Sequential twig selection and biomass consumption of willows by moose calves in winter: a test of optimal patch use theory

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Abstract - A better understanding of how moose *Alces alces* select and browse plants may allow ecologists to make better predictions about how herbivores and plants interact, herbivore food acquisition, and how organisms may shape their own forage supply. This in turn, can lead to a better understanding of animal responses to plant nutrients and defences, and how and why animals move across landscapes, select certain habitats, reproduce, interact with predators and competitors, and survive. Here, we used sequential feeding trials conducted in north-central British Columbia with 4 hand-reared, 9-month-old, orphaned moose calves to study winter shoot selection from ramets cut from native willows *Salix scouleriana*. Our generalized linear models indicated that, when browsing, moose calves generally followed principles of optimal patch use theory and initially selected smaller, less fibrous shoots at the beginning of feeding trials, then switched to larger shoots as smaller, more nutritious shoots were depleted. On average, moose calves removed 20% of the shoot biomass from each ramet trialled and cropped shoots at an average of 5.03mm in diameter. Bite diameters taken by calves were larger when a greater proportion of shoots from ramets had been selected from ramets that had been browsed in previous years and in later feeding trials. Despite some study limitations, our findings provide these and other fine-scaled details contextualized within a backdrop of prior research regarding browse selection by young moose that may help to elucidate connections between browsing behaviours and estimates of intake rate. These findings may help to inform future studies in which forage ecologists are seeking to understand optimal foraging and browse patch depletion dynamics in moose and other species.

Key words: bite, browse, moose, twig, winter.

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Riassunto - Selezione sequenziale dei rametti e consumo di biomassa di salice da parte dei giovani alci in inverno: un test della teoria dell'uso ottimale delle patch alimentari.

Una migliore comprensione delle modalità con cui gli alci *Alces alces* selezionano e brucano le piante può consentire agli ecologi di formulare previsioni più accurate sulle interazioni tra erbivori e vegetazione, sulle strategie di assunzione del cibo da parte degli erbivori e sul modo in cui gli organismi possono influenzare la disponibilità delle proprie risorse alimentari. Ciò, a sua volta, può contribuire a una migliore comprensione delle risposte degli animali ai nutrienti e ai meccanismi di difesa delle piante, nonché delle ragioni e delle modalità con cui essi si spostano nel paesaggio, selezionano determinati habitat, si riproducono, interagiscono con predatori e competitori e sopravvivono.

In questo studio sono stati utilizzati esperimenti di alimentazione sequenziali condotti nella Columbia Britannica centro-settentrionale su quattro giovani alci orfani, allevati a mano e di nove mesi di età, per analizzare la selezione invernale dei germogli appartenenti a rametti recisi di salici autoctoni (*Salix scouleriana*). I modelli lineari generalizzati hanno evidenziato che, durante il brucamento, i giovani alci seguivano generalmente i principi della teoria dell'uso ottimale delle patch alimentari, selezionando inizialmente germogli più piccoli e meno fibrosi all'inizio delle prove di alimentazione, per poi passare a germogli di dimensioni maggiori man mano che quelli più piccoli e nutrienti venivano esauriti.

In media, i giovani alci hanno rimosso il 20% della biomassa dei germogli da ciascun rametto sperimentale e hanno brucato germogli con un diametro medio di 5,03 mm. I diametri dei morsi erano maggiori quando una proporzione più elevata di germogli proveniva da rametti che erano stati brucati negli anni precedenti e durante le prove di alimentazione svolte nelle fasi più avanzate dell'esperimento.

Nonostante alcune limitazioni dello studio, i risultati forniscono informazioni dettagliate, contestualizzate nel quadro delle ricerche precedenti sulla selezione del brucato da parte dei giovani alci, che possono contribuire a chiarire le relazioni tra il comportamento di brucamento e le stime del tasso di assunzione del cibo. Questi risultati potranno inoltre orientare studi futuri in cui gli ecologi delle risorse alimentari intendano comprendere le dinamiche del foraggiamento ottimale e dell'esaurimento delle patch di brucato negli alci e in altre specie.

Parole chiave: alce, brucato, inverno, morso, ramet.

