MOOSE BROWSING ON FELTLEAF WILLOW: OPTIMAL FORAGING IN RELATION TO PLANT MORPHOLOGY AND CHEMISTRY

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ABSTRACT: Moose bite-size selection on feltleaf willow during the winter shows remarkably low variance, despite the large range of bite diameters available on current annual growth twigs. We hypothesized that this apparent selectivity is based on the compromise moose make in their foraging behavior, between the constraints of digestion and rate of food intake. We developed a model of optimal bite diameter based on morphometric and chemical characteristics of current annual growth twigs of feltleaf willow, an important browse species throughout interior Alaska. The model closely predicted the observed bite-size selection of moose, and further showed how differences in twig morphology, spatial density, and forage chemistry affect optimal bite diameter and energy gain per time unit. Twig digestibility, twig volume, clipping rate, and rumen turnover time are all important factors that govern the choice of bite diameter. Numerical analyses showed that, within the plausible range of variation in the field of these parameters, optimal bite diameter is more sensitive to twig morphology and clipping rate than twig chemistry. However, twig chemical characteristics are most important in determining daily energy and nitrogen gain.

Willows represent a major component of the woody browse available to moose in Alaska during winter (Wolff 1976, Risenhoover 1989, MacCracken and Viereck 1990), and the quality and distribution of this forage greatly influences daily activity patterns, range use, and the pattern of browse utilization (Sæther and Andersen 1990).

The frequency distributions of twig diameters at the point of browsing (bite diameter) on woody browse clearly show that moose do not browse at random (Bergström and Danell 1987, Niemelä and Danell 1988, Risenhoover 1989). Moreover, the very low variance of moose bite diameter on feltleaf willow (*Salix alaxensis*) over a wide geographic area (S.E./Mean=1-3%, Kielland, *unpubl.*), despite the large range in potential bite diameters on current annual growth (CAG) twigs (2-10 mm), suggests that some form of "selection" is modifying their feeding behavior. The rate of net energy (or nitrogen) gain from foraging is, in large part, determined by digestibility (Sæther and Andersen 1990). This digestive constraint on energy gain suggests that moose should browse twigs of diameters that are less than the maximal size it can digest (Vivås *et al.* 1991), yet select twigs that are large enough to fill the rumen over the 6-8 hr active period (Risenhoover 1986). Thus, when browsing CAG on winter-dormant twigs moose must compromise between selecting large-diameter twigs with high biomass, but lower digestible energy and nutrient content, versus small-diameter twigs with less biomass, but of higher nutritional quality (Fig. 1).

The purpose of this study was to examine twig-size selection by moose on an important winter forage, feltleaf willow, in
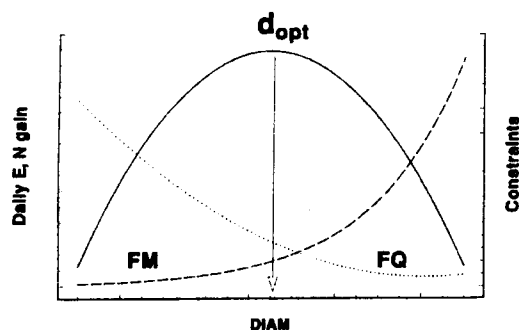
Fig. 1. Hypothetical function for the optimal bite diameter (d_{opt}), solid line, in relation to the empirical constraints of diameter-specific forage mass/volume (FM), dashed line, and forage quality (FQ), dotted line.

regards to the morphometric characteristics and chemical composition of this browse species. We constructed a simple mathematical model and juxtaposed our empirical field observations with the qualitative predictions of optimal foraging theory (Stephens and Krebs 1986), to test the hypothesis that moose attempt to maximize net daily energy/nutrient gain. From these analyses, we also tried to evaluate the chemical and morphological characteristics of the browse that control the optimal browse diameter for free-ranging moose.

