Contrasting Winter Moose Nutritional Carrying Capacity Models on a Dynamic Landscape

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Abstract

Many models used to estimate nutritional carrying capacity (NCC) for ungulates differ structurally, but the implications of those differences are frequently unclear. We present a comparative analysis of NCC estimates for a large herbivore in a dynamic landscape, using models that differ in structure and scope. We compared three model structures across three estimates of winter ranges under three winter-severity scenarios for an isolated, introduced moose Alces alces population on the Copper River Delta of south-central Alaska. Model estimates of NCC ranged from 205 to 4,592 moose, demonstrating the critical influences of model structure and assumptions when applying NCC. Furthermore, population estimates during recent severe winters suggest that past models underestimated NCC on the Copper River Delta. We conducted a sensitivity analysis of a preferred model and determined that model components with the highest and lowest sensitivity were snow depth and lignin- and tannin-caused reductions in forage nutritional quality, respectively. Our low sensitivity values for lignin and tannin influences on NCC contrast with results in other NCC estimates. Overall, our results reinforce the need for, and will hopefully assist, adaptive management in response to landscape, population, behavioral, and climatic changes on the Copper River Delta, and demonstrate the importance of understanding model assumptions and structure in application of NCC estimates in the management of large herbivores in variable ecosystems.

Keywords: Alaska; model structure; moose; nutritional carrying capacity; open-diet selection; winter scenario

Introduction

Nutritional carrying capacity (NCC) is the largest stable population of a specified organism supported by the total available nutritional energy, assuming a stable ecosystem within a defined range and time (Caughley 1979; Monteith et al. 2014). Thus, it acts as an idealized baseline to which further factors may be added to refine population management goals. In highly variable environments, the relationship between a population of animals and its food resource may fluctuate, undermining an equilibrium (Caughley et al. 1987; McLeod 1997).

Therefore, application of NCC requires close consideration of the ecology of the organism and its environment. For ungulates, NCC depends on the species’ foraging behavior relative to the ecology of plant species being consumed (Jefferies et al. 1994; Hobbs et al. 2003; Windels and Hewitt 2011). Within temperate and arctic ecozones, decreases in nutritional quality and availability of browse in winter increase the necessary digestion and foraging time relative to other seasons (Schwartz and Renecker 1997), and thus historically winter was considered the limiting period for temperate ungulates. However, temperate ungulates compensate during...
winter by lowering metabolic rates, decreasing activity periods, and metabolizing fat reserves (McEwan and Whitehead 1970; Mautz 1978b; Regelin et al. 1985; Renecker and Hudson 1986), while using spring and summer months to restore body fat, preparing for the energetically draining behaviors of lactation, rut, and pregnancy (Schwartz and Renecker 1997). Considerable research now suggests that summer forage quality is more influential to NCC for most temperate ungulate populations (Bobek 1977; Merrill and Boyce 1991; Cook et al. 2001, 2004; Beck et al. 2006; Dungan et al. 2010), and determining which season is more significant to a specific population depends on relationships between the animal’s nutritional requirements and seasonal quality and accessibility of forage resources.

Contrasting Carrying Capacity Models S.E. Smythe et al.

Methods for calculating forage available to ungulates vary, but initial “forage supply–animal demand” structures were very simple, assuming equal selection probability of all available forage species (Mautz 1978a). Ungulates, however, preferentially select certain forages over others because of their higher nutritional quality (e.g., crude protein, gross energy) and lower amounts of secondary chemicals (e.g., tannins), and to ensure the proper nutrient ratios (i.e., “gut mixing”) in their diet (Bryant et al. 1992; Windels and Hewitt 2011). Thus, these simple models likely overestimate the forage available and NCC estimates. With increased knowledge of browsing behavior, space use, and forage tolerance to herbivory, estimates of forage biomass within NCC model structures were later constrained by ungulate choice, dietary needs, or ability of forage to recover from consumption. Such models account for ungulate nutritional needs by calculating forage availability relative to its ability to meet ungulate dietary needs or by limiting consumption to highly preferred forages (solely, or in conjunction with, other lesser preferred forages), which are also most vulnerable to overbrowsing (Hobbs and Swift 1985; Hanley and Rogers 1989; Stephenson 1995). However, these structures inform or depend on accurate dietary analyses, which can vary seasonally, regionally, and by methods used (Holechek et al. 1982; Alipayo et al. 1992; Renecker and Schwartz 1997). Furthermore, Hobbs and Hanley (1990) cautioned against assuming ungulate diets are temporally static or inflexible. Thus, more complex models can both misrepresent ungulate diets or underestimate diet flexibility under changing environmental conditions or levels of intraspecific competition. Just as ungulate diets are context-specific, forage tolerance to herbivory is species-, seasonally-, regionally-, and temporally-specific while also influenced by the intensity of herbivory, the length of browsing periods, and soil nutrient loads (Danell et al. 1994; Augustine and McNaughton 1998; Persson et al. 2007). The implications of these different structures are often unclear, and complicate the use of NCC by managers.