INTRODUCTION

Optimal foraging in animals involves complex behavioural and species interaction processes between foragers, the forage base, and predators. Optimal foraging is often defined by ecologists as ways in which animals behave to ensure that the benefits and energy obtained by the forager outweigh costs associated with obtaining food items which can be accompanied by increased risk to predators (Pyke & Starr, 2020). As such, an understanding

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of how animals select what they eat allows ecologists to take better measurements and make better predictions about herbivore-plant interactions, food and energy acquisition, and how herbivores may shape their own forage supply (Cohen *et al*., 1999; Shipley, 2007, 2010). This in turn can lead to a better understanding of how populations and communities are regulated and can help to answer questions in ecology concerning animal responses to plant defences, movements across landscapes, habitat selection, reproductive behaviour, competitor, predator, and parasite interactions, and survival (Cohen *et al*., 1999; Shipley, 2007; Blouin *et al*., 2021; Kramer *et al*., 2024).

The winter foraging ecology of moose *Alces alces* has been studied at the level of the winter range (Hjeljord & Histøl, 1999; Flyktman, 2024; Harris *et al*., 2024), thicket (i.e., dense stand of trees or shrubs; Vivås *et al*. 1991, Shipley and Spalinger 1995) and individual plant (Vivås and Sæther 1987, Stolter *et al*. 2005, Shipley 2007, Rea *et al*. 2015). Selection of winter forage by moose at the scale of the seasonal range and patch appears to be driven by many factors, but in large part by the quantity of available and relatively digestible browse (i.e., browses lower in fibre and anti-herbivore chemicals; Edenius 1991, Andersen and Sæther 1992, Robbins 2012). At the level of individual plants, winter browse selection by moose can be influenced by many factors, including the size of available shoots, but whether moose prioritize the selection of small or large shoots is highly variable and contingent upon factors, such as shoot chemistry and plant architecture (Jia *et al*., 1997; Rea *et al*., 2015).

Foraging behaviours and selection for twig size by moose in winter is dependent on a myriad of factors that vary with the particular circumstances associated with a foraging bout, such as plant species assemblages present, plant phenotype, shoot nutrient quality, the distribution of shoots within a plant, time spent browsing, and sight and chewing sensation (Risenhoover, 1986; Shipley & Spalinger, 1995; Wilson & Kearly, 2003; Rea *et al*., 2015; Breithaupt *et al*., 2025). Additionally, twig diameters that constitute an optimal bite-size for moose in winter may not be generalizable across all moose age- and sex-classes or across populations in different vegetation communities (Andersen & Sæther, 1992; Spaeth *et al*., 2004). For example, browsing behaviours of moose calves in their first winter are different than those of adult moose (Nyström, 1980; Kossak, 1992; Felton *et al*., 2016) which may reflect – among other things – differences in mouth architecture and the inability to process larger bites (Wilson & Kerley, 2003).

Although some differences in specific browsing behaviours of adult moose have been reported across sex classes and body masses (Spaeth *et al*., 2004), how moose calves select and crop shoots from browse plants appears to be complex and poorly understood. Determining browse selection by calves can help to increase our understanding of moose habitat quality in general, but also particularly for sub-adults that require conditions that support their growth, development, and recruitment into breeding age classes of populations occupying specific ranges.

If individual plants upon which moose browse can be thought of as patches in which moose follow optimal foraging rules (Lundberg *et al*., 1990), then according to optimal foraging theory, moose should select shoots that are concurrently most profitable (i.e., high biomass, energy- and protein-rich) and most easily accessible (require low energy expenditures to obtain) from all shoots available. In other words, when encountering a browse plant, a moose should theoretically select bites which are the most nutrient-dense and digestible (within the constraints imposed by the physiognomy of the plant; Vivås *et al*., 1991) then subsequently remove bites which are less and less optimal before moving to the next plant or patch. Habitats rich in optimal bites are habitats that are best suited to support individual fitness and productivity and population growth and expansion (Pyke, 1984; King & Marshall, 2022).

The specific selection of bite size by moose during foraging has been studied through field observations and measurements (Vivås & Sæther, 1987; Shipley *et al*., 1998), including videography and plant sampling (Pastor *et al*., 1999), predictive modelling (Vivås *et al*., 1991; Shipley *et al*., 1999), simulations (Roese *et al*., 1991), and cafeteria/pen trials (Shipley & Spalinger, 1992, 1995; Shipley *et al*., 1999) or some combination of these (Cohen *et al*., 1999). However, an accounting of the biomass and shoot diameters of successive bites taken from individual plants by moose in winter using real time measurements appears to remain unpublished. In this regard, Lundberg *et al*. (1990) suggests that the application of optimal patch use theory can help explain the selection of bites of shrubs and trees by a generalist herbivore such as the moose; Nyström (1980) suggests that counting bites and measuring weights of materials browsed must be included in such endeavours. All of which together may help to inform optimal foraging and patch use theory. Due to its importance in the diets of moose, willow (*Salix* sp.) is a model browse plant for such studies (Shipley, 2010).

