

Research Article

Habitat selection of moose in Sweden in managed boreal forests with *Pinus contorta* and *P. sylvestris*

Maria Bodlund, Fredrik Stenbacka, Fredrik Widemo, John P. Ball, Göran Ericsson and Wiebke Neumann  

Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

Correspondence: Wiebke Neumann (Wiebke.Neumann@slu.se)

Wildlife Biology

2026: e01662

doi: [10.1002/wlb3.01662](https://doi.org/10.1002/wlb3.01662)

Subject Editor: Pete Pekins

Editor-in-Chief: Ilse Storch

Accepted 3 March 2026



[Correction added on July 6, 2026 after first online publication: The first author's surname is updated from "Bolund" to "Bodlund" in the author byline.]

Human land use can take advantage of using exotic species to increase financial benefits. However, the use of exotic tree species might affect ecosystem functioning, potentially including the habitat use and movement behaviour of animals, modifying their ecological impact, and interactions with human land use. The native pine of Sweden is Scots pine *Pinus sylvestris*. In 1920, the Swedish forestry introduced the North American lodgepole pine *P. contorta* to Sweden to increase timber production. We used a two-year data set from GPS-collared adult moose *Alces alces* to examine the annual and seasonal habitat selection of this large keystone herbivore in a managed forest landscape with a relatively higher percentage of *P. contorta* compared to other Swedish boreal regions. Compared to other studies, a central departure point in this work was our focus on whether moose exhibited different selection between the native *P. sylvestris* stands and the exotic *P. contorta* stands.

We found no evidence that moose avoided stands of *P. contorta* within forest landscapes. Instead, our results show that young stands of both *P. sylvestris* and *P. contorta* were a highly preferred habitat for moose year-round, and that selection for *P. contorta* forests depended on the proportion of *P. contorta* at the landscape level and the season. Our work also reveals a diverse selection of forested habitats in almost all seasons, reflecting the differing needs of moose during different times of the year.

Despite being rare in our system, we suggest our findings can have important implications for forestry – *P. contorta* is often planted in the belief that these forests less likely to be browsed by moose than are native *P. sylvestris* forests. Our results do not indicate that the current distribution of different *P. contorta* stands has a limiting effect on how moose distribute across the landscape matrix.

Keywords: *Alces alces*, exotic tree species, forestry, step selection functions

Introduction

In many European countries, human land use largely defines the habitats wildlife can utilize. In such landscapes, wildlife interacts with humans and human interests, thereby



www.wildlifebiology.org

© 2026 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.

generating specific spatial socio-ecological combinations (Raudsepp et al. 2010, Turner et al. 2014, Neumann et al. 2022). Large herbivores (e.g. Cervidae) generate important services for humankind and ecosystem functions (Pascual-Rico et al. 2021, Pringle et al. 2023) and contribute to the global wildlife biomass to a considerable degree (Greenspoon et al. 2023), but also generate sizeable disservices (Gren et al. 2018, Linnell et al. 2020). Understanding cervid movements and how they utilize landscapes managed for different purposes can help in tailoring mitigation measures when human–herbivore conflicts arise (Apollonio et al. 2017). Within forestry, there is great interest in using tree species that increase economic benefits, and indeed tree species have been widely introduced beyond their native ranges to increase timber production (Castro-Díez et al. 2019). Although these introductions of exotic species can have positive economic outcomes, they can also have negative environmental effects and increase other ecosystem disservices.

In 1920 the North American lodgepole pine *Pinus contorta* was first introduced to Sweden (Elfving et al. 2001, Engelman et al. 2001) as a way to overcome a predicted timber shortage (Antonson and Jansson 2011). *P. contorta* was considered to have similar characteristics to the native Scots pine *P. sylvestris* but with greater growth, resistance to pests, and higher survival rates in the early stages, and is less attractive to browsing by moose *Alces alces* (Elfving et al. 2001, Antonson and Jansson 2011). Growth rates of *P. contorta* can surpass those of *P. sylvestris* by more than 1/3 under optimal conditions, which allows for shorter rotation cycles (Elfving et al. 2001, Antonson and Jansson 2011), thereby increasing the overall production of timber. Since 1960, Swedish forest owners have planted or sown *P. contorta* predominately in the northern parts of the country. In 2022, *P. contorta* accounted nationally for about 2% of all productive forest area with about 4% in southern Norrland (counties Gävleborg, Jämtland, and Västernorrland; most stands are currently at an age of 40–60 years; SLU 2022). Using *P. contorta* for timber production in Sweden, however, has not developed as hoped because trees did not grow as well as expected, many were infected by the fungus *Gremmeniella abietina*, and many were damaged as they were unable to withstand high winds and difficult snow conditions (Elfving et al. 2001, Antonson and Jansson 2011).

Compared to *P. sylvestris*, the amount of ground lichen in pine forests is lower in *P. contorta* stands (Horstkotte et al. 2023). Today, ground lichens – a key food item for semi-domesticated reindeer *Rangifer tarandus* in winter – are a decreasing resource in the Swedish managed forest landscape (Sandström et al. 2016), resulting in ongoing conflicts between forestry and reindeer husbandry by the indigenous Sami in northern Sweden (Roos et al. 2022). For environmental and political reasons, plus observed tree damage, the Swedish Forest Agency decided to limit the total annual area allowed for planting *P. contorta* annually, decreasing from 26 000 ha in 1980 to 14 000 ha today (Elfving et al. 2001, Antonson and Jansson 2011). Nevertheless, some forest companies have a great interest in planting *P. contorta* to meet

future timber and fibre demand, both for economic reasons and to meet the country's climate goals. Thus, there is a significant interest and continued need to understand the effect on wildlife of using *P. contorta* within forestry in Sweden.

Despite similarities, *P. contorta* and *P. sylvestris* differ in many characteristics, which leads to them providing different habitat features for forest-dwelling wildlife (Sjöberg and Danell 2001, Roberge and Stenbacka 2014, Horstkotte et al. 2023). For example, *P. contorta* has a denser canopy due to its thicker, lower, and longer branches as compared to *P. sylvestris*, altering the amount of light that can enter through the crown (Bäcklund et al. 2018), thereby altering the conditions for species in the field and ground layer. Furthermore, more needles on the trees result in more litter on the ground, which may also influence understorey species (Sjöberg and Danell 2001, Nilsson and Cory 2010, Bäcklund et al. 2018). *Pinus contorta* has also been found to exhibit higher mortality in older mature forest than *P. sylvestris*, which can generate more forest gaps, thus increasing light influx into the forest (Elfving et al. 2001). Overall, *P. contorta* forests are characterised by more dead, lying wood and fewer dwarf shrubs (*Vaccinium* spp.) (Roberge and Stenbacka 2014). In summary, these structural differences between the two types of pine forests may influence the habitat selection of forest-dwelling species as they affect animals' opportunities to forage and move, and their ability to find cover (Sjöberg and Danell 2001, Roberge and Stenbacka 2014, Horstkotte et al. 2023).

