forage species utilized by moose (*Alces alces gigas*), on the Copper River Delta of south-central Alaska were mechanically treated (hydraulic-axed) to counteract possible earthquake-related increases in non-preferred forage species, and to determine treatment effects on biomass (kg/ha), height (m), nutritional quality (% crude protein, % lignin, and tannin [BSA mg/g]), utilization (%), and snow burial on preferred (willow) and less-preferred (sweetgale, cottonwood, and alder) forage species within 3 winter scenarios (mild, moderate, and severe). Sites were treated in 4 winters (1990–92, 2008, 2010, and 2012) within 5 stand types in 20 locations varying from 0.86–63.40 ha in size. We found few significant differences in treated biomass, height, nutritional quality, utilization, and burial by snow relative to controls. However, our results may be limited by sample sizes (n = 1-9) as visual comparison suggests treatment via hydraulic-axing may be an effective method for increasing willow biomass while decreasing alder biomass without influencing nutritional quality. However, treated willows are significantly shorter than untreated willows ($P = 0.03$). Thus, treatment may result in decreased forage available to moose in severe winters. Our results have implications for habitat management of moose but further research is needed to determine the long-term effects of treatment on willow growth.

INTRODUCTION

Mechanical manipulation of forage is a common strategy in the management of ungulate habitat in North America. Because many deer species rely on early-successional forage, habitat management efforts often focus on delaying forest progression to climax species (Hundertmark et al. 1990, Renecker and Schwartz 1997, Suring and Sterne 1998). These methods have included mechanical shearing, crushing, and axing of overstory vegetation (Scotter 1980, Thompson and Stewart 1997). Mechanical treatment of moose (*Alces alces gigas*) habitat has been used on a limited scale in south-central Alaska on the Copper River Delta (CRD; Delta; Fig. 1) (Stephenson et al. 1998). Moose were introduced to the CRD from 1949-1958, having been naturally excluded by topography (MacCracken et al. 1997). The population has since increased to over 830, divided into western and eastern semi-distinct sub-populations (~ 600 and 230 moose, respectively) separated by the Copper River (C. Westing, Alaska Department of Fish and Game Cordova office, unpublished data). Most management efforts focus on the more accessible and heavily-hunted western population, with a potential range encompassing over

54,000 ha (MacCracken 1992, T. Joyce, USDA Forest Service Cordova Ranger District, personal communication.). However intense winter winds through the Copper River canyon combined with snow depths and drifting, which vary with winter severity, can restrict the range to about 4,800-12,900 ha (MacCracken et al. 1997, Stephenson et al. 2006). This variable seasonal effect restricts the browse accessible to moose and is likely the limiting factor on moose survival during winter (Regelin et al. 1985, Schwartz et al. 1988). Wintering moose on the Delta depend on five willow species, feltleaf willow, Barclays willow, undergreen willow, Hookers willow, and Sitka willow (*S. alexensis, S. barclayi, S. commutata, S. hookeriana, S. sitchensis,* respectively), and only occasionally on black cottonwood (*Populus trichocarpa*), sweetgale (*Myrica gale*), and Sitka alder (*Alnus viridis sinuata*) (MacCracken et al. 1997). A 9.2 magnitude earthquake in 1964 uplifted the area by 1.0–4.0 m (Grantz et al. 1964, Ferrians 1966, Plafker 1969, Stover 1993), initiating changes in hydrology, soil salinity, and vegetation including an acceleration of succession in some stands to stages with lower browse production (Thilenius 1990;2008). The combined effects of winter range restriction and vegetation changes might further limit population performance and persistence (MacCracken et al. 1997, Stephenson et al. 2006).

To address concerns about potential decreases in moose browse, managers (USDA Forest Service Cordova Ranger Station) began experimenting with mechanical treatment of moose habitat through hydraulic-axing (hereafter hydro-axing) in 1990–1992. Additional treatments were completed in 2008, 2010, and 2012 (M. Burcham & T. Joyce, USDA Forest Service Cordova Ranger District, personal communication, Stephenson et al. 1998). Hydro-ax machines use rotary axes to cut down and splinter trees or shrubs up to 15 cm in diameter (Stephenson et al. 1998). Willows in the Kenai National Forest re-sprouted following mechanical treatment while mature red alder (*A. rubra*) stems experienced high mortality (Oldemeyer and Regelin 1980, Harrington 1984). Thus, most treatments on the CRD were sited on established, often alder-dominated stands with remnant willow components in order to encourage willow growth in those stands with the greatest potential for increased browse yields. However, spruce-cottonwood, sweetgale, and willow-dominated stands have also been treated (Table 1). Stephenson et al. (1998) evaluated the success of the initial (1990–1992) treatments 1-3 years post-treatment and found alder mass generally declined in treated sites, while Sitka willow mass increased. Responses by Barclay's willow and sweetgale varied by stand type. Conclusions about biomass responses of cottonwood, feltleaf willow, and undergreen willow were precluded by small samples sizes, and responses by Hooker's willow were unknown as that species was not identified in the study area then (Stephenson et al. 1998, J. MacCracken, personal communication.). Browse utilization by moose varied by plot site, vegetation structure, and snow depths, but only utilization of treated sweetgale and Sitka willow was significantly higher than in adjacent uncut controls (Stephenson et al. 1998). No work was performed to document the effects of mechanical treatment on available biomass, height, nutritional value, or utilization of browse by moose 4+ years post-treatment. In addition, mean height of browse in early-successional and treated stands was often less than mid- or late-successional stands, and snow burial of browse varied by location on the Delta, treatment, and stand type (Stephenson et al. 1998). The researchers hypothesized that full height (5m) Sitka willow in alder- and willow-dominated stands would be especially important in winters with deep snow and heavy drifting. Therefore, if treatment increases the prevalence of early-successional stands with shorter willows, it is possible extensive treatment on the Delta could coincidentally limit browse available to moose in severe winters. Use of hydro-axing is also very challenging on the Delta. Managers need data to evaluate the relative costs to browse benefits of this potential habitat management tool.

Our objectives were to 1) evaluate species-specific and time-since-treatment responses of key winter browse species to mechanical treatment by evaluating available biomass, height, nutritional quality, and utilization and 2) estimate how biomass availability within treated sites might vary with snow depth (winter severity). Based on previous research, succession, and willow regeneration, we hypothesized willow biomass (kg/ha) would increase and alder, cottonwood, and sweetgale biomass would decrease in all treated sites relative to their untreated adjacent controls. Because of regeneration we expected browse biomass to differ between treated and untreated sites, with biomass increasing with time-since-treatment (across the 2012, 2010, 2008, and 1990–1992 sites). We hypothesized treated browse would be shorter (m) than untreated controls, with the exception of those plots cut in 1990–1992, in which we expected the browse would have had sufficient time to regrow to maximize height. Because prior work noted few differences in utilization between treated and untreated browse, we did not expect nutritional quality (% crude protein, % lignin, and tannin [BSA mg/g]) and utilization (%, kg/ha) to differ by treatment. We expected no time-since-treatment effect on nutritional quality or utilization. We hypothesized potential snow burial of browse would be greatest in stand types composed of shorter species (e.g., willows and sweetgale) and in the most recently treated stands (2012). Our results will assist managers in assessment of the relative benefits of hydro-axing as a tool to maintain willow availability for moose in an area subject to earthquake-initiated changes in vegetation.

METHODS

Study Area

The CRD lies within the Chugach National Forest and is bordered by three glaciers, the Chugach Mountain Range, and the Gulf of Alaska (Fig. 1). It is the largest continuous wetland on the Pacific Coast of North America, extending 120 km along the coast and supporting abundant early-successional browse maintained by a moist, relatively mild climate, a lengthy growing season, and continuous channel shifts by glacial streams and the Copper River (USDA-FS, Christensen et al. 2000, Kesti et al. 2007, Thilenius 2008). Using a Satellite Pour l'Observation de la Terre (SPOT version 5 [SPOT5], 2011, Red Castle Resources, Inc.) map, we identified 7 stand types which produce winter browse resources for moose: spruce-hemlock, spruce-cottonwood, cottonwood, alder, alder-willow, willow, and sweetgale (Viereck 1992). Spruce-hemlock, spruce-cottonwood, alder, and sweetgale can all be late-successional stands depending on hydrology, but alder-willow, willow, and sweetgale stands are generally considered early-successional (Boggs 2000). Drainage and desalination resulting from the 1964 earthquake increased the abundance of spruce-hemlock and alder stand types while accelerating succession within some stand types to willow, alder, Sitka spruce (*Picea sitchensis*), and western hemlock stands (*Tsuga heterophylla*) (Boggs 2000, Stephenson et al. 2006, Thilenius 2008). Total winter snow depths range from 83.3–548.6 cm (1994–2013; ACRC 2014), but the area also receives significant rainfall (annual mean of 236 cm) that is frequently interspersed within periods of snowfall (Kesti et al. 2007). This phenomenon varies with winter severity and can significantly affect snow accumulation, drifting, and compaction, complicating efforts to understand the interaction between snow depth, moose behavior, and browse availability.

Treatments and data collection

Prior to initial treatments, managers subjectively evaluated and rated potential treatment site suitability as high, medium, or low using factors of willow composition, encroachment by other woody species, and the level of organic matter in the understory (M. Burcham, USDA Forest Service Cordova Ranger District, unpublished data). Only sites that ranked as highly suitable were treated. Due to logistical constraints related to moving heavy equipment through the wetlands, sites were partially determined by road accessibility and were treated in winter on frozen ground. Managers refined their site selection techniques in later treatment years (2008 and later), focusing on stand types in which species composition held the greatest promise for increased browse production in response to mechanical treatment. In total, from 1990–2012 the Forest Service treated approximately 300 ha. Treatments were applied to 32 sites in 5 stand types varying from 0.86–63.40 ha in the east-central, mid-central, and north-central regions (Table 1 and Figure 1). All sites were unfenced and open to utilization by moose.

We sampled sites during fall (Aug–Sept) 2012–2013 and spring (Apr–May) 2013 to capture maximum growth, and winter utilization and nutrition, respectively. Because of difficulties in accessibility and differences in moose browsing pressure among sites, we selected 20 comparable sites treated in the east-central and mid-central region of the Delta (Table 1 and Figure 1). We selected randomized sampling plots in the treated sites and untreated surrounding areas, categorizing each site by the current stand type of the adjacent control. The plots consisted of three random-start belt transects (1 x 10 m) separated by 5 m. We estimated biomass available to moose (total biomass of twigs with diameter ≤ 8.3 mm; g/stem) with basal diameter-mass regression equations (Table 2; MacCracken and Van Ballenberghe 1993, Stephenson et al. 1998). At every 0.5 m along belt transects we measured basal diameters (mm; above the moss layer) on the 3 stems closest to the transect center. Very large stem basal diameters (> 60.0 mm) increase regression equation heteroskedasticity (MacCracken and Van Ballenberghe 1993). With such stems we instead measured a branch diameter and estimated how many equivalent branches composed the shrub. Within the belt transects, we calculated stem density (stems/ha), and measured shrub height (m) on three replicates of every species. We estimated the available biomass (%) on each stem in 1 m increments of height from 0–6 m to reflect the range of moose browsing in winter on the CRD depending on snow pack conditions (T. Joyce, USDA Forest Service Cordova Ranger District, personal communication.). We calculated the total available biomass (kg/ha; stem biomass x stem density) of every species in each plot.

