WILDLIFE BIOLOGY

Research article

Winter browsing by moose (*Alces alces*) in a forested mountainous landscape of west–central Sweden

Ella Hambeson[1], **Ewa H. Orlikowska**[2] **and Märtha Wallgren**[1,3]

[1]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden
[2]Karlstad University, Department of Environmental and Life Sciences, Biology, Karlstad, Sweden
[3]Forestry Research Institute of Sweden, Uppsala Science Park, Uppsala, Sweden

Correspondence: Ella Hambeson (eaha0008@stud.slu.se)

Wildlife Biology
2025: e01338
doi: 10.1002/wlb3.01338
Subject Editor: Nigel G. Yoccoz
Editor-in-Chief: Ilse Storch
Accepted 13 February 2025

Browsing ecology involving ungulates and their food resource is complex as consumption may reflect responses to various factors, such as quantity and quality of browse species. This study investigated winter browsing by moose *Alces alces* in a mountainous landscape of west–central Sweden, characterized by Norway spruce *Picea abies* production forests with high inclusion of deciduous species. Field data on tree species abundances as well as fresh and previous browsing were collected along moose tracks and control transects, to answer our questions regarding browse selection in relation to availability. The data were analyzed using mainly modelling (generalized linear mixed models) approaches. The results revealed greater amounts of available food trees (< 5 m) in young compared to older forests and along moose tracks compared to control transects. Downy birch *Betula pubescens* was the most abundant independent of forest age class and transect type (i.e. tracks versus controls). Quantitatively, the key winter browse in the study area was a mix of deciduous species, primarily downy birch and willows (*Salix* spp.) complemented by Eurasian aspen *Populus tremula* and grey alder *Alnus incana*. In young forest, aspen, rowan *Sorbus aucuparia* and willows were the most selected species, while common juniper *Juniperus communis* was the least selected. In older forest, alder was most selected, followed by willows and rowan, while aspen and downy birch were the least selected, except for spruce and lodgepole pine *Pinus contorta*. According to Jacobs selectivity index, downy birch, was underused while aspen, rowan and willows were overused in relation to their frequencies. The latter are often limited in today's cultivated forest landscape and thus an increased amount of those species may be utilized to a higher degree by moose than an increase of downy birch. No effect from snow depth was detected and browsing on dwarf shrubs was not observed.

Keywords: boreal, cervids, deciduous, downy birch, dwarf shrubs, Fennoscandia, forage selectivity, foraging, GLMM, Jacobs selectivity index, snow depth, ungulate

NORDIC SOCIETY OIKOS

www.wildlifebiology.org

© 2025 The Author(s). Wildlife Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Browsing ecology is complex and governed by many interacting variables. Herbivore consumption is limited by the availability and quality of vegetation and several studies show a connection between the consumption of plant species and their proportional availability (Morow 1979, Hörnberg 2001, Palo et al. 2015, Bergqvist et al. 2018). In northern and high-altitude ecosystems, strong seasonality impacts wild herbivores through long-duration snow cover, which limits access to browse and restricts movements (Dussault et al. 2005, Lundmark and Ball 2008). Also, limited food availability due to short growing season and low primary production may in turn affect nutritional outcomes, such as calf weights (Paulsen et al. 2000, Ericsson et al. 2002). Browsing can impact the conservation of biologically important deciduous species more notably in areas at high latitudes due to slow vegetation establishment and growth (Moen et al. 2006). Understanding browsing patterns of wild herbivores may therefore increase the possibilities of adapting methods in forestry, agriculture and nature conservation to reduce negative impacts on browse resources and facilitate balance in ecosystems (Reimoser and Gossow 1996, Reimoser and Putman 2011, D'Aprile et al. 2020).

Moose *Alces alces* is a generalist herbivore, but with a strong selective feeding strategy (Wam and Hjeljord 2010). According to a review by Bergström and Hjeljord (1987) covering 43 different studies on moose browsing in Europe, the most important winter browse species are Scots pine *Pinus sylvestris* (hereafter pine), willows (*Salix* spp.), birches (*Betula* spp.), common juniper *Juniperus communis* (hereafter juniper), rowan *Sorbus aucuparia* and Eurasian aspen *Populus tremula* (hereafter aspen). The deciduous species seem to be common also in the summer diet, with significant additions from dwarf shrubs (*Vaccinium* spp.) in the field layer (Spitzer 2019). Norway spruce *Picea abies* (hereafter spruce) is a low-selected species which is browsed to a very limited extent by moose regardless of the season (Bergström and Hjeljord 1987). In all, it seems beneficial for moose to eat a varied diet, demonstrated by Felton et al. (2020) showing positive correlation between higher calf weights and individuals with a varied diet including numerous deciduous trees, compared to a unilateral diet dominated by single or few conifer species. Content of plant toxins is another factor stimulating a varied diet in moose in order to avoid excessively high levels of the same type of toxic substances (Freeland and Janzen 1974, Miquelle and Jordan 1979). However, studies of moose populations in areas of high latitude and altitude in Norway have reported moose winter diets primarily consisting of birches or willows (Sæther et al. 1996), indicating adaptability to a uniform diet when available browse is limited.

In Sweden, moose has a high cultural and symbolic value and the country is estimated to have one of the densest moose populations in the world (Wallgren 2023), in the order of 200 000 individuals after the hunting season of 2023/2024 (Widemo and Leonardsson 2024). The production forests in Sweden are subject to intense forestry focusing on conifers with a relatively low proportion of deciduous trees (Mikusiński et al. 2003), but large local differences occur and young forests are often rich in deciduous trees (Bergqvist et al. 2018).

Most studies of moose browsing in Sweden have been conducted in production forest landscapes within the boreal or boreonemoral zones and preferably in young pine stands (Edenius 1991, Shipley et al. 1998, Wallgren et al. 2013, Nichols et al. 2015, Bergqvist et al. 2018). The present study was carried out on snow-covered ground in mountainous terrain dominated by spruce production forest. We targeted movement patterns and winter browsing choices of individual moose in forests of two age classes: young (average height of dominant tree layer < 6 m) and older (average height of dominant tree layer > 6 m). Specifically, we studied differences in food tree (height < 5 m) distribution along moose tracks compared to random control transects in mountainous forest stands. We investigated utilization and relative selection of tree species in relation to availability and forest age class. Our main questions were: 1) How are food trees distributed between forest age classes in a mountainous forest area of Sweden? 2) What is the difference in food tree utilization between young and older forests? 3) How do browsing moose select between food tree species? and 4) How do forest age class and snow depth affect browsing on dwarf shrubs?