Access to forage and cover are central components of habitat selection by cervids and selection occurs at multiple spatio-temporal scales (Standen et al. 2025). The selective browsing of large herbivores such as cervids can generate strong ecological impacts, particularly in regenerating forests in managed landscapes like temperate and boreal forests (Côté et al. 2004, Stewart et al. 2006, Speed et al. 2013). Within the context of *P. contorta*, the different structural characteristics such as thicker, lower, and longer branches may influence the movement of large animals, in addition to altering forage and cover availability. For example, in semi-domesticated reindeer, habitat selection of *P. contorta* forest stands in winter compared to stands with native *P. sylvestris* is influenced both by proportion of *P. contorta* at the landscape scale and the height of the *P. contorta* stands (i.e. selection against *P. contorta* stands over 3 m tree height and older stands with a higher proportion of *P. contorta* (> 60%, Horstkotte et al. 2023). In contrast, reindeer did not avoid *P. contorta* stands shorter than 3 m tree height (i.e. young forest stands), suggesting that the younger trees had not yet affected ground lichen coverage and did not physically hinder reindeer movement before these forests have grown so dense (Horstkotte et al. 2023).

Moose are a key herbivore and an iconic species in the boreal forests in the Northern Hemisphere where they are an ecosystem engineer (Persson et al. 2005, Niedzialkowska et al. 2022). Moose are important game throughout northern Europe (Jensen et al. 2020) and create socio-economic and cultural value for humankind as well as being a major source of conflicts with forestry (Widemo et al. 2019, Johnson

and Rea 2024). In managed boreal forest landscapes, moose require mosaics of young and older stands to fulfil their daily needs for forage and (thermal) cover (Johnson and Rea 2024). In moose, habitat selection is shaped by multiple context-specific factors including (seasonal) food availability (Bjørneraas et al. 2011, Van Beest et al. 2012, Allen et al. 2016, Widén et al. 2025) and forest structure (Melin et al. 2014), as well as the structural arrangement of habitat patches within the surrounding forest landscape (Guidobaldi Stenbacka et al. 2025).

Animals select habitats and thus resources at multiple scales (Johnson 1980). Habitat preferences are dynamic and reflect context-dependent functional responses that are closely interlinked with animals' exposure and variation in habitat availability (Beyer et al. 2010, Holbrook et al. 2019). Moose show scale- and state-dependent selection, often choosing areas with abundant but low-quality forage at the landscape level while selecting high-quality forage or shelter from predators within their home range (Van Beest et al. 2010). Patch size and continuity further shape habitat selection, particularly when moving in a restricted behavioral state (often considered as an index for foraging and resting behaviour; Guidobaldi Stenbacka et al. 2025). Moose diets vary on a daily and seasonal basis to ensure nutritional balance, thereby benefitting from a foodscape with access to different food items (Felton et al. 2020, Spitzer et al. 2023, 2025). For Scandinavian moose, pine, dwarf shrubs *Vaccinium* spp., and different deciduous trees are staple food items with woody browse such as *P. sylvestris* being the main food in winter (Spitzer et al. 2023). Norway spruce *Picea abies* is generally avoided and very little consumed by moose in this system (Spitzer et al. 2025). Generally, habitat selection follows a seasonal pattern where habitats with higher food availability and quality are preferred and usually reduce the use of space by individual animals (Allen et al. 2016). In winter, moose select for young and mature coniferous forest, while the selection for mixed and deciduous forests as well as wetlands increases in spring (Allen et al. 2016). Findings on moose usage of *P. contorta* are ambiguous. While some previous studies found that moose browse little on *P. contorta* compared to *P. sylvestris* (Sjöberg and Danell 2001, Rea et al. 2014), others found similar browsing pressure on *P. contorta* and *P. sylvestris* (Niemela and Danell 1988, Ball and Dahlgren 2002), or an even higher susceptibility of *P. contorta* to bark stripping by moose (Niemela and Danell 1988). In its native North American range, *P. contorta* is usually little browsed by moose as moose commonly prefer to browse on different *Abies* spp., particularly Douglas fir *Pseudotsuga menziesii*, over all pine species (Hodder et al. 2013, Rea et al. 2014).

The structural differences found between *P. contorta* and *P. sylvestris* forests can affect the use of habitats by large mammals like cervids (e.g. reindeer, Horstakotte et al. 2023). For moose in Sweden, shifts in habitat selection due to the presence of *P. contorta* can have implications for both forestry and moose management, as animals may distribute differently within the managed forest landscape, which in turn can affect their browsing pressure a given forest stand may experience.

Telemetry data allow monitoring of animals 24/7 year-round, which enables us to quantify selection patterns on different spatiotemporal scales and estimate habitat importance within its landscape context. To fill the current knowledge gap of how moose respond to *P. contorta* and the possible ecological impact of this non-native tree species on the largest wild herbivore in Sweden, we studied habitat selection of adult GPS-collared moose roaming in forest landscapes including *P. contorta*.

Specifically, we addressed the following two research questions: 1) what does the seasonal habitat selection of moose look like in forest landscapes including *P. contorta*? and 2) does the seasonal selection for pine forests differ between *P. contorta* and *P. sylvestris*? Such knowledge is important for adding novel information to the ongoing debate on the benefits and disadvantages of using *P. contorta* within the Swedish rotation forestry, where quicker tree growth that shortens rotation times and lower browsing damage by moose are the dominant arguments for using *P. contorta* to try to increase timber production in forestry.

Material and methods

Study area

Our study area covered three counties (Västernorrland, Jämtland, and Västerbotten, i.e. southern Norrland) that harbour one of the highest proportions of *P. contorta* in Sweden (*P. contorta* accounts for 4% of the total standing volume; SLU 2022; Fig. 1). The productive forest land in this region is dominated by native Norway spruce and Scots pine, and together these two conifers account for 80% of the standing timber volume in the region (each species accounting for about 40%). Birch *Betula* spp. (10%) and other deciduous trees make up the rest of the standing timber volume (Roberge et al. 2024). This coniferous forest landscape is interspersed with mires. The average ambient temperature is -8°C in winter, 2°C in spring, 13°C in summer, and 2°C in autumn. Within the study area, winter typically arrives around 25 October, spring on 10 April, summer on 27 May, and autumn on 1 September (SMHI 2024). During most of the winter season, the study area is covered with snow to a depth of 50–100 cm (SMHI 2024).

