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FIELD TEST OF A MOOSE CARRYING CAPACITY MODEL

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Abstract: The amount of moose forage was estimated in each 1 mi^2 exclosure at the Moose Research Center (MRC) near Soldotna, Alaska in July 1983 and 1984. The amount of forage consumed by moose from 15 October to 1 May was calculated using 2 computer simulation models. These models predict daily forage intake of moose based on nutrient requirements, physiological constraints, and forage quality. Each exclosure was stocked during winter with a number of moose to remove a different amount of paper birch current annual growth (CAG). Tagged paper birch shrubs were measured before and after browsing to determine the utilization level of CAG.

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Browsing by hares masked browsing by moose except in the 80-400 cm height strata. Predicted and measured moose utilization levels in the 80+ cm strata were similar in 3 out of the 4 pens. Reason for lack of agreement in the one pen was attributed to inaccurate knowledge of moose forage selection.

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Carrying capacity, the number of individuals a unit of land can support for a unit of time without habitat deterioration, is a term commonly used by the wildlife biologist. However, quantification of carrying capacity has been elusive, and meaningful application of the concept generally nebulous. Early attempts to measure ungulate carrying capacity were based on range or browse transect, indicator plants, or browse utilization methods. Using these techniques, the biologist obtained a better understanding of the relationships between the animal population and its forage base. But, because he could not relate these measurements to the nutritional requirements of the animal, he has seldom been able to quantify numbers of animals that the range could support.

A more recent approach to the problem of quantifying carrying capacity has been to integrate the nutritional needs of the animal with those supplied by the range. This concept of biological carrying capacity requires an understanding of ungulate nutrition, the nutrients the animal must obtain from the range, and the ability of the range to meet those nutritional needs (Moen 1973, Wallmo et al. 1977, Mautz 1978).

This approach to quantifying carrying capacity has been developed and refined through work at the Moose Research Center since 1978. Two computer simulation models (moose submodel) have been developed that predict daily forage intake based upon nutritional physiology of moose (Alces alces), their nutrient requirements, and the quality of available forage. The second part of the carrying capacity equation requires quantification of the amount of biomass available for each forage species. A second model (vegetation submodel) estimates the amount of available forage and nutrients available with different diet mixes and levels of utilization. The final product is an estimate of the potential carrying capacity of the range being evaluated. The term potential carrying capacity is used rather than the actual or realized population level because the 2 may be quite different. Any moose population may have a number of decimating factors (e.g., predation, hunting, starvation) operating upon it at any time.

The purpose of this study was to test the accuracy of these models in a field situation. The 4 large exclosures at the MRC provided an ideal "laboratory" to test the concepts without the complicating factors of seasonal

movements, shifting home ranges, and unknown losses due to predation.

The MRC was established in 1967. It is located on the Kenai National Wildlife Refuge about 40 miles northeast of Soldotna, Alaska. The Alaska Department of Fish and Game constructed and maintains the research facilities under a cooperative agreement with the U.S. Fish and Wildlife Service. Four large moose exclosures, from 239 to 268 ha, were completed in 1971, and digestion cages, feeding pens, and a metabolic chamber were added in 1978-79.

The MRC is located in a mixed birch-spruce forest that was burned by wildfire in 1947. Each pen contains a mosaic of burned and unburned vegetation. Topography is flat to gently rolling in all pens. Approximately one-fourth of Pen 1 was manipulated by tree crushers in 1976. The crushed area is in an earlier successional stage of birch-spruce forest than the remainder of the pens.

The number of moose stocked in each pen has varied greatly since construction due to changing research goals over the past 16 years. In general, the pens have been overbrowsed for several years. Vegetation production is moderate, but continuous browsing pressure has altered species composition. Paper birch (Betula papyrifera) is the dominant hardwood species and aspen (Populus tremuloides) and willows (Salix spp.) are rare compared to areas outside the exclosures.

OBJECTIVES

The goal was to determine the accuracy and precision of a model to predict moose carrying capacity within the exclosures (pens) at the MRC.

Specific objectives were to:

1. Measure forage biomass in each pen within 20% of the mean at the 80% confidence level.

2. Use the simulation models to predict the number of moose days during winter required to utilize the current annual growth of paper birch at various levels during winter.

3. Stock each pen with the appropriate number of moose to utilize paper birch CAG at 4 different levels.

4. Measure the utilization of paper birch CAG in each pen and compare the predicted and measured utilization levels.

METHODS

Moose Submodels

Swift (1983) developed a computer model that simulated the energy and nitrogen (N) balance for wild ruminants and estimated daily energy and N requirements. Daily voluntary intake of food is predicted based on diet digestibility and N content. A key element in this model is rumen volume and

rate of passage because the simulated moose always eats to maximum rumen fill. We modified input variables in Swift's model to be specific for moose based mostly on data collected at the MRC since 1978. Changes incorporated into the model were seasonal metabolic rates (Regelin et al. 1985), rates of passage and rumen turnover time (Hjeljord et al. 1982, Hubbert 1986), protein requirements (Schwartz et al. 1986a), seasonal dynamics of food intake (Schwartz et al. 1984), body weight (Schwartz et al. 1986b), and rumen volume (Gasaway and Coady 1974).

Data on moose food habits (LeResche and Davis 1973, Regelin et al. 1986) and forage quality (Regelin et al. 1986) from the Kenai Peninsula were used as model inputs. Results from the simulation were similar to expected values for daily forage intake of free-ranging moose (Reneker and Hudson 1985) and closely followed the annual cyclic patterns of forage intake and body weight measured with the captive moose at the MRC (Schwartz et al. 1984 and 1986b). These results were encouraging and gave us confidence that the model could correctly simulate energy and N balance in moose and accurately predict daily forage intake.