To calculate moose utilization, we measured every instance of browsing (bite diameters) on the closest stem at every 0.5 m along the transects. We estimated biomass consumed (g/twig) with bite diameter-mass regression equations (MacCracken and Van Ballenberghe

1993) and summed the biomass removed per stem (g/stem). We collected nutritional samples of every browse species found at each plot, stored them fresh-frozen, stripped twigs of any leaves, and sent them to the Washington State University Wildlife Habitat and Nutrition Lab (Pullman, WA) for analysis (crude protein, lignin, and tannin levels). We developed winter scenarios (mild, moderate, and severe) by summarizing data on mean winter snow depth (cm) and length (days from first snowfall to last) from 1917–2012 collected by the Alaska Climate Research Center (ACRC 2014) at Cordova's "Mudhole Smith" Airport weather station. We then estimated the potential effects of snow depth on browse availability by adjusting total available biomass present in each treatment and control plot according to our estimates of mean snow burial under each winter scenario.

To evaluate differences between treated sites and their controls, we used t-tests to compare individual species and total plot available biomass (kg/ha), ratios of willow to alder (willow:alder), height (m), crude protein (%), lignin (%), tannin (mg/g), and utilization (%) of browse species by moose. We found individual willow species effects did not differ significantly and thus they were pooled in subsequent *t*-tests. Feltleaf willow was not recorded in any plot and was removed from further consideration. We initially tested for stand type differences in time-since-treatment effects, but most stand types were not statistically different from their controls or each other. Thus, we pooled all stand types for time-since-treatment analyses and used ANOVAs (Analysis of Variance) to compare treatments across time and winter scenarios. Because the 1990–1992 cut sites were not documented separately, they were analyzed as a single treatment type.

RESULTS

We found treated willow, sweetgale, and total available biomass in 1990–92 treated sites were significantly higher than controls (Table 3; $P = 0.05$, 0.003, and 0.001, respectively), but no other differences in available biomass between treated and untreated sites in any winter browse species or treatment years were detected. When weighted according to their untreated controls (cut/control*100), neither the total relative available biomass nor the relative willow biomass were significantly different across times-since-treatment (Figures 2 and 3). Alder in 2012 plots were significantly shorter than in controls ($P = 0.03$). Average willow height showed no significant effect of time-since-treatment (Figure 4). However, the average treated willow in all sites is significantly shorter than the average untreated willow ($P = 0.003$). There were no statistically significant differences in nutritional quality or utilization by moose across any of our comparisons. The ratio of willow:alder in treated sites was significantly higher than controls in sites 23 years post-treatment and all treatment years differed significantly (*P* = 0.004 and 0.02, respectively, 3 df; Table 4).

We developed three winter scenarios (mild, moderate, and severe) with mean snow depths of 11.4 cm (± 9.9-12.9), 25.8 cm (± 23.3-28.3), and 63.9 cm (± 47.4-80.4), respectively, and mean winter lengths of 147 days (± 139-154), 163 days (± 156-171), and 178 days (±156-200), respectively. Each winter scenario occurred 49, 29, and 11 times, respectively, between 1917–2012, and 6 winters were not categorized due to missing data. Total available biomass across times-since-treatment varied significantly within all snow scenarios (*P* = 0.007-0.03, 4 df; Fig. 5). Biomass in treated 1990–92 plots differed significantly across the snow scenarios (*P* = 0.04, 3 df), with total available biomass decreasing 61% from mild to severe winters. Total available willow biomass across times-since-treatment also varied significantly within all snow scenarios (*P* = 0.01-0.05, 4 df; Fig. 6). Treated 2008 plot willow biomass differed significantly across snow scenarios (*P* = 0.05, 3 df), decreasing by 95% from mild to severe winters.

DISCUSSION

Our sample sizes and variability within our samples likely limited our ability to detect statistically significant differences (*n* = 1–9 treated stands). Given the observed variability, our a posteriori power analyses suggested sample sizes of 9–17 would be necessary to detect significance in comparisons of willow-only and all-species browse. However, visual examination of the data suggests treatment via hydro-axing produces notably more total and willow biomass, with the effect increasing with time since treatment. Furthermore, treatment significantly increased the ratio of willow:alder over time. This suggests hydro-axing may be an effective method for increasing willow biomass to counter earthquake-initiated or successional increases in alder. Hydro-axing does not seem to influence the nutritional quality of the treated browse, as suggested by the insignificant differences in crude protein (%), lignin (%), tannins (BSA mg/g), and utilization (%) by moose, though our findings may again be limited by small sample sizes. The high variability in height (m) of treated willows makes it difficult to determine if hydro-axing affects final regrowth height. Because the average treated willow is shorter yet more productive than the average untreated willow, hydro-axing may be changing the growth form of treated willows to be bushier, with more biomass concentrated in many smaller shoots from the recovering stem. A changed architecture may explain the larger decrease in available biomass relative to controls in sites treated in 1990–92 as winter severity and snow depth increased. However, after 23 years of regrowth, mean available biomass in severe winters is similar to the mean available biomass provided by controls, suggesting increases in overall treated biomass availability may compensate for losses due to snow burial.

MANAGEMENT IMPLICATIONS

Overall, our results suggest mechanical treatment of moose winter browse species via hydro-axing could be a useful method for increasing the ratio and biomass of willow available to moose on the CRD after 23 years of regrowth. However, extensive treatment could limit browse availability to moose in more extreme winter scenarios relative to untreated stands for a few decades until regrowth can occur. Managers should be cautious in applying this technique across large areas concurrently. Furthermore, because of the large gap between the 2008 and 1990–92 treatments, we were unable to determine when the regrowth asymptote occurs. Further research at graded intervals is needed to determine the regrowth pattern and long-term effects of mechanical treatment on the moose forage species of the CRD.

TABLES AND FIGURES

Figure 4.1. Sites mechanically-treated (hydraulic-axed) in 1990–92, 2008, 2010, and 2012 on the west Copper River Delta of south-central Alaska to improve the availability of willow forage for wintering moose.

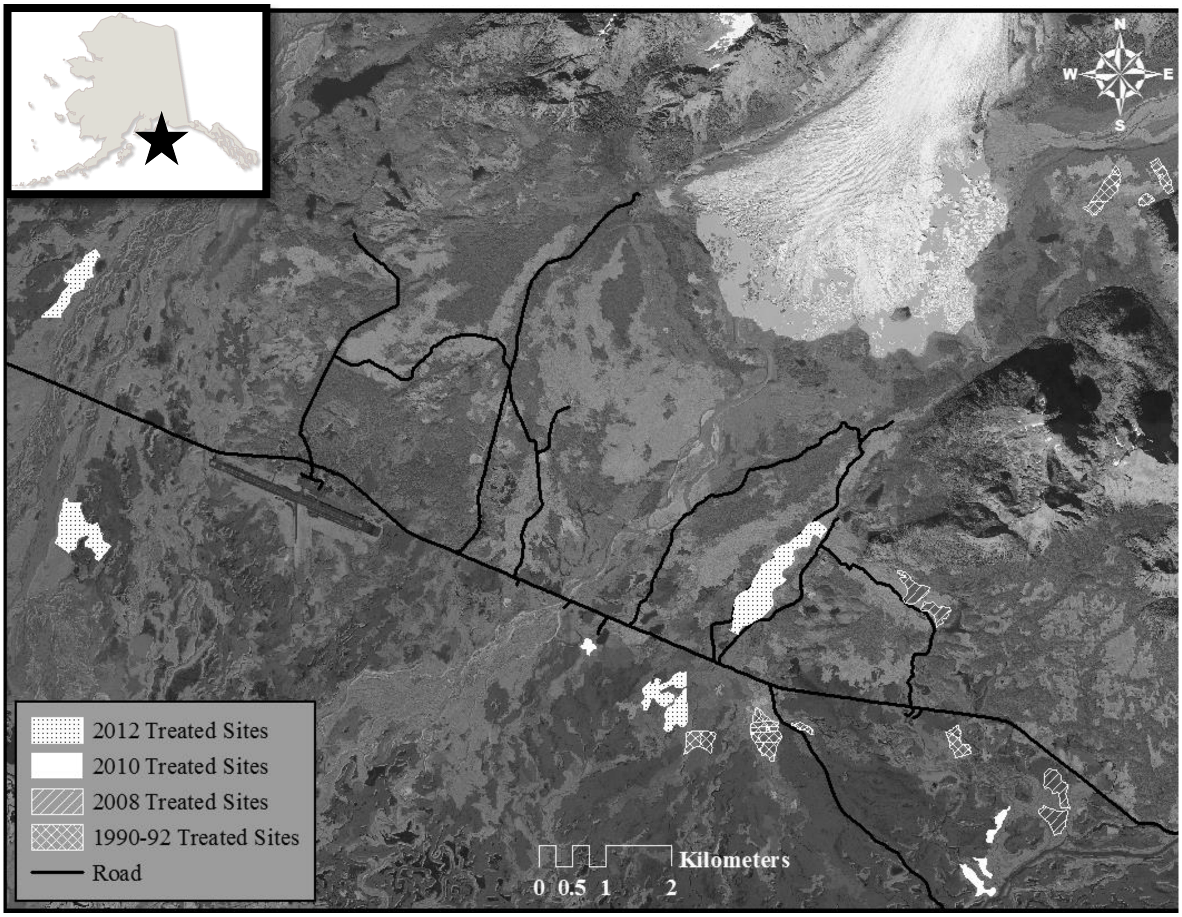


Table 4.1. Characteristics of mechanically treated (hydraulic-axed) sites sampled (2012–2013) for moose winter browse on the western region of the Copper River Delta, Alaska, including site age (years since treatment), control stand type, soil type, area (ha), and sampling replicates.

Age (years)	**Winter Treated**	**Control Stand Types**	**Soil Type**[a]	**Size (ha)**	**Replicates (*n*)**
1	2012/2013	Spruce-Cottonwood	AST	57.87	1
		Alder	AST	23.87, 63.40	2
3	2010/2011	Alder	OPN	3.42	1
		Sweetgale	AST	7.96, 3.38, 5.69	3
5	2008/2009	Spruce-Cottonwood	GM	10.71, 7.64	2
		Willow	AST	11.84, 10.54	2
22–23	1990–1991	Spruce-Hemlock	OPN	0.86, 1.53	2
	& 1991–1992	Alder	AST/OPN	2.99, 2.24	2
		Alder-Willow	AST	0.89, 4.92	2
		Willow	AST	1.53	1
		Sweetgale	OPN	2.58, 0.85	2

[a] Soil Types include AST = alluvium and stream terrace deposits , OPN = glacial outwash plains, nonforested , GM = undifferentiated glacial moraines (Davidson and Harnish 1978).