Methods

Study area

The study was carried out in the vicinity of Ottsjö village in Jämtland county of west–central Sweden (Fig. 1), at 500–650 m a.s.l. The climate in the mountainous region of Jämtland is cold temperate (continental subarctic climate zone; Arnfield 2023), but because of the closeness to the North Atlantic winters are generally mild with extensive precipitation (SMHI 2023a). The annual mean temperature was 2.3°C in 2022 and 1.8°C for the period 1991–2020 (SMHI 2022a), while the total annual precipitation was 865 mm in 2022 and the average total for the period 1991–2020 was 815 mm (SMHI 2022b). In January, when most of the data collection took place, the average temperature of the area is −5.9°C and the average precipitation 44.6 mm (data for normal period 1991–2020) (SMHI 2023b). The average number of days with snow cover is 205 per year (for the period 1904–2013) (Wren 2015).

Data were collected in production forests of two age classes: young and older, defined by the stand-forming tree layer being lower respectively higher than 6 m. This delineation was based on results in Bergqvist et al. (2018): young forest up to ca 6 m generally have the largest amount of browse within moose feeding height, which according to Nichols et al. (2015) extends up to a maximum of 3 m. In forests with tree heights exceeding 6 m the amount of available browse decreases rapidly (Bergqvist et al. 2018).

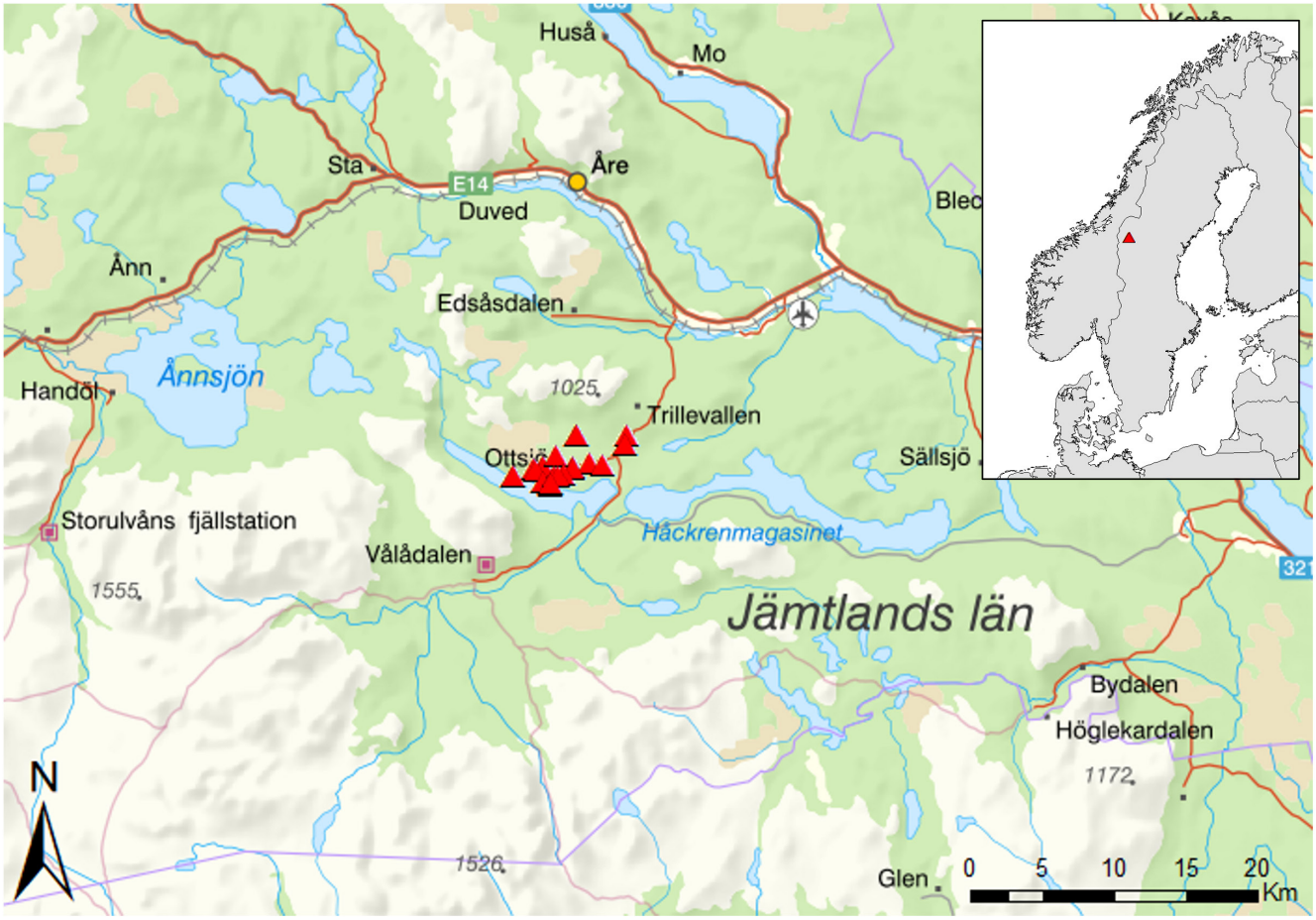


Figure 1. Map of study area in Jämtland county of west–central Sweden, in forested terrain proximate to the Scandinavian Mountain chain. Red triangles show the placement of the surveyed transects.

Jämtland has a low proportion of deciduous trees in a national context within Sweden (Mikusiński et al. 2003), with 3.8% of deciduous forest (% of productive forest area) and 8.4% of mixed conifer–deciduous forest (SLU 2019). The surveyed stands are located in mountainous terrain dominated by spruce forests and mixed conifer–deciduous forests (SEPA 2022). The predominating ground vegetation types in the area are rich-herb and low-herb with bilberry *Vaccinium myrtillus* (SLU 2021), and the main soil type is till, occasionally overtopped by thin layers of clay and silt (SGU 2023). The main land use is silviculture with even-aged stands in a rotational forest management system. According to figures from the County Administrative Board of Jämtland (2021), moose density in the area in 2021 was estimated to 0.91 moose per km^2. All surveyed forest stands were owned by non-industrial private landowners.

In western Jämtland competition between moose and other cervids is limited to roe deer *Capreolus capreolus*, which reaches comparatively modest density in the area, and reindeer *Rangifer tarandus*, which generally do not use trees as food during the winter other than for eating tree lichens (Danell et al. 1994), although some studies have shown presence of birch in reindeer winter diet (Mathiesen et al. 2000). Large predators present in the area are brown bear *Ursus arctos*, wolverine *Gulo gulo* and lynx *Lynx lynx*. Grey wolf *Canis lupus* may occasionally pass through, but territorial establishment is prohibited as the study area is within a region used for traditional reindeer husbandry with free ranging reindeer.