Swift's model assumed that moose always ate to rumen fill, but studies of food intake in moose (Schwartz et al. 1984) indicate that other factors probably affect voluntary intake. Also, in Swift's model, rumen volume has a major influence on intake levels. We were unable to measure rumen volume in moose and used values presented by Gasaway and Coady (1974). These data were based on measurements of rumen fill and were highly variable. Due to these concerns, Hubbert and Schwartz (Hubbert 1986) developed a new simulation model that could predict daily voluntary intake of food based on body condition and energy demand.

The Hubbert-Schwartz model estimates daily food intake based on the seasonal body condition and energy requirements. The dynamics of animal body condition (% fat) and energy requirements are used as drivers in the model to predict food intake under the constraints of seasonal diet quality and maximum rumen capacity. Maximum rumen capacity was established as a constant throughout the year, while rumen fill changed seasonally, allowing for flexibility in intake with changing forage availability, quality, and energy demands. This modeling concept allows daily forage intake to be controlled by both physical means (rumen volume, rate of passage as altered by forage quality) and physiological needs (energy requirements and body condition).

Body condition values were estimated through controlled feeding experiments (Schwartz et al. 1987) to establish fat levels for moose by season. Fat levels were measured using tritiated water.

The Hubbert-Schwartz model also changed how the fat and protein stores were anabolized and catabolized. Swift's original model had an animal lose all of its fat reserves before protein was catabolized. Also, an animal

in positive energy balance first regained only muscle mass until expected lean body mass was reached, then fat was added. Based on data from mule deer (Odocoileus hemionus) (Torbit 1985), the Hubbert-Schwartz model catabolizes 70% fat and 30% protein when the moose is in negative energy values and anabolizes the reverse proportions when it is in positive energy balance. The modified Swift model also uses these proportions for anabolism and catabolism of body stores.

Estimates of daily forage intake produced by both the Swift and Hubbert-Schwartz models are used to predict the amount of paper birch CAG that will be consumed over winter at different stocking rates. The accuracy of these predictions was assessed by measuring the level of utilization of paper birch CAG in each pen at the end of winter.

Estimation of Forage Biomass

A random sampling design was used to estimate forage biomass in each pen. All biomass measurements were made between 18 July and 10 August in both 1984 and 1985. Each pen was subdivided into 4 quadrats of approximately equal size. Transects were located in each quadrat by drawing random numbers between 1 and 800 that equated to distances in meters from a pen corner. Along each transect line, 8 random points (between 1 and 800) were selected for location of a 1 x 5 m plot. The 1 x 5 m plots were established using a 5-m cable stretched between 2 pins and a meter stick. A 20 x 50 cm subplot was nested within the lower righthand corner of each plot. Distances to transects and plots were determined by pacing and direction maintained using a compass. The number of transects measured in each quadrat is shown in Table 1.

Table 1. Number of transects in each quadrat used to estimate forage biomass in the pens at the Moose Research Center in 1983 and 1984. Eight plots were located along each transect.

	Pen							
	1		2		3		4	
Quadrat	1983	1984	1983	1984	1983	1984	1983	1984
A	6	8	6	8	16	8	18	8
B	20	16	12	8	12	20	10	24
C	33	16	14	8	18	12	6	24
D	10	20	11	8	26	16	18	28
Total	69	60	43	32	72	56	52	84

The number of stems of paper birch, aspen, and willow rooted within each plot were counted for density estimates. Stems exceeding a diameter of 5 cm at 10 cm above the ground or less than 40 cm in height were ignored. The stem of each hardwood species within the plot and nearest the lower righthand corner was measured for height, diameter at 10 cm above the ground, and clipped. Shrubs were divided into 3 height strata for clipping, 0-40, 41-80, and

81-400 cm. Plant material above 400 cm was discarded. Leaves and CAG from each strata were sacked and weighed separately. All mountain cranberry (*Vaccinium vitis-idaea*), rose (*Rosa acicularis*), and fireweed (*Epilobium angustifolium*) located in or overhanging the 20 x 50 cm subplot were clipped to ground level and each species sacked separately. All clipped material was dried at 100°C for 48 hours and weighed to the nearest 0.1 g.

Epson HX 20 computers were used as field data recorders. All data on plant density, height, and basal diameter collected in the field as well as weight data measured in the laboratory were entered into the field computer. These data were electronically transferred to a Fujitsu Micro 16 personal computer each evening. After 6 transects had been completed in each quadrat, data were analyzed and variance estimates used to predict the number of transects required to estimate CAG biomass within 20% of the mean at the 80% confidence level. Once the estimated number of transects had been completed, another analysis was conducted to ensure the biomass estimates were within the desired level of precision. Additional transects were measured if necessary.

The shrub biomass and density measurements were combined at the plot level to provide an estimate of the biomass on each 1 x 5 m plot. The means and variances of biomass estimates in each quadrat were combined for each pen by the following formulas:

$$\bar{\bar{X}} = \frac{1}{4} \times \sum_{i=1}^{4} \bar{X}_i$$

$$S^2_{\bar{\bar{x}}} = \frac{1}{16} \times \sum_{i=1}^{4} (S_{X_i})^2/n_i \, .$$

Degrees of freedom for the estimators were approximated by the formula:

$$df_{\bar{\bar{x}}} = \left[16 \times S^2_{\bar{\bar{x}}}\right]^2 \Big/ \sum_{i=1}^{4} \left[(S_{X_i})^2/n_i\right]^2 \Big/ (n_i - 1).$$

Paper Birch Utilization

Individual plants of paper birch were randomly selected and permanently marked for measurement of utilization of CAG during late winter. Within each of the 4 quadrats in each pen, 12 transects were randomly established in the same manner as the biomass transects. Along each transect a random starting point between 1 and 800 m was selected. Ten sampling points were established on each transect at 20 m intervals beginning at the random starting point. If the random starting point was 601 or greater, there was not adequate distance to establish 10 plots before reaching the end of the quadrat. In these cases, all possible points were established on the original transect and the remainder placed on a parallel transect 5 m to the right running in the opposite direction. This procedure ensured that plants near the ends of the transect had an equal probability of being selected as all other

plants. The number of paper birch plants marked in each quadrat is shown in Table 2.