Table 4.2. Regression equations used to estimate species-specific forage biomass available (g/stem) and biomass consumed (g/twig) by moose wintering on the Copper River Delta, AK. Equations for biomass available and consumed are derived from measurements of basal diameters (BD, mm) and bite diameters (bD, mm), respectively. Available biomass equations were developed in both mechanically-treated (hydraulic-axed) and untreated control sites. Treated site equations are presented according to their site age (time since treatment, as of sampling in 2012 & 2013).

Browse Species	**Time Since Treatment**				**Untreated**[c]	**Consumption**[c]
	1 Year[a]	3 Years[a]	5 Years[b]	22-23 Years[b]		
Cottonwood (*Populus trichocarpa*)	$= \exp(-4.22)(BD^{2.85})$	$= 0.64(BD)$	$= 0.15(BD^{1.97})$	[g]--	$= 2.37(BD)$	$= 0.04(bD^{2.6})$
Alder (*Alnus viridis sinuata*)	$= \exp(-3.89)\ (BD^{2.77})$	$= \exp(-2.45)(BD^{1.8})$	$= 0.03(BD^{2.58})$	$= 4.12(BD)$	$= 2.33(BD)$	[d]$= 0.03 + 0.06(bD^{2.5})$ or $= 0.34(bD^{4})$
Sitka Willow (*Salix sitchensis*)	$= \exp(-3.16)\ (BD^{2.52})$	$= \exp(-0.93)(BD^{1.46})$	$= 0.13(BD^{2.02})$	$= 0.21(BD^{1.8})$	$= 11.07(\ln BD)$	$= 0.03 + 0.06(bD^{2.5})$
Barclay Willow (*S. barclayi*)	[e,f]$= \exp(-3.50)\ (BD^{2.72})$	[f]$= 0.98(BD)$	$= 1.74(BD)$	$= 2.56(BD)$	[e]$= 0.14(BD^{1.93})$	$= 0.05 + 0.03(bD^{2.7})$
Hooker's Willow (*S. hookeriana*)	[e,f]$= \exp(-3.50)\ (BD^{2.72})$	[f]$= 0.98(BD)$	$= 0.11(BD^{2.09})$	$= 1.43(BD)$	[e]$= 0.18(BD^{1.80})$	$= 0.05 + 0.03(bD^{2.7})$

Table 4.2. Continued…

Browse Species	**Time Since Treatment**				**Untreated**[c]	**Consumption**[c]
Undergreen Willow (*S. commutata*)	$= \exp(-3.12)\ (BD^{2.48})$	$= 0.56(BD)$	$= 1.51(BD)$	$= 1.40(BD)$	$= 0.55(BD)$	$= 0.05 + 0.03(bD^{2.7})$
Sweetgale (*Myrica gale*)	$= 0.12\ (BD)$	$= 0.22(BD)$	$= 1.26(BD)$	$= 1.70(BD)$	$= \exp(-3.33)(BD^{2.15})$	[d]$= 0.05 + 0.03(bD^{2.7})$ or $= 0.12(bD^{2})$

[a] developed by Stephenson et al. (1998)
[b] developed by Smythe et al. (current)
[c] developed by MacCracken and Van Ballenberghe (1993)
[d] revised by Stephenson et al. (1998)
[e] revised by Smythe et al. (current); negative added to coefficient
[f] separate equations were not developed for Hooker's and Barclay willows (Smythe et al. in prep)
[g] sample size was insufficient to develop a regression equation

Table 4.3. Species-specific and total mean (± SD) available biomass (kg/ha), height (m), crude protein (%), lignin (%), tannin (mg/g), and use (%) of winter browse for moose in mechanically treated (cut, via hydraulic-ax) and untreated (control) sites on the Copper River Delta, AK. Treated sites were sampled 1, 3, 5, or 23 years post-treatment (age) in 2012 & 2013.

Browse Species	Cut Age (years)	Treatment	Biomass (kg/ha)	Height (m)	Crude Protein (%)	Lignin (%)	Tannin (mg/g)	Use (%)
Black Cottonwood	1	Cut	10.89 (--)	1.0 (--)	^{a}--	^{a}--	^{a}--	^{a}--
(*Populus trichocarpa*)		Control	2343.00 (--)	6.0 (--)	^{a}--	^{a}--	^{a}--	^{a}--
	3	Cut	^{b}--	^{b}--	^{b}--	^{b}--	^{b}--	^{b}--
		Control	^{b}--	^{b}--	^{b}--	^{b}--	^{b}--	^{b}--
	5	Cut	15.18 (11.05)	2.3 (1.2)	8.16 (2.56)	12.47 (0.65)	0.00 (0.00)	18.47 (0.32)
		Control	573.53 (522.92)	4.0 (2.8)	5.45 (--)	13.28 (--)	0.00 (0.00)	0.00 (0.00)
	23	Cut	^{b}--	^{b}--	^{b}--	^{b}--	^{b}--	--
		Control	21.49 (51.19)	4.5 (2.1)	4.74 (--)	18.7 (--)	0.00 (--)	18.47 (--)
Sitka Alder (*Alnus*	1	Cut	18.15 (13.43)*	1.0 (0.0)**	^{a}--	^{a}--	^{a}--	^{a}--
viridis sinuata)		Control	605.42 (307.10)*	4.7 (1.2)**	^{a}--	^{a}--	^{a}--	^{a}--
	3	Cut	3.78 (4.99)	1.5 (0.7)	^{c}7.64 (--)	^{c}14.7(--)	^{c}31.6(--)	57.05 (15.20)
		Control	138.59 (240.04)	6.0 (--)	^{c}7.64 (--)	^{c}14.7(--)	^{c}31.6(--)	0.40 (--)
	5	Cut	^{b}--	^{b}--	^{b}--	^{b}--	^{b}--	^{b}--
		Control	125.48 (149.59)	4.0 (0.0)	7.64 (--)	14.7(--)	31.6(--)	0.00 (0.00)
	23	Cut	143.42 (430.25)	5.0 (--)	7.64 (--)	14.7(--)	31.6(--)	0.00 (--)
		Control	257.49 (429.99)	4.5 (1.29)	7.64 (--)	14.7(--)	31.6(--)	7.17 (12.41)

Table 4.3. Continued…

Browse Species	Cut Age (years)	Treatment	Biomass (kg/ha)	Height (m)	Crude Protein (%)	Lignin (%)	Tannin (mg/g)	Use (%)
Willow spp. (*Salix* spp.)	1	Cut	78.13 (75.01)	1.3 (0.6)	[a]--	[a]--	[a]--	[a]--
		Control	279.81 (253.04)	3.9 (1.9)	[a]--	[a]--	[a]--	[a]--
	3	Cut	386.19 (416.60)	1.4 (0.5)	7.04 (0.71)	11.87 (0.48)*	49.07 (17.64)	14.50 (10.87)
		Control	405.41 (244.35)	2.3 (0.7)	6.91 (0.89)	15.47 (2.08)*	44.51 (19.55)	12.67 (5.03)
	5	Cut	550.79 (370.05)	1.6 (0.5)	7.91 (1.13)	15.53 (1.47)	32.28 (30.92)	3.25 (4.27)
		Control	260.67 (112.35)	3.7 (1.5)	6.85 (1.18)	13.71 (1.29)	43.52 (3.03)	0.00 (0.00)
	23	Cut	1225.01 (614.71)**	2.0 (0.5)	7.06 (0.54)	15.60 (1.67)	48.26 (16.92)	16.17 (15.45)
		Control	522.89 (408.90)**	2.5 (0.7)	7.07 (0.64)	15.61 (0.54)	37.48 (30.56)	11.83 (8.35)
Sweetgale (*Myrica gale*)	1	Cut	21.06 (36.47)	1.0 (--)	[a]--	[a]--	[a]--	[a]--
		Control	0.04 (0.08)	1.0 (--)	[a]--	[a]--	[a]--	[a]--
	3	Cut	76.63 (86.54)	1.0 (0.0)	8.50 (0.64)	22.42 (0.86)	44.53 (1.33)	53.00 (23.07)
		Control	250.13 (221.49)	1.0 (0.0)	6.85 (--)	22.61 (--)	98.90 (--)	33.50 (21.92)
	5	Cut	403.28 (547.33)	1.0 (0.0)	6.75 (--)	17.00 (--)	41.00 (--)	10.80 (6.22)
		Control	[b]--	[b]--	[b]--	[b]--	[b]--	[b]--
	23	Cut	503.02 (560.63)**	1.0 (0.0)	7.53 (0.46)*	21.73 (0.59)*	56.98 (27.95)*	7.75 (8.18)
		Control	56.30 (103.77)**	1.0 (0.0)	6.91 (0.11)*	22.51 (0.17)*	95.37 (6.12)*	40.00 (40.15)

Table 4.3. Continued…

Browse Species	Cut Age (years)	Treatment	Biomass (kg/ha)	Height (m)	Crude Protein (%)	Lignin (%)	Tannin (mg/g)	Use (%)
Total Winter Browse Species	1	Cut	120.96 (80.93)	1.17 (0.29)*	[a]--	[a]--	[a]--	[a]--
		Control	1666.26 (1292.39)	4.13 (1.63)*	[a]--	[a]--	[a]--	[a]--
	3	Cut	466.59 (476.44)	1.35 (0.47)	7.52 (0.27)	14.80 (1.27)	43.66 (6.70)	23.28 (12.00)
		Control	794.12 (212.15)	2.38 (1.19)	6.94 (0.80)	16.40 (2.53)	51.06 (23.13)	16.00 (15.09)
	5	Cut	969.24 (852.05)	1.76 (0.77)	8.13 (1.50)	14.47 (0.23)	23.79 (23.96)	5.00 (5.83)
		Control	959.69 (663.60)	3.44 (1.50)	6.81 (0.55)	14.13 (0.83)	30.43 (8.34)	0.00 (0.00)
	23	Cut	1871.44 (711.48)**	1.96 (0.56)*	7.19 (0.38)	16.77 (2.04)	46.76 (16.92)	10.67 (4.23)
		Control	858.17 (454.79)**	2.86 (1.01)*	7.06 (0.60)	16.20 (1.30)	40.75 (29.50)	9.33 (7.58)

[a] Re-growth of sites had not occurred by the time of spring nutritional sampling in one-year-old sites, but had occurred by the time of fall biomass sampling

[b] Species did not occur in site

[c] Alder samples combined for nutritional analysis

**T-test *P* ≤ 0.05 between cut and control

* T-test *P* = 0.06–0.10 between cut and control

Figure 4.2. Total relative biomass (cut/uncut*100, ± SD) of browse species available to wintering moose within mechanically treated (via hydraulic-ax between 1990–2012) sites on the Copper River Delta, Alaska as of 2012–13 sampling. The dashed line represents treated site recovery of pre-treatment biomass (100%). Relative biomass across the 4 treatments was not significantly different (*P* = 0.15, 3 df).