An isolated moose Alces alces population on the Copper River Delta (CRD; Delta) in south-central Alaska (Figure 1), established by translocations starting in 1949 in an area previously unavailable to moose, provides a simplified single-ungulate system in which to evaluate NCC models. Estimates of NCC with varying definitions of available biomass have been used to set population management goals for moose on the CRD in the face of landscape change and strong seasonal fluctuations in resource availability (MacCracken et al. 1997; Stephenson et al. 2006), while recent changes in population size and distribution complicate the applicability of past estimates. As such, this research area serves as a case study in demonstrating the need to gauge the impact of modeling decisions and assumptions on NCC estimates. Highly variable winters and changes in moose winter ranges since the establishment of the new moose population further complicate estimation of NCC on the CRD. From 1917 to 2012, winter length (total days from first snow until last) ranged from 65 to 221 d, with annual snow depths averaging 2.7–108.0 cm (WRCC 2015). Thus, effects of winter severity on forage availability (snow burial) vary by year (Visscher et al. 2006). Furthermore, past research that included NCC estimates (1987–1989; MacCracken et al. 1997) found 90% of collared moose wintered within primary and secondary ranges of 4,800–12,900 ha (Figure 1), presumably because of forage availability, snow drifting, and extreme winter winds (−40°C wind chill) from the Copper River Canyon. Although detailed space-use data are unavailable for the current population, recent (2012–2014) aerial surveys suggest the moose population has expanded its winter range beyond those described in 1987–1989 to encompass most of the west Delta. Nevertheless, these same surveys indicate the highest moose densities may still occur within the 1987–1989 primary range (C. Westing, Alaska Department of Fish and Game, personal communication). Whether this range expansion is due to exploration from the release points, population growth, or changes in vegetation resulting from climate- or earthquake-driven succession is unknown, but the increased forage availability could significantly affect NCC estimates.

Here, we evaluate different approaches to estimating winter NCC in order to guide management of a large herbivore on a dynamic landscape. We developed three model structures of energy-based winter NCC with varying levels of forage availability and plant tolerance to herbivory. To maintain historical precedent set by previous studies (MacCracken et al. 1997; Stephenson et al. 2006), we assumed that winter was the limiting season and compared model estimates of NCC across different winter scenarios (mild, moderate, and severe) and winter

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Contrasting Carrying Capacity Models S.E. Smythe et al.
range sizes (12,995–54,735 ha). Our objectives were to 1) calculate the digestible energy available to moose in different stand types and develop a set of energy-based NCC models, varying in structure and assumptions, in order to represent the diverse factors that managers on the CRD may consider relevant to the moose population with their current knowledge of CRD moose ecology; 2) compare estimates from these models to demonstrate the differences resulting from NCC model structures and assumptions; 3) perform a sensitivity analysis to determine the relative influence of factors within one model, range, and winter scenario within that combination.

**Study Area**

The CRD is the largest continuous wetland (>283,000 ha) in the Pacific Northwest (Kesti et al. 2007). Presumably excluded from the Delta by topography in the past, moose were introduced (n = 23; 1949–1958) as a subsistence resource for the town of Cordova (MacCracken et al. 1997). The population has since split into two semidistinct populations (west and east; 600 and 230 individuals, respectively) separated by the Copper River (C. Westing, Alaska Department of Fish and Game, unpublished data; Figure 2). We address the western population, which is better understood and managed. Hunting began in 1960 and is the greatest source of mortality in adult moose, although heavily harvested wolf *Canis lupus* and brown bear *Ursus arctos alascensis* populations contribute to adult and calf mortality (MacCracken et al. 1997). The population supports a relatively high twinning rate (58–65%; C. Westing, Alaska Department of Fish and Game, unpublished data).
The west Delta (~55,000 ha, 0–300 m elevation) is encircled by the Pacific Ocean, glaciers, the Chugach Mountain Range (>2,000 m elevation), and the Copper River (Figure 1), which channels winter gusts up to 193 km/h through its canyon. Soil types include aeolian and alluvial sands, gravels, and marine glacial silts (Davidson and Harrish 1978). Mean annual (1909–2014) precipitation, winter snow depth, and temperature were 230 cm, 23 cm, and 4.0°C (monthly range –8.9–16.3°C; WRCC 2015). The CRD has 336 annual growing-degree days (base 50°F or 10°C) on average. Hydrological dynamics and channel changes determine vegetation distribution on the Delta (MacCracken 1992; Boggs 2000). Woody browse important to wintering moose include feltleaf, Barclay’s, undergreen, Hooker’s, and Sitka willow Salix alaxensis, S. barclayi, S. commutata, S. hookeriana, and S. sitchensis, as well as Sitka alder Alnus viridis sinuata, black cottonwood Populus trichocarpa, and sweetgale Myrica gale (MacCracken et al. 1997). These eight forage species are found in seven stand types classified via a map generated by Satellite Pour l’Observation de la Terre, version 5 (SPOTS; 2011, Redcastle Resources, Inc., Salt Lake City, UT): spruce–hemlock Picea–Tsuga, spruce–cottonwood Picea–Populus, cottonwood, alder Alnus, alder–willow Alnus–Salix, willow, and sweetgale Myrica. A 1964 earthquake (9.2 magnitude) 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, especially Sitka alder, sweetgale, and Sitka spruce P.sitchensis (Ferrians 1966; Stover and Coffman 1993; Boggs 2000; Thilenius 2008).