Table 2. Number of paper birch plants marked in each quadrat and used to measure utilization in the pens at the Moose Research Center during spring 1984 and 1985.

	Pen			
Quadrat	1	2	3	4
A	36	67	74	78
B	58	53	64	74
C	48	72	75	75
D	54	76	54	52
Total	196	268	267	279

The paper birch stem over 40 cm tall, but less than 5 cm in diameter, nearest each random point was selected for sampling. The distance from the random point to the chosen paper birch was measured so utilization could be weighted for plant density. Shrub density could influence the probability of a plant being browsed, with shrubs in locally high-density areas having a reduced probability of being selected. The weighting factor $\frac{1}{d^2}$, where d was the distance from the random point to the nearest paper birch, was used to correct for differences in paper birch density. If no paper birch occurred within a 5 m radius of the point, no plant was measured. This resulted in unequal numbers of paper birch stems sampled in each quadrat.

The selected paper birch plant was marked with a metal tag, its height and basal diameter measured, the number of CAG twigs counted, and the diameter of each CAG twig measured to the nearest 0.1 mm just anterior to the bud scale scar. CAG counts and measurements were recorded separately for 3 height strata, 0-40, 41-80, and 81-400 cm above ground level. Each plant was permanently marked with a metal band at 40 and 80 cm in 1984 and 1985 so height strata could not vary.

Concurrently, unbrowsed CAG twigs of adjacent paper birch plants were clipped at the bud scale scar. Two hundred CAG twigs were collected in each quadrat in 1984. The diameter at the bud scale scar was measured, the twigs dried at 100°C for 48 hours, and each CAG twig weighed. Regression equations for each pen were calculated to relate stem diameter to weight. The weight of CAG twigs on each permanently tagged shrub was estimated using these regression equations for both 1984 and 1985.

The next spring just prior to leaf burst, each permanently tagged paper birch was examined for utilization by moose and snowshoe hare (*Lepus americanus*). If the plant had been browsed, the number of unbrowsed CAG was counted and their diameter measured. The browsed CAG twigs had their diameter measured at the point of browsing and the bud scale scar. The proportion of CAG weight remaining on each shrub was calculated and the average utilization in each quadrat and pen determined. Utilization percentages

were also calculated in 1985 based on the number of CAG leaders browsed and unbrowsed and on the number of shrubs browsed and unbrowsed.

Estimating Utilization by Quadrat

When combining information from individual trees to form an estimate for utilization in a quadrat, we had to take into account that our sampling plan did not give all shrubs an equal probability of being measured. The probability of any shrub being sampled was inversely related to the density of paper birch in the immediate area, so we weighted the observations for individual trees with their local density. As we lacked an absolute measure of local density, we used the multiplicative inverse of the distance from point to birch squared ($w = (1/d)^2$ where w = weighting and factor and d = distance from point to birch).

When calculating our utilization estimate and its sampling variance, we treated each weighted observation as a random sample from the quadrat.

Average utilization ($\bar{Y}$) was estimated:

$$\bar{Y} = \sum_{i=1}^{n} w_i u_i \Big/ \sum_{i=1}^{n} w_i c_i$$

where w_i was the weight for the ith tree

u_i was the dry weight of CAG removed from the tree

c_i was the dry weight of CAG available before winter

n was the number of trees sampled per quadrat. The sampling variance of this estimate ($S^2(\bar{Y})$) is:

$$S^2(\bar{Y}) = \frac{n}{\left(\sum_{i=1}^{n} w_i c_i\right)^2}\left(\frac{\left(\sum_{i=1}^{n} (w_i u_i)^2\right) - 2\bar{Y}\left(\sum_{i=1}^{n} w_i^2 u_i c_i\right) + \bar{Y}^2\left(\sum_{i=1}^{n} (w_i c_i)^2\right)}{n-1}\right).$$

When performing hypotheses tests or constructing confidence intervals, we used the value $n' - 1$ for degrees of freedom, where n' is the number of transects, generally 12. This formula for degrees of freedom is not consistent with the calculation of sampling variance, but is most consistent with the sampling procedures.

Estimating Utilization by Pen

Utilization for a pen was estimated by combining the utilization rates for the 4 quadrats within a pen where we weighted each quadrat with the total paper birch CAG biomass estimate from the summer sampling. For a pen the estimated utilization rate (U) is calculated:

$$U = \sum_{i=1}^{4} X_i \bar{Y}_i \Big/ \sum_{i=1}^{4} X_i$$

where X_i is the estimate of total paper birch CAG biomass in pen i and $\bar{Y}_i$ is the estimated utilization rate in quadrat i.

The formula for the sampling variance for this estimator is not nearly as intuitively obvious as the formula for the estimator. If the X_i's were known values, the

estimator would be a simple linear function of random variables (the $\bar{Y}_i$'s). However, the X_i's are estimates, thus random variables rather than known quantities, so we must also consider their variability when attempting to estimate the sampling variance of U. The formula is an approximation based on a fourth order Taylor's series expansion of the function:

$$f = \left(\left(\sum_{i=1}^{4} X_i \bar{Y}_i \Big/ \sum_{i=1}^{4} X_i\right) - \left(\sum_{i=1}^{4} E(X_i) E(\bar{Y}_i) \Big/ \sum_{i=1}^{4} E(X_i)\right)\right)^2$$

around the expected values of the $\bar{Y}$'s and X's.