Data collection

Data collection took place between 7 January and 5 February 2023. It was done by locating and following fresh moose tracks (hereafter tracks) in the snow, as well as randomly placed control transects in the same forest stands. Only one track and one control transect were surveyed per forest stand and hence all replicates came from different stands. The age of the tracks was estimated by the appearance in relation to past days weather. Number of tracks was limited and any fresh track was located either by daily drives by car along the main road leading to the village of Ottsjö, or along trails or offroad on foot or by skis. Tracks crossing the travelled line were inspected for freshness and the first stretch qualifying

for survey was selected. The basic criterion for suitable tracks included at least 50 m of individual track from a single moose, which turned out to be challenging as several moose often seemed to walk together (likely a cow with a calf) or use the tracks of other moose. Furthermore, because the study targeted browsing and not traveling by moose, a minimum number of trees with fresh browsing along a 50 m stretch was set to 4. The minimum distance to the closest road of any section of the track or control transects had to be at least 10 m for small roads with low traffic (< 250 cars per day) and at least 50 m for major roads with more frequent traffic (> 400 cars per day) (Swedish Transport Administration 2016). The first stretch of 50 m moose track fulfilling the above-mentioned criteria was surveyed.

Track and control transect surveying was carried out by foot. The tracks were followed in the opposite direction of the moose travel in order to avoid disturbing an individual moose remaining in the area. The track length was measured with a 25 m rope following the movement pattern of the moose. For the control transects the rope was laid out perpendicular to the track, first establishing a 25 m buffer distance to the track (in order to avoid direct interference of the chosen path of the moose). A 50 m standard length of data collection was applied to both moose tracks and control transects, except in dense stands where collection ended at 25 m if more than 50 trees had been registered at that point. Nevertheless, the entire 50 m track or transect was always inspected, visually verifying that the first 25 m were representative for the whole stretch in terms of tree abundance and species composition. The sampling length was treated as a covariate for dense or sparse forest in the subsequent analyses.

The trees surveyed were those reaching at least 0.3 m above the snow and growing within 1.5 m, i.e. 'browsing distance', of either side of the track or control transect. In cases where trees had branches hanging within browsing distance these were included in the survey sample even if the stem center was located outside. Tree height was estimated to the nearest 0.5 m up to heights of 5 m and thereon noted as > 5 m.

Along the tracks all trees were recorded as being freshly browsed (presumably by the moose whose track was followed) or not. Furthermore, the number of freshly browsed shoots was counted for all tree species and the proportion of freshly browsed shoots of the total amount available was estimated for each tree to the nearest 5%, calculated by dividing the number of freshly browsed shoots with the estimated total amount of shoots available. No estimate of total amount of shoots was recorded for trees that were not freshly browsed. Previous browsing, i.e. any non-fresh (i.e. dried and greyed) bite surfaces, was recorded as present or not (i.e. 1/0). Previous browsing was recorded along tracks and control transects, whereas fresh browsing was only applicable along the tracks. Snow depth was measured at 3–5 representative points along both tracks and control transects and an average depth assigned for the whole unit. The percentage of exposed (not snow-covered) dwarf shrubs in the track ground area (i.e. 50 × 3 m) was also estimated and any browsing on dwarf shrubs recorded as present or not (i.e. 1/0).

Statistical analyses

The statistical analyses were performed using SAS 9.4 (SAS Institute Inc. 2016) and specifically generalized linear mixed models (GLMMs, using PROC GLIMMIX). GLMMs are suitable for analyses of blocked designs and a range of responses, e.g. count, binary and proportional. The responses tested were applicable on either of two spatial scales: transect (including both moose tracks and control transects) or individual tree. The variables moose track (versus control), young forest (versus older forest), tree species and presence of previous browsing were treated as fixed effects. Transect length was used as a proxy for forests of two density classes: dense (i.e. 25 m transects) and sparse (i.e. 50 m transects) and also applied as a fixed effect in GLMMs of transect responses (such as total number of trees). This was done to improve the model fit, but the effect of forest density class on the response variables was not interpreted further, as it was not part of the aim. For individual tree data we used transect identity as random variable. The details for setups of all GLMMs are presented in Supporting information. Post hoc testing was performed with Tukey–Kramer test for multiple comparisons.

Trees ≥ 5 m can be considered the limit for when essentially no significant contribution of shoots is offered within browsing height (approximately < 3 m) and side-shoot browsing is likely of marginal importance for the tree. However, because these trees take up space and may compete with smaller trees their frequencies and distributions are still of interest but must be separated from smaller trees, which are relevant for assessing browse selection and utilization parameters. The total number of trees ≥ 5 m per transect, depending on young or older forest and moose track or control, was tested with GLMM.

To test whether there was a difference in number of trees < 5 m, snow depth and browsing variables between moose tracks and controls in young versus older forests GLMMs were done separately for each of the response variables. Tests of differences in browsing history on individual tree level between moose tracks and controls in young versus older forests were conducted. Finally, differences in browsing variables on tree scale between young versus older forests or depending on tree species or browsing history were also tested with GLMMs.

Jacobs selectivity index E (Jacobs 1974) was calculated for each tree species and data pooled for all moose tracks:

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

where r_i represents the proportion of use (i.e. fresh browsing, binary measure) of tree species i and p_i its proportion of the total availability of trees. E varies between 1 (overuse) and –1 (underuse), with 0 reflecting exact proportional use. A positive value signals that a species is selected for in the diet, whereas a negative value can mean that it is either avoided or utilized less than proportional to its availability.

Results

General

A total of 16 moose tracks and 8 control transects were surveyed, evenly distributed between the two forest age classes based on heights: young (< 6 m) and older (≥ 6 m) forests. In addition, two tracks in older forests, but none in young forest, were discarded in advance based on the criterion of < 4 trees with fresh browsing within 50 m. This means that the overall fresh browsing in older forest within our study area was somewhat lower than presented by our results. Our methodology resulted in seven 25 m and one 50 m moose track samples in young forests and two respectively six in older forests. Corresponding numbers for the control transects were two 25 m and two 50 m in young forest and three respectively one in older forest. All test statistics are given in Table 1–7.

All tree species encountered were included, resulting in a total of 1920 tree individuals representing 9 species or species groups: pine, spruce, downy birch *Betula pubescens*, aspen, rowan, willows (of the genus *Salix*, in the study area species such as *Salix caprea* and *Salix pentandra*), grey alder *Alnus incana* (hereafter alder), juniper and lodgepole pine *Pinus contorta* (hereafter contorta).

Trees ≥ 5 m summed to 236 individuals, or 12% of all trees surveyed. The number of trees ≥ 5 m was significantly larger in older compared to young forest, but there was no difference between moose tracks and controls nor any interaction effect (Table 1). All trees ≥ 5 m were excluded from further analyses as they were considered to not affect moose browsing routes within forest age class. Remaining were 1684 trees < 5 m, also referred to as food trees when excluding spruce. The most common food tree species along both moose tracks and controls and irrespective of forest age class was downy birch and the least common was pine (Table 2).

Food tree distribution

There were significantly more food trees in young forest compared to older forest, and along moose tracks compared to controls (Table 3). Quantitatively, there was double density (2.4 compared to 1.2 ind. m^{-1} of moose track/control transect) of food trees in young forest compared to older forest, but a smaller difference between moose tracks and control (1.8 to 1.5 ind. m^{-1}). The interaction effects showed slightly different results as moose tracks in older forest tended to encounter more food trees than controls, while the opposite was true in young forest (Table 3). Interestingly, there was no significant difference in the number of forage trees along moose tracks depending on forest age class.