Methods

Modeling nutritional carrying capacity

Calculating digestible energy and development of NCC model structures. To evaluate the effects of model type, winter severity, and winter range on NCC estimates, we developed three digestible energy-based NCC models (Figure 3) using the “forage supply–animal demand” structure (Mautz 1978b; Hobbs et al. 1982). All three models incorporated species- and stand-type-specific estimates of nutritional quality and available biomass (kg/ha) to calculate the digestible energy (kcal/ha) available within the seven stand types. Nutritional quality estimates incorporated effects of secondary chemicals (reduction of available protein due to tannins, and reduction of digestible dry matter due to lignin; Windels and Hewitt 2011), gross energy, and neutral detergent fiber. 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 energy values and to provide estimates of within-stand-type variability. We then multiplied the within-stand variability of digestible energies by range-specific estimates of stand-type areas (ha) to estimate median stand-type digestible energies. We summed the total median stand digestible energies, and compared the total calculated winter scenario- and range-specific digestible energy with the total energy required by an average adult female moose (500 kg) for maintenance (Schwartz et al. 1988) across a scenario-specific winter length (days) to determine the total number of moose supported within a specified range (see Figure 3 footnotes for maintenance requirements, all NCC formulas, and associated references).

The three models differed in their approach to available biomass.

1) In our “open-diet” model (a historically relevant standard, and digestible energy-based modification of the model used by MacCracken et al. 1997), we assumed equal selection probability for all forage species (i.e., did not consider forages “preferred” or “nonpreferred”). Because complete (100%) consumption of all available forage is ecologically, physiologically, and managerially unrealistic (Miquelle and Jordan 1979; Renecker and Schwartz 1997) but the tolerance level for consumption of shrubs on the CRD are unknown, we conservatively reduced the available biomass of forage species to 25% (i.e., 25% use) to simulate sustainable browsing of forage species (Singer and Zeigenfuss 2002; Dungan et al. 2010).

2) Our “diet-restricted” model reduces available biomass to the most preferred (and at-risk for overconsumption) forage as determined by proportional occurrence in diet analyses (Bryant et al. 1992; Windels and Hewitt 2011). Moose fecal analyses conducted by MacCracken et al. (1997) determined willows were most abundant in the CRD moose diets, although their analyses could not differentiate among species. Thus, we used the total available biomass of willows as the limiting forage.

3) Lastly, because the “diet-restricted” model assumes 100% availability of available willow biomass, we
developed a third model, which conservatively limited willow biomass to 25% (“diet-restricted, 25% use”).

Development of winter scenarios. We developed winter scenarios (mild, moderate, and severe) by categorizing winters based on mean winter snow depth (cm) and length (days from first snowfall to last) collected from 1917 to 2012 by the Alaska Climate Research Center (ACRC 2014) weather station at Cordova’s “Mudhole Smith” Airport on the west Delta. We determined categories by plotting winter total snow depths and noting natural breaks. We then calculated winter lengths by averaging the number of days from first snowfall to last for each winter in each category. We used analysis of variance to compare scenarios, and then adjusted scenario NCC model components of available biomass and winter length by mean snow depths and numbers of days.

Delineation of winter ranges and estimation of stand type areas. We initially defined two ranges relevant to the wintering moose population (Figure 1): 1) an aggregate of the primary and secondary ranges (hereafter, “total past observed range”) as determined using previously Very High Frequency-collared moose (n = 200; 1987–1989; MacCracken et al. 1997), and 2) the entire west Delta, to incorporate evidence from recent aerial surveys showing range expansion of the population (C. Westing, Alaska Department of Fish and Game, unpublished data). Our vegetation sampling plots were subject to logistical and safety restrictions and fell ≤1.5 km from CRD roads, which function as levees; therefore, we investigated effects of plot distance from roads (m) on nutritional energy using linear regression models to account for potential hydrological effects of roads on vegetation. We determined which stand types differed significantly (regression P-value ≤ 0.05) in nutritional energy with increasing distance from roads, retested to determine at what distance the effect became nonsignificant, and then developed a third range definition (hereafter, “adjusted west delta range”), which re-estimated nutritional energy in affected stands beyond the significant distance. We then recalculated the total nutritional energy across the Delta by summing separate estimates of nutritional energy beyond the significant distance for each affected stand type with estimates of nutritional energy within the significant distance, as well as total nutritional energy regardless of road distance for unaffected stands (Figure S1, Text S2, Data S2, Supplementary Material). This statistical adjustment to our forage biomass estimates relative to the levee-like road thus provides the least-biased correction for our forage estimates created by the logistical restrictions placed on our sampling size and design. To estimate stand type areas (ha) within winter ranges, we used the SPOT5 (2011) vegetation map, which determined the vegetation stand-type categories we used, and Graphical Information System (GIS)–based tools to sum the total area of each stand type. We corrected stand area estimates of the SPOT5 map according to an error matrix developed by Red Castle Resources, Inc. (Salt Lake City, UT) via “spot-proofing” (randomly visiting points within the study area to verify the accuracy of satellite classifications), and by visually checking stand categorization accuracy at our randomized points across the Delta.

Estimation of biomass availability and nutritional quality

To estimate the biomass available to and utilized by moose, we used GIS-based programs and the SPOT5 map to generate 7–9 randomized points within each of the 7 stand types (53 total). We restricted points to ≤ 1.5 km of roads because of logistical and safety constraints. Upon reaching each point, we verified the SPOT5 classification of the stand type (Viereck 1992) and established three 10 × 1-m belt transects. Two belt transects ran north and the third ran west, with start points ≥ 5 m apart. To capture maximum forage growth, we collected autumn (September–October 2012, 2013) basal diameters, stem densities, and stem heights, and to sample browse nutrition prior to green-up, we collected late-winter (April–May 2013) samples of the eight browse species.

