

EFFECTS OF WILLOW QUALITY ON MOOSE DISTRIBUTION IN A MONTANE ENVIRONMENT

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ABSTRACT: Plant communities in Rocky Mountain National Park are influenced by a steep elevation gradient. Therefore, we hypothesized that summer forage quality of willow (*Salix* sp.) communities varies with elevation. Moose (*Alces alces shirasi*) in Colorado rely heavily on willow for summer browse, and browse patches differ in size as well as productivity in mountainous environments. We also hypothesized that moose distribution within the park is influenced by willow forage quality and that moose would distribute themselves by sex and age class across the elevation gradient in accordance with their need for forage quality and quantity. We measured crude protein and fiber content for 3 of the most abundant willow species. Where present, willows were collected at 3 different elevations during 5 sampling periods throughout the summers of 2003 and 2004. Because elevation influenced both chemical and physical properties of willow, we found its relationship with browse quality to be more complex than that reported for herbaceous forage. Whereas the relationship is often linear with herbaceous forage, we hypothesize that an apex in browse quality may be reached between the extremes of an elevation gradient. Although higher elevation willow communities often offered chemically superior forage (e.g., more nutritious), it was also physically inferior (e.g., lower achievable intake rates). Mid and high elevation sites were used predominantly by females. Therefore, moose with smaller body sizes (and thus smaller absolute energy requirements) probably exploit the most nutritious willow communities more efficiently, while larger moose (adult males) likely encounter intake constraints at higher elevations because of their higher absolute energy requirements. However, elevation-specific intake rates are needed to determine at which elevation moose are assimilating the greatest amount of nutrients.

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In 1978 and 1979, the Colorado Division of Wildlife introduced 2 groups of 12 moose (*Alces alces shirasi*) to an area northwest of Rocky Mountain National Park (RMNP) (Nowlin et al. 1979). Shortly after the introduction, moose began colonizing RMNP (Stevens 1988), especially the Kawuneechee Valley (KV) that is carved by the Colorado River and houses the park's largest willow (*Salix* sp.) communities. More than 25 years later little is known about the distribution of moose outside the KV. RMNP is largely managed as a legally designated wilderness area with access provided by a limited number of

hiking trails. Visitor access to trailheads is provided via a trans-park road that parallels the Colorado River through the KV before climbing up the continental divide and descending into the eastern portion of the park. As a result of limited access, existing data on moose distribution has been primarily limited to chance observations made from the road in areas where it passes through relatively low-elevation willow communities.

Higher elevations offer ungulates more nutritious forage because the shorter growing season demands rapid growth correlated with high nutritive quality (Klein 1970, Bergström

and Danell 1986). The later onset of the growing season offers more digestible plants at earlier phenological stages that contain higher protein and lower fiber contents (Van Soest 1994). Indeed, spring migrations of moose moving up-slope have frequently been shown to coincide with “green-up” (LeResche 1974), and Edwards and Ritcey (1958) speculated that migratory females in British Columbia experience a higher incidence of twins. Regardless of elevation, summer nutrition influences over-winter survival (Schwartz et al. 1988) and reproductive condition (Franzmann and Schwartz 1985). Because nutrition is so closely coupled with willow communities for the RMNP moose herd, its health is dependent upon the vigor of the park’s willow communities.

Willows are important forage for moose in western North America (Peek 1974), especially in montane environments where forbs and aquatic plants may not be as prevalent as in other habitat types (Van Ballenberghe et al. 1989). Food habit studies from Colorado, Montana, and Wyoming indicate that moose browse willow extensively during the summer, often relying on it for > 85% of their diet (McMillan 1953, Houston 1968, Dorn 1970, Dungan and Wright 2005). In Colorado, moose use willow communities for food and shelter in all seasons (Kufeld and Bowden 1996).

Moose seem to be increasing their numbers, distribution, seasonal migration patterns, and browsing effects, although definitive data to document any of these conditions are lacking. Park resource managers desire a more complete understanding of moose distribution and their forage preferences. This is based, in part, on concern over forage and spatial competition with abundant Rocky Mountain elk (*Cervus elaphus*) that can reach winter range densities of 12-13 elk/km², similar to Yellowstone National Park (Singer et al. 1998), and have been shown to reduce maximum height, densities, and crown volumes of willows in RMNP (Singer et al. 2002). The objective of

this study was to identify relationships between willow phenology, forage quality, and moose distribution so that park managers might better understand the interaction between RMNP’s ungulate and willow communities.