Downy birch and willows were more abundant in young forest compared to older forest (1.4 versus 0.7 ind. m^{-1} for downy birch and 0.3 versus 0.2 ind. m^{-1} for willows) and there was more downy birch along moose tracks compared with controls (1.2 versus 0.8 ind. m^{-1}, Table 3). There was also a significant interaction effect for both downy birch and willows in older forest with higher abundances along moose tracks than controls and the opposite for willows in young forest. Juniper and spruce were less abundant in younger forest (juniper: 0.1 versus 0.2, spruce: 0.3 versus 0.2 ind. m^{-1}) and along moose tracks than the alternatives (juniper: 0.1 versus 0.2, spruce: 0.4 versus 0.2 ind. m^{-1}). For the remaining species (alder, aspen, contorta, pine and rowan) the tests showed non-convergence of data. Furthermore, food trees along moose tracks in young forest were significantly higher than those along controls in young forest (average heights 1.3 versus 1.1 m).

Food tree utilization – previous and fresh browsing

The number of previously browsed food trees showed higher frequencies in young forest and along moose tracks than the alternatives (Table 4). There were also significant interactions for the amount of previously browsed forage trees: more along moose tracks than controls in older forest, but opposite for young forest. There were significant differences in browsing properties along moose tracks depending on forest age class (Table 4). Moose tracks in young forest had a higher number of trees with fresh browsing compared to those in older forest (0.7 versus 0.3 ind. m^{-1}). However, there was no corresponding difference in proportions of food trees being browsed. Nevertheless, both the number and proportion of shoots with fresh browsing were significantly higher in young forest compared to older forest.

A total of 24% of all food trees, 21% if considering all species including spruce (for which no fresh browsing was observed), along the moose tracks were freshly browsed to some extent. The number of trees with fresh browsing, pooled across tracks and forest age classes, was dominated by downy birch, followed by aspen and willows, while pine comprised the smallest fraction of freshly browsed trees (Table 5). In total 90% of all freshly browsed trees had visible signs of previous browsing. The species-specific rebrowsing rate was highest in aspen and willows (98%) and lowest in pine (33%), excluding spruce and contorta (0%). There was a significant positive relationship between fresh browsing and previous browsing for all food trees pooled, as well as for downy birch (Table 4).

Table 1. Test results of GLMMs fitted to the number of trees ≥ 5 m along the transects for young versus older forest and moose tracks versus controls in a mountainous landscape of Jämtland, west–central Sweden. ns = non significant.

Dependent variable (scale)	Independent variable	df	F	p-value	Direction of effect
Number of trees ≥ 5 m total, all species (transect)	Young forest	16	76.10	< 0.001	Negative
	Moose track	16	3.22	ns	–
	Young forest × Moose track	16	0.02	ns	–
	Dense forest	16	0.82	ns	–

Table 2. Average species composition (i.e. proportions) of trees (< 5 m heigh) along moose tracks and control transects in a mountainous landscape of Jämtland, west–central Sweden. Mean proportions are given with standard error, minimum and maximum and sample size (= n). NA = Not applicable.

Transect	Moose track						Control					
Forest	Young forest (8)			Older forest (8)			Young forest (4)			Older forest (4)		
age (n)	Mean (SE)	Min; max	n	Mean (SE)	Min; max	n	Mean (SE)	Min; max	n	Mean (SE)	Min; max	n
Alder	0.07 (0.03)	0; 0.54	44	0.05 (0.04)	0; 0.36	12	0 (NA)	NA	0	0 (NA)	NA	0
Aspen	0.09 (0.02)	0; 0.44	62	0.04 (0.02)	0; 0.31	33	0 (NA)	NA	0	0 (NA)	NA	0
Contorta	0.04 (0.01)	0; 0.24	35	0 (NA)	NA	0	0.11 (0.02)	0; 0.26	56	0 (NA)	NA	0
Downy birch	0.58 (0.01)	0.17; 0.85	385	0.5 (0.01)	0.24; 0.84	276	0.52 (0.01)	0.35; 0.74	156	0.36 (0.03)	0.03; 0.62	74
Juniper	0.02 (0.01)	0; 0.06	10	0.13 (0.01)	0; 0.27	55	0.05 (0.01)	0.03; 0.10	16	0.16 (0.03)	0; 0.39	30
Pine	0.01 (0.01)	0; 0.08	6	0.01 (0.01)	0; 0.03	2	0 (NA)	NA	0	0,00 (0.01)	0; 0.02	1
Rowan	0.03 (0.01)	0; 0.08	21	0.01 (0.01)	0; 0.06	3	0.06 (0.02)	0; 0.17	11	0 (NA)	NA	0
Spruce	0.10 (0.01)	0.01; 0.17	57	0.13 (0.01)	0.05; 0.29	59	0.1 (0.01)	0.05; 0.18	28	0.44 (0.04)	0.14; 0.97	73
Willows	0.05 (0.03)	0;0.38	25	0.14 (0.02)	0; 0.47	70	0.15 (0.02)	0; 0.31	77	0.03 (0.03)	0; 0.14	7

Selection of food trees

Freshly browsed individuals in relation to the availability of the respective species showed that willows, aspen and rowan were the most selected species in young forest, while alder was the most selected species in older forest (Table 5). In this comparison, fresh browsing was treated as a binary variable and no weight was given to the amount of browsing per tree. However, the proportion of browsed shoots differed significantly depending on tree species, such that willows (on average 10% of the shoots) and rowan (18%) were more browsed than juniper (2%) and downy birch (2%), and rowan was also more browsed than alder (4%) and aspen (8%, Table 6).

Jacobs selectivity indices (Fig. 2) revealed that moose selected for alder, aspen, willows, rowan and pine in the diet, while downy birch and juniper were underused in relation to availability. Contorta and spruce did not display any fresh browsing and were not included in the calculations of Jacobs selectivity indices.

Snow depth and browsing on dwarf shrubs

Snow depth varied between 0.1–0.5 m between transects and showed no significant difference between transect or forest age class (Table 7). Exposed (i.e. not covered by snow) dwarf shrubs were observed on < 1% of the total surveyed track area and there was no sign of digging for or browsing on them along any of the surveyed tracks. No test was conducted due to absence of data.

Discussion

General

The lack of difference in number of trees ≥ 5 m between moose tracks and control transects suggests that moose are either indifferent to the big trees as these do not provide relevant amounts of food, or that there is simply low variation within forest age classes in terms of trees ≥ 5 m. The study area is intensively managed for rotational forestry and low variation in stem densities of larger trees (i.e. after precommercial and commercial thinning operations) is a desired overall characteristic.