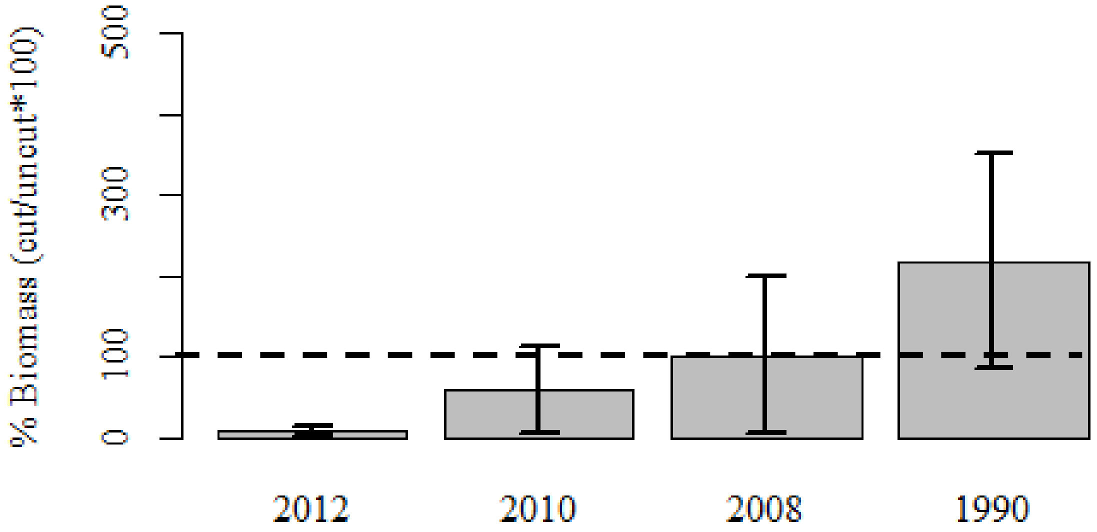


Figure 4.3. Relative willow (*Salix* spp.) biomass (cut/uncut*100, ± SD) available to wintering moose within mechanically treated (via hydraulic-ax between 1990–2012) sites on the Copper River Delta, Alaska as of 2012–2013 sampling. The dashed line represents treated site recovery of pre-treatment biomass (100%). Relative biomass across the 4 treatments was not significantly different (*P* = 0.13, 3 df).

Figure 4.4. Mean height (m, ± SD) of willows (*Salix spp*.) present in sites mechanically treated (hydraulic-axed) from 1990/92–2012 relative to the mean height of untreated willows (2.85 m, dashed line) on the Copper River Delta, Alaska as of 2012–2013 sampling. The average treated willow is significantly shorter than the average untreated willow (*P* = 0.003), but treated willow heights across treatment years are not significantly different (*P* = 0.13, 3 df).

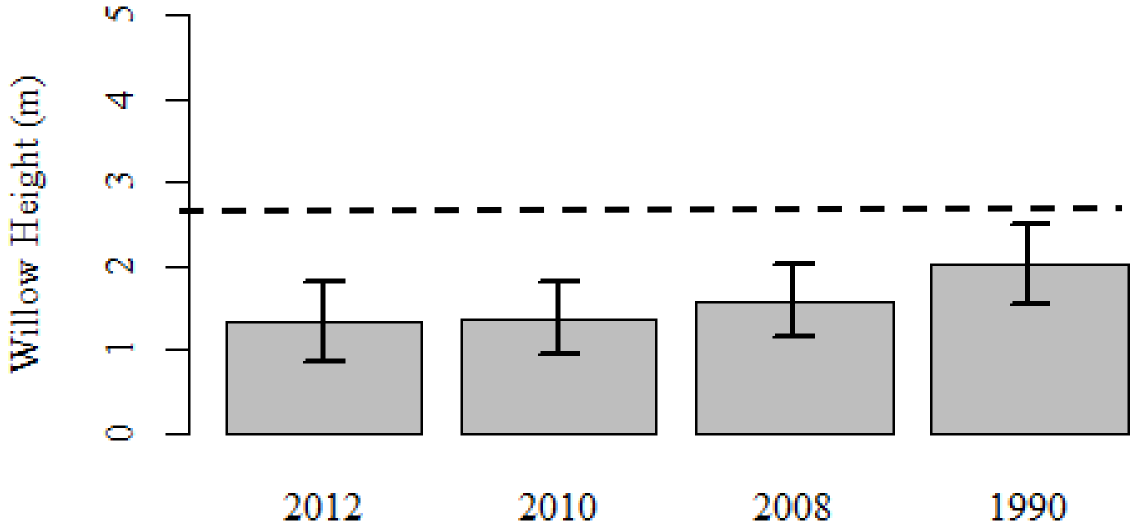


Table 4.4. Ratios of available biomass for willow (*Salix* spp.) and alder (*Alnus viridis sinuata*; willow:alder) in mechanically-treated (hydraulic-axed) and untreated (control) sites across 4 different treatment years prior to this study (2012–2013) on the Copper River Delta, Alaska.

	1 Year	**3 Years**	**5 Years**	**23 Years**
Control	0.77	360.11	74.38	205.82
Treated	11.26	323.63	550.79	1163.37
Significance between treated and control (*t*-test)	0.33	0.91	0.08	0.004
Significance across all treatments (ANOVA, 3 df)				0.02

Figure 4.5. Reductions in total forage biomass (kg/ha, ± CI, as of 201–13) available to wintering moose due to mean snow depths in 3 winter scenarios (mild, moderate, severe) in mechanically-treated (hydraulic-axed) sites cut from 1990/92–2012 on the Copper River Delta, Alaska. All biomass differences within winter scenarios are significant (*P* = 0.007–0.03, 4 df), and the 1990–92 across-scenario differences are significant (*P* = 0.04, 3 df).

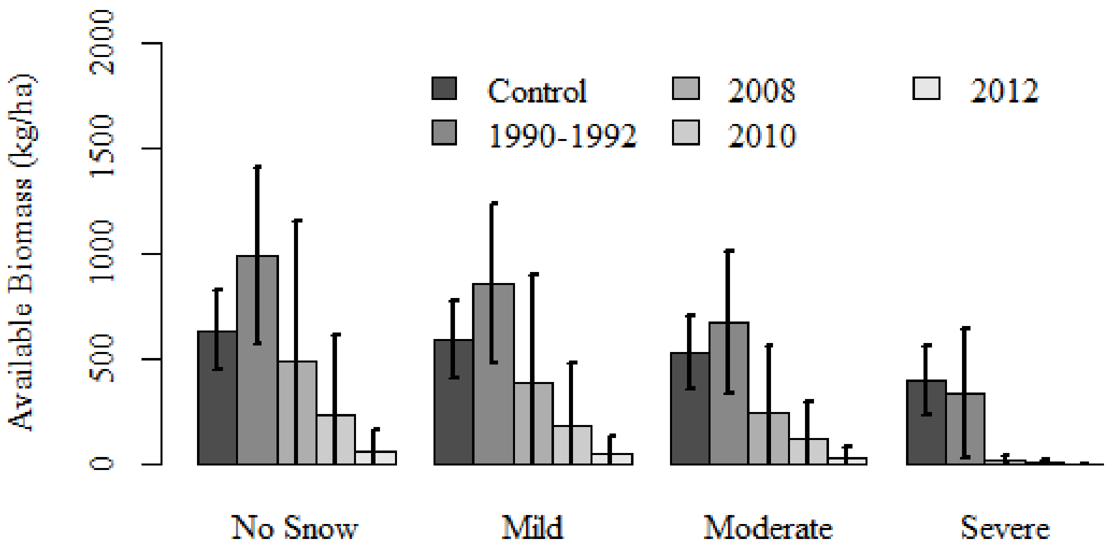
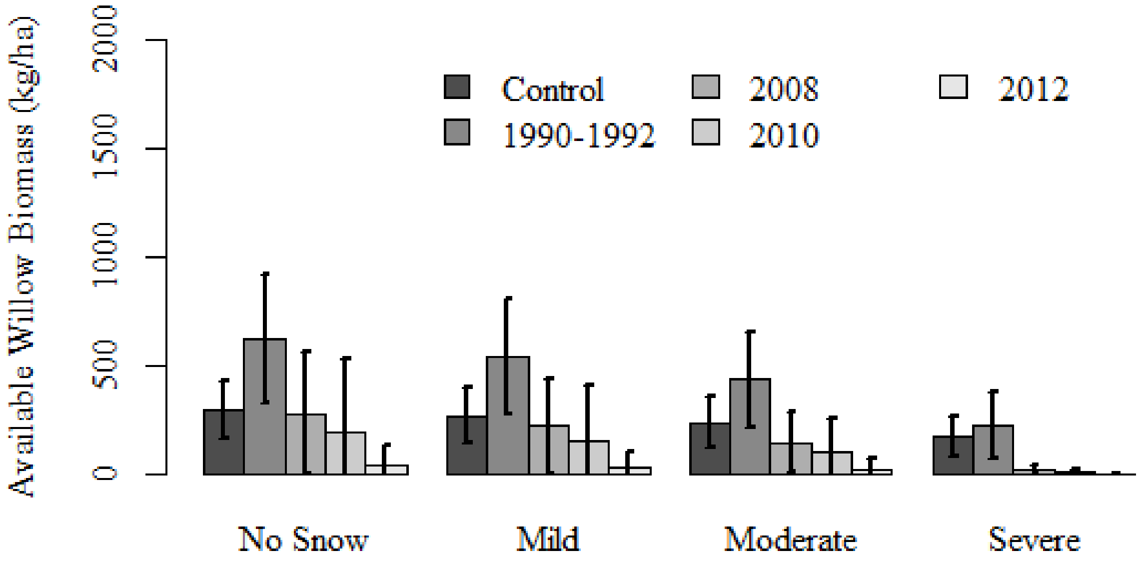


Figure 4.6: Reductions in willow (*Salix* spp.) biomass (kg/ha, ± CI, as of 2012–13) available to wintering moose due to mean snow depths in 3 winter scenarios (mild, moderate, severe) in mechanically-treated (hydraulic-axed) sites cut from 1990/02–2012 on the Copper River Delta, Alaska. All biomass differences within winter scenarios are significant (*P* = 0.01–0.05, 4 df), and the 2008 across-scenario differences are significant (*P* = 0.05, 3 df).