STUDY AREA

RMNP is located in north central Colorado (Lat. 40°20' N., Long. 105°40' W.), is bisected by the continental divide, and lies near the southern extent of moose range in North America. This study was conducted in the western portion of RMNP where willow communities are present from its lowest elevations, 2,560 m, to beyond tree line at approximately 3,425 m. Because moose rarely use willow communities above tree line, the study area’s upper bound was determined by the elevation of the uppermost riparian meadow (3,291 m) below tree line. For sampling purposes, the study area was divided into 3 elevation strata: low (2,560 – 2,803m), mid (2,804 – 3,047m), and high (3,048 – 3,291 m). In terms of moose habitat, the dominant landscape feature within the park is the KV occurring in the low elevation strata. Outside the KV, riparian meadows (and associated willow communities) occur as islands in a forest dominated by lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*) at lower elevations, with subalpine fir (*Abies lasiocarpa*) replacing lodgepole pine at higher elevations. A detailed physiographic description of the study area is given by Baker (1989).

Willow communities occurring above the valley floor are supported by the network of streams that make-up the headwaters of the Colorado River and differ markedly from those of the KV. The steep elevation gradient between the continental divide and valley floor influences 3 characteristics of willow communities: (1) species richness; (2) height; and (3) patch size. All are inversely related to elevation.

METHODS

Forage Sample Collection

We observed moose foraging in all elevation strata throughout the summers of 2003 and 2004. Moose were habituated and tolerant of human presence, often to within 10-15 m. From this distance we were able to observe how moose crop willow and identify the specific parts of the plant that were taken. For example, once a moose selected a particular stem to feed on, it would begin to gather leaves with its tactile lips before placing its mouth either around or over the terminal end of the stem, depending on the plant height. Having gathered as many leaves as possible in its mouth, a moose would then grip the stem with its teeth and rake its mouth towards the terminal end of the stem, which serves to harvest some leaves before cropping the stem at a suitable diameter. In late summer when willow leaders and stems are fully developed, moose may strip the leaves without cropping the stem. This technique allows moose to crop highly digestible bites by maximizing leaf intake (more digestible) and minimizing stem intake (less digestible). Given the objectives of this study, we believed it more important to understand the nutrition moose achieved in each bite rather than the nutrition available in each plant part.

Plant morphology and phenology varied among elevations, and moose bite sizes varied accordingly. When collecting samples for forage quality analysis, we mimicked the moose cropping technique with our hands. One hand would be placed around a stem or over its terminal end while using fingers to gather as many leaves as possible. The researcher would then tighten his grip and rake his hand toward the terminal end of the stem. As he felt the diameter of the stem begin to taper (to a point comparable to what we observed moose cropping), the stem was cropped with pruners.

Our sampling technique accounted for the progression of willow development

throughout the summer. Plant parts collected throughout the summer were similar to those taken by Stewart et al. (1976) at 4 phenological stages (described as twig, leaf bud enlargement, leaf expansion, and leaf flush), although sampling continued beyond leaf flush. As plants age beyond leaf flush, nutritive quality generally declines, in part, as a result of a decreased proportion of leaves to stems (Van Soest 1994). Therefore, to accurately track this decline (and compare the nutrition offered by species with different morphologies or a single species at different phenological stages) leaves and stems must be collected and analyzed together in the proportion they are cropped by herbivores.

Plant tissues from the 3 most abundant willow species, *S. geeyeriana*, *S. monticola*, and *S. planifolia* var. *planifolia* (Dorn 1997), were collected at 5 sampling intervals between June 15th and August 15th in 2003 and 2004. Because forage quality varies little within riparian browse species collected at a common site, forage samples combined material from multiple plants (Oldemeyer 1974). Each species was collected at, or as near as possible, the elevation center of each stratum (2,682 m, 2,926 m, and 3,170 m). Collection sites were consistent between sampling periods and years with the exception of mid-elevation *S. planifolia*. It was collected at different sites in 2003 and 2004, but the collection site remained consistent within a given year. Samples were air-dried for the remainder of the summer. They were then oven-dried at 40°C for 48 h and ground in the fall following collection.

Forage Quality Analyses

Crude protein — Nitrogen content of willow samples was measured with the Kjeldahl technique (A.O.A.C. 1980) and then converted to an estimate of crude protein (percent nitrogen x 6.25). Duplicates were run for each sample and mean values were accepted as accurate when the coefficient of

variation (CV) was < 5 .