In this study, we quantified specific patterns of shoot removals from whole ramets (i.e., co-dominant main stems) of willows by 9-month-old moose calves in winter to ascertain whether moose adhere to rules governing optimal foraging and patch use. We recruited all young moose calves at a wildlife shelter who had been orphaned and raised in the absence of their mothers since being neonates. All calves were of the same age and size which minimized possible variability in browsing responses due to differences in age and body mass. We measured the number and diameter of repeated bites taken from ramets and the amount of biomass removal from ramets that were presented to moose one at a time. We tested how the diameters (and by correlation, the biomass of shoots) at which moose took bites from individual plants changed as browsing progressed. We predicted that if moose foraged optimally, they would first consume smaller (i.e., more digestible) shoots within feeding bouts, then begin incorporating larger, more fibrous bites as smaller bites became less available with progressive browsing. We also hypothesized that as moose became more satiated over the course of consecutive trials and hours of browsing, that their interest in each new willow ramet offered would wane and browsing by moose would become more selective with moose browsing only the thinnest and most

nutritious shoots from each new ramet. Our trials were designed to help us answer questions around optimal winter browsing by moose calves that could lead to more informed decision-making about what to provide for calves in shelters and zoos (Ramont *et al*., 2025) but also across native winter ranges (Andersen & Sæther, 1992).

METHODS

Study Area and Field Methods

On February 11, 2013, we collected 35 willow ramets (ramets were approximately 1.5 to 2 m tall with branching architecture to about 1 m wide) of similar shape and form from about 2 dozen different individual willow clumps along the shores of Tezzeron Creek in the John Prince Research Forest (JPRF; 54.677801, -124.308929), near Fort St. James, British Columbia (BC), Canada. The JPRF is a 16,500-ha public forest nestled between two large lakes that contain extensive wetland complexes (Crowley *et al*., 2012). The research forest is within the Sub-Boreal Spruce biogeoclimatic zone where logging has been extensive and persistent over the last 75 years (Crowley *et al*., 2012) and has likely altered the diet composition and foraging dynamics of moose (Koetke *et al*., 2023).

After cutting, we transported the willow ramets to the University of Northern British Columbia (UNBC), Prince George, BC, Canada. At UNBC, plants were temporarily stored outdoors in subzero temperatures. During all transportation and storage, willow ramets were wrapped and sealed in tarps to minimize excessive loss of plant moisture and dehydration which could influence browsing and biomass measurements. On February 22, 2013, willows were transported to the Northern Lights Wildlife Shelter (Smithers, BC) for feeding trials with 4, 9-month-old moose calves over a 2-day period. Calves were hand-reared at the shelter after losing their mothers but had been living on an open range behind the shelter since 4-months of age with access to native browse plants, including several species of willow. Animal Care and Use Applications were approved (ACUC Protocol Numbers: 2012-07) by the Animal Care and Use Committee at the University of Northern BC.

Prior to feeding trials (defined as consecutive feeding bouts on an individual ramet), ramets were individually and randomly removed from the tarp, numbered on the base of the plant, weighed to the nearest tenth of a gram in a sheltered building, and as part of a larger project, photographed against a white backdrop (Fig. 1a); they were then re-photographed upon completion of each trial (Fig. 1b). During each feeding trial, an individual ramet was held from inside an enclosed area and offered over a fence to moose calves in a series of sequential feeding bouts. This was done to ensure that each ramet could be retracted back into the enclosure and protected from further browsing while measurements were taken between successive feeding bouts.

During each bout, ramets were held by the experimenter at the base of each cut ramet main stem with crowns directed outward and over the fence to the area where calves were waiting to feed (Fig. 2). During most feeding bouts, a single moose browsed the ramet. However, during some feeding bouts, two or three moose browsed the willow ramet concurrently or sequentially. An individual feeding bout (but not the trial) ended when moose had taken one or more (up to 8) bites that required measurements to be taken before the next bout. Ramets were then retracted and the diameter of bitten shoots were measured to the nearest tenth of a mm using digital callipers. The same ramet was then again presented to calves for another and several consecutive feeding bouts, with the ramet retracted between bouts for measurements until moose showed a lack of interest in browsing the ramet any further. A new, unbrowsed ramet was then presented to moose and the process was repeated until all ramets had been trialled.