STUDY AREA

Browse surveys were carried out along a 30 km stretch of the Koyukuk River, Alaska, between the lower and upper mouth of Three-Day Slough (65°27'N, 157°11'W, elevation 400 m) during March and April 1995. The climate is continental and the average precipitation is approximately 25 cm, most of which falls as snow. The temperature difference between summer and winter can be as much as 80°C (+30°C and -50°C, respectively). The soils are composed of alluvium and glacial debris, as well as eolian sand and silt. The vegetation is bottom-land mixed spruce and birch forests with a riparian zone that is heavily

dominated by extensive stands of feltleaf willow. The sampling areas were located in 5-15 year old stands of feltleaf willow that were 1.5-3.5 m tall. Younger and older stands were generally unavailable to moose during winter because they were covered by snow or were taller than the maximum browse height for moose (Wolff and Zazada 1979). The population density in the area is approximately 12 moose / mi² (Osborne, *unpubl. data*).

METHODS
Field sampling
At each site (*n* = 5), we measured the diameter at the point of browsing (dpb) to the nearest 0.1 mm and the diameter at the base of the CAG of approximately 200 randomly selected feltleaf willow twigs. Concomitant with the browse measurements, we sampled CAG twigs for morphometric and chemical analyses (Kielland, *unpubl.*).

Laboratory analyses
For the purpose of this paper, we define forage quality in terms of *in vitro* dry matter digestibility (%IVDMD) and nitrogen concentration (%). IVDMD trials were carried out using the two-stage procedure (Tilley and Terry 1963) using rumen liquor from captive caribou that had been conditioned on feltleaf willow twigs for at least two weeks prior to the trials. Total nitrogen was analyzed on a LECO 200 CNS elemental analyzer. These chemical analyses were conducted on a diameter-specific basis (2, 3,..,9 mm) on CAG twigs (*n* = 20 per diameter class), dried to a constant weight at 60°C, and ground in a 20 mesh Wiley mill (Kielland, *unpubl.*).

Modeling optimal twig size selection
After identifying the morphological and chemical characteristics of feltleaf willow (Kielland, *unpubl.*), we constructed a modi-

fied deterministic model of optimal bite-size selection based in part on the work by Vivås et al. (1991). The model attempts to predict the bite diameter of a given forage species that results in maximal net daily energy gain, rather than determining absolute energy gain *per se*. The main parameters of the model are: gross energy content per volume unit of consumed twigs of diameter d (GE_d), bite rate (B_d), rumen fill time (F_d), time spent digesting a given volume of twigs (expressed as rumen turnover time, RTT_d), and, twig digestibility per diameter class (D_d).

The net energy (NE_d) of filling the rumen with browse of diameter d is

$$NE_d = (GE_d * D_d) * V \qquad (1)$$

where V is the volume of the rumen (set at 30 L). The time needed to obtain and process the food is the sum of time spent feeding plus the digestion time. The time required to fill the rumen at a given bite rate is

$$F_d = (V*B_d)/v_d \qquad (2)$$

where v_d is the volume of a twig clipped at diameter d.

The total time required to process the food is incremented by the average time available for digestion, RTT_d (Hungate 1966, Hjeljord et al. 1982, Schwartz et al. 1987). Thus, the total time (T_d) necessary to extract the energy is

$$T_d = F_d + RTT_d \qquad (3)$$

The optimal bite diameter (d_{opt}) per feeding cycle is then the diameter that maximizes the function

$$f(d) = NE_d/T_d \quad \text{or,} \qquad (4)$$

$$\partial(NE_d/T_d)/\partial(d) = 0 \qquad (5)$$

which yields the maximum daily net energy/nitrogen gain when browsing twigs of diameter d (*sensu* Vivås et al. 1991).

Linear and non-linear regression equations were developed for the relationship between twig diameter (d), and the various parameters needed to construct the model:

Twig weight = $0.55-0.34(d)+0.03(d)^3$

Twig volume = $3.16(d)4.30$

Twig density = $1.28(d)-0.37$

We ran the model both for energy and nitrogen intake, using the product of digestibility and crude protein as an approximation of "digestible protein", and substituting the diameter-specific crude protein concentration for energy in the equations above.

We used an estimated foraging rate calculated from winter activity patterns (Risenhoover 1986) and body-mass specific daily intake rates (Schwartz et al. 1984, Renecker and Hudson 1986), given a moisture content of 40% of winter-dormant feltleaf willow (Kielland, *unpubl. data*). This foraging rate (6 bites/min) corresponded closely to that reported by Vivås et al. (1991), but is lower than those reported by Renecker and Hudson (1986).