Because the 8 random variables in the formula for U are independent, many combinations of odd ordered terms drop out. By taking the expected value of the expansion and substituting our estimates for their expected values, we arrive at the approximation:

$$S^2(U) = \sum_{j=1}^{4}\left[\frac{\left(\sum_{i=1}^{4} X_i(\bar{Y}_j - \bar{Y}_i)\right)^2}{\left(\sum_{i=1}^{4} X_i\right)^4} S^2(X_j)\right] + \sum_{j=1}^{4}\left[\frac{-2\left(\sum_{i=1}^{4} X_i(\bar{Y}_j - \bar{Y}_i)\right)^2}{\left(\sum_{i=1}^{4} X_i\right)^5} S^3(X_j)\right]$$

$$+ \sum_{j=1}^{4}\left[\frac{X_j^2}{\left(\sum_{i=1}^{4} X_i\right)^2} S^2(\bar{Y}_j)\right] + \sum_{j=1}^{4}\left[\frac{3X_j^2 - 4X_j\left(\sum_{i=1}^{4} X_i\right) + \left(\sum_{i=1}^{4} X_i\right)^2}{\left(\sum_{i=1}^{4} X_i\right)^4} S^2(X_j) S^2(\bar{Y}_j)\right]$$

$$+ \sum_{k=1}^{4} \sum_{\substack{j=1 \\ j \neq k}}^{4}\left[\frac{3X_k^2}{\left(\sum_{i=1}^{4} X_i\right)^4} S^2(X_j) S^2(\bar{Y}_k)\right] + \sum_{j=1}^{4}\left[\frac{3\left(\sum_{i=1}^{4} X_i(\bar{Y}_j - \bar{Y}_i)\right)^2}{\left(\sum_{i=1}^{4} X_i\right)^6} S^4(X_j)\right]$$

$$+ \sum_{k=1}^{4} \sum_{\substack{j=1 \\ j \neq k}}^{4}\left[\frac{3(\bar{Y}_j^2 + 4\bar{Y}_j\bar{Y}_k + \bar{Y}_k^2)\left(\sum_{i=1}^{4} X_i\right)^2 - 18\left(\sum_{i=1}^{4} X_i \bar{Y}_i\right)\left(\sum_{i=1}^{4} X_i(\bar{Y}_j + \bar{Y}_k - \bar{Y}_i)\right)}{\left(\sum_{i=1}^{4} X_i\right)^6} S^2(X_j) S^2(X_k)\right].$$

To simplify our application of this formula, we used X_i equal to the mean biomass per hectare rather than X_i = total biomass. This is allowed because all quadrats in a pen are nearly identical in area.

To get the terms $S^3(X_i)$, we took advantage of the rules: (1) the skewness of a distribution of sample means is equal to $1/\sqrt{n}$ times the skewness of the population where n is sample size; and (2) the kurtosis of a distribution of sample means is equal to 1/n times the kurtosis of the population. We estimated 3rd and 4th central moments from our biomass data, calculated sample skewness and kurtosis, applied the above rules to arrive at values for skewness and kurtosis for mean biomass estimates, and then approximated 3rd and 4th central moments for the sample means ($S^3(X_i)$ and $S^4(X_i)$) from definitions for skewness and kurtosis.

When constructing confidence intervals around utilization estimates, we let degrees of freedom be equal to the smallest number of degrees of freedom associated with the 8 estimates used in the formula for U. This approach is conservative but we thought it appropriate because of our lack of knowledge about the stability of the sampling variance approximation.

Estimation of Food Habits

Accurate knowledge of moose food habits is an essential ingredient in calculating nutritional carrying capacity. We lacked data on diet selection of moose in each pen prior to the study. To begin the study and make decisions on stocking rates, we made gross estimates of food habits in all pens based on data from LeResche and Davis (1973) and Regelin et al. (1986). More accurate data on diet selection within each pen were collected during the study by analyzing moose feces and observing the moose as they foraged. Predicted utilization levels of paper birch were adjusted to account for differences in diet selection.

Fecal pellets from each moose in each pen were collected during the 1984-85 winter at approximately 10 day intervals from 1 December through 15 April. Each moose was observed until it defecated to ensure fresh pellets were collected. Approximately 15 pellets were collected from each fecal group and frozen. Samples were sent to the Composition Analysis Laboratory at Colorado State University for microhistological analysis. A slide of each sample of fecal material was prepared according to the methods of Sparks and Malechek (1968) and 20 fields per slide examined to determine species composition.

Moose were observed during January-March 1986 in another study to determine activity patterns. The amount of time moose spent foraging on different species was recorded during these observations. These data were tabulated to provide food habits data.

Stocking of Pens

Pens were stocked each year on 15 October with the projected number of adult moose required to remove 35, 50, 75, and 100% of the paper birch CAG by 30 April. These desired utilization levels were based on estimated intake of forage predicted by the simulation model and the original gross estimates of food habits in Table 3. Predicted utilization levels were altered when more accurate data on food habits in each pen became available.

Table 3. Original estimates of diet selection by moose in the pens at the Moose Research Center during winter 1983-84.

	Percent of diet						
Species	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Paper birch	50	60	60	60	70	70	60
Willow	20	20	20	20	5	5	15
Aspen	15	10	10	5	--	--	10
Mountain cranberry	5	10	10	15	25	25	10
Rose	5	--	--	--	--	--	5

Moose eat some old-growth material as they browse on paper birch plants. The ratio of CAG to old-growth consumed is an important factor when calculating the

predicted utilization level of paper birch; however, we had no data on which to base values. To calculate initial stocking rates and utilization levels, we made several assumptions and used estimated values for the ratio. During the study we collected data to determine the ratio of CAG to old-growth paper birch consumed in each pen and then adjusted the original values. For the original estimates we assumed the amount of old-growth consumed would increase as the utilization level of CAG increased. We then arbitrarily assigned the following ratios to calculate the amount of CAG consumed.

% CAG utilized	% paper birch that is old growth
35	25
50	30
75	40
100	50

Later, the amount of old-growth and CAG of paper birch consumed in each pen was based on twig diameter:weight relationships and diameter at point of browsing by moose in each pen. The weight of CAG twigs on each was calculated as was the total weight removed from each shrub and the proportion of old-growth to CAG consumed determined.