Fiber analysis — Neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) were determined by sequential fiber analysis (Goering and Van Soest 1970) employing filter bag technology (Komarek 1993, Komarek and Sirios 1993). Duplicates were run for all samples, and mean NDF and ADF fraction values obtained were accepted as accurate when the CV was < 5 (Bruce Davitt, Wildlife Habitat Lab, Washington State University, personal communication). However, the nature of sequential analysis rendered the application of this stringent quality control measure cost-prohibitive for ADL determination. Despite this fact, 72.5% of duplicates (29 of 40) maintained a CV < 5 . The highest CV recorded for an ADL value was 13.90.

Moose Distribution

Transects were surveyed regularly to track the progression of moose distribution throughout the summer by comparing the proportional change in moose occurrence between elevation strata. Eight transects were surveyed 6 times each throughout the course of each summer. Each round of sampling was completed just before one of the 5 corresponding rounds of vegetation sampling with an additional round of moose location inserted at the beginning of the summer to determine initial moose distribution. Four transects (mean length = 3.2 km) were located wholly within low-elevation willow communities, 3 of which paralleled the Colorado River through the KV. To best detect moose on broad floodplains containing tall willow communities, these transects were surveyed with double observers walking along opposite sides of the KV. The remaining 4 transects began at low elevation sites, continued up-slope to high-elevation sites and could be effectively surveyed by 1 observer because of the narrower riparian zones and/or shorter willow heights outside the KV (mean length = 12.8 km). A discrepancy in transect length

was necessary to represent the full spectrum of willow communities found in the study area. Transects spanning the elevation gradient were not located wholly within willow communities. Instead, they ran adjacent to Colorado River tributaries through large forested tracts punctuated with willow-containing riparian meadows. Although a rare occurrence, moose sightings within the forest were recorded, as it was assumed that the moose were traveling between willow communities within the given stratum.

Moose were located by direct observation. Location and elevation were recorded with a handheld GPS unit. A solitary animal as well as a group of animals was considered a sampling unit. Each observation was classified as male, female, or mixed. Female groups were further described by the presence or absence of calves.

Statistical Analyses

Forage quality values were evaluated with analysis of variance (ANOVA) to determine the effects of variables (i.e., year, species, sampling period, elevation). Moose distribution data were also analyzed with ANOVA to test for differential use of elevation between the sexes. When unequal means were detected in ANOVA tests, Fisher's least significant difference (LSD) test was performed to identify inequalities. A chi-square test of equal proportions was used to compare the frequency of moose observations to the proportion of land area in each stratum. Pearson's correlation coefficient was employed to determine the relationship between group size and elevation.

RESULTS

Forage Sample Collection

During the course of the summer, moose cropped stems from previous years' growth (old growth, OG) as well as stems and leaves of the current annual year's growth (CAG). Willows initiated leaf growth before stem

growth and moose could not efficiently exclude OG from their bites until after the initiation of new stem growth. When moose cropped willow leaders early in the growing season, they were ingesting the previous years' stem growth along with the current year's leaf growth. The current year's leaf crop appeared from lateral and terminal buds that would eventually become the current year's leaders. Leaves are the most nutritious willow plant part followed by CAG stems and OG stems (Regelin et al. 1987). Therefore, it benefits moose to take bites that offer them the largest proportion of leaves. As the summer progressed moose were better able to meet their intake needs from CAG. In early summer the leaf-to-stem ratio (but probably better stated as leaves-to-OG) was largely determined by the phenologic stage of the plant. After stem growth initiation, the leaf-to-stem ratio of CAG available to moose was largely determined by leader length.

In early summer before willow leaves matured, moose consumed both stems and leaves. However, in late summer when willow leaders were long and leaves mature (e.g., after mid-July in the low stratum), moose were observed leaf-stripping. Therefore, as the summer progressed, leaves comprised a greater percentage of moose diet. This progression was reflected by our sampling scheme in that the ratio of leaves to stems per sample increased throughout the summer. This trend held true at all elevations. However, leaf-to-stem ratios were not constant across elevations. As elevation increased, willows assumed a shorter growth form, were increasingly hedged, and produced shorter leaders unsuitable for leaf-stripping (Fig. 1). Therefore, the proportion of leaves per sample was greater at lower elevations. This influences the interpretation of the results as forage quality values are indicative of the ratio at which moose select leaves and stems (CAG and OG) and is not uniform across the growing season or elevation strata.

Only 1 species, *S. planifolia*, was present throughout the range of all 3 elevational strata.