At the end of each trial, biomass measurements were re-recorded before a new ramet was offered in the next feeding trial. All calculations were made using green or fresh wet mass without any drying procedures conducted between the time of collection and feeding as per Lundberg *et al*. (1990) and Rea *et al*. (2015). No corrections were made for water losses in plant mass because such losses were previously determined to be negligible during similar trials at similar temperatures (Rea *et al*. 2010). Willows were wrapped in tarps for all transportation and remained tarped except during the trials (from ~5-20 minutes long) when presented to moose. All trials and measurements were completed within 12 days of the collection of willow ramets.

Data Analysis

We used a linear model to explore how consecutive browsing opportunities affected the diameters of bites. In this model, each bite was treated as an observation. We tested for an effect of previous browsing (i.e., whether the ramet had been browsed by moose before collection for feeding trials), pre-trial weight of the ramet, order of the feeding trial, order of the feeding bout within each trial, and proportion of the pre-trial weight consumed during feeding trials on the diameters of bites taken by moose calves (Tab. 1).

We fit a beta regression using the *betareg* package (Cribari-Neto & Zeileis, 2010) in RStudio (R Core Team, 1999+; RStudio Team, 2026) to explore how browsing history influenced the proportion of the ramet browsed. In this model, each feeding trial (i.e., ramet) was treated as an observation and the proportion of the ramet browsed was calculated as the difference between the pre-trial and post-trial weights of the ramet divided by the pre-trial weight. We tested for an effect of previous browsing, pre-trial weight of the ramet, order of the feeding trial, and the total number of bites taken across the feeding bouts within each trial (Tab. 2).

In both models, variables representing the order of the feeding trial and order of the bout within each feeding trial were treated as numeric indices to avoid overparameterizing the models and to allow inference about linear trends across trials and bouts. We were unable to track which individual moose made each bite, so we did not control for variation in bite size across individual moose calves. However, all moose included in the study were 9 months of age and of similar size, so they likely had similar oral capacities and were likely clipping twigs at similar bite sizes. For both models, we calculated robust



Fig. 1 - Research assistant, Jenna Rea marks the identity of each willow (in this case willow ramet #15) and its condition in preparation for photographic records being taken both prior to (A) and after (B) it has been browsed by moose calves. Note B shows the typical condition of a ramet at the end of all bouts of feeding within the trial of that ramet. / L'assistente alla ricerca, Jenna Rea, identifica ciascun salice (in questo caso il ramet di salice n. 15) e ne registra lo stato in preparazione alla documentazione fotografica, effettuata sia prima (A) sia dopo (B) il brucamento da parte dei piccoli di alce. La figura B mostra la condizione tipica del ramet al termine di tutte le sessioni di alimentazione previste nella prova sperimentale relativa a quel ramet.



Fig. 2 - A camera equipped with a fish-eye lens captures the process used during the feeding trials, with moose being presented with a ramet over the fence of an enclosure. All ramets were stored in the enclosure wrapped in tarps with ramets being presented one at a time over the fence for bouts of feeding until the trial was complete. This procedure was necessary so that moose could be kept away from each ramet and the browse supply while measurements were made between bouts and trials. / Una macchina fotografica dotata di obiettivo fisheye riprende la procedura utilizzata durante le prove di alimentazione, nelle quali ai giovani alci veniva presentato un ramet di salice oltre la recinzione del recinto. Tutti i ramet venivano conservati all'interno del recinto, avvolti in teli protettivi, e presentati agli animali uno alla volta oltre la recinzione per successive sessioni di alimentazione, fino al completamento della prova. Questa procedura era necessaria per impedire agli alci di accedere ai singoli ramet e alla riserva di materiale vegetale durante l'esecuzione delle misurazioni tra una sessione di alimentazione e la successiva e tra una prova sperimentale e l'altra.

standard errors using the *sandwich* package (Zeileis *et al*., 2020). We conducted all data analyses in RStudio (R Core Team, 1999+; RStudio Team, 2026).

RESULTS

We measured bites taken and biomass removed by moose calves on 32 of the 35 willow ramets we had originally collected. Ramets that we collected showed no signs of browsing during the winter of collection; however, some (n = 6) had evidence of minimal browsing in previous years. On average, ramets were used for 6.78 bouts of feeding per trial (standard deviation (SD) = 3.12, range = [2, 15]) before moose showed a lack of interest in browsing the trialed ramet any further. The number of feeding bouts per trial was not correlated with the order

Table 1 - Descriptions of independent variables used to model two dependent variables (bite diameter and proportion of ramet browsed) to explore browsing choices by moose (*Alces alces*) calves from north-central British Columbia. / Descrizioni delle variabili indipendenti utilizzate per modellare due variabili dipendenti (diametro del morso e percentuale di rametti brucati) al fine di analizzare le scelte alimentari dei giovani alci (*Alces alces*) della Columbia Britannica centro-settentrionale.