RESULTS

Food Habits

Analysis of the fecal material indicated the diet of moose in all pens consisted of 84 to 99% willow bark throughout winter. Such results were not possible because willow plants were rare in all pens and could have comprised only a minor part of the diet. We requested the laboratory at Colorado State University reexamine the samples. Their response was that the willow bark had been misidentified and it was really paper birch bark. The laboratory also noted that the samples were very trashy with a high level of unidentifiable material. We doubt the accuracy of the fecal analysis data. LeResche and Davis (1973) found that moose in the pens consumed 72% paper birch and 21% mountain cranberry. On a "depleted" range the diet contained 22% paper birch and 51% mountain cranberry. All of the pens were heavily used and Pens 2 and 4 could be considered a "depleted" range. We find it doubtful that the moose diet in Pen 4 could have averaged 91% paper birch over winter. Also, moose at the MRC refused to eat a diet containing 100% paper birch CAG. The food habits data from fecal analysis were not used to predict utilization rates of paper birch. They are only presented for the reader's interest (Table 4).

Table 4. Diet selection of moose in each pen at the Moose Research Center during winter 1984-85 based on analysis of fecal material. These data are not used in the model.

	December				January				February			
	Pen				Pen				Pen			
Species	1	2	3	4	1	2	3	4	1	2	3	4
Reed grass				0.8	1.5							
Sedge					1.5							
Labrador tea			0.9	0.7			0.9					
Lichen	0.5		0.9									
Rose						1.3						
Willow leaves		1.4	1.7	0.7			1.5	0.5	1.7	0.8		
Willow bark	86.8	89.9	83.8	92.7	86.3	95.6	92.2	89.0	97.4	95.8	89.2	98.3
Mountain cranberry	12.0	8.0	12.9	5.1	10.0	3.1	5.5	10.5	0.8	3.3	10.8	1.7

	March				April			
	Pen				Pen			
Species	1	2	3	4	1	2	3	4
Reed grass								
Sedge								
Labrador tea	0.5	0.5			1.0			
Lichen								
Rose	0.7	1.0	0.8				0.8	
Willow leaves	0.5		0.8	2.5	2.0			
Willow bark	93.1	96.2	98.3	85.8	95.0	99.1	98.3	91.2
Mountain cranberry	5.0	2.2		11.8	2.0	0.9	0.8	8.8

Direct observation of moose during winter 1985-86 in Pens 1 and 4 indicated lower utilization of paper birch than by the fecal analysis (Table 5). Moose were observed for 44 hours in Pen 1 and 40 hours in Pen 4. Moose in Pens 2 and 3 were not observed with similar intensity, so these data are less definitive. Observers indicated the diet in Pen 2 contained a minimum of 60% mountain cranberry, about 5% Labrador tea, and the remainder of the diet was paper birch and fallen leaves. We used the value of 22% paper birch in the diet based upon the data reported by LeResche and Davis (1973) for a depleted range. We have the least food habits data from Pen 3. The few direct observations that were made indicated that paper birch was a major food item. Because we lacked data for this pen, we used the data reported by LeResche and Davis (1973) for normal winter ranges. Pen 3

Table 5. Diet selection of moose in Pens 1 and 4 at the Moose Research Center during winter 1985-86 based on direct observation of moose.

Species	Pen 1	Pen 4
Birch	49.3	30.5
Aspen, willow	2.8	17.0
Mountain cranberry	39.8	33.5
Leaves (fallen)	3.5	3.5
Spruce	3.6	--
Aspen bark	0	7.0

is not depleted and has large amounts of paper birch, so this value may be a reasonable approximation.

The percentages of paper birch in the diet in each pen used to predict utilization levels of paper birch were: Pen 1, 49.3%; Pen 2, 22%; Pen 3, 72%; and Pen 4, 30.5%.

The ratio of CAG to old-growth of paper birch consumed varied between pens but the differences were not significant ($\underline{P} \geq 0.20$). The percentage of CAG in the paper birch diet (±80% CI) in each pen was: Pen 1, 55.4 ± 9.2%; Pen 2, 40.4 ± 6.6%; Pen 3, 53.6 ± 6.8%; and Pen 4, 48.8 ± 6.3%.

Forage Intake Estimates

The modified Swift submodel predicted that an adult female moose weighing 365 kg on 15 October would consume 1502 kg of oven-dry forage from 15 October to 30 April. Dry matter intake of forage varied from 9.9 to 5.1 kg/day and averaged 7.7 kg/day over winter. Highest intake occurred in October and early November and lowest intake in late March. For modeling purposes we assumed all moose weighed 365 kg with 55 kg of body fat (15%) on 15 October. Body fat peaked at 68 kg on 3 December (17.6% of total body weight) and then gradually declined to 6.2 kg on 1 May. Total body weight decreased by 14.2% over winter and 89% of the fat stores were catabolized.

Digestibility and crude protein content of the diets used as input variables in the simulation model are shown in Fig. 1. Digestibility and crude protein content of the diet are determined by diet selection. During winter the digestibility and crude protein content of the important forage species varied little (Regelin et al. 1986). Because changes were small, we did not alter the digestibility and crude protein content inputs into the model to account for differences in diet selection between pens. Rather, we did a sensitivity analysis to determine the influence of increasing or decreasing diet digestibility and crude protein by 10%. Increasing digestibility of the diet by 10% (from an average of 39 to 43%) had a negligible effect on daily forage intake. Total forage intake over the entire winter increased by only 14 kg, but simulated body weight and fat content were significantly higher. The moose lost only 11% of its body weight and 67% of its body fat according to the modified Swift model.