CHAPTER 5: CONCLUSION TO THE THESIS

The objectives of this thesis were to 1) explore the factors influencing nutritional carrying capacity for moose on the west Copper River Delta (CRD; Delta), while combining updated remote sensing and field-collected data to estimate nutritional carrying capacity (NCC), and 2) assess the effects of mechanical treatment on production of moose browse across stand types and over time. To that end, we compared past (1988–89) regressions of Barclay's willow (*Salix barclayi*; possibly including Hooker's willow, *S. hookeriana* data) with regressions developed with recent (2013) data for both Barclay's and Hooker's willows to determine past and present differences in biomass estimation, and evaluate the inclusion of Hooker's willow in past samples. We could not determine with certainty whether Hooker's willow had been included in past regressions, but found equations developed from recent samples predicted 1.9–2.2*x* more available biomass relative to prior models. Possible causal factors behind this increase include earthquake-initiated increases in woody species, stand aging, utilization by moose, or increased annual summer temperatures. Our study was limited in focus (only Barclay's and Hooker's willow) so we could not evaluate whether similar differences in regression estimates of biomass existed for other browse species. However, our results suggest that older equations are likely under-predicting the biomass available to wintering moose on the CRD. This has significant implications for regression application and NCC estimation. We recommended cautious use of older regressions and encouraged the redevelopment of biomass-predicting regression equations regularly.

We then developed and compared 5 NCC models (open diet/25% use, diet-adjusted/100% use, diet-restricted/100% use, diet-adjusted/25% use, and diet-restricted/25% use) within 4 winter ranges (the west Delta, road-bias adjusted west Delta, inference, and past observed ranges) and under 3 winter-severity scenarios (mild, moderate, and severe) to evaluate their effects on forage availability and NCC estimates. After comparing our results, we conducted a sensitivity analysis on our final model to identify the most influential factors on its NCC estimate. Lastly, we compared past and present estimates of species available biomass, stand areas, and NCC estimates over time, while evaluating the effects of including forage nutritional quality and satellite-estimated stand areas on NCC estimates relative to previous models lacking nutritional data and utilizing estimates of stand areas derived from aerial photography maps (MacCracken et al. 1997, Stephenson et al. 2006).

Our most conservative models (diet-adjusted and restricted with 25% use in plot inference and past observed ranges under severe winters) provided estimates suggesting the current moose population (~600 moose) may be above NCC. However, these models require potentially problematic assumptions relative to the flexibility of the moose diet, the extent of the moose winter range, and the occurrence of severe winters on the CRD. Our models within the road-bias adjusted range produced the highest estimates of NCC (581–5,228 moose), but our sample sizes and scope for detecting road bias on plot available biomass were limited, potentially decreasing the accuracy of our results. Thus, our final model used the open-diet (25% use) structure within the west Delta range. This model produced estimates of NCC between 2,198–3,471 moose, depending on the winter scenario, and suggested the current moose population is below NCC. These results are supported by other lines of evidence including low forage utilization rates, high twinning rates, high rump fat estimates in post-winter females, and potentially stable (or only slightly decreasing) estimates of NCC in the glacial outwash plains (Stephenson et al. 2006; C. Westing, 2013, unpublished data). These NCC estimates would produce moose densities comparable to those found in surrounding game management units (P. Harper, 2010, unpublished data). However, the precision of our results is limited because we lacked detailed, multi-season, and multi-year data from which to estimate current space use behavior of the wintering moose, were unable to fully evaluate the extent to which the 7 forage species can recover from herbivory, and could only partially evaluate the potential effects of the geological forces (glacial, river, tidal, and earthquake) and climate-related changes on forage availability and growth rates. Our models incorporated the best knowledge currently available, however we recommend further research to supplement these areas of incomplete knowledge and increase the precision of future models.

Past authors have recommended using estimates from severe winter scenarios for developing management goals, and our sensitivity analysis on our final model suggests snow depth is the greatest determining factor in NCC for the CRD moose. However because detailed data on daily snow depths, drift formation, melt rates, and compaction are absent for the CRD, we relied on snowfall data collected at the Mudhole Smith Airport. We are therefore cautious in weighting that factor beyond the quality of the data, and recommend that concerted efforts be invested in learning more about this potentially important factor. Furthermore, while there are valid reasons for choosing conservative estimates to manage the population (Stephenson 1995, MacCracken et al. 1997, Stephenson et al. 2006), overreliance on the severe winter scenarios might be rendered irrelevant in the future if severe winters become increasingly rare. Thus, management goals designed around moderate winter scenarios may be more appropriate. Because a primary motive of increasing the CRD moose population is to increase harvest rates, we also recommend consideration of population management theory, including maximum sustained yield within variable environments, when selecting management goals. Our sensitivity analysis also suggested the nutritional quality of forage minimally influenced NCC estimates. However, our comparison between model estimates produced with and without consideration of forage nutritional quality suggest inclusion of those factors significantly decreases NCC, paralleling results those found by Windels and Hewitt (2011). Thus, we recommend inclusion of nutritional quality of forage species in future estimates of NCC. Furthermore, previous NCC models have assumed 100% use of available biomass of forage species. Because of species-specific variability in browsing tolerance, we suggested that such an approach might produce inherently risky estimates for long-term management of ungulate habitat. Thus, we recommended restraining available biomass within NCC models to levels of utilization that allow for forage recovery. Lastly, current literature has advised cautious use of NCC estimates in highly variable environments, and suggested NCC estimates performed on summer forage may more accurately model the nutritionally-limiting period in ungulate ecology (Bobek 1977, Mautz 1978a, Merrill and Boyce 1991, McLeod 1997, Schwartz and Renecker 1997, Sayre 2008, Dungan et al. 2010). Thus, we recommended managers recognize the inherently temporary nature of NCC estimates in the incredibly dynamic CRD ecosystem, and we recommended consideration of summer-based estimates of NCC in future studies.

We also evaluated the effectiveness of mechanical treatment (hydraulic-axing or hydro-axing) as a technique for increasing production of moose browse, especially willow biomass. Because the treatments were not designed collectively as an experiment and because sample sizes were low, our ability to make statistical comparisons was limited. Therefore our ability to detect significant differences was also limited, but visual examination and comparison of the data suggested treatment via hydro-axing produced notably more total (all-species) browse and willow biomass, with the effect increasing with time-since-treatment. Furthermore, treatment significantly increased the ratio of willow:alder as time-since-treatment increased. These results suggest hydro-axing might be effective in increasing willow biomass to counter successional increases in alder. Managers will likely find these results useful in deciding whether to invest time and resources in further treatments, which are logistically difficult. However, treatment also likely influences shrub height and architecture, making treated shrubs shorter and "brushier." These structural differences may limit the forage available to moose during sever winters relative to untreated sites. Furthermore, because of the significant gap between the original (1990-92; 23 years since treatment) and next treatment in the series (2008; 5 years since treatment), we were unable to determine when the asymptote in regrowth occurred. Thus, treatment of an extensive area over a relatively limited number of years could limit browse availability to moose. Further research based on a systematic experimental design would be needed to better estimate the potential long-term and landscape scale effects of mechanical treatment on the moose forage species of the CRD.

Management concerns about potential earthquake-initiated landscape-level changes in stand ranges and related effects on the moose population prompted our investigation. The processes influencing stand type, stand area, and successional sequence are complicated (Appendix; Boggs 2000). However, studies on the vegetation dynamics of the CRD suggest the earthquake-initiated changes in vegetation may be relatively stabilized (Boggs 2000, Thilenius 2008). If so, our estimate of browse availability and NCC suggest the moose population can grow. Hydro-axing may not be necessary to ensure the future of the moose population, though it could be used to counter increases in alder biomass which are likely within certain successional sequences (Boggs 2000). However, a greater threat to the future of the moose population might be climate change as it will likely influence both the habitat and the moose themselves. Average temperatures, rates and patterns of succession, nutritional quality and growth rates of forage species, hydrology (e.g., glacial melt, sea level fluctuations, changes in evaporation rates, and altered precipitation amounts, forms, and seasonality), winter severity, and moose dietary, space use, or thermoregulatory responses could all be affected. Some changes would likely increase forage production while others would negatively affect the vegetation. An ideal management tool would be a model capable of exploring how the moose population will be affected with respect to these complicated and interacting processes.

The inherently dynamic nature of the CRD makes the application of any managerial tool (biomass-predicting regressions, mechanical habitat manipulation, and especially modeling) difficult. As demonstrated by the differences in past and present biomass regressions, constant ecosystem change will likely render every tool utilized by the CRD managers as only temporarily applicable. If so, from a managerial and scientific perspective, the dynamic nature of the Delta is both its greatest difficulty and its greatest advantage. Successful management in variable and complex ecosystems will always be challenging, especially when managing for long-term ideals. However, that guarantees a constant need for further investigation, redevelopment, and reapplication of tools for ungulate management, ensuring that the moose of the CRD will remain an important resource for researching and refining the tools of ungulate management worldwide.

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APPENDIX

GEOLOGICAL, ZOOLOGICAL, AND ANTHROPOGENIC FORCES INFLUENCING THE VEGETATION AVAILABLE TO MOOSE ON THE WEST COPPER RIVER DELTA, ALASKA

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INTRODUCTION

The Copper River Delta (CRD; Delta) in south-central Alaska (Fig. 1) encompasses a Critical Habitat Area, a State Game Refuge, and a National Forest. Its significance is derived through supporting millions of migrating shorebirds and thousands of breeding waterfowl, including the only breeding population of the dusky Canada goose (*Branta canadensis occidentalis,* USDA-FS), along with several other species of concern to the state or federal governments (Chapman et al. 1969, Kesti et al. 2007). Furthermore, the Delta supports an economically-important population of moose introduced to provide a harvestable resource for the west-Delta town of Cordova (MacCracken et al. 1997). The species richness and heavily-managed moose population of the Delta are dependent on the ecology of the vegetation and landform of the Delta. However, these are determined by several complex, landscape-level, and geological forces including: 1) glacial growth and retreat, 2) glacial or lake stream flooding, sedimentation, erosion, and channel cutting, 3) river flooding, sedimentation, and erosion, 4) tidal flooding, soil and water salification, sedimentation, and erosion, and 5) earthquake-caused cycles of uplift and subsidence (Boggs 2000). The vegetation of the CRD is further complicated by zoological factors including beaver (*Castor canadensis*) and the moose themselves, as they influence the vegetation through feedback mechanisms, or localized anthropogenic factors including the construction of the Copper River Highway and mechanical treatment or logging of moose habitat (Chapter 4) (Maurer and Ray 1992, Danell et al. 1994, MacCracken et al. 1997, Christensen et al. 2000, Wright et al. 2002, Stephenson et al. 2006, Cooper 2007). Together, these forces create a very dynamic landscape with vegetation processes and patterns that are interactive, opposing, or difficult to model. This creates a challenging task for the wildlife managers of the CRD as they attempt to establish long-term goals for the moose population which balance the subsistence needs of the local Cordova populace with the delicate ecology of the critically-important Delta. Their task if further complicated by the effects of climate change, which will likely influence most if not all of the current forces (Melack et al. 1997, Moore et al. 2009). Our objectives in this report are to 1) summarize the current research relevant to the landscape-level forces determining the vegetation communities and processes on the west CRD and 2) evaluate how recent and potential changes in the vegetation communities might impact the western moose population during winter. Our hope is that this report may assist managers in practically managing a moose herd whose future may be too complex to see clearly.