Moose data

We captured adult moose near the village of Junsele in the municipality of Sollefteå in the county of Västernorrland in March 2022 and March 2023. Moose were immobilised from a helicopter with a pre-pressurized dart using a CO_2 -powered rifle (DANiNJECT) injecting a combination of 50 mg Xylazine (Xylased® 500 mg) and 4.45 mg Etorphine (Captivon® 98 Etorphine HCl, 9.8 mg ml^{-1}). Immobilisation was reversed using Naltrexone and Atipamezole (Kreeger and Arnemo 2007). Immobilisation and capture occurred during March while moose were in their winter range. The procedure to handle free-ranging wildlife is described in more detail by Græsli et al. (2020). We programmed the

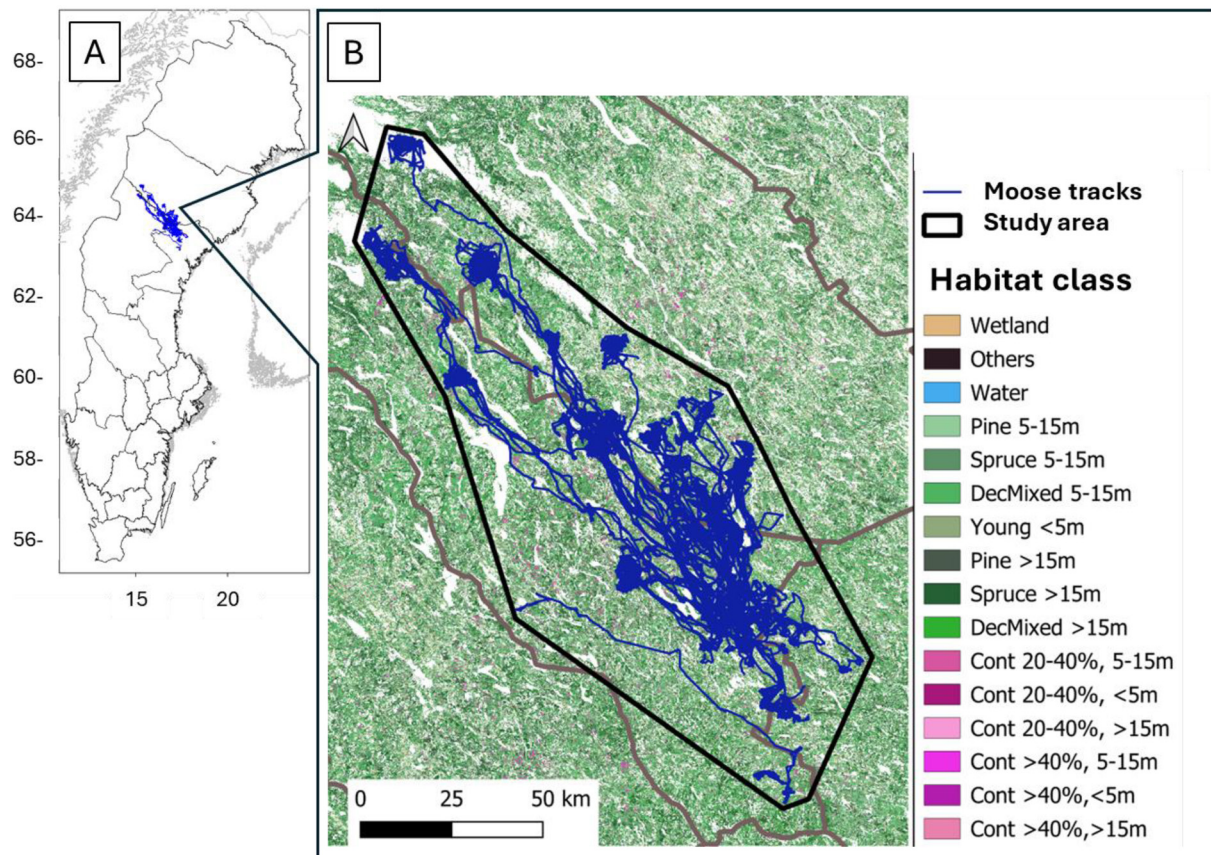


Figure 1. (A) Distribution of the movement tracks (in blue) of the studied adult moose in northern Sweden, 2022–2024, and (B) in relation to county borders (brown lines) and habitat classes, including share of contorta (pink coloured classes). Study area indicated as black-lined polygon.

GPS tracking devices (Vectronic Aerospace GmbH) to position fixation rate of 30–180 min intervals, depending on season (e.g. tighter intervals during the calving season for females), and data were stored and managed in the Wireless Remote Animal Monitoring (WRAM) database system for data security and management at the Swedish University of Agricultural Sciences (Dettki et al. 2014).

To apply the same time intervals over the annual cycle, we sub-sampled the data set to three-hour intervals. For the present study, we used position data collected between 1 April 2022 and 1 March 2024, including position data from a total of 29 different moose (21 females and 8 males), resulting in a total of 96 857 observations (an average of 2028 positions per moose $\pm$ 248). The number of moose that could be followed a given year differed, and in total our analysis included 60 moose-year combinations (year 2022: $n=20$, 2023: $n=24$, 2024: $n=16$).

Environmental variables

To classify and characterise different forest habitats and differentiate between stands dominated by the two *Pinus* species (*P. contorta* and *P. sylvestris*), we merged information given by four different maps: the National Land Cover map (NMD), the additional height cover map 0.5–5.0 m, the additional

height cover map 5.0–45.0 m, and the *P. contorta* proportion map (Table 1).

We started by re-classifying the land cover classes from the NMD map into five different habitat classes that were deemed biologically relevant for moose: ‘Pine’, ‘Spruce’, ‘Mixed Forest’, ‘Young < 5 m’ (forest with a tree height < 5 m regardless of stand composition), ‘Wetland’, and ‘Others’. The NMD map did not inform on tree species present in ‘Young < 5 m’ habitat class (even though in most cases they were probably mainly *P. sylvestris*), nor did it include specific information about *P. contorta* (Supporting information). We therefore used the map on volume timber stock (provided in the SLU tree species map) to define the habitats including *P. contorta* (Table 1). We spatially linked this map to our map on the six habitat classes. We classified stands with *P. contorta* as belonging to two proportion classes: ‘Contorta 20–40%’ and ‘Contorta > 40%’ (representing *P. contorta* proportion of 20–40% and > 40%, respectively). For this step, we restricted our grouping to forested habitats only (i.e. ‘Pine’, ‘Spruce’, ‘Deciduous’, ‘Mixed Forest’, or ‘Young < 5 m’). We based the threshold of the *P. contorta* proportion on a prior study on reindeer habitat selection that used the proportion 20–60% and > 60% (Horstkotte et al. 2023). Due to the lack of areas with a proportion of *P. contorta* stands with more than 60% in

Table 1. Information on the environmental data used for the habitat classification in this study. ¹Swedish EPA 2019. The maps represent official open-source national data that are produced through co-processing of different satellite and laser data, and other existing maps (Table 2; https://geodata.naturvardsverket.se/nedladdning/marktacke/NMD2018/NMD_Produktbeskrivning_NMD2018Basskikt.pdf [In Swedish]), https://geodata.naturvardsverket.se/nedladdning/marktacke/NMD2018/NMD2018_ProductDescription_ENG.pdf, <https://www.naturvardsverket.se/verktyg-och-tjanster/kartor-och-karttjanster/nationella-marktackedata/ladda-ner-nationella-marktackedata/>. ²The map is produced through co-processing of field data from the Swedish National Forest Inventory as well as aerial images and satellite images; <https://www.slu.se/en/environment/statistics-and-environmental-data/environmental-data-catalogue/slu-forest-map/>.