Decreasing digestibility of the diet by 10% increased winter forage intake by 18 kg, an insignificant amount over the 196-day winter period. However, a reduction of 10% in digestibility caused a total depletion of fat reserves and a weight loss of 28%. Altering the crude protein content of the diet by 10% also had a negligible effect on predicted forage intake during winter. The average values for diet digestibility and crude protein content shown in Fig. 1 were used to predict intake in all pens.

The Hubbert-Schwartz model predicted a total forage intake of 1261 kg for a female moose weighing 365 kg during

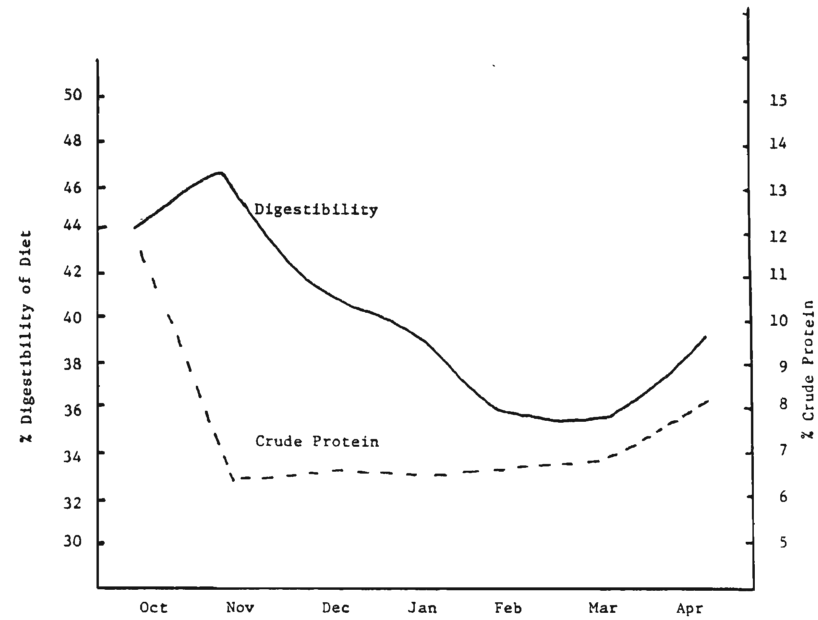

Fig. 1. Digestibility and crude protein content of the diet of moose used as input variables in the simulation models used to predict forage intake.

the winter period, an average of 6.4 kg/day. This is 16.1% lower than the intake predicted by the modified Swift model. The Hubbert-Schwartz model predicts a lower forage intake during March and April than expected based on empirical data from the tame moose. Altering digestibility of the diet by plus or minus 10% of the average value had a negligible effect (<2%) on forage intake. Both simulation models predict intake rates within the range measured with tame moose on a pelleted diet.

Biomass Estimates

Total biomass in 1983 in the pens varied from 422 to 606 kg/ha and was measured within at least 10.7% of the mean at the 80% confidence level (Table 6). Total forage biomass decreased by about 27% (a statistically significant decline ($\underline{P} \leq 0.20$) in Pens 2 and 3 from 1983 to 1984. Total forage biomass in Pen 1 decreased while biomass increased slightly in Pen 4 from 1983 to 1984, but these differences were not statistically significant ($\underline{P} \geq 0.20$). Total biomass in 1984 was measured in each pen within at least 13.8% of the mean at the 80% confidence level (Table 7).

The amount of paper birch CAG varied greatly between pens in both 1983 and 1984 (Tables 6 and 7). A significant decrease ($\underline{P} \leq 0.20$) in biomass of paper birch CAG occurred in Pens 1, 2, and 4 from 1983 to 1984. The proportion of

Table 6. Total forage biomass of individual species and plant parts in each pen at the Moose Research Center in late August 1983.

	kg/ha ± 80% Confidence Interval			
	Pen			
	1	2	3	4
Total biomass	422 ± 36	506 ± 47	523 ± 51	606 ± 65
Birch CAG, 0-400cm	14.4 ± 2.6	7.7 ± 1.5	11.8 ± 2.3	4.4 ± 0.7
All shrub CAG,[a] 0-400cm	14.6 ± 2.6	7.8 ± 1.6	12.2 ± 2.3	4.7 ± 0.7
Paper birch leaves	90.5 ± 15.9	58.2 ± 12.5	90.1 ± 19.9	17.9 ± 4.8
All shrub leaves[a]	91.2 ± 16.0	58.4 ± 12.5	91.0 ± 19.9	18.8 ± 4.9
Mountain cranberry	311.5 ± 34.7	394.8 ± 48.0	384.1 ± 43.3	562.5 ± 65.2
Rose	25.4 ± 4.9	37.6 ± 22.8	31.8 ± 14.9	15.5 ± 4.4
Fireweed	30.9 ± 7.2	7.2 ± 2.1	3.7 ± 0.8	4.8 ± 1.3
Total ha	239	260	239	268

[a] Includes paper birch, willow, and aspen.

Table 7. Total forage biomass of individual species and plant parts in each pen at the Moose Research Center in late August 1984.

	kg/ha ± 80% Confidence Interval			
	Pen			
	1	2	3	4
Total biomass	365.6 ± 35.5	374.5 ± 51.6	373.0 ± 41.7	617.0 ± 37.8
Paper birch CAG 0-400 cm	9.5 ± 1.8	3.6 ± 0.7	9.1 ± 1.5	2.7 ± 0.5
All shrub CAG[a] 0-400 cm	9.8 ± 1.8	3.6 ± 0.7	9.6 ± 1.5	3.5 ± 0.5
All shrub leaves[a]	85.4 ± 19.2	40.3 ± 10.6	74.6 ± 12.8	13.2 ± 2.7
Paper birch leaves	84.6 ± 19.2	40.2 ± 10.6	73.4 ± 12.8	11.6 ± 2.7
Mountain cranberry	227.9 ± 25.1	309.1 ± 45.0	269.1 ± 39.4	573.2 ± 50.0
Rose	16.5 ± 4.0	9.7 ± 3.1	15.1 ± 2.8	13.2 ± 2.4
Fireweed	28.3 ± 6.0	11.7 ± 7.2	4.6 ± 1.1	5.6 ± 1.7
Total ha	239	260	239	268

[a] Includes paper birch, willow, and aspen.

paper birch CAG and leaves in each height strata was similar in Pens 1, 2, and 3 in both 1983 and 1984. Most paper birch CAG and leaves occurred in the 81 to 400 cm strata (Table 8). In Pen 4, more of the paper birch CAG occurred in the 0-40 cm strata due to past overbrowsing. Paper birch CAG comprised a small amount of the total forage biomass, varying from 0.4 to 3.4% of the total. Mountain cranberry was a large component of the biomass in each pen, varying from 62 to 93% (Table 8).