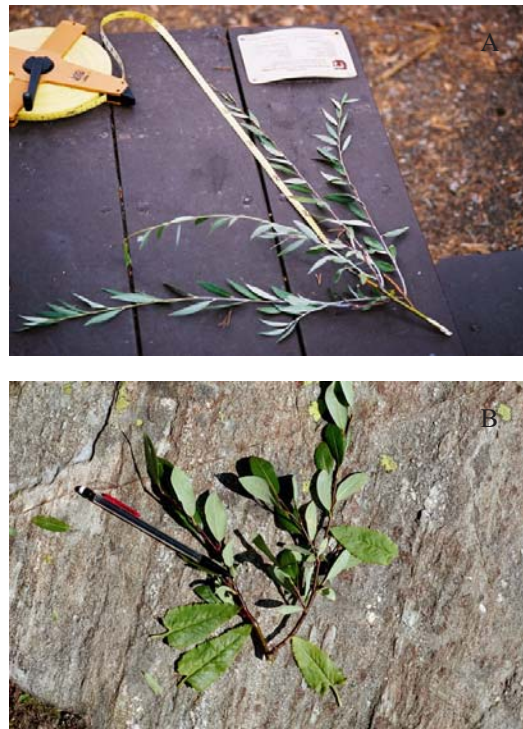


Fig. 1. Comparison of willow leader lengths on 15 Aug 2004 at low and high elevations. (A) *S. geeyeriana* leaders in excess of 50 cm in length and clipped at 2,720 m (low stratum) 15 Aug 2004. (B) *S. planifolia* leaders approximately 15 cm in length and clipped at 3,170 m (high stratum) 15 Aug 2004. Annual bud scars are marked with Arrowleaf senecio (*Senecio triangularis*) leaves.

Therefore, comparisons among elevation strata were based on values recorded for *S. planifolia* and species comparisons were limited to the low elevation stratum.

Forage Quality Analyses

Crude protein — Crude protein (CP) content varied with species and sampling period but not by elevation or year. However, within each sampling period, CP varied with elevation and year, except that elevation was not a significant factor during the August 15th sampling period nor was year on July 30th.

Peak CP content occurred earlier in 2004 than in 2003 for all low elevation species (Fig. 2). The rank of elevation stratum, ordered

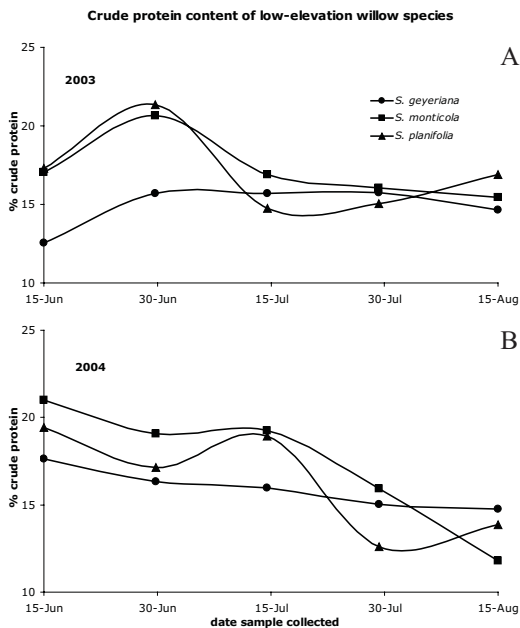


Fig. 2. Comparison of crude protein content for the 3 most abundant willow species of the Kawuneechee Valley (low elevation stratum), Rocky Mountain National Park, CO, 2003-2004.

by CP content, varied between years (Fig. 3). Additionally, low elevation plants rarely recorded the highest CP content for any given sampling period (Fig. 3).

Fiber analysis— Neutral detergent fiber varied with year, species, and sampling period but not by elevation. However, when *S. planifolia* (the only species occurring at the upper and lower bounds of the study area) data were analyzed separately, elevation only narrowly missed ($P = 0.073$) the standard of statistical significance, $\alpha = 0.05$.

Lignin content (i.e., ADL) varied with species and sampling period but not by year or elevation. However, when *S. planifolia* data were analyzed separately, year, elevation, and sampling period all became determinant variables. The individual analysis of each sampling session revealed little differentiation between the remaining variables (i.e., year and elevation).

The rank of elevation stratum, ordered by fiber content (e.g., NDF, ADL), was not

constant between years (Fig. 4). Additionally, low elevation *S. planifolia* rarely recorded the lowest fiber content after mid-summer (Fig. 4).