RESULTS

Predicted optimal bite diameters based on energy and nitrogen gain per unit time were very similar (Fig. 2), attesting to the fact that these parameters are largely controlled by the variance in the same fundamental factor, namely the diameter-specific bark:wood ratio of the twig (Kielland,
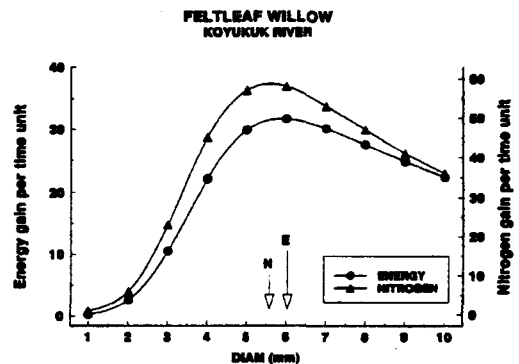
Fig. 2. Predicted optimal bite diameter for moose browsing feltleaf willow that represents maximum energy and nitrogen intake per time unit.

unpubl.).

To test the hypothesis that moose in the study area forage optimally, i.e. in a fashion that maximizes daily net energy/nitrogen gain, we superimposed the theoretical curves generated by the model on the observed frequency distribution of the dpb. The close match of the peaks in the model curves both for energy (Fig. 3a) and nitrogen (Fig. 3b) to the observed average bite diameter (5.7 mm), show that the model predicted twig size selection reasonably well , and moose appear to forage in an optimal fashion.

Thus viewed in the context of optimal foraging theory, these results explain why a large proportion of the annual browse production is not consumed by moose even when the browse frequency per plant is very high (Kielland, *unpubl.*).

Evaluation of model parameters

Variation in the main model parameters: twig volume, bite rate, digestibility, rumen turnover time (RTT), and nitrogen concentration, affected both net energy/ nitrogen gain and the predicted optimal bite diameter (d_{opt}). However, there were notable differences in the magnitude and direction of the responses depending on whether the parameter under consideration pertained to morphological or chemical attributes of the twig.

Increasing the twig volume at a given diameter (as in a stem with less taper, as found on species such as *Salix pulchra* and *Salix arbusculoides*) decreased d_{opt}, but increased energy gain (Fig. 4). This prediction is consistent with the much lower observed dpb of diamondleaf willow (*Salix pulchra*) relative to feltleaf willow, despite the fact that these species show substantial overlap in CAG diameters in the study area (Kielland, *unpubl.*). Likewise, increasing bite rate increased nitrogen gain in a similar fashion (Fig. 5), and decreased d_{opt}.

Digestibility, which may vary in two different ways as a function of twig diameter, exhibited two distinct modes of response. First, large differences in digestibility had no effect on d_{opt} as long as the proportional changes in digestibility as a
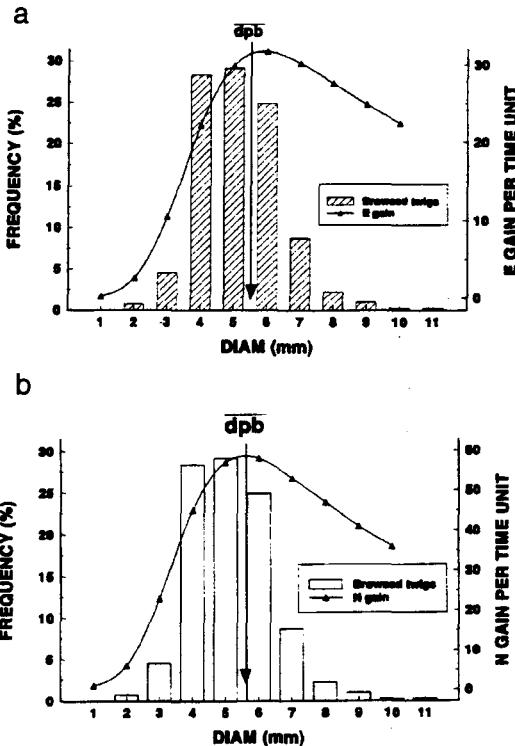
a