Predicted Utilization Levels of Paper Birch

The predicted utilization levels of paper birch in each pen were calculated based on model predictions of daily forage intake, food habits of moose, and the ratio of CAG utilization to consumption of paper birch old-growth (see page 20). Predicted utilization levels in 1983-84 ranged from 24 to 57% using the modified Swift model (Table 9) and 22 to 48% using forage intakes generated by the Hubbert-Schwartz model (Table 10). Predicted utilization rates during the 1984-85 winter ranged from 26 to 54% (Table 11) using the modified Swift model and 21 to 45% (Table 12) using the Hubbert-Schwartz model.

Table 8. Proportion of paper birch in each height strata and proportion of total biomass comprised of various species and plant parts in the pens at the Moose Research Center in 1983 and 1984.

Forage component	Pen 1		Pen 2		Pen 3		Pen 4	
	1983	1984	1983	1984	1983	1984	1983	1984
% paper birch CAG 0-40 cm	22.1	17.0	9.3	7.5	6.9	11.7	28.4	45.5
% paper birch CAG 41-80 cm	23.9	18.1	5.1	9.4	12.6	10.2	36.6	21.8
% paper birch CAG 81-400 cm	54.0	64.9	85.6	83.1	80.6	78.1	35.0	32.7
% paper birch leaves 0-40 cm	10.2	6.1	2.4	0.9	2.2	2.8	14.3	21.6
% paper birch leaves 41-80 cm	15.6	10.8	3.3	2.4	5.6	5.3	26.3	20.5
% paper birch leaves 81-400 cm	74.2	83.1	94.3	96.7	92.2	91.9	59.4	57.9
% paper birch CAG of total shrub CAG	96.4	97.1	98.2	99.4	96.9	95.4	91.1	75.6
% paper birch leaves of total shrub leaves	99.2	99.0	99.6	99.8	98.5	98.4	95.4	87.9
% paper birch leaves of total biomass	21.4	23.1	11.5	10.7	17.2	19.7	3.0	1.9
% paper birch CAG of total biomass	3.4	2.6	1.5	1.0	2.3	2.4	0.7	0.4
% mountain cranberry of total biomass	61.6	62.3	78.0	82.5	73.5	72.2	93.0	92.8
% rose of total biomass	6.1	4.5	7.4	2.6	6.1	4.0	2.5	2.1
% fireweed of total biomass	7.4	7.7	1.4	3.1	0.7	1.2	0.8	0.9

Table 9. Predicted intake and utilization of paper birch CAG by moose in each pen at the Moose Research Center from 15 October 1983 to 30 April 1984. Intake based on the modified Swift submodel.

Pen	Total forage intake kg	Total birch intake kg	Birch CAG intake kg	Birch CAG available kg	Predicted CAG utilization %
1	3493	1722	954	3441	28
2	5649	1243	502	2002	25
3	4141	2982	1598	2820	57
4	1864	569	278	1179	24

Table 10. Predicted intake and utilization of paper birch CAG by moose in each pen at the Moose Research Center from 15 October 1983 to 30 April 1984. Intake based on the Hubbert-Schwartz model.

Pen	Total forage intake kg	Total birch intake kg	Birch CAG intake kg	Birch CAG available kg	Predicted CAG utilization %
1	2924	1442	799	3441	23
2	4735	1042	421	2002	21
3	3536	2546	1365	2820	48
4	1712	522	255	1179	22

Table 11. Predicted intake of paper birch CAG and predicted utilization of paper birch CAG by moose in each pen at the Moose Research Center from 15 October 1984 to 30 April 1985. Intake based on the modified Swift submodel.

Pen	Desired utilization %	Total forage intake kg	Total birch intake kg	Birch CAG intake kg	Birch CAG available kg	Predicted CAG utilization %
1	35	2125	1381	1036	3372	30
2	100	3018	1056	528	936	56
3	50	3018	1811	1268	2366	54
4	75	1509	151	90	702	12

Table 12. Predicted intake and utilization of paper birch CAG by moose in each pen at the Moose Research Center from 15 October 1984 to 30 April 1985. Intake based on the Hubbert-Schwartz model.

Pen	Total forage intake kg	Total birch intake kg	Birch CAG intake kg	Birch CAG available kg	Predicted CAG utilization %
1	1766	871	482	2270	21
2	2509	552	223	936	23
3	2509	1806	968	2175	45
4	1254	382	187	724	26

Measured Utilization of Paper Birch

Utilization levels of paper birch CAG measured in 1984 include all CAG leaders from ground level up to 400 cm. Field measurements attributed nearly all browsing to snowshoe hares. We think moose consumed a large portion of the CAG, but hares browsed the same twigs later in the winter. We were unable to determine how much paper birch CAG remained on the twigs when they were browsed by hares. Hares undoubtedly consumed some CAG even though they prefer old-growth material because it contains lower concentrations of secondary compounds (Bryant and Kuropat 1980). Total utilization of paper birch CAG by both moose and hares during the 1983-84 winter ranged from 41 to 68% (Table 13). It is not valid to compare the measured and

Table 13. Predicted and measured utilization levels (±80% confidence interval) of paper birch CAG biomass in each pen at the Moose Research Center during winter 1983-84.