Moose Distribution

Transects intersected 91.5% of the study area’s 739.3 ha of riparian willow communities. The proportion of willow communities surveyed in each elevation stratum (low-80.9%, mid-17.0%, and high-2.1%) was very similar to the distribution of willow communities in the study area (low-80.1%, mid-16.9%, high-3.0%).

Of the 199 moose observations recorded in 2003 and 2004, 62% ($n = 123$) were female groups, 24% ($n = 48$) male, and 14% ($n = 28$) mixed. Of the female groups, 47% ($n = 58$) were cows with 1-2 calves. Mean group size was 1.36 (SD=0.89) not including calves. Mean group size was similar among

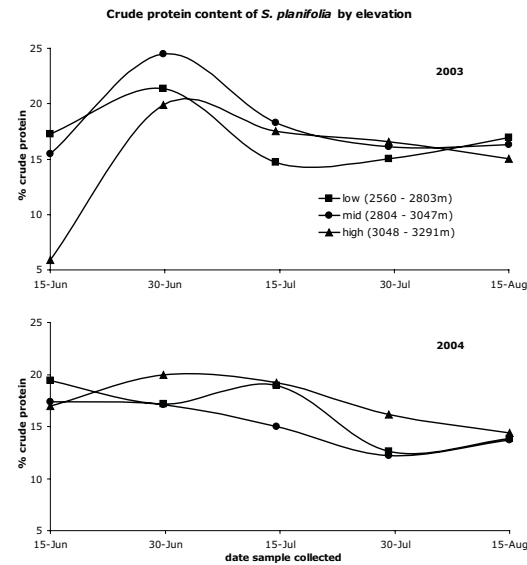


Fig. 3. Comparison of crude protein trends for *Salix planifolia* across an elevation gradient in Rocky Mountain National Park, CO, 2003-2004. Note: because insufficient sample was collected, values displayed at mid and high elevations on 30 Jun 2003 are estimates based on other species at similar elevations. These estimates were used for visual display only and not included in statistical analyses.

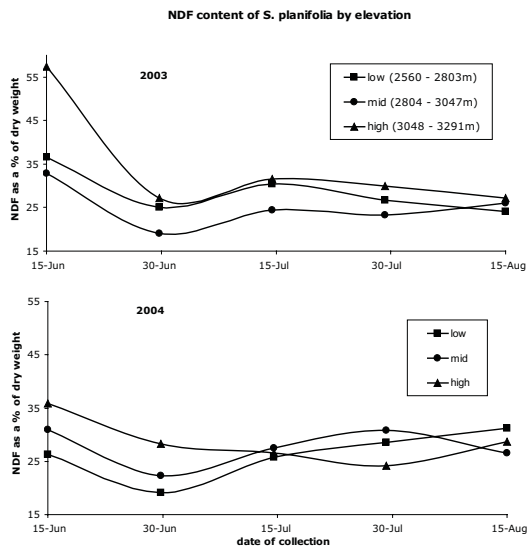


Fig. 4. Comparison of trends in neutral detergent fiber content for *Salix planifolia* across an elevation gradient in Rocky Mountain National Park, CO, 2003-2004.

sampling sessions throughout the summer ($F = 1.30$, $P = 0.27$) but declined with elevation ($R = 0.22383$, $P = 0.0015$).

Of the 39 observations recorded at mid and high elevation sites, only 6 (5 male, 1 mixed) were not female groups. Therefore, mid and high elevation sites were used almost exclusively by females. Elevation of female groups varied by sampling period ($F = 5.29$, $P = 0.0002$) with mean elevations for sampling periods exhibiting an increasing trend throughout the summer ($\bar{x}_1 = 2,710\text{m}$, $\bar{x}_2 = 2,707\text{m}$, $\bar{x}_3 = 2,716\text{m}$, $\bar{x}_4 = 2,811\text{m}$, $\bar{x}_5 = 2,808\text{m}$, $\bar{x}_6 = 2,892\text{m}$). Females selected for low elevation willow communities from late May until the end of June ($\chi^2 = 6.83$, $P < 0.05$) and mid and high elevations from early July through mid August ($\chi^2 = 40.33$, $P < 0.001$). Elevation of females with calves and females without calves was not significantly different ($F = 1.44$, $P = 0.232$).