Map	Information	Year	Resolution	Coordinate system	Source
National land cover map	Different land cover types	2019	10 × 10, raster	SWEREF99 TM (EPSG:3006)	Swedish Environmental Protection Agency ¹
Contorta proportion	Percentage <i>P. contorta</i> of standing volume	2018	10 × 10, raster	SWEREF99 TM (EPSG:3006)	SLU Forest map ²
Additional layer object height 0.5–5.0 m	Height of vegetation objects under 5.0 m as an indication for shrubs	2019	10 × 10, raster	SWEREF99 TM (EPSG:3006)	Swedish Environmental Protection Agency ¹
Additional layer object height 5.0–45.0 m	Height of objects over 5.0 m as an indication for trees	2019	10 × 10, raster	SWEREF99 TM (EPSG:3006)	Swedish Environmental Protection Agency ¹

our study area, we decided on the threshold of 40%. We also incorporated the tree height of *P. contorta*, which has been identified as being important for reindeer (with a threshold of 3 m tree height; Horstkotte et al. 2023). Since we were also interested in differentiating between moose selection in relation to different tree heights, we further divided all forest habitats into three height classes: ‘less than 5 m (< 5 m)’, ‘5–15 m’, and ‘more than 15 m (> 15 m)’ using the height class maps and information from the NMD map (i.e. ‘Young < 5 m’). For the *P. contorta* habitats, we thus ended up with six different classes as given by the two proportion groups and the three height classes (Table 2). In the end, we had 15 habitat classes that we considered as being biological meaningful for moose (Table 2).

Statistical analyses

In our study system, seasonality affects moose foraging opportunities and thus habitat use (Allen et al. 2016, Spitzer et al. 2025). We therefore also examined seasonal variation in moose habitat selection. We divided our position data into four seasons (winter, spring, summer, and autumn), following mean timing of season arrival in a given region and year as given by official maps from the Swedish Meteorological and Hydrological Institute (SMHI 2024; Supporting information).

To test for both annual and seasonal selection of different forest habitats by moose in an area where *P. contorta* is relatively common, we applied step selection functions (SSF) (R package ‘amt’, Signer et al. 2019; www.r-project.org). The

Table 2. Classification and definition of the 15 habitat classes applied in this study to test for moose habitat selection of different forest types, Sweden 2022–2024. Percentage of each habitat class to the terrestrial area (excluding water) in the study area (black polygon in Fig. 1). In parentheses: habitat classes percentage in proximity to the moose as given by the random steps.

Habitats	Percentage	Definition
Pine 5–15 m	21.9 (6.8)	Minimum crown cover of 10%, crown cover of at least 70% of pine, tree height 5–15 m
Spruce 5–15 m	10.8 (1.2)	Minimum crown cover of 10%, crown cover of at least 70% of spruce, tree height 5–15 m
DecMixed 5–15 m	25.5 (6.8)	Minimum crown cover of 10% where coniferous crown cover can reach up to 70%, but deciduous crown cover can reach > 70%, tree height 5–15 m
Contorta 20–40% 5–15 m	2.9 (2.2)	Forestland with the proportion of 20–40% <i>P. contorta</i> , tree height 5–15 m
Contorta > 40% 5–15 m	0.5 (1.0)	Forestland with the proportion of > 40% <i>P. contorta</i> , tree height 5–15 m
Pine > 15 m	7.3 (14.7)	Minimum crown cover of 10%, crown cover of at least 70% of pine, tree height above 15 m
Spruce > 15 m	8.9 (8.7)	Minimum crown cover of 10%, crown cover of at least 70% of spruce, tree height above 15 m
DecMixed > 15 m	5.7 (9.4)	Minimum crown cover of 10% where coniferous crown cover can reach up to 70%, but deciduous crown cover can reach > 70%, tree height above 15 m
Contorta 20–40% > 15 m	0.03 (1.4)	Forestland with the proportion of 20–40% <i>P. contorta</i> , tree height above 15 m
Contorta > 40% > 15 m	0.001 (0.4)	Forestland with the proportion of > 40% <i>P. contorta</i> , tree height above 15 m
Young < 5 m	9.3 (34.6)	Temporary non-forest land with a tree height below 5 m that is expected to grow into a forest, e.g. clearcuts, fire-damaged forests, wind damaged forests
Contorta 20–40% < 5 m	0.1 (1.7)	Forestland with the proportion of 20–40% <i>P. contorta</i> , tree height below 5 m
Contorta > 40% < 5 m	0.005 (0.3)	Forestland with the proportion of > 40% <i>P. contorta</i> , tree height below 5 m
Wetlands	4.1 (7.1)	Open land where water for a large part of the year is close by, in or just above the ground surface
Others	3.4 (6.1)	Not forest related habitat: arable land, Inland/marine water, open land, roads and buildings

SSF compares a given observed step with a set of random steps to quantify animals' selection in relation to the reference habitat (in our case: *P. sylvestris* forest with a tree height of 5–15 m, hereafter 'Pine 5–15 m', which was the most common coniferous habitat, Table 2) and all habitat availability in the surrounding area (Thurfjell et al. 2014). We generated the random steps by fitting a parametric distribution of the observed steps' length and angle of rotation of the observed animal using the gamma distribution and von Mises distribution (Thurfjell et al. 2014, Signer et al. 2019). For each observed step, we created 10 random steps with a tolerance of 1 h (Thurfjell et al. 2014). We spatially linked the end of each step with our habitat map, thereby addressing animals' habitat selection (Signer et al. 2019). We applied a conditional logistic regression with a significance level of $\alpha < 0.05$ to test for the selection for or against a given habitat in relation to our reference habitat (which was 'Pine 5–15 m') and all other habitats. For the annual habitat selection, we used all data and for the seasonal selection, data belonging to a given season following positions' timestamp.

All data handling and processing including processing of maps and habitat classification was performed using the programming software R ver. 4.4.1 (www.r-project.org).

Results

Many of the GPS-collared moose migrated long distances so that their positions at different times in the annual cycle reached into the neighbouring provinces (Västerbotten and Jämtland; Fig. 1).

On an annual basis, moose selected all other forest habitats over 'Pine 5–15 m' forest stands, except the two *P. contorta* habitats above 15 m tree height, and in relation to the occurrence of these forested habitats in the landscape, animals selected against 'Wetlands' and 'Other areas' (Fig. 2). Notably, the three coniferous habitats with trees below 5 m were the three most selected ones compared to 'Pine 5–15 m' and all other habitats: 'Young < 5 m', 'Contorta 20–40% < 5 m', and 'Contorta > 40% < 5 m'. The forest habitats with a tree height 5–15 m (i.e. 'DecMixed 5–15 m', 'Contorta 20–40% 5–15 m', and 'Contorta > 40% 5–15 m') were similarly selected, and more than 'Spruce 5–15 m' or forests with trees above 15 m.