Independent variable	**Description**	**Dependent variable**	
		Bite diameter	Proportion of ramet browsed
Previously browsed	Binary; whether ramet experienced moose browsing before collection for feeding trials	X	X
Pre-trial weight	Weight (g) of willow ramet before feeding trials	X	X
Feeding trial	Order of feeding trial (i.e., ramet)	X	X
Feeding bout	Order of feeding bout within each trial (i.e., per ramet)	X	
Proportion eaten	Proportion of pre-trial weight consumed during feeding trials	X	
Number of bites per trial	Total number of bites taken across the trial		X

Table 2 - Candidate models and model selection statistics used to predict the diameter of bites and the proportion of ramets browsed during feeding bouts by moose (*Alces alces*) calves from north-central British Columbia. Independent variables were defined in the text and in Tab. 1. Bolded variables indicate a statistically significant ($p < 0.05$) relationship with the dependent variable. / Modelli candidati e statistiche di selezione dei modelli utilizzati per prevedere il diametro dei morsi e la percentuale di rametti brucati durante l'alimentazione dai giovani alci (*Alces alces*) della Columbia Britannica centro-settentrionale. Le variabili indipendenti sono state definite nel testo e nella Tab. 1. Le variabili in grassetto indicano una relazione statisticamente significativa ($p < 0,05$) con la variabile dipendente.

Dependent variable	**Rank**	**Independent variables**	**ΔAICc**	**AICc w**
Bite diameter	1	**Previously browsed** + Feeding trial + **Proportion eaten**	0.00	0.70
	2	**Previously browsed** + **Feeding trial** + Feeding bout + Pre-trial weight + **Proportion eaten**	1.76	0.29
	3	**Previously browsed** + Feeding trial + Feeding bout	9.83	0.01
	4	**Previously browsed** + Feeding trial + Feeding bout + Pre-trial weight	11.86	<0.01
	5	**Previously browsed** + Feeding trial + Pre-trial weight	12.51	<0.01
	6	Null model	34.89	<0.01
Proportion of ramet browsed	1	Null model	0.00	0.41
	2	Feeding trial	2.28	0.13
	3	Pre-trial weight	2.28	0.13
	4	Previously browsed	2.28	0.13
	5	Number of bites per trial	2.29	0.13
	6	Feeding trial + Pre-trial weight	4.72	0.04
	7	Feeding trial + Number of bites per trial	4.73	0.04
	8	Previously browsed + Feeding trial + Pre-trial weight + Number of bites per trial	10.19	<0.01

of feeding trials (Spearman's rank correlation; $r = 0.25$, $p = 0.17$). Willow ramets weighed, on average, 721.8 g (SD = 224.3, range = [386.0, 1164.4]) before and 573.2 g (SD = 180.7, range = [301.6, 921.8]) after feeding trials. The proportion of the ramet eaten by weight, across feeding trials varied from 12.6% to 32.2% (mean = 20.6% of total ramet biomass). During most feeding bouts (n = 146), only one moose calf browsed the ramet, but in some bouts, ramets were browsed by two (n = 54) or three (n = 11) moose calves either concurrently or sequentially. An average of 3.4 bites (range = [1, 8]) were taken by moose in each bout of feeding. The average bite diameter was 5.03 mm (SD = 1.35, range = [1.10, 9.70]; Fig. 3).

The feeding trial, proportion of the ramet eaten, and whether the ramet had been browsed (yes/no) in previous years were significantly associated with the diameter of bites (Fig. 4, Tab. 2). Bite diameters were larger when a greater proportion of the ramet had been eaten ($\beta = 3.22$, robust SE = 0.93, degrees of freedom (df) = 715, $p < 0.01$), on ramets that had been browsed in previous years ($\beta = 0.64$, robust SE = 0.20, df = 715, $p < 0.01$) and in earlier feeding trials ($\beta = -0.01$, robust SE < 0.01, df = 715, $p = 0.03$) (Tab. 2). There was no statistically significant relationship between bite diameters and the feeding bout ($\beta = 0.03$), robust SE = 0.02, df = 715, $p = 0.11$) or pre-trial weight ($\beta = 0.00$, robust SE < 0.01, df = 715, $p = 0.60$) (Tab. 2). None of the variables included in the model were significantly associated with the proportion of each ramet eaten (previous browsing: $\beta = 0.13$, robust SE = 0.17, $p = 0.44$; pre-trial weight: $\beta = 0.00$, robust SE = 0.00, $p = 0.51$; order of feeding trial: $\beta = 0.00$, robust SE = 0.01, $p = 0.83$; number of bites: $\beta = 0.01$, robust SE = 0.01, $p = 0.29$) (Tab. 2).