In the autumn, we measured basal diameters (0.01 mm) above the moss layer on the three closest stems every 0.5 m along the transects, and then estimated available biomass (g/stem) with regression equations (MacCracken and Van Ballenberghe 1993; Stephenson et al. 1998; Smythe 2015). Very-large-stem basal diameters (>60.0 mm) increase heteroscedasticity of biomass estimates (MacCracken and Van Ballenberghe 1993). Thus, for large stems we measured a branch diameter, estimated the number of equivalent branches on the stem, and summed the branch biomasses. We counted the number of stems and calculated stem density (n/30 m²) of each forage species, measured the height (m) of three stems per species (when available) per transect and, to allow for changes in available biomass with increasing snow depth, we visually estimated the biomass (%) present on those stems in 1-m increments from 0 to 6 m (the height range of browse available to moose in mild to severe winters). We calculated the species-specific mean available biomass (stem biomass × stem density, kg/ha, and % available by incremental height classes), and height (m) within each stand type.

Finally, to estimate forage nutritional quality, we collected samples of available biomass for every browse species observed in each plot. The maximum bite diameter recorded on the Delta was 8.3 mm (MacCracken et al. 1997), so 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 where they were oven-dried and ground prior to analyses of gross energy (cal/g; bomb calorimetry), crude protein (%), lignin (%), 72% sulfuric acid method), tannin levels (mg/g, Martin and Martin
Figure 3. General model structure used to estimate nutritional carrying capacity of the Copper River Delta, Alaska, for moose *Alces alces* wintering in 2012–2013. Model structure was applied across model types (open-diet 25% use, diet-restricted 100% use, and diet-restricted 25% use), winter ranges (total past observed including primary and secondary ranges, whole west Delta, adjusted west Delta), and winter scenarios (mild, moderate, severe).

Footnotes:
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 Smythe (2015).
5. NDF = neutral detergent fiber (% of DM).
6. NDS = neutral detergent solubles (g/100 g DM); Spalinger et al. (2010).
1982), and neutral detergent fiber (%, Van Soest/Ankom sequential fibers). From these values, we calculated the mean species-specific nutritional values within each stand type.

**Sensitivity analysis**

We conducted a sensitivity analysis on one model, range, and winter scenario combination to determine the relative influence of factors within the representative combination. On the “open-diet, 25% use” model in the road-bias-adjusted range during a severe winter, we increased nine factors (protein reduction due to tannins, lignin content, gross energy, stem biomass, stem density, snow depth, stand type area, winter length, energy needed by wintering moose, and moose mass) by 5% and calculated the change (%) in NCC and the proportional sensitivity.

**Results**

Although we encountered feltleaf willow near the Scott Glacier and Copper River (S.E. Smythe, personal observation, 2013), it never occurred within our randomized plots and we subsequently removed it from our analyses. The seven remaining forage species in the seven stand types varied in mean available biomass (kg/ha), gross energy (cal/g), crude protein (%), lignin (%), tannin (mg/g), and neutral detergent fiber (%) levels (Tables S1 and S2, Text S3, Data S2, Suppemental Material). Winter length in mild, moderate, and severe winter scenarios averaged 147 (±7), 163 (±8), and 178 (±22) d, while annual mean snow depths averaged 11 (±2), 26 (±2), and 64 (±17) cm, respectively. Between 1917 and 2012, mild, moderate, and severe winter scenarios occurred 49, 29, and 11 times, while 6 winters were unclassified on account of incomplete data (Text S4, Data S3, Supplemental Material). Winter ranges varied in size (12,995–54,735 ha) and stand type composition (Table 1, Text S5).

Digestive energy available to moose varied by stand type and winter scenario (Figure 4, Text S6). Of the seven stand types, only digestible energy estimates in cottonwood, alder–willow, willow, and sweetgale stands were significantly affected by plot distance (m) from the Delta roads (linear regression: P ≤ 0.05; Table S3, Text S2, Data S2, Supplemental Material). The effect disappeared in plots >100 m from roads in cottonwood stands, and >200 m from roads in alder–willow, willow, and sweetgale stands.

Estimates of NCC across all models, ranges, and scenarios ranged from 205 to 4,592 moose (1.0–12.5 moose/km²; Figure 5, Text S7, Data S2, Supplemental Material). Mean estimates of NCC in the three ranges (total past observed, whole west Delta, and road-bias-adjusted west Delta) across all winter scenarios and models were 849, 2,359, and 2,407 total moose, respectively. Thus, NCC estimates using the adjusted west Delta range were 2.0% higher than the west Delta range, while estimates using the total past observed range were 64.0% lower. However, our models estimated the highest moose densities (moose/km²) within the total past observed range (Figure 5; Text S7, Data S2, Supplemental Material). Mean NCC estimates using “diet-restricted (100% use)” models across all ranges and winter scenarios were 20.1% higher, respectively, than estimates using the “open-diet” model, though estimates declined by 75.0% when we limited available biomass (“diet-restricted, 25% use”). Mean NCC estimates across all models decreased by 18.9% and 32.5% as winter severity increased to moderate and severe, respectively. Percent changes in NCC from the sensitivity analysis on the “open-diet, 25% use” model in the road-bias-adjusted winter range model during a severe winter varied from −4.76 to 11.18% (Table 2; Text S8, Data S2, Supplemental Material). Proportional sensitivity ranged from −0.95 to 2.24, with the smallest and largest
proportional sensitivity attributed to protein reduction (due to tannins) and snow depth, respectively.