Moose varied their habitat selection with season, although some habitats were always selected (Fig. 3). For example, 'Young < 5 m' forests were always selected more than 'Pine 5–15 m' and were one of the most selected habitats through all seasons. On the other hand, moose always selected 'Wetlands' less than 'Pine 5–15 m' stands. Compared to other seasons, moose selected for only a few habitats other than 'Pine 5–15 m' in summer. In this season, animals focused on 'Young < 5 m', and the two *P. contorta* habitats with tree height 5–15 m, whereas they selected against 'Pine > 15 m' stands and 'Wetlands'. Moose selected for the remaining forest habitats similarly as for 'Pine 5–15 m' and to habitats' availability in the landscape. In autumn, the habitat selection

of moose became again increasingly diverse and more active as they included a selection of more habitats. In this season, animals selected all forest habitats more than 'Pine > 5 m' stands, except for 'Spruce 5–15 m' and 'Cont > 40% > 15 m'. In winter, forests below 5 m in tree height were the dominant habitats, but animals also selected for forests with trees greater than 15 m in height, 'DecMixed 5–15 m' and 'Contorta 20–40% 5–15 m'. Habitat selection in spring largely mirrored selection during winter.

Discussion

Using GPS-marked adult moose, we examined annual and seasonal habitat selection over two years in a managed forest landscape including *Pinus contorta*. A central departure point in this work was our focus on testing whether moose selected differently between the two pine forest types – *P. contorta* (exotic) and *P. sylvestris* (native). We have three main findings. First, within this landscape young forest stands were highly preferred habitats for moose year-round. Second, moose habitat selection was least diverse in summer where animals actively selected fewer forested habitats. Third, and most important, moose selected *P. contorta* forest stands, particularly the lower height classes, similarly to how they selected *P. sylvestris* stands in most seasons.

Throughout all seasons, the most selected habitat for moose was young forests ('Young < 5 m'), which underscores the relevance of young successional (coniferous) forests for this large browser all year, in accordance with previous research in this system (Guidobaldi Stenbacka et al. 2025). In other systems (e.g. North America), moose selection for young forests varied, depending for example on stand age (Johnson and Rea 2024). Such context-specific responses suggest that, in managed landscapes, forest practices (e.g. clear-cut sizes) are major drivers in shaping their attractiveness for large herbivores like moose. Within an extensively managed forest landscape like Sweden, forestry activity can lead to landscape heterogeneity, although individual forest stands are usually monoculture in terms of tree species and stand age. A mosaic of different forest types has been highlighted as central for fulfilling daily needs for moose in managed forest landscapes (e.g. access to forage, cover, and thermal shelter; Borowik et al. 2024, Johnson and Rea 2024, Widén et al. 2025). In our study area, moose select a broad set of different forest types in terms of tree height and composition. However, thus far, previous research provides little guidance on how planting exotic tree species like *P. contorta* may affect the resource availability and thus habitat selection of mobile browsers in this landscape matrix. For example, denser coniferous forest where less light enters the floor (such as *P. contorta*; Bäcklund et al. 2018) likely will provide a different field layer for browsers than more open coniferous forest stands, both in terms of composition and nutritional value (Felton et al. 2026). For example, *Vaccinium* ssp. show lower coverage in exotic *P. contorta* stands compared to stands of native Scots pine (Roberge and Stenbacka 2014).

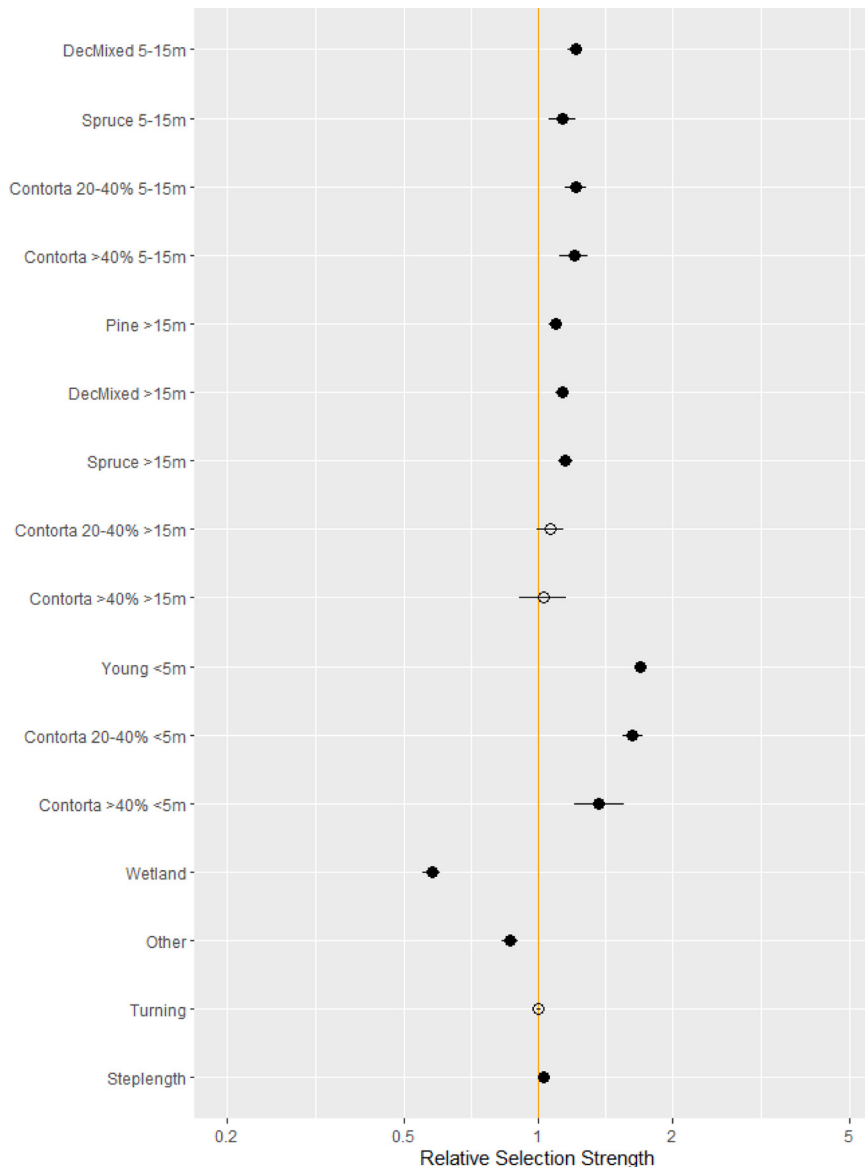


Figure 2. Estimates of the annual relative selection strength on habitat selection of adult moose *Alces alces* as given by a conditional logistic regression, Sweden 2022–2024. Stands of *Pinus sylvestris* with a tree height of 5–15 m and more (pine 5–15 m) was the reference habitat (orange line). Values larger than one indicate selection for a given habitat in relation to the reference habitat and in relation to habitats' availability, values smaller than one selection against a given habitat. The black horizontal bars represent the confidence intervals. If the confidence intervals do not cross the reference line, the selection is significantly different from the reference habitat.