Food tree distribution

Comparison of total number of food trees, i.e. trees < 5 m excluding spruce, along moose tracks versus control transects suggests that moose actively seek out paths with high number of food trees. As the amount of food trees in older forests is generally low, it may suggest that the best strategy for moose is to select sites providing comparatively high quantity while browsing there. In young forests on the other hand, showing the opposite trend in our study, the amount of food trees may be sufficient to instead select for quality, i.e. certain tree species or a balanced intake (c.f. Felton et al. 2020). Furthermore, older forests may provide advantages in

Table 3. Test results of GLMM fitted to the number and heights of trees < 5 m along the transects for young versus older forest and moose tracks versus controls in a mountainous landscape of Jämtland, west–central Sweden. ns = non significant.

Dependent variable (scale)	Independent variable	df	F	p-value	Direction of effect
Number of trees < 5 m					
Total food trees, (i.e. all trees excluding spruce) (transect)	Young forest	1	85.22	< 0.001	Positive
	Moose track	1	28.04	< 0.001	Positive
	Young forest × Moose track	1	56.88	< 0.001	0 × 0 < 0 × 1 1 × 0 > 1 × 1
	Dense forest	1	23.00	< 0.001	0 × 1 = 1 × 1 Positive
Downy birch (transect)	Young forest	1	39.93	< 0.001	Positive
	Moose track	1	30.79	< 0.001	Positive
	Young forest × Moose track	1	20.07	< 0.001	0 × 0 < 0 × 1
	Dense forest	1	27.47	< 0.001	Positive
Juniper (transect)	Young forest	1	18.39	< 0.001	Negative
	Moose track	1	7.88	< 0.05	Negative
	Young forest × Moose track	1	0.38	ns	–
	Dense forest	1	13.45	< 0.01	Negative
Spruce (transect)	Young forest	1	13.79	< 0.01	Negative
	Moose track	1	8.48	< 0.01	Negative
	Young forest × Moose track	1	4.50	< 0.05	0 × 0 > 0 × 1
	Dense forest	1	2.97	ns	–
Willows (transect)	Young forest	1	9.86	< 0.01	Positive
	Moose track	1	0.26	ns	–
	Young forest × Moose track	1	44.67	< 0.001	0 × 0 < 0 × 1 0 × 1 > 1 × 1
	Dense forest	1	1.81	ns	1 × 0 > 1 × 1 –
Height of trees < 5 m excluding spruce (individual tree)	Young forest	1	1.07	ns	–
	Moose track	1	2.03	ns	–
	Young forest × Moose track	1	8.64	0.0033	1 × 0 < 1 × 1

Table 4. Test results of GLMM fitted to previously and freshly browsed food trees (< 5 m, not including contorta and spruce) along the transects for young versus older forest and moose tracks versus controls in a mountainous landscape of Jämtland, west–central Sweden. ns = non significant.

Dependent variable (scale)	Independent variable	df	F	p-value	Direction of effect
Number of trees < 5 m with previous browsing (transect)	Young forest	1	24.14	< 0.001	Positive
	Moose track	1	26.88	< 0.001	Positive
	Young forest × Moose track	1	62.23	< 0.001	0 × 0 < 0 × 1 0 × 1 > 1 × 1
	Dense forest	1	28.93	< 0.001	1 × 0 > 1 × 1 Positive
Number of trees < 5 m with fresh browsing (transect)	Young forest	1	10.43	< 0.05	Positive
	Dense forest	1	0.00	ns	–
Proportion of trees < 5 m with fresh browsing (transect)	Young forest	1	1.86	ns	–
	Dense forest	1	3.39	ns	–
Number of shoots with fresh browsing (transect)	Young forest	1	66.50	< 0.001	Positive
	Dense forest	1	6.02	< 0.05	Positive
Proportion of shoots with fresh browsing (transect)	Young forest	1	5.86	< 0.05	Positive
	Dense forest	1	3.09	ns	–
Fresh browsing (individual tree)	Previous browsing	1	75.17	< 0.001	Positive
Fresh browsing per species	Previous browsing per species				
Alder	Alder	1	0.13	ns	–
Aspen	Aspen	1	0.25	ns	–
Downy birch	Downy birch	1	8.58	< 0.01	Positive
Juniper	Juniper	1	3.70	ns	–
Pine	Pine	1	0.51	ns	–
Rowan	Rowan	1	1.10	ns	–
Willows (individual tree)	Willows	1	0.14	ns	–

Table 5. Proportion of trees < 5 m with fresh browsing along moose tracks in two types of forests in a mountainous landscape of Jämtland, west–central Sweden. NA = not applicable.

	Proportion freshly browsed trees of total freshly browsed		Proportion freshly browsed trees of available		Proportion rebrowsed of freshly browsed (%)
	Young (%)	Older (%)	Young (%)	Older (%)	
Alder	11	10	39	75	92
Aspen	26	4	66	12	98
Contorta	0	NA	0	NA	NA
Downy birch	43	35	18	12	83
Juniper	1	14	10	24	86
Pine	2	0	50	0	33
Rowan	7	1	52	33	92
Spruce	0	0	0	0	NA
Willows	11	36	68	47	98
Total	100	100	24	18	90

addition to the browse provided, e.g. more vegetative shelter and lower snow accumulation in winter which facilitates movement. Bjørneraas et al. (2011) found that young forest stands in Norway provided higher amounts of selected browse species compared to older stands, but also noted an increase in selection for older forest stands in winter compared to the rest of the year, suggesting less snow accumulation and rich cover of dwarf shrubs in older forests to be the main reasons. Aspen and alder were the species that showed the strongest connection to moose tracks, as they were exclusively recorded there. Somewhat unexpectedly, a high abundance of downy birch seemed to consistently attract moose despite that it was the overall most common food tree in the area, which emphasizes the importance of high quantity food resources for moose in winter. Willows on the other hand did not display the same pattern although it is known as a highly selected food tree (Shipley et al. 1998, Månsson et al. 2007). In fact, willows were under-represented along moose tracks in young forest, which seems like a rare observation. However, in this study willows were not identified to species and perhaps differences in palatability and species composition underlies this unusual result. Juniper and spruce were quite common but avoided by browsing moose. Underrepresentation of spruce was particularly pronounced for moose tracks in older forest, possibly because there were less food trees overall and browsing in older forests required higher selectivity in terms of site.

As there were more trees to choose from in young forest compared to older forest moose appear to select paths with taller trees, which provide larger shoot biomass (Scholten 2023).