DISCUSSION

Our findings provide empirical support for various components of optimal patch use theory at the scale of individual bites, illustrating nuanced foraging behaviour in moose calves browsing on shoots of individual and sequentially presented willow ramets. Initial bites from newly presented ramets tended to be of smaller diameter, and as feeding progressed, calves consumed increasingly larger shoots. This pattern suggests selective exploitation of more digestible browse early in a feeding trial, followed by tolerance of larger and presumably less desirable and less nutritious shoot materials (Wilson and Kerley, 2003) as the optimal components were depleted (McNamara, 1982) similar to results reported for white-tailed deer and moose (Shipley & Spalinger, 1995; Jia *et al*., 1997).

Regarding the size of individual bites taken, this foraging strategy is particularly critical for calves, whose smaller mouths may impose anatomical limitations compared to adult moose (Spaeth *et al*., 2001). Calves are likely to be under greater pressure to select thinner, more digestible twigs to meet nutritional needs efficiently (Shipley, 2007). Consequently, patterns elucidated here suggest it may be beneficial for cow moose with calves at heal to select feeding patches with higher densities of thinner shoots to improve their calves' access to the most nutritious and suitable browse to increase calf survival (Monestier *et al*., 2015).

The tendency for calves to take larger bites from the 20% of our ramets that had been browsed in previous years agrees with the findings of others (Danell & Huss-Danell, 1985; Bowyer & Bowyer, 1997; Shipley *et al*. 1998; Bowyer & Neville, 2003) and may also support optimal patch use theory. The influence of prior browsing on bite size may simply reflect the consequences of plant compensation (i.e., the absence of smaller shoots being available to the calves) or may be a response by calves targeting larger, but highly nutritious shoots, that were produced by plants in response to previous browsing events (Danell & Huss-Danell, 1985; Rea & Gillingham, 2001), all of which may help calves increase browse intake per bite when the patch (ramet) is revisited (Possingham & Houston, 1990).

These dynamics underscore how herbivore interactions can shape patterns of resource use at fine spatial scales and how plant response to previous browsing can

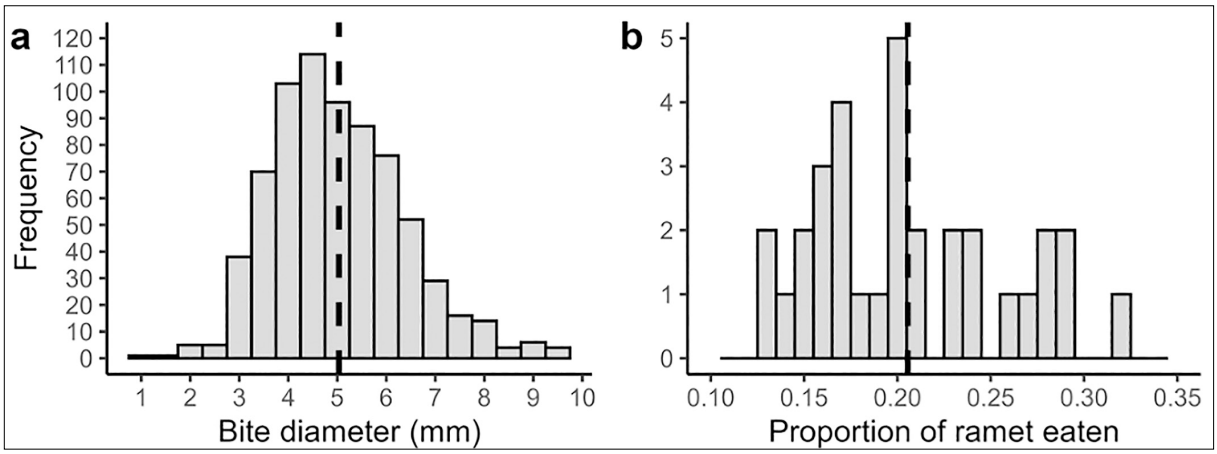


Fig. 3 - Distribution of the diameter (mm) of bites taken (a) and proportion of eaten (b) by moose calves on willow shoots across feeding trials. The dashed line represents the mean of the distributions. / Distribuzione del diametro (mm) dei bocconi prelevati (a) e della proporzione di germoglio consumata (b) dai giovani di alce sui germogli di salice nel corso delle prove di alimentazione. La linea tratteggiata rappresenta la media delle distribuzioni.