b

Fig. 3. Relationship between average bite diameter observed in the field and the optimal bite diameter predicted from the model, with respect to (a) energy and (b) nitrogen.
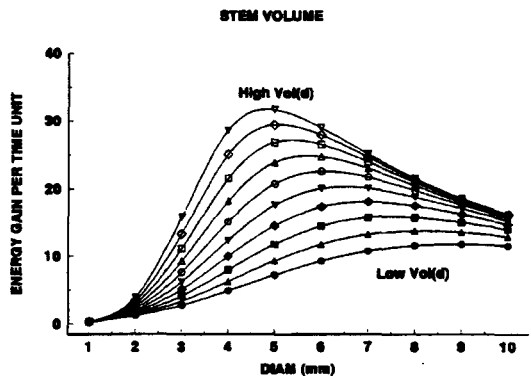

Fig. 4. Effects of increasing diameter-specific stem volume and predicted optimal bite diameter and energy gain.
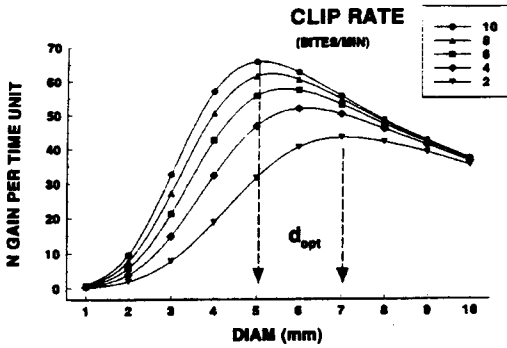
Fig. 5. Effects of increasing clip rate on optimal bite diameter and nitrogen gain.

function of twig diameter (D_d) remained the same, i.e. similar regression coefficients, but different intercept. But twigs of lower digestibility, of course, conferred lower energy/nitrogen gain. However, an increase in the rate of change of D_d (Fig. 6a) decreased both d_{opt} and the energy gain (Fig. 6b). In an analogous fashion, increasing RTT decreased both d_{opt} and energy gain per unit time (Fig. 7).

Changes in twig nitrogen concentration (Fig. 8a) had relatively little effect on d_{opt}, but had a large effect on nitrogen gain per time unit (Fig. 8b), as shown by the three-fold increase in nitrogen gain at d_{opt} with the proportional increase in overall stem nitrogen concentration. Thus, both plant chemistry and plant morphology may alter the energy/nitrogen gain of the animal, as a function of the selection of bite diameter.

DISCUSSION

Several important inferences that govern moose-forage relations can be drawn from this modeling exercise. First, "selectivity" appears to be best defined with respect to d_{opt}, rather than being simply inversely proportional to bite diameter (cf. Molvar and Bowyer 1994), because below d_{opt} the energy/nitrogen return diminishes at a rapid rate. Second, d_{opt} is very sensitive to bite rate, suggesting that the spatial density of the twigs, both with respect to canopy
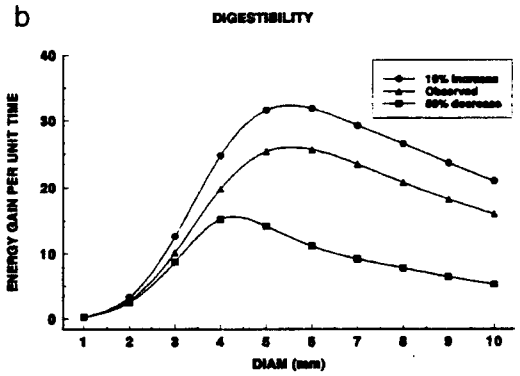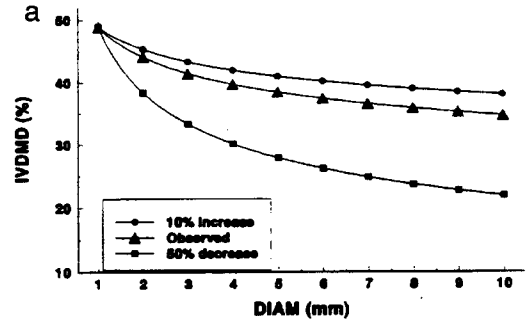