Food tree utilization – previous and fresh browsing

Previous browsing is a strong factor connected to present moose food utilization. The fact that moose revisited previously browsed transects and trees in this system is in line with several previous studies of moose feeding patterns (Bergström 1983, Wallgren et al. 2013, Mathisen et al. 2017). Previous research has demonstrated rebrowsing for young pine forests (Wallgren et al. 2013), but our findings extend this understanding, indicating that moose selection of feeding sites is driven by analogous mechanisms in forests of completely different tree species composition: a strong dominance of spruce and downy birch. Also, a noteworthy finding is that rebrowsing was more common along moose tracks in older forest than young forest, probably indicating that fewer food trees in older forest further increases the likelihood of rebrowsing. There is higher quantitative utilization of food trees as well as number of shoots in young forests compared to older forests. However, the proportional use of food trees remains at the same level as in older forests, whereas the proportional use of shoots is higher in young forests, perhaps as an effect

Table 6. Test results of GLMMs. Browsing properties on individual freshly browsed food trees (< 5 m, not including contorta and spruce) along moose tracks in a mountainous landscape of Jämtland, west–central Sweden.

Dependent variable (scale)	Independent variable	df	F	p-value	Effect
Browsed proportion (% shoots browsed) (individual tree)	Species	6	6.95	< 0.001	See posthoc test*
*Posthoc (individual tree)	Willows > Alder Willows > Downy birch Willows > Juniper Rowan > Alder Rowan > Aspen Rowan > Downy birch Rowan > Juniper				

Table 7. Test results of GLMM fitted to snow depth and previous browsing along the transects for young versus older forest and moose tracks versus controls in a mountainous landscape of Jämtland, west–central Sweden. ns = non significant.

Dependent variable (scale)	Independent variable	df	F	p-value	Direction of effect
Snow depth (transect)	Young forest	1	0.06	ns	–
	Moose track	1	0.79	ns	–
	Young forest × Moose track	1	0.33	ns	–
	Dense forest	2	0.95	ns	–

of heavy browsing on highly selected species like alder and aspen which only occurred there.

Selection of food trees

The utilization level (in terms of proportion of individuals that are freshly browsed) of downy birch was found to be low compared to basically all other deciduous species and pine. This pattern aligns with a strategy of mixing diet based on uneven food occurrences (Felton et al. 2020), also in a system with high dominance of deciduous browse and low levels of pine, which is the bulk winter food of moose in pine dominated areas, counting for 39% of the productive forest area in Sweden (SLU 2019). Furthermore, as moose in our area selected for routes containing more downy birch when browsing in older forest but not in young forest, it might reflect feeding goals in young forest leaning towards more highly selected tree species occurring in larger quantities there (c.f. Hörnberg 2001).

Juniper was avoided even though it has been referred to as relatively high-ranked by moose (Bergström and Hjeljord 1987), although less so in a context with more highly selected food species like rowan, aspen and willows. Spruce was avoided, an expected result as it is essentially not a food species (although 2.8%, or 10 out of the 355 spruce trees carried signs of previous browsing).

Aspen, rowan, willows and alder were utilized in high proportions, patterns which have been shown repeatedly for the first three species and explained by their beneficial nutritional composition (Felton et al. 2021), but reports on the importance of alder for moose are scarce. Alder has previously been considered an avoided species (Bergström and Hjeljord 1987, Edenius 1991), and selection for alder has not been shown before to our knowledge. Shipley et al. (1998) found alder to be used in proportion to availability in northern coastal Sweden. Perhaps the low occurrence of alder in our study area makes it more attractive for moose. In fact, Jacobs selectivity index indicated similar selectivity for alder as for aspen, rowan and willows. The index takes into account the availability of each species among all individuals of all species and just marginally downgrades alder relative to aspen, rowan and willows.

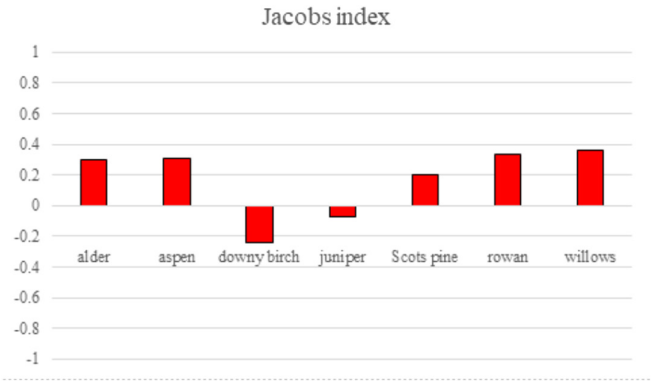


Figure 2. Jacobs selectivity indices, indicating moose browsing selection per tree species in a mountainous landscape of Jämtland, west–central Sweden. Data includes incidence of fresh browsing (binary variable) and is pooled for all moose tracks. Lodgepole pine and Norway spruce are excluded as no fresh browsing was observed on these species (their Jacobs selectivity indices were –1, signaling total avoidance).

According to Jacobs selectivity index pine was also selected for by browsing moose in the area. Pine is a main food source of moose in Sweden in winter (Shipley et al. 1998) and there are documented positive health effects from pine consumption due to its ample biomass (Fohringer et al. 2021). Pine is obviously palatable and in the light of moose striving to achieve a mixed diet, pine could be expected to be highly selected for by moose in areas where pine is sparsely distributed. In support of that, 50% of the available pines in young forest were indeed freshly browsed by moose, to be compared to e.g. 52% of available rowans.

The most intense browsing in terms of percentage of shoots browsed on individual trees was found for willows and rowan. While rowan had about twice the percentage of shoots browsed compared to willows, the absolute number of shoots browsed on rowan was instead only half of that on willows. This puts rowan forward as more selected for in the diet of moose, but willows probably being the most quantitatively important browse among the highly selected tree species.

Apart from spruce, contorta was the only tree species without signs of fresh browsing along the moose tracks. Nevertheless 35%, or 33 of the 93 contortas found carried signs of previous browsing. Other studies indicate that contorta is utilized as a food resource by moose in Sweden (Sjöberg and Danell 2001). The lack of fresh browsing on contorta in this study could be explained by the presence of other more highly selected food species, e.g. alder along one of the two contorta dominated moose tracks.

Snow depth and browsing on dwarf shrubs

Movement strategies are central for browsing efficiency over the seasons, though most research done is of large-scale patterns of migration (Andersen 1991, Borowik et al. 2020). No effect was noted from variation in snow depth within the

study area, likely due to the limited variation in combination with low maximum depth (50 cm) not affecting the energy expenditure of moose other than marginally. Other studies have shown restrictions in movement at depths of 30–40 cm (Melin et al. 2023) and 76 cm (Prescott 1968), as well as for migration behavior (Lundmark and Ball 2008) and home-range size at long durations of snow > 70 cm deep (Sweanor and Sandegren 1989).

The importance of dwarf shrubs as food for moose and other deer species has been increasingly emphasized in research literature over the past half-decade (Felton et al. 2020, Spitzer et al. 2021). Still, neither exposed field layer nor browsing on dwarf shrubs was found along any of the moose tracks, despite thin snow cover and signs of digging in the snow from roe deer and reindeer in the surroundings. However, this observation agrees with results from several studies compiled by Bergström and Hjeljord (1987) where moose did not feed from the field layer at snow depth of 30 cm or more. This may represent a trade-off where the energy expenditure required does not justify its use if alternative food is available elsewhere.