In Sweden, dwarf shrubs are key forage for moose in Sweden, and improved calf weights as an index for population quality has been linked to shrub availability, suggesting a diverse diet to be important for moose (Felton et al. 2020, Spitzer et al. 2025). Moreover, browsing damage on pine may be indirectly linked to access to dwarf shrub (i.e. no shrubs available with snow depths beyond 30 cm; Pfeffer et al. 2021).

Our findings highlight that young forests are attractive habitats in all seasons, suggesting that these stands provide relevant resources year around for moose in our study area, as has also found in other areas in Sweden (Sand et al. 2021, Guidobaldi Stenbacka et al. 2025, Widén et al. 2025). Logging activities are going on continuously at landscape level

in Sweden (i.e. there are multiple clear-cuts every year within the home range of most moose; www.skogsstyrelsen.se). This makes young forests a somewhat heterogenous type of habitat for herbivores in terms of forage and cover – depending on the time since clear-cutting (i.e. tree height) and whether pre-commercial thinning has taken place or not (which greatly affects the amount of deciduous trees available in the stand). Stands with lower tree heights attract moose (e.g. 2–7 m; Melin et al. 2013). Non-thinned young forests can have large amounts of young successional deciduous trees (in our case birch *Betula* spp., aspen *Populus tremula*, rowan *Sorbus aucuparia*, and willows *Salix* spp.), which are all desirable food sources for moose all year around in Sweden (Spitzer et al.

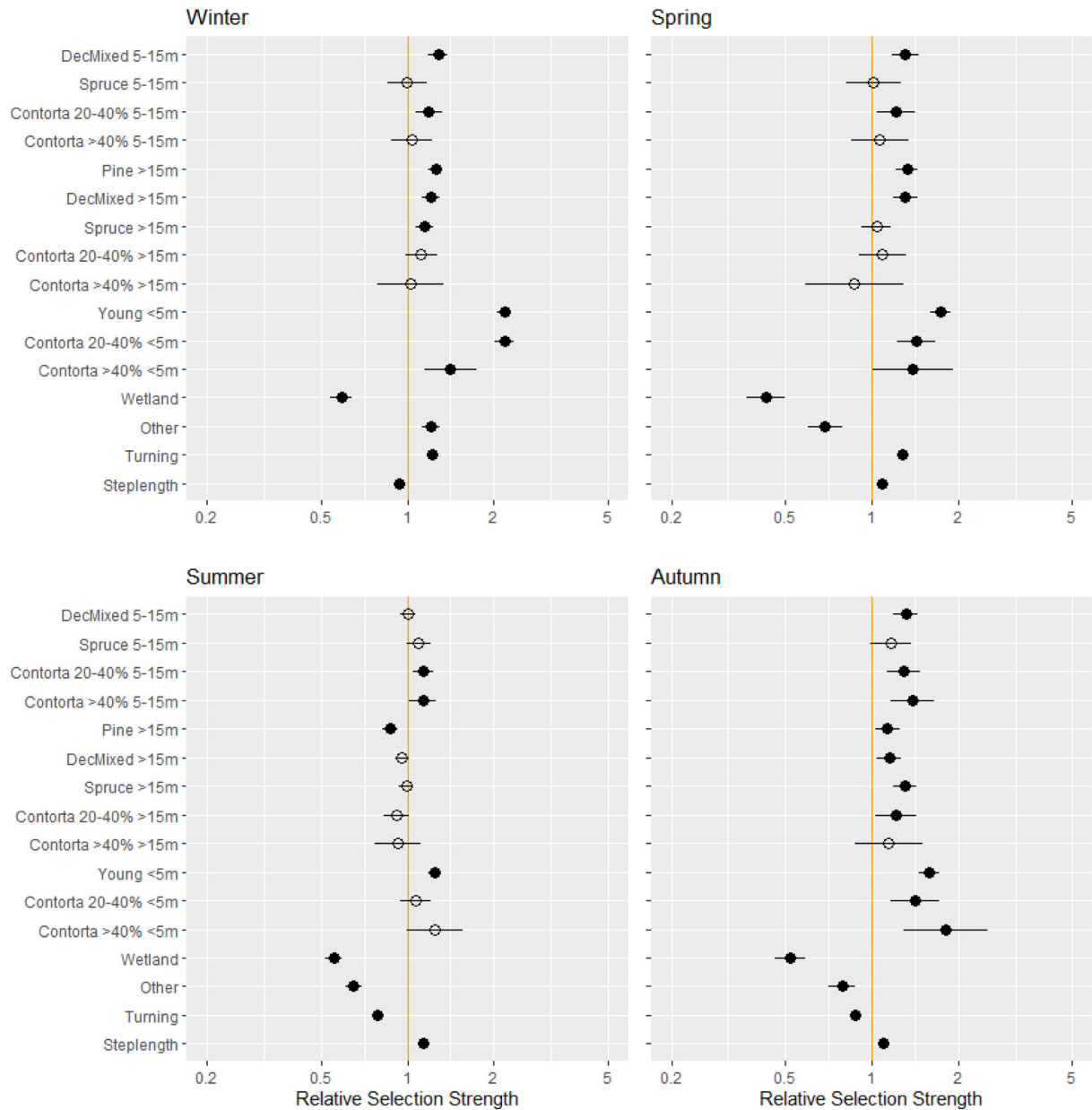


Figure 3. Estimates of the seasonal relative selection strength on habitat selection of adult moose *Alces alces* as given by a conditional logistic regression, Sweden 2022–2024. Stands of *Pinus sylvestris* with a tree height of 5–15 m and more (pine 5–15 m) was the reference habitat (orange line). Values larger than one indicate selection for a given habitat in relation to the reference habitat and in relation to habitats' availability, values smaller than one selection against a given habitat. The black horizontal bars represent the confidence intervals. If the confidence intervals do not cross the reference line, the selection is significantly different from the reference habitat.

2025). Yet, in winter, twig browsing on pine becomes usually more efficient for a larger browser like moose because a bite of pine contains much more biomass than one of birch, for example, which in most cases is the main alternative.

Unfortunately, at present there are no open, accessible, remotely sensed data on thinning status in forest stands at a national level (but for an attempt to estimate forage availability for cervids based on field and remotely sensed data, see Graf et al. 2025). Thus, we were unable to include this (potentially important) feature in our analysis to more directly test

whether the seasonal selection of 'Young < 5 m' correlated with the degree of deciduous forage. Within this context, it is important to note that thinned mature forests of *P. sylvestris* provide important forage for moose too (i.e. Ericaceae shrubs, Spitzer et al. 2021, 2025), except when covered by more than 30 cm of snow (Cederlund and Nyström 1981). Occurrence and the maturity level of Ericaceae shrubs, however, are heavily influenced by forestry actions, which in turn likely affect their attractiveness as foraging habitats for moose. For example, bilberry *Vaccinium myrtillus* abundance is positively

related to stand age (e.g. increases until stand age of about 125 years; Eldegard et al. 2019), is negatively affected by heavily closed tree cover because not enough sun reaches the field layer (Kardell and Eriksson 2011), and decreases with increasing forest volume (Hedwall et al. 2013). In Swedish forestry, a pre-commercial thinning is done to remove competing trees during the young forest stage and thus determine the future tree species composition of a given stand, and also defines the forage available for herbivores (Karlsson et al. 2010, Ara et al. 2022). In summary, within managed forest landscapes, forestry measures and practices largely determine the composition and structure of habitats with available food resources which moose can find on the landscape scale.