THE WEST CRD MOOSE POPULATION AND STUDY AREA

The moose of the CRD were introduced (23 individuals) from 1949–1958 to develop a harvestable resource for the town of Cordova (MacCracken et al. 1997). Though ubiquitous throughout much of Alaska, moose likely were excluded naturally from the CRD by surrounding mountains and glaciers. Since their introduction, the moose population has divided into two semi-distinct sub-populations (west and east), geographically separated by the Copper River, and grown to an estimated 600 and 230 individuals, respectively (as of 2013; C. Westing, 2014, personal communication). Because of its proximity to Cordova, the western population is more heavily managed, studied, and hunted (C. Westing and T. Joyce, 2014, personal communication). Furthermore, because of a potentially restricted winter range, winter has traditionally been assumed to be the most limiting season for the CRD moose (MacCracken et al. 1997). Winter browse available to the CRD moose includes 5 willow species: feltleaf willow, Barclays willow, undergreen willow, Hookers willow, and Sitka willow (80% of winter diet; *Salix alexensis, S. barclayi, S. commutata, S. hookeriana,* and *S. sitchensis,* respectively), Sitka alder (*Alnus viridis sinuata;* 3.0% of winter diet), black cottonwood (*Populus trichocarpa;* 1.0% of winter diet), and sweetgale (*Myrica gale;* 7.0% of winter diet) (MacCracken et al. 1997). Preferred willow forages (e.g., willow spp.) occur mainly in willow-dominated and alder-willow co-dominated stand types, but willow species can also make up a notable portion of the biomass available in sweetgale-, cottonwood-, and spruce-cottonwood dominated stands. The proportion of willow in herbaceous-, alder-, or spruce-hemlock (*Picea sitchensis-Tsuga heterophylla*) dominated stands is generally minimal (Chapter 3, MacCracken et al 1997).

The CRD is the largest continuous wetland (>283,000 ha) in the Pacific Northwest (USDA-FS, Kesti et al. 2007). The western region of the CRD encompasses over 54,000 ha, averages 236 cm in annual precipitation, and sustains mean temperatures of -9.3–16.3 °C (Kesti et al. 2007). Ranging from sea level to 300 m, the west Delta is hemmed by the Chugach Mountain Range and glaciers reaching over 2000 m in height (Kesti et al. 2007). Soil types include deposits of aeolian sands, alluvial sands and gravels, and marine glacial silts with very fine sands (Davidson and Harnish 1978). Boggs (2000) identified 42 successional sequences on the CRD, with 75 stand types. Stand type location, successional rate, and climax type are determined primarily by the interacting physical and chemical factors of hydrology and sediment supply (Boggs 2000, Kesti et al. 2007). These factors function on different spatial and temporal scales on the three major ecoregions of the west Delta: the glacial outwash plains, uplifted marsh, and tidal marsh (Fig. 1; Boggs 2000).

THE ECOLOGY OF THE GEOLOGIC FORCES, VEGETATION, AND MOOSE POPULATION ON THE ECOZONES OF THE WEST CRD

The Glaciers, Glacial Streams, and Glacial Outwash Plains

Three glaciers flow south or southwest and drain onto the west CRD, shaping the geography and hydrology: the Scott Glacier, Sheridan Glacier, and the Sherman Glacier (Fig. 1). The Scott Glacier covers over 17,000 ha and creates the Scott River which drains a watershed incorporating almost 53,000 ha within and beyond the west Delta (Kesti et al. 2007). The Sherman Glacier (5,400 ha) drains directly into Sheridan Lake (10, 000 ha; the largest lake on the west CRD), while collectively supplying Sheridan River and a watershed encompassing over 32,000 ha (Kesti et al. 2007). Together these 3 glaciers create, destroy, or change land available for vegetation directly (through glacial retreat or growth) and indirectly (through effects by their glacial streams).

In the past 200–300 years, the CRD glaciers have mostly receded with only occasional, small advances (Blanchet 1996). Glacial growth reduces the area available for vegetation, while glacial retreat creates new areas subject to primary succession, eventually encouraging herbaceous and shrub colonization after several decades of soil development (Crocker and Major 1955, Chapin et al. 1994, Boggs 2000). However, direct effects of the glaciers on vegetation are minimal relative to effects produced by their streams. Heavy glaciation of the mountainous portions of the west CRD likely prevents streams in the northern regions, but on the more level areas of the Delta glacial streams continuously reshape the landscape (Boggs 2000, Kesti et al. 2007). Through seasonally-periodic and variously-intense flooding during glacial and snow melt (June–September), glacial streams change course, remove established vegetation, and scour or create new stream banks through erosion and sedimentation. This process creates new areas for primary succession, distributes soil material, and can lead to the formation of ponds in old channels in distal areas, which then develop their own successional processes determined by sedimentation rates and species colonization (Boggs 2000).

The ecozone most influenced by these continuously-changing glacial watersheds is the glacial outwash plains. The outwash plains are the most widespread landscape on the CRD, encompassing the northern portions of the west Delta (Boggs 2000). They are not tidally-influenced and, as a result, they are dominated by salt-intolerant species of peat mosses (*Sphagnum* spp.), herbs, shrubs, and trees (Boggs 2000). The rate of glacial and snow melt and resulting frequency and intensity of floods, channel changes, and ground water levels determine vegetation stand composition, age, and successional sequence (Boggs 2000, Kesti et al. 2007). Thilenius (1990) initially noted some succession from shrub-dominated (e.g., willow and alder) to cottonwood-dominated stands and hypothesized spruce as the climax-stage species in the outwash plains, depending potentially on the nitrogen-fixation rate of alder. Later, Boggs (2000) identified 13 successional sequences on the glacial outwash plains ending in peatland, alder, or forest species. He also classified spruce-hemlock forests as late-successional in plains proximal to glaciers, but described the vegetation immediately below glaciers as absent or in permanently early seral stages (e.g., herbaceous spp., alder, willows, and cottonwood) due to more frequent flooding. Distal outwash plains maintain climax stands of peatland in old channels with stringers of shrub and forest on old levees (Boggs 2000).

Because moose on the CRD subsist mainly on willow species which favor scarified ground and primary succession (Walker et al. 1986), the constant reformation of the glacial outwash plains through flooding of the glacial streams will likely provide a continuous source of forage for the future moose population. Barring changes to the hydrology of the glacial outwash plains, the geophysical properties of the Delta (its large area and slight slope) will likely maintain the “braiding” effect of the glacial streams with continual disruption and regrowth of vegetation. However, Stephenson et al. (2006) developed a Markov-chain model using vegetation changes from 1959–1986 on the glacial outwash plains to predict the effects of glacial retreat and earthquake-caused uplift on vegetation distribution 238 years after the 1964 earthquake. Their model predicted further increases in spruce and hemlock stands as glacial-related disturbance decreased (due to convergence of glacial streams and increased areas of glacial lakes) in the glacial outwash plain (Stephenson et al. 2006). If Stephenson’s model is correct and the effects of glacial-related flooding lessen, proximal regions of the glacial outwash plains may eventually convert to alder-, spruce-, or hemlock-dominated stands, reducing the forage available to future moose populations.

The Uplifted Marsh, McKinley Lake, and the Copper River

South of the glacial outwash plains, a combination of glacial streams, lake streams, and the Copper River influence the dynamics of the uplifted marsh (Fig. 1; Boggs 200, Kesti et al. 2007).

This ecozone consists of levees, freshwater streams, ponds, sea cliffs, and tidal creeks that resulted when the pre-1964 earthquake tidal marsh was raised mostly above tidal influences (Boggs 2000). The uplifted marsh has therefore lost tidal salt effects and marine sediment loads except in tidal creeks at its southern edge, which experience twice-daily 4 m tides (Boggs 2000). The most distal portions of the Scott and Sheridan glacial streams continue to branch into the western portion of the uplifted marsh, while the Copper River shapes the eastern edge (Kesti et al. 2007). In between these two forces, streams within 7 sub-watersheds originating from McKinley Lake drain over 13,000 ha (Kesti et al. 2007). The landscape-forming processes of erosion and deposition occur on the uplifted marsh through all three of these sources, but at much slower rates than on the glacial outwash plains. The factor with the greatest potential to initiate change is the Copper River. Dividing the eastern and western regions of the Delta, the Copper River (Fig. 1) is almost 20 km across at its mouth and has winter winds which reach gusts of 193 km/h through the Copper River Canyon. Over 460 km long with a watershed covering over 6 million ha, the Copper River drains the 6th largest basin in Alaska (Kesti et al. 2007). Glacial melt mainly determines the rate and intensity of its flow, but the Copper River carries on average more than 62 million metric tons of sediment per year, more than twice the sediment load of any other Alaskan river (Brabets 1996, Boggs 2000, Kesti et al. 2007). When this sediment load reaches the Pacific Ocean, the waters of the Copper River slow and deposition of the sediment load occurs quickly (Boggs 2000). This sediment deposition, along with the loess channeled by winds through the Copper River Canyon, make the Copper River the largest factor in creating and maintaining the Delta. However, except during high flow, little of the river sedimentation occurs within the uplifted marsh (Boggs 2000). Similarly, only during flooding do glacial, lake, or tidal influences quickly shape the channels and levees of the uplifted marsh. Instead, overall levee development and water flow is steady in the uplifted marsh, with some locations maintaining water velocities slow enough to support anaerobic activity.

Vegetation processes in the uplifted marsh parallel its land development. The slow, constant waters support stands dominated by herbaceous and water-tolerant shrubs (e.g., sweetgale), with stringers of willow and alder on raised levees (Boggs 2000). Occasional floods or stream channel-cutting change the hydrology to allow colonization of new levees or growth of less water-tolerant species on more drained levees, but peatland with stringers of shrub and forest are classified as the late-successional stages (Boggs 2000). Currently, bands of willow and alder form an ecotone between the uplifted marsh and the glacial outwash plains (Crow 1968, Boggs 2000, Thilenius 2008). Vegetation closer to the Copper River and exposed to the winter winds experiences a different micro-climate relative to the rest of the uplifted marsh, with lower annual precipitation, lower temperatures, and longer snow persistence (MacCracken et al. 1997). It is likely the dynamics of vegetation in that region function differently. However, the overall hydrology and vegetation communities on the uplifted marsh seem relatively stable and static (Boggs 2000, Thilenius 2008). The current abundance of willow forage makes the uplifted marsh a resource stronghold for the current moose population (MacCracken et al. 1997). Depending on the stochastic influences of flooding, some shrub stringers within the uplifted marsh might remain in relatively early seral stages or eventually become dominated by taller, bushier, or woodier willows and alders. Unless willows attain heights and architecture sufficient to escape moose browsing, or local succession leads to alder- or forest-dominated stands, willow distribution and biomass in the uplifted marsh will likely continue to benefit moose. However, eventual erosion of the tidal creek banks (currently up to 2 m) at the southern edge of the uplifted marsh may gradually increase salification of the area, reducing the shrub component and resources available to future moose (Boggs 2000). Currently the uplifted marsh seems to be eroding slowly, possibly due to the fine-grained, clay bank soils and dense bank vegetation (Boggs 2000). Thus, this threat to the available moose forage is likely very distant.