DISCUSSION

Forage Sample Collection

We attempted to mimic the variation in moose plant part selection among willow spe-

cies (which exhibit varying leader lengths) and across an elevation gradient (which may elicit varying growth forms from a single species). The converse strategy is to collect a uniform portion of each plant such as CAG. Because moose do not select bites consisting of a constant leaf-to-stem ratio across elevations, a uniform collection scheme would not have accurately represented the nutrition achieved by moose. If only CAG was sampled, the perception of forage quality would be greater than that achieved by the moose during early summer when OG and CAG are taken. Conversely, forage quality might be underestimated late in the summer at low elevations if all of the CAG was collected when moose strip leaves from willow leaders. Because plants parts collected were not uniform throughout the course of the summer, our sampling scheme is subject to some human bias. However, we believe that adhering to a less subjective sampling scheme would fail to account for the gradient in willow morphology and phenology, thereby obstructing an accurate perception of the foraging choices presented to moose across an elevation gradient.

Forage Quality

Ultimately, all the forage sample variables (i.e., year, species, sampling period, and elevation) influenced the observed fiber and CP values. Analysis of Variance tests identified "species" and "sampling period" as significantly influencing forage quality when all data were analyzed together. However, the cyclic nature of forage quality required parsing of the data set so that the influence of "elevation" and "year" could be truly understood. The forage quality of deciduous browse species predictably reaches a base level each year that coincides with dormancy and occurs after leaf fall (Short et al. 1966). Forage quality remains low until the onset of the preceding growing season. Because willow collection spanned the 2003 and 2004 growing seasons, forage quality could be expected to

approach minimum values in early and late summer. Therefore, means calculated for the entire summer are heavily influenced by the base forage quality. In other words, it is not surprising that ANOVA tests did not detect a significant difference among elevations (or between years) when data from an entire growing season were analyzed together. In order to realize the effect of forage quality on moose distribution, mean values for a particular elevation (or year) were not as important as the timing and magnitude of those peaks, so sampling periods were evaluated individually.

Regardless of how the data were grouped for analysis, forage quality always varied by sampling period (date of collection). This demonstrates the strong relationship between plant phenology (and the resulting leaf-to-stem ratio) and forage quality. In 2003, CP content peaked for most low elevation species around June 30th (Fig. 2a). In 2004, the peak in CP presumably occurred at or before the first sampling period as CP exhibited a decreasing trend for most species between June 15th and 30th (Fig. 2b). We began sampling just after the onset of the growing season and suspect that the difference between years on June 15th can be explained with anecdotal evidence. In 2003, Colorado received heavy, late-season snows and the snow pack persisted down to 2,900 m through June, whereas the snow pack had disappeared up to 3,050 m by late May in 2004. Therefore, the growing season probably began earlier in 2004 yielding a more advanced phenology during the initial sampling period.

Another, but less explainable, difference between years was the change in rank of elevations ordered by both CP and fiber values. Perhaps microclimate (which affects phenology) or herbivory pressure (which affects plant morphology) varied among sampling sites, which were consistent with respect to elevation but not location between years. Regardless, low elevation willow communities were gener-

ally not the highest-ranking elevation stratum in terms of CP in either year. In 2004, the low elevation stratum contained the lowest fiber content (highest quality) until July 15th, but maintained an intermediate quality in 2003 (Fig. 4). The varying forage quality among willow species and elevation stratum provides motivation for moose and other ungulates to forage selectively between and within willow communities.

Given the limitations of a 2-year dataset and the variation encountered between 2003 and 2004, a consistent relationship between browse quality and elevation was not evident. Albon and Langvatn (1992) reported that forage quality of herbaceous vegetation increases asymptotically with elevation. A possible explanation for the discrepancy between the linear relationship these authors report for forage quality and elevation and the findings of this study is that woody species may present a more complex relationship as a result of the difference in forage quality between stems and leaves. In early stages of development in herbaceous forage, there is little difference between the nutritive quality of plant parts (Laca et al. 2001). In contrast, the relative qualities of woody plant parts vary dramatically (Kubota et al. 1970, Oldemeyer et al. 1977, Larter and Nagy 2001). For woody species, forage quality is largely determined by the leaf-to-stem ratio ingested, with leaves being the more nutritious of the 2 plant parts. However, the greater presence of secondary compounds in browse compared with grasses (Bø and Hjeljord 1991) adds additional complexity to the calculation of browse forage quality.

Because the highest qualities measured in this study occurred at mid and high elevation sites despite a less favorable leaf-to-stem ratio, the nutritive quality of browse leaves likely increases with elevation and even compensates for lesser leaf-to-stem ratios. An elevation threshold may exist past which leaves at an earlier phenologic stage do not compensate

for poor leaf-to-stem ratios or it could be expected that moose would forage on alpine willow communities. Above the hypothetical threshold, an ungulate migrating up-slope will encounter forage of reduced quality when fiber fractions become a large enough portion of the diet to reduce nutrient intake.