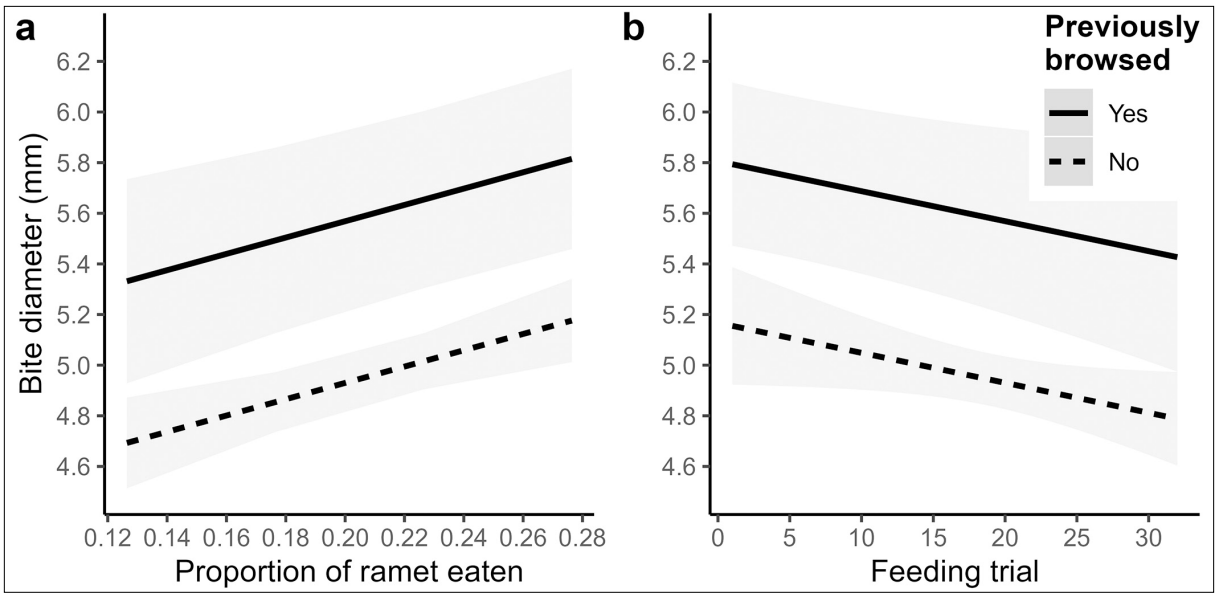


Fig. 4 - Diameter (mm) of bites taken by moose calves on ramets that had and had not been browsed in previous winters as a function of the proportion of the ramet eaten and the order of the feeding trial. The lines represent the relationship between bite diameter and proportion of the ramet eaten (a) or the feeding trial (b) as predicted by the average of the two most parsimonious linear models predicting bite diameters taken. The shaded area represents the 95% confidence interval (CI) of the predicted bite diameter. Solid lines and CIs represent ramets that had been browsed in previous years and dashed lines and CIs represent ramets that had not been previously browsed. / Diametro (mm) dei bocconi prelevati dai piccoli di alce su ramet che erano stati e non erano stati brucati negli inverni precedenti, in funzione della proporzione del ramet consumata e dell'ordine della prova di alimentazione. Le linee rappresentano la relazione tra il diametro dei bocconi e la proporzione del ramet consumata (a) oppure la prova di alimentazione (b), come previsto dalla media dei due modelli lineari più parsimoniosi utilizzati per stimare il diametro dei bocconi. L'area ombreggiata rappresenta l'intervallo di confidenza al 95% (CI) del diametro dei bocconi previsto. Le linee continue e gli intervalli di confidenza corrispondono ai ramet che erano stati brucati negli anni precedenti, mentre le linee tratteggiate e gli intervalli di confidenza corrispondono ai ramet che non erano stati precedentemente brucati.

influence animal-plant interactions (Skarpe & Hester, 2008; Mathisen *et al*., 2017). This may be especially important for twin calves, who may face heightened intra-pair competition for high-quality forage. In such cases, browsing of smaller-diameter forage by one twin could intensify resource limitation and force the other to adopt a less selective feeding strategy (Altman, 1958).