Fig. 6. Effects of change in (a) the rate of change of diameter-specific digestibility and (b) optimal bite diameter and energy gain.
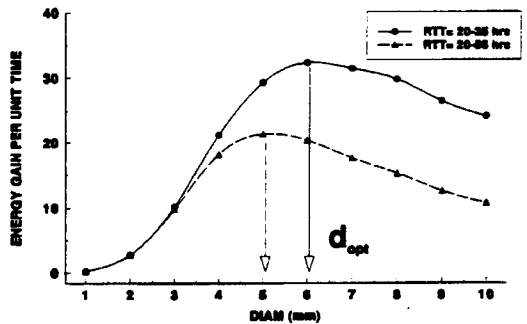

Fig. 7. Effects of varying rumen turnover times (RTT) on optimal bite diameter and daily energy gain.

architecture and plant density, exerts significant control over feeding behavior (Vivås and Sæther 1987). Likewise, differences in CAG morphology that affects twig volume also greatly affects d_{opt}. However, this situation is most relevant in comparing different species, since intraspecific differences in twig morphology are much less
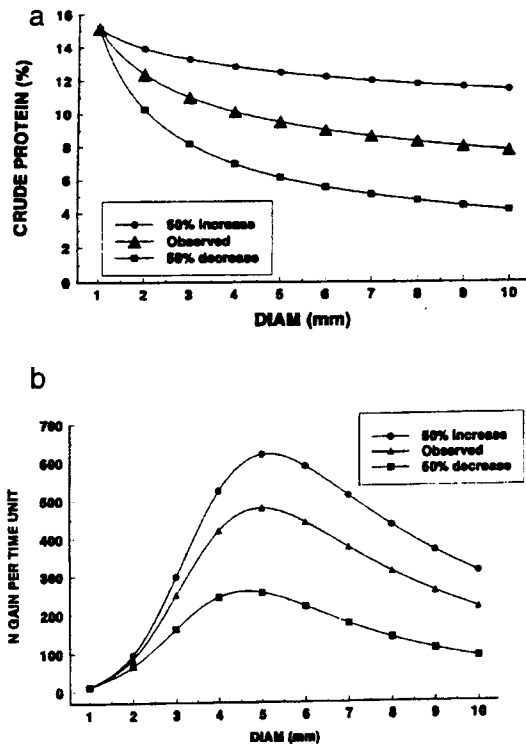
Fig. 8. Effects of changes in (a) the rate of change in diameter-specific crude protein concentration and (b) optimal bite diameter and nitrogen gain.

than among species.

We recognize that some of the model parameters are not independent, although treated as such in our parameter evaluation. We did this on the basis of making a more conservative estimate of the effects that changing parameter values have on the model. For example, bite rate and bite size (volume) are inversely related (Risenhoover 1987), but this effect is very small over the range of harvest rates presented here (cf. Schwartz 1992).

We would like to emphasize that the principal insight this model provides, is a reasonable theoretical framework for interpreting observed deviations from the predicted values, rather than simply to predict d_{opt} per se. For example, smaller average bite diameter than predicted may indicate

greater forage availability, independent of absolute forage biomass (Risenhoover 1987), whereas larger bite diameters may indicate that the animals are nutritionally stressed. Moreover, the sensitivity analyses of plant chemistry and morphology allows us to evaluate the relative importance of these plant characteristics in controlling the energy/nitrogen gain by moose during winter.

The results have several ramifications for moose and their winter forage base:

(1) An optimally foraging moose should select twigs substantially smaller than the maximal size it is able to digest; and,

(2) Variation in browse plant morphology, both twig size and canopy architecture greatly affects intake rate/rumen fill time.

Within the expected variation of these plant characteristics in the field, it appears that variation in *morphology* alone can have substantial effects on optimal bite diameter, but comparatively less of an effect on daily energy/nitrogen gain. By contrast, at a given (constant) cropping rate and twig morphology, the numerical analyses also show how very small variations in bite diameter may reflect substantial variation in *forage chemistry*, which in turn is manifested by large differences in daily energy/ nitrogen gain for the animal (cf. White 1983).

We conclude that our model may be useful in providing *a priori* estimates of twig-diameter selection by moose, and help interpret observed patterns of browse utilization in the field. Thus, this approach could be used to assess forage quality and forage availability in the context of the carrying capacity of moose winter ranges.

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