Moose Distribution

If moose select feeding sites based solely on chemical properties of forage, it would be expected that a greater proportion of the moose population in RMNP would use the mid and high elevation strata and that utilization would not be restricted to females. Shipley et al. (1998) demonstrated that moose also select forage based on physical properties of plants such as morphology. In their study, moose selected plants with few large twigs over those with many small twigs, presumably to increase intake rate (Shipley and Spalinger 1992). The fact that herbivores would make diet choices based on physical properties of plants broadens the definition of forage quality from merely chemical composition to any physical qualities influencing foraging mechanics.

Spalinger et al. (1988) found that intake rate will decrease as bite size decreases despite an attempt by the animal to compensate by increasing bite rate. Bite size is then of critical importance to an animal with large requirements because its ability to trade-off intake rate for nutrient content becomes diminished. In a sexually dimorphic species like moose, bite size may be more limiting for males, the larger sex. Although male moose within RMNP are probably responsive to variation in willow chemistry at the stand level, the variation in productivity among elevations might explain their absence from the highest elevations on summer ranges. The subset of moose with the next highest forage requirements are cows with calves. A lactating cow provides a singleton calf as much as 342 g protein dry matter/day in addition to meeting its own requirements (Reese and Robbins 1994). However, the fact

there was no difference between the elevation use of non-lactating and lactating females suggests that forage requirements are not the only factor determining elevation use, at least where calf-rearing is involved.

Because bite size is coupled with plant morphology, willow offer decreasing bite sizes with increasing elevation. This relationship may be further exacerbated in RMNP as a result of heavy utilization by cervids. Outside the low elevation strata, a decrease in intake rate may be partially compensated for by a higher rate of nutrient assimilation as result of higher forage quality. Because we did not measure intake rates of moose in this study, trade-offs between intake rate and forage quality are hypothetical. Moose with the smallest energy requirements (smallest body size) are the most capable of making trade-offs between intake rate and forage quality. Thus, large males may be precluded from higher elevations because they are unable to meet daily requirements due to a reduced intake rate. Conversely, females may be better able to forage on willow communities at different elevations and make trade-offs between intake rate and forage quality.

Another constraint possibly placed on males at mid and high elevations is the absolute abundance of forage. Absolute abundance of forage affects intake rates on an ultimate, or seasonal, scale whereas bite size affects intake rates on a proximate or daily scale. Mid and high-elevation sites occur in much smaller patch sizes (e.g., mean size 4-5 ha) and lack the continuity of willow communities occupying a broad floodplain. If a large male was to spend the summer foraging at higher elevations, and was indeed constrained by absolute forage abundance, any advantage that might be gained over rivals by consuming superior forage could be negated by the travel costs accrued while frequently moving between foraging patches in a mountainous environment. This assertion assumes that not only are females able to use all elevation strata

because of their lesser absolute abundance requirements, but that foraging patch size in mid and high elevation sites must fall between minimum thresholds for females (lactating and non-lactating) and males. Although we are reporting that males did not use the higher elevation stratum within the study area, it should not be inferred they are not migratory. RMNP occurs at the highest elevation in the local area. It is probable that male moose not wintering in the park must migrate up-slope to reach the park during the summer months. This assertion is consistent with the findings of Kufeld and Bowden (1996) who reported that moose in north central Colorado winter at the lowest elevations of their yearly home range. Therefore, park boundaries probably do not encompass the entire moose population or the yearly home ranges of all individuals.

If chemical forage quality dictates female foraging-site selection, females should not use low elevation willow communities for almost the entire duration of the summer. Curiously, females did not seem to take full advantage of higher elevation willow communities in late June when the differences in willow chemistry between the elevations were greatest. However, females do utilize these willow communities shortly after the peak in chemical quality and then continue to increase their elevation throughout the summer. The fact that females undertake a "delayed" migration indicates that they are sensitive to differences in plant chemistry but may be constrained by intake rates early in the growing season. But, as the summer progressed and leaves matured, females increased their elevation and utilized the highest quality forage in terms of plant chemistry. We hypothesize that it is not until leaves near maturity and offer larger bite sizes that it becomes profitable for female moose to forage at higher elevations. Presumably, the bite-size threshold required for males to forage profitably at mid and high elevations is never reached. The fact that only 5 male groups were observed above the low elevation stratum, ir-