**Discussion**

Variability in model structure strongly influenced NCC estimates generated from our three model structures, winter scenarios, and winter ranges. Thus, evaluating different winter NCC models for moose on the CRD highlighted the importance of matching model structure to species’ behavioral, ecological, and topological constraints, and the difficulty of comparing NCC estimates even within the same system. The model structures that resulted in the greatest limitations of forage (‘diet-restricted’ with 25% use, severe winter scenarios) estimated NCC below the current population, and may explain the 15–20% population decrease following the 1970–1971 severe winter, when space use by, and thus forage availability for, moose may have been highly constrained (MacCracken et al. 1997). Observations that the current population persisted through another severe winter in 2011–2012 (Figure 2; Text S1, Data S1, Supplemental Material) suggest the restricted range used in those models no longer adequately describes the area over which moose are currently accessing resources. Aerial surveys suggest moose have expanded their winter range; therefore, increased access to forage potentially buffered the 2011–2012 population in a historically severe winter (mean snow depth = 101 cm). This suggests that models dependent on assumptions of restricted winter range size (total past observed) are not currently accurate. Assessing space use in severe and mild winters should be a prerequisite for future attempts to measure NCC here and in similar systems.

Density-dependent and seasonal factors in herbivores and forage may influence browsing behavior or diets over time and space (Vivas and Saether 1987). In this analysis, the “diet-restricted” structures constrained diet preferences to those observed in 1987–1989, but potential for seasonal and temporal shifts in diet preference since then were poorly understood. Hobbs and Hanley (1990) cautioned against assuming that herbivores are limited to the diets observed during a specific period. In Kruger National Park, 10 of 11 ungulates studied displayed significant seasonal changes in grass and shrub consumption (Codron et al. 2007b), while Codron et al. (2007a) noted regional differences may explain disparities in diet recorded for African ungulates, and a study in Japan found notable differences in diets across individual serows Capricornis crispus during winter (Jiang et al. 2008). Seasonally specific free-choice diets are unknown for the CRD moose, but the recent severe winter survival (2012) and our record of

**Figure 4.** Digestible energy (kcal/ha) of moose Alces alces winter forage within dominant stand types on the Copper River Delta, Alaska, as estimated across three winter scenarios (mild, moderate, and severe) from samples collected in 2012–2013.

| Range                  | Total area  | Spruce–hemlock | Spruce–cottonwood | Cottonwood | Alder | Alder–willow | Willow | Sweetgale |
|------------------------|-------------|----------------|-------------------|------------|-------|--------------|--------|-----------|
| Whole west Delta*      | 54,735d     | 7,538          | 1,524             | 294        | 13,674| 1,372        | 1,735  | 9,463     |
| Adjusted west Deltab   | 54,735      | 7,538          | 1,524             | 294        | 13,674| 1,372        | 1,735  | 9,463     |
| Primary observedc      | 8,184       | 571            | 783               | 61         | 1,663 | 782          | 928    | 1,864     |
| Secondary observedd    | 4,811       | 275            | 548               | 32         | 1,522 | 410          | 415    | 534       |
| Total past observedd   | 12,995      | 846            | 1,331             | 93         | 3,185 | 1,192        | 1,343  | 2,398     |

*Encompasses the entire study area.

b Includes different estimates of biomass available in cottonwood, alder–willow, willow, and sweetgale plots 100–200 m from the roads.

c Primary, secondary, and total (summed) past observed ranges represent winter ranges used by collared moose in 1987–1989 (MacCracken et al. 1997).

d Totals also include nonmoose habitat such as water, bare ground, etc.
Table 2. Changes (%) and proportional sensitivities ($S_x$) of the independent components in an open-diet (25% use of all forage species) model used to estimate nutritional carrying capacity (NCC) for moose within the road-bias-adjusted west Delta winter range in a severe winter on the Copper River Delta, Alaska. Samples used within the model were collected in 2012–2013.

| Model variable | % Adjusted | NCC | % Change | $S_x$ |
|----------------|------------|-----|----------|-------|
| No change      | 0          | 2,167 | —        | —     |
| Protein reduction | +5%   | 2,167 | -0.02    | 0.00  |
| Lignin         | +5%       | 2,168 | 0.03     | 0.01  |
| Gross energy   | +5%       | 2,315 | 6.81     | 1.36  |
| Stem biomass   | +5%       | 2,324 | 7.23     | 1.45  |
| Stem density   | +5%       | 2,333 | 7.64     | 1.53  |
| Snow depth     | +5%       | 2,409 | 11.18    | 2.24  |
| Area           | +5%       | 2,291 | 5.71     | 1.14  |
| Winter length  | +5%       | 2,064 | -4.76    | -0.95 |
| Moose energy   | +5%       | 2,064 | -4.76    | -0.95 |
| Moose mass     | +5%       | 2,089 | -3.59    | -0.72 |

high sweetgale use (Smythe 2015) suggests the limited diet assumed by the “diet-restricted” models underestimates the amount of forage available, and that applying models with limited diets in any system would require detailed understandings of diet preferences under different conditions. Considering this unknown variability, the “open-diet” model could be seen as a physiologically generous alternative, appealing to the indefinite limits of ungulate diet selection. However, the open-diet model contradicts well-studied models of ungulate diet selection and preference, which cannot be ignored even if they are not currently ecologically complex enough. Seasonally comprehensive and long-term diet studies are needed to resolve this issue.