Our findings show a broad habitat selection, including different forested habitats, in all seasons except during summer, which contrasts with earlier research. Borowik et al. (2024) showed that moose in Poland strongly selected deciduous forests during summer and Nikula et al. (2004) describe a more varied habitat choice in summer than in winter for moose in Finland. The moose population in our study area had a high proportion of migratory individuals, where some animals migrated northwest to the belt of mountain birch forest along the mountain forest border, whereas others stayed below this border in the interior (Fig. 1). The lack of an active selection for deciduous and mixed forests in summer suggests that these forests still might be a common feature for most animals in their summer landscape, and they thus do not need to be specifically selected. Our findings underscore on one hand the importance of ‘different forests of both 5–15 m and > 15 m tree height’ (all forest types, except Contorta > 40%) as a winter habitat but also highlighted the general importance of coniferous forests with a tree height below 5 m (‘Young < 5 m’ and ‘Contorta 20–40% < 5 m’) during this season. Going beyond land cover and season only, Guidobaldi Stenbacka et al. (2025) showed how context-specific attributes can further shape the selection of forested habitats in moose (e.g. patch size and connectivity, behavioural state). These should be incorporated in further research on *P. contorta* and moose to deepen our understanding of animal response to forest stands, including exotic tree species, within their landscape context.

Moose in our study area were less likely to select wetlands than pine forests with a tree height of 5–15 m and all other forested habitats, regardless of season. This can indicate two things: first, wetlands might be such a common feature that they do not need to be specifically selected (4% in the study area but 7% in animals’ proximity – i.e. as indicated by the random steps – of all terrestrial surface excluding water (Table 2), nationally up to 22% of all terrestrial surface is wetland and open land, www.scb.se); and second, that pine forests with trees between 5 and 15 m might provide relatively more resources for moose than wetlands in our study area. Surprisingly, we did not find increased selection for forests with greater tree height during summer but a similar selection as for ‘Pine 5–15 m’. Unexpectedly, animals selected against ‘Pine > 15 m’ in summer. We do not have a good explanation for the observed selection pattern. These

forests covered 7% within the study area and almost 15% in animals’ proximity (Table 2), which does not suggest an availability extent that needs to be avoided. Forests with taller trees can provide important habitats during warmer times of the year (Felton et al. 2024), likely due to thermal refuge as concluded by studies of moose in other – even though warmer – regions further south (Van Beest et al. 2010, 2012, Borowik et al. 2020, Verzuh et al. 2023). Habitats with more shrubs also have been highlighted as important components to provide thermal shelter within managed forest landscapes (Widén et al. 2025), indicating that ‘Young < 5 m’ forests might not only provide forage, but can also act as thermal shelter.

Most importantly, comparing selection of *P. sylvestris* and *P. contorta*, we found that moose selected similarly (or even more) for *P. contorta* forests than for *P. sylvestris* forests – depending on the proportion of *P. contorta* and tree height. This is an interesting point, from both a conservation and a forestry perspective. Next to higher growth rates, lower susceptibility for browsing pressure by moose is a reason used to justify planting *P. contorta* in Sweden (Sjöberg and Danell 2001, Rea et al. 2014). A study evaluating species composition and browsing pressure along snow tracks of moose across different forest stands in a landscape with a higher share of *P. contorta* suggests low utilization of *P. contorta* by moose, both in terms of little *P. contorta* along moose tracks (compared to control sites) and lack of freshly browsed twigs, yet older signs of browsing did occur (35% *P. contorta* measured; Hambeson et al. 2025). Our findings point out that moose selected for young forests in our study area – regardless of whether they contained *P. sylvestris* or *P. contorta*. It is important to note that despite being more common than in other parts of Sweden, stands with *P. contorta* were still a rare habitat in our setting (Table 2).

Quantifying the selection of rare habitats can be challenging (Thurfjell et al. 2014, Northrup et al. 2022). Moose roam over large areas (Singh et al. 2012), with their home ranges covering multiple habitats (Allen et al. 2016). Thus, the relevance of rare habitats (here *P. contorta* stands) might be relatively low for moose, even though rare foraging species might be preferred within the given landscape matrix. For example, moose switch preference between silver birch *Betula pendula* and downy birch *Betula pubescens* depending on availability, where animals seem to select the less common species (Widemo et al. unpubl.). We did not assess browsing pressure or damage but focused on the habitat selection by individual moose, which does not inform on whether a given moose browsed on *P. contorta* or other food sources while in this habitat. Nevertheless, selection of a given habitat likely increases the probability that animals will utilize the resources available there.

Previous research show that browsing on *P. contorta* by moose can be like browsing on *P. sylvestris* (Ball and Dahlgren 2002), or even greater (e.g. bark stripping; Niemela and Danell (1988). Moreover, *P. contorta* is susceptible to bark stripping by red deer *Cervus elaphus* (Gill 1992), which have expanding populations northwards (Linnell et al. 2020). We

encourage future research to study the link between habitat usage and browsing pressure in these two pine forests – specifically by moose, but possibly also by other relevant herbivores. If moose browse preferably on *P. sylvestris*, forestry planting more *P. contorta* in areas with high winter moose browsing pressure can be beneficial as it reduces the number of trees lost due to browsing within such stands. However, it could also increase browsing pressure on remaining *P. sylvestris* stands close to these *P. contorta* stands. Moreover, in areas with more *P. contorta*, the forage landscape available for moose would be reduced, especially in winter, which in turn would hamper management goals to balance the moose population with their forage resources and damage to forestry (www.naturvardsverket.se). The composition of the nutritional landscape available for herbivores is increasingly discussed in terms of herbivore well-being (Youngentob et al. 2025).

In line with findings on reindeer (Horstkotte et al. 2023), our results do not suggest that forests with lower proportions of *P. contorta* represent ‘totally lost’ habitats, particularly not those with tree height lower than 5 m. In contrast to reindeer, however, our findings also suggest that older forests and those with a higher proportion of *P. contorta* are used by moose too. In winter, we found animals to select as much for young successional *P. contorta* (‘Contorta 20–40%, < 5 m’) as for *P. sylvestris* (‘Young < 5 m’), suggesting no major differences between these two forest types for moose during this time of the year in our study area. We want to acknowledge, however, in the present landscape matrix, that stands with *P. contorta* 20–40% < 5 m were only a small percentage of the availability of stands with *P. sylvestris* (‘Young < 5 m’). This may lower both their overall relevance and obstacles for moose. Yet different cervid species can respond differently to stands with exotic tree species. Horstkotte et al. (2023) pointed out that mature *P. contorta* may hamper the movement of reindeer in older stands with larger trees due to their denser growth, lower and larger branches, and more lying deadwood compared to corresponding *P. sylvestris* forests (Roberge and Stenbacka 2014). At present, there is no map that helps in estimating the amount of lying larger obstacles that might hamper movement of larger animals across forest stands. In our study, we did not find evidence that moose avoided *P. contorta* forests > 5 m, except those stands with trees > 15 m and a proportion of more than 40% of *P. contorta*. Our findings point instead in the opposite direction, as we found that animals partly selected *P. contorta* forests with trees 5–15 m in summer and autumn. At present, we do not know the underlying driver for the observed selection pattern and can only speculate. For example, the denser canopies of *P. contorta* forests > 5 m may provide better shade than *P. sylvestris* forests (Sjöberg and Danell 2001, Bäcklund et al. 2018), which might be attractive for a large-bodied herbivore like moose that have been found to select for denser forests during warm or sunny days (van Beest et al. 2012, Widén et al. 2025). Here, future researchers targeting the relevance of forest structure for moose, including exotic species, might be able to provide additional insights (Melin et al. 2014).