The average diameter of bites from shoots (~5mm) per ramet decreased with progressive feeding trials, indicating increasing selectivity over time. This may reflect decreasing hunger or interest in the shoots of offered ramets with progressive trials (Nyström, 1980) and thus reduced tolerance for less digestible shoots or a developing ability among calves to discriminate more effectively between shoot sizes. Calves displayed considerable plasticity in bite diameter, spanning nearly an order of magnitude (from 1-10mm) which was similar but somewhat larger than diameters taken by moose and reported by Andersen & Sæther (1992), Shipley *et al*. (1999), and Rea *et al*. (2015). Such variation may arise from individual differences in preference or feeding strategy between calves or the accidental intake of older shoot materials (or thinner shoot tips) into bites, but it could also indicate flexibility in response to ramet morphometry/chemistry and shoot availability.

These fine-scale observations – at the level of individual bites and ramets – build on prior work across coarser spatial scales (e.g., seasonal ranges, thickets, and whole plants; Cassing *et al*., 2006; Månsson *et al*., 2007; De Jager *et al*., 2009) and helps to improve our understanding of moose winter browsing, at least for hand-reared calves. By focusing on within-plant selection and bout-to-bout decision-making, our results reveal how moose calves respond (at an innate level without prior learning from a mother) not only to overall shoot availability but also to subtle features of forage structure that are often overlooked in broader-scale studies. In doing so, we highlight the relevance of optimal patch use theory across nested spatial hierarchies. For example, selection for thinner twigs may influence which ramets are preferred within a plant, which plants are favoured within a thicket, and which thickets are ultimately selected within a seasonal range. Recognizing this continuum – from individual bites to landscape-level decisions – is essential for understanding how herbivores like moose shape and are shaped by their environment at multiple ecological scales (Belovsky, 1986; Pastor *et al*., 1988; Shipley, 2010; Koetke *et al*., 2023; Johnson & Rea, 2024).

In contrast to bite diameter, the proportion of ramet browsed in each feeding trial was not influenced by the order of the ramet offered in the consecutive feeding trials or by browsing during previous years. The proportion of ramet browsed represents the aggregated result of multiple bites, which may have been confounded by which calf or calves browsed ramets, variation in ramet structure/geometry, shoot chemistry/morphometry, orientation, or

feeding position or the interactions of all these or other factors (Kielland & Osborne, 1998; De Jager *et al*., 2009; Pastor & De Jager, 2013). These factors can obscure subtle patterns of selectivity within ramets, whole plants, patches, or larger heterogeneous foraging environments (Searle *et al*., 2005) and should be further investigated. For example, willow ramets we trialed differed in branching and twig density, which can influence the proportion of the ramet that can be cropped by and is palatable for moose calves. As such, metrics based on moment-to-moment browsing behaviours, such as shoot placement on ramets and the diameter of each bite, may offer more nuanced and ecologically meaningful insights into foraging strategies at this scale.

Several limitations of this study should be acknowledged. The moose were hand-reared and observed under controlled feeding trial conditions, so these results may not fully reflect how moose of different age and sex classes might behave in the wild. As underscored by Nyström (1980), calves also lacked a role model and may have made different choices if they were imitating the browsing behaviours of their mothers. Markgren (1966), however, suggests that hand-reared, motherless moose calves showed 'fairly good agreement' with those of wild moose, implying food choice is probably innate.

All moose calves engaged in our trials were the same age and size and differences in the sex of moose does not appear to influence bite size (Spaeth *et al*., 2004). Only four individual calves were included in our trials, however, and the individual identities of the calves browsing and in which order were not recorded, which may reduce the generalizability of our findings. Finally, although we used robust standard errors, some residual autocorrelation may remain among ramets in the bite diameter analysis. Thus, effect sizes should be interpreted cautiously, but the direction and consistency of the patterns align with established ungulate foraging principles, and the controlled setting reduced environmental noise.

Our findings may have broader ecological implications beyond the trials themselves, since ungulate bite size directly affects estimates of intake rate, forage quality, and depletion dynamics (Trudell & White, 1981; Shipley *et al*., 1994; Wilson & Kerley, 2003; Kazimierski *et al*., 2016). Understanding these patterns at fine spatial scales may enable ecologists to undertake more informed modelling approaches to herbivore-plant interactions. Future studies of optimal patch use theory at the scale of bites within bouts should consider other plant species, chemical defences, and the nutritive value of bites taken, in addition to tracking the identity of each individual taking bites. How such findings may help to inform theories related to movements, reproductive success, and predator-prey dynamics across various spatial and temporal scales remains to be determined (Burkepile & Parker, 2017).

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