The Tidal Marsh and Tides of the Pacific Ocean

The effects of the freshwater streams and Copper River continue into the tidal marsh where they are met and interact with tidal influences from the Pacific Ocean. The tidal marsh (Fig. 1) is delineated by the portion of the Delta newly exposed after the uplift and where true primary succession is occurring (Boggs 2000). The tidal marsh includes mudflats, marshes, tidal creeks, and some shrub-dominated areas, and is mostly influenced by two primary sources of sediment and erosion: the Copper River and the Pacific Ocean. These two forces determine the shape and development of tidal regions as deposition by the river counteracts tidal erosion, and to a lesser degree tidal deposition offsets stream erosion. Growth of the Delta is thus limited by sedimentary loads while Delta elevation is determined by tide height (Boggs 2000). Together these forces create a very dynamic ecozone as land is eroded, developed, and shifted continuously. Thus, the tidal marsh is dominated by sedges and herbs with stringers of shrubs and halophytic species (Boggs 2000). Herbs and sedges are late-successional within the tidal flats until steady accretion of silt develops levees and allows shrub and tree expansion (Boggs 2000). However, the community gradation from herbs to shrubs to trees might represent zonation rather than succession on the tidal marsh. The tidal marsh does not provide appreciable browse for moose on the CRD, though halophytic plants may provide a potentially important source of sodium (Botkin et al. 1973, MacCracken et al. 1997). Rather, the main benefit of the tidal marsh for the moose seems to be its position as a buffer to tidal effects on the uplifted marsh. However, if the tidal marsh continues to increase or adjust with oceanic and river influences (Boggs 2000), creating new areas of primary succession and enabling later seral stages in other vegetated areas, it may minimally benefit moose.

The Geologic Cycle and the 1964 Earthquake

The final geologic force affecting the CRD vegetation is the cycle of earthquake-initiated uplift and subsidence. Unlike the more constant geologic forces (glaciers, streams, rivers, and tides), earthquakes on the CRD likely have a more sporadic, widespread, and immediate influence over the Delta landscape, interacting with the other geological forces, and changing the mechanism or intensity of their influence. As a result, the geologic cycle has the potential to dramatically and quickly affect the vegetation available to current and future moose populations.

Plafker (1990) first described the cycle of coseismic (immediate effects of an earthquake) uplift followed by interseismic (post- or between-earthquake responses) subsidence that shapes the CRD. Coseismic uplift results in a less tidally-influenced and increasingly-drained delta, allowing salt- or water-intolerant species such as fresh water peat, shrubs, and trees to expand their distribution (Boggs 2000, Thilenius 2008). However, eventually tectonic subsidence combined with eustatic (global) sea level rise results in a slow submergence of the Delta and return to vegetation types dominated by salt marsh plants (Plafker 1990). Geologic evidence obtained through radiocarbon-dated peat and wood suggests this process has occurred for at least 3500 years with at least 4 separate coseismic uplifts prior but equivalent to the 1964 uplift (Plafker 1990). Plafker (1990) hypothesized the overall characteristics of the Delta would remain relatively constant through this cycle, with uplift and intertidal accumulation of silt balancing with submergence (Reimnitz 1966). However, Boggs (2000) hypothesized this geologic cycle would result in the slow expansion of the Delta's marshes and land.

The most recent phase in this cycle was initiated with the 1964 earthquake. Initial magnitude estimates of the earthquake ranged from 8.4–8.75 (Ferrians 1966, Thilenius 2008), but the United States Geologic Survey ([USGS] 2012) revised the estimate to 9.2 following improvements in technology. One of the earliest geologic assessments of the affected areas concluded that the CRD had uplifted by 6.5–7.5 ft (2.0–2.3 m) and hypothesized that landscape-level changes would be permanent along the coast ((Grantz et al. 1964). Later investigators varied in their estimation of the uplift (from 1.0–4.0 m) and vegetation changes (Plafker 1990, Kesti et al. 2007, Thilenius 2008), but all agreed the uplift included the entire Delta. Uplift resulted in no major river channel changes and generally decreased in magnitude further inland (Plafker 1969, Kesti et al. 2007). As a result, the 1964 earthquake affected the hydrology and vegetation of the 3 ecozones differently.

Glacial Outwash Plains—Because the glacial outwash plains are not tidally influenced and uplift effects on elevation in the plains were minimal, Boggs (2000) hypothesized that the uplift had no effect on species distribution or succession. DeVelice et al. (2001) developed a model of succession for the CRD predicting changes in vegetation since the 1964 earthquake over 100 years in 10-year time steps. Their model predicted vegetation composition of the glacial outwash plains would be relatively stable at the landscape scale. If Boggs and DeVelice et al. are correct, then the 1964 earthquake likely had little effect on the vegetation available to moose on the glacial outwash plains. However, if the 1964 earthquake significantly lowered the water table through increased drainage on the glacial outwash plains, then succession may change to favor further increases in taller, forested species, eventually decreasing the browse available to moose (MacCracken et al. 1997, Boggs 2000, Kesti et al. 2007).

Uplifted Marsh—Thilenius (1990) summarized qualitative reports of post-earthquake vegetation changes on the uplifted marsh. By 1979, the bands of alder, willow, and herbaceous species had become less distinct as alder developed on the channel levees and established willows increased in height and biomass. Reports suggested that sweetgale might also have become more abundant. However, by 1988 the rate of succession seemed to have decreased (Thilenius 1990). Later, Thilenius (2008) confirmed reports of less distinct vegetation bands and the appearance of a “shrub invasion,” either due to actual establishment of new shrubs or increased biomass in those already present. Boggs (2000) found no late-successional shrub or forest communities on levees during his study. He noted vegetation along new channels and on alluvium seemed even-aged, and that halophytic species or communities described as common in previous studies (Crow 1968) were rare or absent (Boggs 2000). The model by DeVelice et al. (2001) predicted significant vegetation changes on the uplifted marsh, with total acreage of woody vegetation on both uplifted and tidal marshes increasing 8.6*x* in 100 years. Thus, post-earthquake changes in vegetation within the uplifted marsh seem to have largely benefited the moose population with increased shrub (including willow) availability (MacCracken et al. 1997). Because of regular inundation, complete forestation of the uplifted marsh is unlikely and the hydrology of the uplifted marsh seems to be relatively stable (Boggs 2000, Thilenius 2008). With occasional flooding, newly developing levees, and barring further seismic events in the near future, it is likely that this ecozone will remain productive for moose browse.

Tidal Marsh—In his post-earthquake work, Thilenius (1990) documented succession on the tidal marsh as sedge marshes developed from mudflats within 10 years, expanded within 15 years, and stabilized within 25 years. Simultaneously, shrub distribution expanded seaward (Thilenius 1990). By the time of his study (1995), Thilenius (2008) described an expansion of the tidal marsh by 1.5 km. Christensen et al. (2000) also described the formation of new land and retreat of the shoreline. New channels developed immediately following the earthquake, but within 15 years they were again filled with sediment and flooded. DeVelice et al. (2001) expected the greatest changes in vegetation composition to occur on the tidal ("new") marsh, with development from bare ground to a mosaic of 8 landcover (vegetation-dominated) classes within 100 years. However, while the 1964 earthquake increased the land available for vegetation development, this new land remains dominated by herbaceous species which compose a small portion of the moose diet. Unless an increase in sedimentation or further uplift allow the tidal marsh to escape salt influences, tidal flooding, and enable further shrub development, it seems unlikely that the earthquake-caused tidal marsh will factor significantly in the CRD moose ecology.

FEEDBACK EFFECTS OF BEAVER AND MOOSE ON THE CRD VEGETATION

While geologic factors likely dominate vegetation development on the CRD, significant changes to vegetation communities and processes can originate through biological mechanisms. Zoological factors with the potential to cause landscape level changes on the CRD vegetation include mainly two species: beaver and moose. Beaver seem to have significantly benefited from the increased shrub availability in the uplifted marsh since the 1964 earthquake, as their population shifted south and increased (Boggs 2000, Cooper 2007). As known habitat architects which selectively utilize some woody species and whose damming activities back-flood the landscape, beavers have the potential to significantly adjust the hydrology and suitability of land to favor growth of certain species. From 1959–1996, beavers on the uplifted marsh increased surface water area from 0–20% with their damming activities. This increase in water table depth, decreased flow, and selective cutting of shrubs will likely favor growth of willows and water-tolerant species (e.g., sweetgale), potentially adjusting the successional trajectory for areas under their influence (Naiman et al. 1986, Martinsen et al. 1998, Boggs 2000, Wright et al. 2002, Cooper 2007). As a result, beaver activity should largely benefit browse availability for moose. However, beavers also preferentially store and consume willows during winter and might directly compete with moose for forage (Allen et al. 1983). Depending on the magnitude of these opposing effects, the moose population might be positively or negatively affected by beaver activities and population density.

Similarly, the moose themselves may support or hinder development of their own food base. Moose on the CRD selectively browse willow species and cottonwood (MacCracken et al. 1997). Anecdotal evidence and observations of an exclosure established in the early 1990s suggests the moose may be limiting cottonwood recruitment (T. Joyce and S. Smythe, personal communication and observation), but no study has evaluated the long-term effects of moose introduction on the CRD vegetation. Results from studies evaluating the effects of moose use on forage availability and nutrition vary (Bergstrom and Danell 1987, Danell et al. 1994, Bowyer and Neville 2003, Pastor and Danell 2003), but a review by Augustine and McNaughton (1998) found that intermittent herbivory (e.g., due to migration or non-herding) and nutrient-rich ecosystems were key factors in supporting the regrowth capacity of palatable species. A later study by Persson et al. (2007) confirmed that regrowth ability varied along a habitat productivity gradient and found birch (*Betula pubescens* and *B. pendula*) could tolerate 25–40% use in productive sites. Considering the relatively minimal herding observed by the CRD moose and influx of nutrients both tidally and glacially on the Delta, preferred forages on the CRD may be able to support high levels of consumption by moose (MacCracken et al. 1997). However, because the CRD moose are also an introduced species, the forage species of the CRD may have developed lower browsing tolerances prior to the introduction. Alternatively, moose browsing may indirectly benefit willow growth by increasing the prevalence of actinorhyzal species (e.g., alder and sweetgale), simultaneously increasing the availability of soil nitrogen (Kesti et al. 2007). Currently, the vegetation on the CRD is not showing signs of over-utilization (Chapter 3). However, much of the ecology between this introduced moose population and its isolated forage base are simply not known. Current knowledge suggests the Delta ecosystem can sustain a higher moose population (Chapter 3), but the vegetation should be monitored if the CRD moose population is increased.