As in other studies of NCC, our attempts to determine ecologically reliable estimates of NCC for the west CRD moose were hampered by several factors. Lack of recent detailed data on space use and resource selection by moose obscured the appropriate definition of a current moose winter range. Although the observed range defined by MacCracken is overly restrictive, moose are likely not using the full west Delta range equally or entirely. We estimated capacity for higher moose densities within the observed range, suggesting some areas could be preferred by moose. The factors contributing to this preference are largely unknown, but could include past population occurrence and exploration, human factors, or predator influences, among others beyond the influence of snow depth and forage availability discussed. Both humans and predators are known to influence ungulate space use (Brown 1999; Theuerauf and Rouys 2008), often restricting ungulate movement to areas with less abundant or lower quality forage associated with decreased predation risk. Ungulates may also select for areas associated with humans—elk Cervus canadensis in Banff National Park utilized refugia created by human activity to decrease risk of wolf predation (Hebblewhite and Merrill 2009). In areas with limited predator effects, energy expenditure associated with increasing range sizes may function as the only significant limit to population distribution, such as with caribou Rangifer tarandus in northern Quebec (Messier et al. 1988). Nutritional carrying-capacity models that lack behavioral, predatory, or physiological restraints to a population’s range risk overestimating the forage available.

The browsing tolerance of forage species is unknown on the CRD and in many other systems. 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 changes in secondary chemicals and nutrition. Neither study evaluated the long-term effects of high utilization (MacCracken and Viereck 1990; Miquelle et al. 1992). A review by Augustine and McNaughton (1998) found that intermittent herbivory (e.g., due to migration or nonherding) and nutrient-rich ecosystems aided the regrowth capacity of palatable forage species. 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 through tidal, glacial, and actinorhizal sources on the Delta, forage may be able to support greater levels (>25%) of consumption, and NCC models that restrict forage use may underestimate the forage consumable by populations without causing ecological damage. Alternatively, moose, as large herbivores, are a relatively recent pressure on forage species; therefore, it also possible the browsing tolerance of shrubs on the CRD may be <25% use, in which case sustainable NCC estimates must be reduced.

The dynamic nature of the forces governing the CRD vegetation make all estimates of NCC temporary. The hydrology, soil quality, land area, form, and successional patterns of the vegetation of the Delta are dictated by several landscape-level forces including glacial, stream, and tidal flooding, sedimentation, erosion, and salinization, along with periodic earthquake-initiated cycles of uplift and subsidence (Boggs 2000). These geological factors may interact with zoological and human influences (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; Smythe et al. 2016) to influence forage availability in opposing ways (potentially increasing or decreasing forage available to moose; reviewed in Smythe 2015). Furthermore, as a result of its levee-like action of trapping water north of the road, and reducing both the rate and dynamics of flow south of the road, the Copper River highway acts as a constant manmade influence on the hydrology and, in turn, the vegetation growing within its influence. Our approach to estimating the spatial reach of road effects on vegetation biomass would have benefitted from additional sample size designed specifically to address that effect. Full understanding of the complex, longer term hydrological and ecological influences of the road on the Delta vegetation warrants a separate, more detailed investigation.

Climate change will likely influence many factors within NCC models and is expected to have disproportional strongly influences in other high-latitude ecosystems (IPCC 2007). We found potential evidence of...
Figure 5. Estimates of nutritional carrying capacity (NCC; no. of moose *Alces alces* predicted, with SE bars) on the Copper River Delta, Alaska, in 2012–2013 using three models (“open-diet/25% use,” “diet-restricted/100% use,” and “diet-restricted/25% use”), across three ranges (total past observed including primary and secondary ranges, whole west Delta, adjusted west Delta), and under three winter scenarios (mild, moderate, and severe). The “open-diet” model allowed equal use of all seven winter forage species, while the “diet-restricted” models limited forage biomass to preferred willows. Percent use restricted biomass availability to allow forage recovery (25% use) or complete consumption (100% use). Winter range areas (ha) used in modeling ranged in size from largest, consisting of the entire study area (whole west Delta), to smallest being a range determined by space use by moose tracked in an earlier study (total past observed; MacCracken et al. 1997), with primary and secondary subranges being used in both mild and moderate winter severities, but only the secondary subrange being used in severe winters. Intermediate in area was the west Delta with estimates of available forage biomass adjusted relative to road levee effects (adjusted west Delta). Numerical estimates of NCC (total abundance and moose/km²) are summarized in Table S4 (Supplemental Material) by model, range, and winter scenario.
increased willow stem biomass relative to 1988–1989 data (Smythe 2015), possibly due to increased mean temperatures across Alaska (ACRC 2014), while severe winters on the CRD have diminished from four in the 20-y period from 1917 to 1936 to one thus far in 1997–2015. Rates and patterns of succession may increase with further increases in temperature, nutritional quality of forage may benefit from earlier or increased growing seasons, and snow effects on forage availability may decrease as winter severities continue to lessen. Alternatively, forage biomass and nutrition may experience earlier senescence or endure harsher summer conditions with warmer temperatures, possibly creating mismatches in peak forage nutrition and peak nutritional need for lactating moose. Furthermore, as in some parts of the lower 48 states, the temperatures in Alaska may eventually exceed those physiologically manageable by moose. The CRD managers would benefit from monitoring and research in these areas.