		Predicted utilization%		Measured utilization %
Pen	Number shrubs	Swift model	Hubbert-Schwartz model	Combined hare and moose use
1	196	28	23	41 ± 11
2	268	28	21	42 ± 10
3	267	57	48	34 ± 14
4	279	24	22	68 ± 10

predicted utilization levels of paper birch during 1983-84 because we were unable to separate browsing by moose and hare.

During 1984-85, each tagged paper birch shrub was marked at heights of 40 and 80 cm so we could measure utilization levels at 3 height strata. It was not possible to protect shrubs from hare browsing, yet permit moose browsing, but we thought hare browsing would not occur above a height of 80 cm. Results indicated that some hare browse occurred in the 80+ cm height strata but the levels were less than 5% of the total utilization. Hare browsing again masked the amount of moose browsing in the 2 lower height strata. However, measured utilization levels in the 80+ cm strata were similar ($P \leq 0.20$) to predicted levels in 3 of the 4 pens using the forage intake estimates generated by the Hubbert-Schwartz model (Table 14). We had the most reliable food habits from Pens 1, 2, and 4 and these were the pens where we accurately predicted the utilization level of paper birch CAG. The lack of agreement between predicted and measured utilization levels in Pen 3 is most likely due to inaccurate food habits data. Obviously, the diet in Pen 3 did not contain 72% paper birch. This is the value reported by LeResche and Davis (1973) for normal range and was used because it was the best information available.

The predicted utilization levels based on the modified Swift model were about 5% higher than estimates based on

the Hubbert-Schwartz model. These increases in predicted utilization caused significant differences to occur between the Swift model based on predictions and measured utilization levels in Pens 1 and 2. However, the differences between predicted and measured rates were only 7 and 11% in Pens 1 and 2, respectively (Table 14). The small amount of hare browsing in the 80+ cm strata did likely mask some moose browsing and true moose utilization values have been slightly higher.

Table 14. Predicted and measured utilization levels (± 80% confidence interval) of paper birch CAG biomass in each pen at the Moose Research Center, Soldotna, Alaska during winter 1984-85.

	Predicted utilization %		Measured utilization %		
Pen	Swift model	Hubbert-Schwartz model	All strata hare and moose	40 cm+ strata hare and moose	80 cm+ strata hare and moose
1	26	21[a]	41 ± 7	29 ± 6	19 ± 6
2	28	23[a]	23 ± 4	18 ± 6	17 ± 5
3	54	45	31 ± 7	23 ± 6	16 ± 5
4	31[a]	26[a]	66 ± 6	40 ± 8	44 ± 14

[a] Significant ($P \leq 0.20$) agreement between predicted and measured values.

Measured utilization levels were slightly lower than predicted values in Pens 1 and 2 while the reverse was true in Pen 4. This may be due to the extremely overbrowsed conditions in Pen 4 and the shorter height of most paper birch plants in Pen 4.

Utilization levels of paper birch shrubs during winter 1984-85 were calculated by 3 methods. The measured utilization values presented in Table 14 are the percent of CAG biomass removed from each tagged shrub during winter. The percent of CAG twigs browsed and unbrowsed was also calculated as well as the percent of shrubs that had been browsed. There was a close relationship between the utilization levels calculated for biomass removed and twig use (Table 15). The percent of trees browsed was higher than the percent CAG biomass removed or twigs browsed (Table 15).

Table 15. Comparison of 3 methods of measuring browse utilization levels of paper birch CAG at the Moose Research Center, Soldotna, Alaska during winter 1984-85.

	% Utilization[a] ± 80% Confidence Interval		
Pen	CAG biomass removed	CAG stems	Individual plants
1	41 ± 11	37 ± 7	52 ± 7
2	23 ± 10	20 ± 4	40 ± 6
3	31 ± 14	32 ± 6	63 ± 5
4	66 ± 10	60 ± 7	69 ± 5

[a] Includes browsing by both hare and moose for all height strata.

CONCLUSION

Browsing by hare on paper birch created problems in measuring utilization by moose. Hares apparently browsed the paper birch twigs to obtain old-growth material after the moose had browsed the CAG, thus masking utilization by moose. During the second year of the study we measured utilization by height strata. Hare browsing did occur in the 80+ cm height strata, but only to a small degree (less than 5% of utilization). We used the utilization level of the 80+ cm height strata to make comparisons between the predicted and measured utilization of paper birch.

We found significant agreement ($P \geq 0.20$) between the predicted utilization and measured utilization in the 80+ cm strata for paper birch in 3 of the 4 pens. The measured utilization in Pen 3 was much lower than the predicted level. We attribute this difference to unreliable information on food habits in Pen 3. These results indicate that the concept of nutritional carrying capacity is valid and that it is possible to accurately predict utilization levels based on intake rates from simulation models and accurate food habits data.

Several other important contributions were made during this study. The Hubbert-Schwartz model provides a new conceptual framework for assessing nutritional carrying capacity. It will become a valuable tool for measuring habitat quality and carrying capacity using body condition of moose as the unit of measurement. This will reduce the need for expensive and time-consuming vegetation measurements in many management applications.

Sampling and statistical procedures were derived that provide an accurate measure of variance for forage biomass and utilization data. One technique combines variance estimates of shrub density and shrub biomass into a single estimate of variance. This technique has numerous applications in wildlife biology. The other procedure provides a method to combine variance estimates of a shrub utilization from individual plants, transects, and sample quadrats to a single variance estimate for the study area.

Estimates of shrub utilization based on the number of CAG twigs browsed are similar ($P \geq 0.20$) to estimates based on biomass of CAG removed. The time and money required to estimate weight of CAG on shrubs before and after browsing can be reallocated to counting twigs on more plants and a more precise estimate of utilization obtained.

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