Conclusions

The novelty of this study, compared to most previous studies of moose winter browsing in Sweden, is the low presence of Scots pine. Instead, the bulk winter browse resource in the area is a mix of deciduous tree species, such as downy birch and willows complemented by aspen and alder. Nevertheless, some patterns similar to those expressed in young pine forests are revealed. Moose seem to balance quality with quantity, choosing a variation of browse species with different nutritional values when available, while also utilizing significant amounts of the most common species, in this case downy birch. Moreover, rebrowsing of previously browsed trees is high, both at transect and individual tree scales, in line with what has been documented numerous times for pine.

These consistent patterns imply how browsing behavior may be expressed in forests with different tree compositions. Given that the diets of large wild herbivores may interfere with human interests like forestry, understanding these dynamics may be valuable for mitigating negative browsing effects, such as browsing damage to pine. For example, it may suggest that the most important effort is not to create huge quantities of common alternative browse (often birch) but instead focus on adapting forestry methods to favor highly selected browse species that are limited in todays cultivated forest landscape, e.g. aspen, rowan and willows. A higher diversity of deciduous species has also shown positive relationships with several ecosystem services like bilberry production (Gamfeldt et al. 2013), which in turn offers another alternative food resource for moose. However, browsing ecology is complex with various factors affecting animals across both temporal and spatial scales. Further understanding of the key variables driving moose browsing behavior would be of importance in the attempts to mitigate negative effects from human activities on moose habitat. In addition, many more studies are needed to get a better idea of the utilization of dwarf shrubs year-round in areas where the ground is covered by snow in the winter.

Acknowledgements – We thank Olivia Teghararian, Alicia Ström and Johan Watz for providing constructive comments on early drafts of the manuscript and the private forest owners in Ottsjö area for being supportive towards the study. We thank the journal editor and an anonymous reviewer for careful reading and commenting on the manuscript. The field study was financed by Skogforsk (the Forestry Research Institute of Sweden).
Funding – The field study was financed by Skogforsk (the Forestry Research Institute of Sweden).

Author contributions

Ella Hambeson: Conceptualization (supporting); Investigation (lead); Writing - original draft (equal); Writing - review and editing (equal). **Ewa H. Orlikowska**: Conceptualization (supporting); Supervision (supporting); Writing - original draft (supporting). **Märtha Wallgren**: Conceptualization (lead); Formal analysis (lead); Supervision (lead); Writing - original draft (equal); Writing - review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01338.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5mkkwh7dz (Hambeson et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Andersen, R. 1991. Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. – J. Appl. Ecol. 28: 102–108.

Arnfield, J. 2023. Koppen climate classification. – https://www.britannica.com/science/Koppen-climate-classification.

Bergqvist, G., Wallgren, M., Jernelid, H. and Bergström, R. 2018. Forage availability and moose winter browsing in forest landscapes. – For. Ecol. Manage. 419–420: 170–178.

Bergström, R. 1983. Rebrowsing on birch (*Betula pendula* and *B. pubescens*) stems by moose. – Alces J. Devoted Biol. Manage. Moose 19: 3–13.

Bergström, R. and Hjeljord, O. 1987. Moose and vegetation interactions in northwestern Europe and Poland. – Swed. Wildl. Res. 1: 213–228.
Bjørneraas, K., Solberg, E. J., Herfindal, I., Moorter, B. V., Rolandsen, C. M., Tremblay, J.-P., Skarpe, C., Sæther, B.-E., Eriksen, R. and Astrup, R. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. – Wildl. Biol. 17: 44–54.
Borowik, T., Ratkiewicz, M., Maślanko, W., Duda, N. and Kowalczyk, R. 2020. The level of habitat patchiness influences movement strategy of moose in eastern Poland. – PLoS One 15: e0230521.
County Administrative Board of Jämtland 2021. Management plan for moose. – Älgskötselplan Vällistefjällets Älgskötselområde 2022–2024.
D'Aprile, D., Vacchiano, G., Meloni, F., Garbarino, M., Motta, R., Ducoli, V. and Partel, P. 2020. Effects of twenty years of ungulate browsing on forest regeneration at Paneveggio Reserve, Italy. – Forests 11: 612.
Danell, K., Mikael Utsi, P., Thomas Palo, R. and Eriksson, O. 1994. Food plant selection by reindeer during winter in relation to plant quality. – Ecography 17: 153–158.
Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L. and Jolicoeur, H. 2005. Linking moose habitat selection to limiting factors. – Ecography 28: 619–628.
Edenius, L. 1991. The effect of resource depletion on the feeding behaviour of a browser: winter foraging by moose on scots pine. – J. Appl. Ecol. 28: 318–328.
Ericsson, G., Ball, J. P. and Danell, K. 2002. Body mass of moose calves along an altitudinal gradient. – J. Wildl. Manage. 66: 91–97.
Felton, A. M., Holmström, E., Malmsten, J., Felton, A., Cromsigt, J. P. G. M., Edenius, L., Ericsson, G., Widemo, F. and Wam, H. K. 2020. Varied diets, including broadleaved forage, are important for a large herbivore species inhabiting highly modified landscapes. – Sci. Rep. 10: 1904.
Felton, A. M., Wam, H. K., Felton, A., Simpson, S. J., Stolter, C., Hedwall, P.-O., Malmsten, J., Eriksson, T., Tigabo, M. and Raubenheimer, D. 2021. Macronutrient balancing in free-ranging populations of moose. – Ecol. Evol. 11: 11223–11240.
Fohringer, C., Dudka, I., Spitzer, R., Stenbacka, F., Rzhepishevska, O., Cromsigt, J. P. G. M., Gröbner, G., Ericsson, G. and Singh, N. J. 2021. Integrating omics to characterize eco-physiological adaptations: how moose diet and metabolism differ across biogeographic zones. – Ecol. Evol. 11: 3159–3183.
Freeland, W. J. and Janzen, D. H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. – Am. Nat. 108: 269–289.
Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J. and Bengtsson, J. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. – Nat. Commun. 4: 1340.
Hambeson, E., Orlikowska, E. H. and Wallgren, M. 2025. Data from: Winter browsing by moose (*Alces alces*) in a forested mountainous landscape of west-central Sweden. – Dryad Digital Repository, https://doi.org/10.5061/dryad.5mkkwh7dz.
Hörnberg, S. 2001. The relationship between moose (*Alces alces*) browsing utilisation and the occurrence of different forage species in Sweden. – For. Ecol. Manage. 149: 91–102, https://doi.org/10.1016/S0378-1127(00)00547-8.
Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. – Oecologia 14: 413–417.
Lundmark, C. and Ball, J. P. 2008. Living in snowy environments: quantifying the influence of snow on moose behavior. – Arct. Antarct. Alp. Res. 40: 111–118.
Månsson, J., Kalén, C., Kjellander, P., Andrén, H. and Smith, H. 2007. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. – Scand. J. For. Res. 22: 407–414.
Mathiesen, S. D., Haga, Ø. E., Kaino, T. and Tyler, N. J. C. 2000. Diet composition, rumen papillation and maintenance of carcass mass in female Norwegian reindeer (*Rangifer tarandus tarandus*) in winter. – J. Zool. 251: 129–138.
Mathisen, K. M., Milner, J. M. and Skarpe, C. 2017. Moose–tree interactions: rebrowsing is common across tree species. – B.M.C. Ecol. 17: 12.
Melin, M., Matala, J., Mehtätalo, L., Pusenius, J. and Packalen, T. 2023. The effect of snow depth on movement rates of GPS-collared moose. – Eur. J. Wildl. Res. 69: 21.
Mikusiński, G., Angelstam, P. and Sporrong, U. 2003. Distribution of deciduous stands in villages located in coniferous forest landscapes in Sweden. – AMBIO J. Hum. Environ. 32: 520–526.
Miquelle, D. G. and Jordan, P. A. 1979. The importance of diversity in the diet of moose. – Alces J. Devoted Biol. Manage. Moose 15: 54–79.
Moen, J., Andersen, R. and Illius, A. 2006. Living in a seasonal environment. – In: Large herbivore ecology, ecosystem dynamics and conservation. Conservation biology. Cambridge Univ. Press, https://doi.org/10.1017/CBO9780511617461.
Morow, K. 1979. Competition between moose and red deer in the Augustow forest. – Alces J. Devoted Biol. Manage. Moose 15: 388–408.
Nichols, R. V., Cromsigt, J. P. G. M. and Spong, G. 2015. DNA left on browsed twigs uncovers bite-scale resource use patterns in European ungulates. – Oecologia 178: 275–284.
Palo, R. T., Öhmark, S. M. and Iason, G. R. 2015. Distribution of winter browsing by moose: evidence of long-term stability in northern Sweden. – Alces J. Devoted Biol. Manage. Moose 51: 35–43.
Paulsen, J., Weber, U. M. and Körner, Ch. 2000. Tree growth near treeline: abrupt or gradual reduction with altitude? – Arct. Antarct. Alp. Res. 32: 14–20.
Prescott, W. H. 1968. A study of winter concentration areas and food habits of moose in Nova Scotia. – MSc thesis, Acadia University, Canada.
Reimoser, F. and Gossow, H. 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. – For. Ecol. Manage. 88: 107–119.
Reimoser, F. and Putman, R. 2011. Impacts of wild ungulates on vegetation: costs and benefits. – In: Ungulate management in Europe: problems and practices. Cambridge: Cambridge Univ. Press, pp. 144–191. https://doi.org/10.1017/CBO9780511974137.007.
Saether, B.-E., Andersen, R., Hjeljord, O. and Heim, M. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. – Ecology 77: 1493–1500.
SAS Institute Inc. 2016. SAS® 9.4 Language Reference: Concepts, Sixth Edition. Cary, NC: SAS Institute Inc.
Scholten, J. 2023. Effects of moose browsing on natural regeneration of deciduous trees, forage availability and field layer vegetation. – MSc thesis, Swedish University of Agricultural Sciences, Sweden.