The CRD landscape is highly dynamic, and McLeod (1997) questioned the validity of calculating carrying capacity within any nonequilibrium ecosystem. Our current winter NCC estimates will, however, inform management goals in the near future and serve as an updated benchmark as geological, hydrological, successional, climatic, zoological, and cultural influences continue to drive vegetation change. Our work serves as a reminder of the change inherent to most ecosystems and its continuous effect on animal populations, even within relatively stable landscapes. Estimates of NCC on the Delta will need to be recalibrated periodically to guide management as habitat changes, but future efforts will be informed by the lessons from this comparative study. Similarly, NCC estimates globally may require periodic reevaluation, depending on the stability of the system and factors affecting model components.

Our NCC models with larger winter ranges generally suggest that a larger moose population could be sustained on the CRD, depending on the winter scenario. Past authors used severe winter scenarios for developing conservative management goals, and our sensitivity analysis indicates snow depth is the most influential model factor, and winter length contributed to overall declines in NCC with increasing winter severity. However, the severe winter scenario may decrease in relevance if climate change reduces the frequency of those conditions, and moderate winter scenarios may be more appropriate for management goals. Delta-wide data on daily snow depths, drift formation, melt rates, and compaction are not currently available but would aid managers in weighting this factor. Given the importance of moose hunting for subsistence in the region, we further recommend managers consider setting population size targets at some margin above the level at which maximum sustained yield would be obtained (e.g., half of NCC; Caughley 1976) but lower than total NCC, depending on the model deemed most appropriate with current knowledge (which should likely be a summer-based NCC model; see below). That margin would protect against issues associated with inaccurate population estimates or within a highly variable environment that can lead to delayed recognition of over- or underharvest, population instability, and ecosystem damage (Larkin 1977; Lande et al. 1997; McCullough 2001). Given that moose are an introduced megaherbivore in this Critical Habitat Area (Alaska Department of Natural Resources 2007), managers also must carefully consider the effect of a higher moose population on vulnerable native species. More reliable and continuous space use and vitality data would greatly aid management of this population. Our sensitivity analyses suggest that managing for higher stem densities or larger areas with forage would most efficiently improve forage availability, supporting current mechanical treatment (e.g., hydraulic-axing) efforts on the CRD (Stephenson et al. 1998; Smythe et al. 2016).

Despite the low proportional sensitivity of tannins and lignin in our analysis, inclusion of nutritional quality and use of energy-based models can dramatically influence NCC estimates (Windels and Hewitt 2011; Smythe 2015). We recommend models of NCC incorporate species-specific nutritional values, and constrain available biomass (<100% use) within NCC models to allow forage recovery (Singer and Zeigenfuss 2002). We also strongly recommend estimating summer-based NCC on the CRD in the future because 1) considerable research finds ungulate reproductive success (milk yields, calf growth and viability, etc.) depends on fat reserves gained during spring and summer rather than reserves lost during winter; and 2) the forage available to the CRD moose is no longer limited by a restricting winter range; therefore, consideration of full-year forage availability may be important to understand the population’s current limiting factors (Bobek 1977; Mautz 1978a; Merrill and Boyce 1991; Cook et al. 2001, 2004; Beck et al. 2006; Dungan et al. 2010). Alternatively or in complementary fashion, we recommend estimates of carrying capacity conducted via “animal indicators” (Franzmann and Schwartz 1985; Stephenson 1995; Cook et al. 2013; Monteith et al. 2013) as a supplementary method for estimating the sustainability of this population within a nuanced environment.

Supplemental Material

Please note: The Journal of Fish and Wildlife Management is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Text S1. Program R code to create population graph (Figure 2) in conjunction with Data S1 (Supplemental Material) Excel data to estimate moose population abundance on the West Copper River Delta, Alaska. Found at DOI: https://doi.org/10.3996/122017-JFWM-104.S1 (2 KB R).

Text S2. Program R code to test the relationship between nutritional energy for moose (Copper River Delta, Alaska) in vegetation plots relative to their distance from the roads (Figure S1, Table S3, Supplemental Material) as a baseline for the road buffer defined the
adjusted west Delta range; in conjunction with Data S2 (Supplemental Material) Excel data.

Text S3. Program R code to derive summarized nutritional values for moose forage species on western Copper River Delta of Alaska (Tables S1 and S2, Supplemental Material) in conjunction with Table S2 Excel data.

Text S4. Program R code to summarize snow depths specific to winter scenarios (see Results) on the western Copper River Delta, Alaska, in conjunction with Data S3 (Supplemental Material) Excel data.

Text S5. Winter-range total sizes (ha) and range-specific stand-type components (ha) for moose on the western Copper River Delta, Alaska, were determined using NCCRCCode and Geographic Information System-based calculations of landcover rasters (SPOT 5 2011; U.S. Forest Service).

Text S6. Program R code to summarize digestible energy values of moose forage species present by stand type on the western Copper River Delta, Alaska (Figure 4) in conjunction with Data S2 (Supplemental Material) Excel data.