respective of higher forage quality, indicates that it may be misleading to speak in terms of selection when considering males. Mid and high elevation sites may not be available to males as a result of some foraging constraint such as absolute forage abundance or intake rate as previously discussed. Some support for the absolute abundance assertion is provided by the negative correlation between group size and elevation use. Willow communities decrease in size with increasing elevation. If the absolute abundance of forage was not a limiting factor in moose group distribution, then it would be expected that: (1) no correlation between elevation and group size would exist; and (2) large groups would occasionally use the mid and high elevation stratum. However, observations support the hypothesis that absolute abundance of willow communities does limit group size above the KV.

If moose were randomly distributed (exhibited no selection) throughout willow communities across the study area, moose distribution should be proportional to willow community occurrence and should not be influenced by forage quality or willow community elevation. Female moose appear to select for low elevation sites during the summer until June 30th and select mid and high elevation sites thereafter. Statistical support for this assertion was provided with a chi-square analysis. However, expected high elevation counts are below what Cochran (1954) suggests for an accurate approximation of the chi-square distribution. Agresti (1990) refutes the notion that a single rule governing sample can apply to all cases. We included the results of the analysis because of the strength of selection beyond June 30th in each year.

If females utilizing mid elevations are able to convert higher quality forage to an improved body condition, mid-elevation foraging sites may contribute disproportionately to demographic parameters such as fecundity and survival. For example, females using mid-elevations might have higher fecundity rates

or higher calf and over-winter survival rates relative to females inhabiting lower elevations. Studies of other cervids (Klein 1970, Albon and Langvatn 1992) have demonstrated the benefits of migration with respect to body mass. However, a review of some studies assessing moose fitness across elevation and latitudinal gradients was inconclusive.

Hjeljord and Histol (1999) claim the relationship between forage quality and elevation does not elicit the same response in moose as it does in other cervids. They support their claim with data showing a negative relationship between calf and yearling body mass and elevation. Moose populations under study were migratory. Ericsson et al. (2002) also reported that moose calves inhabiting higher elevation sites exhibited a negative relationship between October (growth cessation) body mass and elevation. This relationship is attributed to the shorter growing season length at higher elevations. Therefore, the presumed higher quality forage could not compensate for a shorter growing season. The authors make no mention of migratory behavior, implying that moose elevation remains static.

Alternatively, Sand et al. (1995) found that moose inhabiting more northern latitudes (harsher climates similar to higher elevations) exhibited a larger body mass in autumn yet similar skeletal size relative to moose inhabiting more southerly latitudes. This finding suggests that differences in body mass can be attributed to muscular and fatty tissues. Data were acquired when moose body mass was at its yearly maxima. The authors acknowledge that their data do not necessarily imply a higher fitness for more northerly animals, but that these animals may experience larger amplitudes in their yearly body mass cycles. If this is the case, the relationship between body mass and latitude could change with the seasons. However, late summer or early fall body condition is especially important to moose as they enter both the ensuing rut and winter.

Although body mass and nutritional plane have definite implications for fitness, fitness is not realized until over-winter survival or successful mating occurs. Edwards and Ritcey (1958) were able to attribute the higher fitness (fecundity) of migratory moose to an assumed increased plane of nutrition during summer months. Although all of the aforementioned authors speculate about the quality of forage at various elevations as an extrapolation of moose body condition, none of them measured forage quality empirically.

If the interaction between elevation and forage quality is to be understood in the context of moose fitness, empirical values of forage quality must be associated with some aspect of fitness. We did not collect data related to moose fitness in this study. But, our findings concerning the relationship between elevation and browse quality divulge the danger in assuming a linear relationship. Moose feeding at the apex of forage quality (possibly intermediate elevations) likely experience the greatest body mass gains through the height of the growing season. If researchers are not aware of where the browse forage quality apex occurs on the landscape, faulty conclusions could be reached. For example, if moose populations are sampled from only above and below elevations where the apex of forage quality occurs, relationships between elevation and measures of fitness will appear linear.

As measured in 2003 and 2004, the apex of willow forage quality in RMNP occurs between 2,804 and 3,047 m of elevation approximately 400 m below tree line. At the aforementioned elevation, body mass gains afforded by the high forage quality could be counterbalanced by the shortened growing season. Therefore, migration probably benefits moose most in montane environments where the elevation gradient is sufficiently steep to offer moose both the highest quality forage and relatively long growing seasons.

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