HUMAN-CAUSED CHANGES TO THE CRD VEGETATION

Human management practices and developments on the CRD also have the potential to significantly influence the browse available to moose. Both timber harvest and mechanical treatment (hydraulic-axing) of moose habitat have been performed to directly impact the CRD vegetation. Since 1950, almost 3,600 ha of timber have been cut for personal or state use, and between 1990–2012, almost 300 ha of moose habitat were treated to encourage willow growth (Chapter 4, Kesti et al. 2007). No study has evaluated the effects of timber harvest on the CRD moose. However, as an herbivore which favors early-successional shrub species, timber harvest will likely increase the forage available to moose (MacCracken et al. 1997, Rempel et al. 1997, Fisher and Wilkinson 2005). Hydraulic-axing effects on moose browse were mostly statistically inconclusive (Chapter 4, Stephenson 1995), but suggest mechanical treatment may eventually increase the willow biomass available to moose while decreasing alder biomass. Depending on the extent to which these practices are used, the magnitude of their effects on browse resources, and duration of their use, timber harvest and hydraulic-axing might benefit future moose populations.

Development on the CRD is minimal, consisting of a small number of cabins, buildings, and the Cordova airport (Kesti et al. 2007). These structures likely do not significantly influence the CRD vegetation. However, water flow and vegetation communities have been altered by the construction of the Copper River and Northwest Railroad bed (from 1906–1911) which currently supports the Copper River Highway (Christensen et al. 2000). Because of the conflict between static bridges within dynamic watersheds, bridges significantly restrict the river braiding in some areas (Kesti et al. 2007). Flood control dikes and spur dikes were constructed upstream to help control flow, often only temporarily (Kesti et al. 2007). No studies have evaluated the effects of the highway on sedimentation, erosion, or vegetation. However, Kesti et al. (2007) suspected the highway minimally affected water quality or flow quantity, though it may affect the timing of flows in the larger glacial rivers. They expected eventual aggradation upstream of the highway, possibly reaching the elevation of the highway, and in areas where bridge width is much narrower than the river system, they suspected increased channel scour occurs. Overall, they rated the significance of changes to channels and sediment deposition as “moderate”. The available biomass found in cottonwood, alder-willow, and willow stands within 1.5 km of the road system significantly decreased as distance from the roads increased, while biomass available in sweetgale stands significantly increased with distance from the roads (Chapter 3). No differences in available biomass were found between plots north or south of the road, but sample sizes were small (n = 7–9). This suggests the vegetation available to moose may be affected by the differences in hydrology and sedimentation caused by the highway (what is essentially a large levee), but the magnitude, extent from the road, and varying effects north or south of the road are mostly unknown. Depending on the continued interaction between the bridges and glacial streams (rates of aggradation, scour, and flow), the effect of the Copper River Highway on vegetation available to moose may be significant.

CLIMATE CHANGE AND THE CRD VEGETATION

The final, and least predictable, factor with the potential to initiate vegetation changes on the CRD is climate change. Annual mean temperatures across Alaska have risen by 1.7°C since 1949 ([ACRC] 2014), and we have found evidence of increased willow growth relative to 1988-89 data (Chapter 2). The occurrence of severe winters on the CRD, as we defined them, has diminished from 4 in the 20 year period from 1917-1936, to 1 in the period from 1997-2014. No research has been done to estimate how the hydrology and vegetation on the CRD will respond to further increases in temperature, increased growing degree days, or decreased snow loads. However, if temperature and winter severity trends continue, it is likely that climate change will influence most, if not all, of the factors already described. Melting rates of glaciers will increase, affecting the frequency and intensity of flooding on glacial streams and the glacially-fed Copper River. This, in turn, will affect rates of sedimentation, erosion, channel-cutting, deposition, and overall development of the Delta land area. Tidal influences will be determined by changes to currents and overall sea level. The hydrology of the Delta will be further impacted by rates of precipitation via snow or rain and evaporation. The distribution of the CRD vegetation will respond to these changes in landscape and hydrology, while their growth rates, successional processes, and community ecology will adjust to changes in temperature and soil quality. These vegetation responses will, in turn, partially determine the ecology of the animals on the CRD, as they adjust their resource selection according to their metabolic and thermoregulatory needs, possibly initiating further animal-plant feedback cycles. Overall, climate change and its interactive effects on the geological and zoological forces determining the landscape and ecology of the CRD have the potential to create a very different ecosystem in which humans must live and manage.

CONCLUSION

Ultimately the direction of vegetation changes and corresponding influences on the CRD moose population are unknown. The characteristics of the CRD are determined by complex and interacting geologic forces and environmental processes of glacial retreat or growth, stream channel changes, sedimentation, and erosion, effects of the Copper River, tidal erosion and deposition, earthquake uplift, subsidence, vegetation growth rates and succession, animal-plant feedback cycles, human modifications, and climate change (Table 1). Studies of the geologic, zoologic, and human forces on the CRD suggest they maintain a dynamic ecosystem that could be largely beneficial or neutral for the CRD moose, supporting and renewing large regions with willow biomass. Alternatively, the processes on the CRD could interact to significantly decrease the forage available to moose by simultaneously eroding or succeeding to less-preferred vegetation types. However, climate change may alter most if not all of these factors through mechanisms and in magnitudes that are difficult to predict. How does one manage a population in such a complex, unknowable, and vital landscape? The answer clearly cannot be simple, but we can hope, through further investment in understanding the forces at work on the Delta and continued monitoring of the species affected, practical solutions may arise.

TABLES AND FIGURES

Figure A.1: Map of the western region of the Copper River Delta delineating the 3 ecoregions (glacial outwash plains, uplifted marsh, and tidal marsh; Boggs 2000), the 3 glaciers (Scott, Sheridan, and Sherman), the Copper River, and the town of Cordova in south-central Alaska.

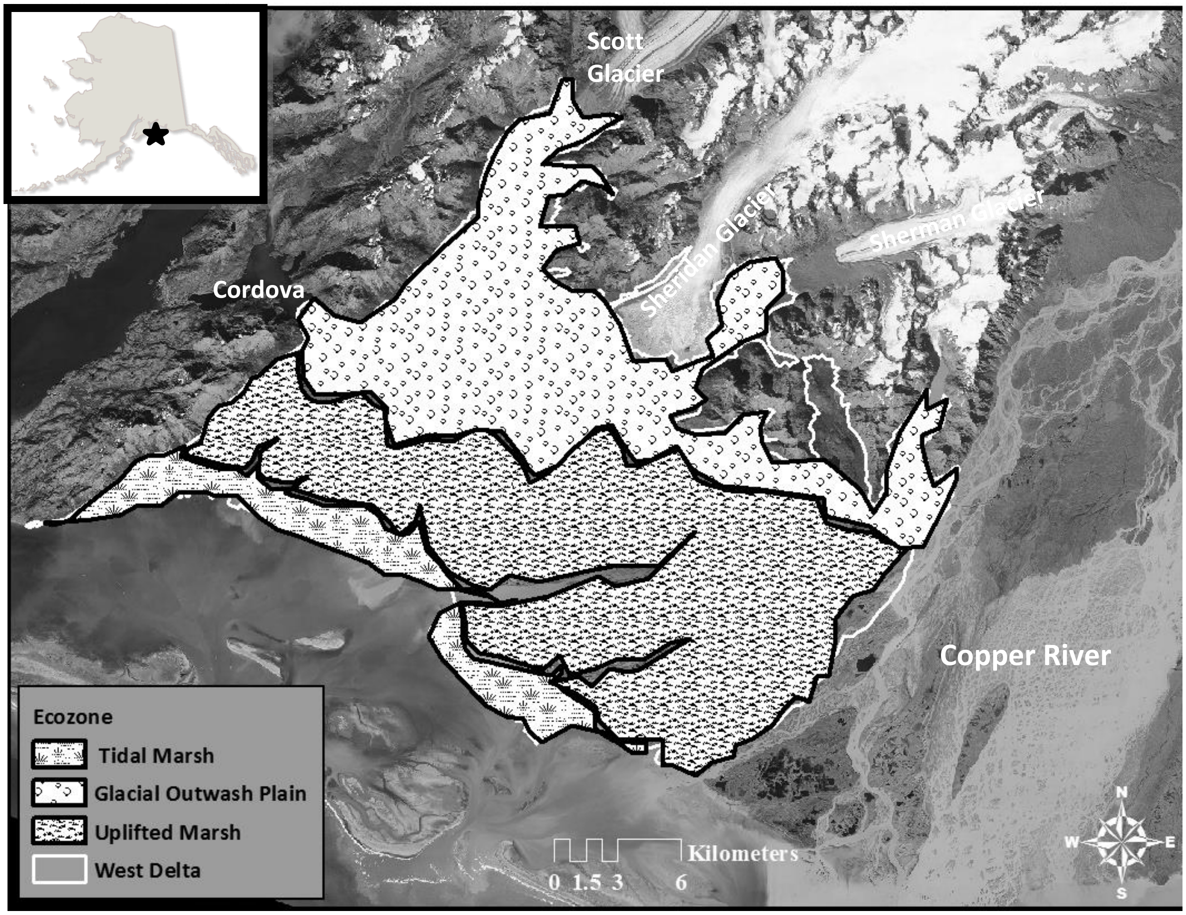

Table A.1: Summary of the geological, zoological, and anthropogenic forces affecting the vegetation available to current (2012–13) and future wintering moose on the Copper River Delta, AK. Listed are the ecozones (glacial outwash plains, uplifted marsh, or tidal marsh) affected by the forces and the estimated direction (+, ±, –; i.e., positive, mixed, or negative) of the effect relative to the availability of moose forage as determined by current literature.

Geological, Zoological, or Anthropogenic Force	**Ecozone(s) Affected**	**Direction of Effect on production of moose browse**
Glacial growth and retreat	Glacial outwash plains	±
Glacial/lake stream flooding, sedimentation, erosion, and channel cutting	Glacial outwash plains, uplifted marsh	+
Copper River flooding, sedimentation, and erosion	Uplifted marsh, tidal marsh	+
Tidal flooding, soil and water salification, sedimentation, and erosion	Uplifted marsh, tidal marsh	±
Cyclical earthquake-caused uplift and subsidence (relative to, specifically, the 1964 earthquake)	Glacial outwash plains (minimally), uplifted marsh, tidal marsh	±
Beaver damming and shrub utilization	Uplifted marsh	±
Moose shrub utilization	Glacial outwash plains, uplifted marsh	±
Copper River Highway damming, bridge scouring, and aggradation	Glacial outwash plains, uplifted marsh	±
Timber logging	Glacial outwash plains	+
Mechanical treatment of moose habitat (hydraulic-axing)	Glacial outwash plains, uplifted marsh	+