SEPA 2022. Nationella Marktäckedata 2018. – https://metadatakatalogen.naturvardsverket.se/metadatakatalogen/GetMetaDataById?id=8853721d-a466-4c01-afcc-9eae57b17b39.

SGU 2023. Soil types 1:25 000-1:100 000. – https://www.sgu.se/en/products/maps/map-viewer/jordkartvisare/soil-types-125-000-1100-000/.

Shipley, L. A., Blomquist, S. and Danell, K. 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. – Can. J. Zool. 76: 1722–1733.

Sjöberg, K. and Danell, K. 2001. Introduction of lodgepole pine in Sweden – ecological relevance for vertebrates. – For. Ecol. Manage. 141: 143–153.

SLU 2019. Skogsdata 2019 - Aktuella uppgifter om de svenska skogarna från SLU Riksskogstaxeringen. – Tema: Skogens struktur. – https://www.slu.se/globalassets/ew/org/centrb/rt/dokument/skogsdata/skogsdata_2019_webb.pdf.

SLU 2021. Kartor över dominerande markvegetationstyper i svensk skogsmark 1983–1987. – https://www.slu.se/institutioner/mark-miljo/miljoanalys/markinfo/standort/vegetation2/vegetation/.

SMHI 2022a. SMHI: året 2022 – Lufttemperatur. – Års-Och Månadsstat, https://www.smhi.se/pd/klimat/pdf_stats/year/SMHI_vov_temperature_22.pdf.

SMHI 2022b. SMHI: året 2022 – Nederbörd, solsken och strålning. – Års- och Månadsstat, https://www.smhi.se/pd/klimat/pdf_stats/year/SMHI_vov_precipitation_sunshine_22.pdf.

SMHI 2023a. SMHI: Jämtlands klimat. – https://www.smhi.se/kunskapsbanken/klimat/klimatet-i-sveriges-landskap/jamtlands-klimat-1.4996.

SMHI 2023b. SMHI: Dataserier med normalvärden för perioden 1991–2020. – https://www.smhi.se/data/meteorologi/dataserier-med-normalvarden-forperioden-1991-2020-1.167775.

Spitzer, R. 2019. Trophic resource use and partitioning in multispecies ungulate communities. – PhD thesis, Swedish University of Agricultural Sciences, Sweden.

Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N. J., Taberlet, P., Widemo, F. and Cromsigt, P. G. M. 2021. Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over *Vaccinium* shrubs in the field layer. – For. Ecol. Manage. 480: 118768.

Sweanor, P. Y. and Sandegren, F. 1989. Winter-range philopatry of seasonally migratory moose. – J. Appl. Ecol. 26: 25–33.

Swedish Transport Administration 2016. Vägtrafikflödeskartan. – https://vtf.trafikverket.se/SeTrafikinformation.

Wallgren, M. 2023. Sveriges älgstam fortfarande i topp. – https://www.skogforsk.se:443/kunskap/kunskapsbanken/2023/sveriges-algstam-fortfarande-i-topp/.

Wallgren, M., Bergström, R., Bergqvist, G. and Olsson, M. 2013. Spatial distribution of browsing and tree damage by moose in young pine forests, with implications for the forest industry. – For. Ecol. Manage. 305: 229–238.

Wam, H. K. and Hjeljord, O. 2010. Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. – Eur. J. Wildl. Res. 56: 745–755.

Widemo, F. and Leonardsson, K. 2024. Älgstammens utveckling och älgförvaltningen i siffror – årsrapport för jaktåret 2023/24. – https://www.naturvardsverket.se/4a4754/globalassets/algforvaltningen-i-siffror-prepublicering.pdf.

Wren, L. 2015. Snödjup i sverige 1904/05 – 2013/14. – Meteorologi, https://www.diva-portal.org/smash/get/diva2:948146/FULLTEXT01.pdf.