Text S7. Program R code to summarize the NCC of moose specific to each model type, winter scenario, and winter range on the western Copper River Delta, Alaska (Figure 4, Data S3, Supplemental Material) in conjunction with Data S2 (Supplemental Material) Excel data.

Text S8. Program R code to summarize percent changes and proportional sensitivities of model components in moose NCC models for the western Copper River Delta, Alaska (Table 2); to be used in conjunction with Data S2 (Supplemental Material) Excel data.

Data S1. MoosePop Excel; used to plot changes in the moose Alces alces population on the west Copper River Delta in south-central Alaska from 1949 to 2014 using different survey methods. Accompanied by a ReadMe file.

Data S2. MooseRData Excel; used to support generation of nutritional values of forage species collected in 2012–2013 and consumed by moose Alces alces on the Copper River Delta, Alaska. Data were analyzed by species and stand type, used in subsequent estimates of nutritional carrying capacity across three winter scenarios (Text S2 and Text S4, Supplemental Material), and also provides data for sensitivity analyses (Text S2, Supplemental Material) for the nutritional carrying capacity models. Accompanied by a ReadMe file.

Data S3. SnowScenarioData Excel; Used for calculation of total snow depths and winter lengths from 1914 to 2014 on the Copper River Delta, Alaska. Accompanied by a ReadMe file.

Figure S1. Changes in plot nutritional energy (a product of forage biomass and factors contributing to nutritional quality; see manuscript Methods; kcal/ha) relative to plot distance (m) from road structure in different stand types (black = spruce–hemlock, red = spruce–cottonwood, blue = cottonwood, green = alder, purple = alder–willow, orange = willow, and yellow = sweetgale). Winter forage species for moose found in the seven stand types were Barclay’s willow, undergreen willow, Hooker’s 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. These were used to estimate moose Alces alces nutritional carrying capacity on the Copper River Delta, Alaska, using forage samples from 2012 to 2013. We tested for effects of plot distance from roads on nutritional energy via linear regression. Nutritional energy in cottonwood, alder–willow, willow, and sweetgale plots was significantly (P < 0.05) affected. To define the modeling (winter) range accounting for this effect, we retested for significance after successively removing points for stands located at increasing distances from the roads (e.g., <100 m, <200 m). Nutritional energy in cottonwood plots >100 m from roads, and from alder–willow, willow, and sweetgale plots >200 m from roads, were no longer significantly affected. Using these results, we then re-estimated the nutritional energy available (see manuscript Methods and Figure S3) in the affected stands using plots sampled nearer and beyond their respective significant distances (from roads) and calculated total nutritional energy available for each stand type across the modeling range we refer to as the adjusted west Delta range.

Table S1. Stand-type- and species-specific values of mean gross energy (GE; cal/g), crude protein (CP; %), lignin (L; %), tannin (T; mg/g BSA), and neutral detergent fiber (NDF; %), digestible energy (DE; cal/g) and 95% confidence intervals (±) for the seven winter forage
species Barclay’s willow, undergreen willow, Hooker’s 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 seven stand types (spruce–hemlock, spruce–cottonwood, cottonwood, alder, alder–willow, willow, and sweetgale) important to wintering moose *Alces alces* sampled in late winter (April–May) of 2012–2013 on the west Copper River Delta, Alaska.

Found at DOI: [https://doi.org/10.3996/122017-JFWM-104.S13](https://doi.org/10.3996/122017-JFWM-104.S13) (41 KB DOCX).

**Table S2.** Stand-type- and species-specific estimates of mean available biomass (AB, kg/ha; no snow burial or height limit) and consumption (Use, %) by moose *Alces alces* for the seven winter forage species Barclay’s willow, undergreen willow, Hooker’s 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 seven stand types (spruce–hemlock, spruce–cottonwood, cottonwood, alder, alder–willow, willow, and sweetgale) relevant to moose winter ecology and sampled August–September 2012–2013 (biomass) and April–May 2013 (use) on the west Copper River Delta, Alaska.

Found at DOI: [https://doi.org/10.3996/122017-JFWM-104.S14](https://doi.org/10.3996/122017-JFWM-104.S14) (32 KB DOCX).

**Table S3.** Regression results for stand-specific digestible energy (kcal/ha, y variable) available to moose *Alces alces* relative to the distance (m, x variable) of sampling plots from the Copper River Highway sampled in 2012–2013 on the Copper River Delta, Alaska.

Found at DOI: [https://doi.org/10.3996/122017-JFWM-104.S15](https://doi.org/10.3996/122017-JFWM-104.S15) (22 KB DOCX).

**Table S4.** Nutritional carrying capacity estimates (no. of moose [density of moose/km²]) for the seven winter forage species Barclay’s willow, undergreen willow, Hooker’s 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 seven stand types (spruce–hemlock, spruce–cottonwood, cottonwood, alder, alder–willow, willow, and sweetgale) important to wintering moose *Alces alces* using 2012–2013 forage data and estimated according to different model structures (“open-diet or diet-restricted” with 25% or 100% use of forage species), winter ranges (west Delta, road-bias-adjusted west Delta, and total past observed), and winter severities (mild, moderate, and severe) on the Copper River Delta, Alaska.

Found at DOI: [https://doi.org/10.3996/122017-JFWM-104.S16](https://doi.org/10.3996/122017-JFWM-104.S16) (23 KB DOCX).

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