No study is without its limitations, of course. Even though our study area had relatively more *P. contorta* than many other areas of Sweden, *P. contorta* is still a relatively uncommon tree species at the landscape scale compared to *P. sylvestris* or *Picea abies* (SLU 2022), and in general the use of uncommon habitats is challenging to estimate (Northrup et al. 2022). Also, the present Swedish land cover map does not distinguish between young forests dominated by *Pinus sylvestris* and *Picea abies*, thereby limiting the possibility to formally test for difference among different types of young forest in relation to *Pinus contorta*.

Conclusion

Our work shows that young successional forests, of both *P. sylvestris* and *P. contorta*, are habitats selected by moose all year round in our study area. We also found varied habitat selection during most seasons, suggesting multiple needs during different times of the year, including diet, cover, and shelter. Next to faster growth, one major argument for the forest industry to plant more *P. contorta* is the anticipation that these stands are less susceptible to browsing by moose than are those of *P. sylvestris*. However, we did not find any evidence that moose avoided forest stands of *P. contorta* but, surprisingly, the opposite. This can have implications for forestry in cases where *P. contorta* has been planted in the belief that moose are utilizing these forests less. We recommend future research to investigate the link between selection patterns and browsing pressure on *P. sylvestris* and *P. contorta*, which was beyond the scope of the present study. We suggest that paying attention to the potential effects of exotic tree species at various scales may lead to better management of forests (including management of herbivore damage), and more sustainable moose management, even in the face of climate change.

Acknowledgements – We acknowledge the field staff and all the contributing members of the public.

Funding – SLU funding ensured animal marking and working time.

Conflict of interest – The authors declare no conflict of interest.

Permits – All personnel handling the moose were certified in accordance with the demands of the Swedish Animal Welfare Agency and the Swedish Board of Agriculture standards. All animal marking and handling has been approved by the Animal Care Committees in Umeå (DNR A14-15, A11-2020). Animal ethical permits are A14-15 and A11-20.

Author contributions

Maria Bodlund: Data curation (equal); Formal analysis (lead); Validation (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Fredrik Stenbacka:** Data curation (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Fredrik Widemo:** Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **John**

P. Ball: Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Göran Ericsson:** Funding acquisition (lead); Resources (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Wiebke Neumann:** Conceptualization (lead); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (lead); Validation (equal); Visualization (equal); 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/wlb3.01662>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6djh9w1gt> (Neumann et al. 2026).

Supporting information

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

References

- Allen, A. M., Månsson, J., Sand, H., Malmsten, J., Ericsson, G. and Singh, N. J. 2016. Scaling up movements: from individual space use to population patterns. – *Ecosphere* 7: e01524.
- Antonson, H. and Jansson, U. 2011. Agriculture and forestry in Sweden since 1900: geographical and historical studies. – The Royal Swedish Academy of Agriculture and Forestry (KSLA).
- Apollonio, M. et al. 2017. Challenges and science-based implications for modern management and conservation of European ungulate populations. – *Mamm. Res.* 62: 209–217.
- Ara, M., Felton, A. M., Holmström, E., Petersson, L., Berglund, M., Johansson, U. and Nilsson, U. 2022. Pre-commercial thinning in Norway spruce–birch mixed stands can provide abundant forage for ungulates without losing volume production. – *For. Ecol. Manage.* 520: 120364.
- Bäcklund, S., Jönsson, M., Strengbom, J. and Thor, G. 2018. Tree and stand structure of the non-native *Pinus contorta* in relation to native *Pinus sylvestris* and *Picea abies* in young managed forests in boreal Sweden. – *Scand. J. For. Res.* 33: 245–254.
- Ball, J. P. and Dahlgren, J. 2002. Browsing damage on pine (*Pinus sylvestris* and *P. contorta*) by a migrating moose (*Alces alces*) population in winter: relation to habitat composition and road barriers. – *Scand. J. For. Res.* 17: 427–435.
- Ball, J. P., Nordengren, C. and Wallin, K. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. – *Wildl. Biol.* 7: 39–47.
- Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M. and Matthiopoulos, J. 2010. The interpretation of habitat preference metrics under use–availability designs. – *Philos. Trans. R. Soc. B* 365: 2245–2254.
- Bjørneraas, K., Solberg, E. J., Herfindal, I., Moorter, B. V., Rolandsen, C. M., Tremblay, J., 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., Kowalczyk, R., Ratkiewicz, M., Maślanko, W., Duda, N. and Zmihorski, M. 2024. A highly variable habitat selection in moose across diel and seasonal scales. – *Mov. Ecol.* 12: 69.
- Borowik, T., Ratkiewicz, M., Maślanko, W., Duda, N. and Kowalczyk, R. 2020. Too hot to handle: summer space use shift in a coldadapted ungulate at the edge of its range. – *Landsc. Ecol.* 35: 1341–1351, <https://doi.org/10.1007/s10980-020-01018-4>.
- Castro-Díez, P. et al. 2019. Global effects of non-native tree species on multiple ecosystem services. – *Biol. Rev.* 94: 1477–1501.
- Cederlund, G. and Nyström, A. 1981. Seasonal differences between moose and roe deer in ability to digest browse. – *Ecography* 4: 59–65.
- Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C. and Waller, D. M. 2004. Ecological impacts of deer overabundance. – *Annu. Rev. Ecol. Syst.* 35: 113–147.
- Dettki, H., Ericsson, G., Giles, T. and Norrskén-Ericsson, M. 2014. Wireless remote animal monitoring (WRAM) – a new international database e-infrastructure for telemetry sensor data from fish and wildlife. – In: The European society of telemetry. Proceedings 2012: convention for telemetry, test instrumentation and telecontrol.
- Eldegard, K., Scholten, J., Stokland, J. N., Granhus, A. and Lie, M. 2019. The influence of stand density on bilberry (*Vaccinium myrtillus* L.) cover depends on stand age, solar irradiation, and tree species composition. – *For. Ecol. Manage.* 432: 582–590.
- Elfving, B., Ericsson, T. and Rosvall, O. 2001. The introduction of lodgepole pine for wood production in Sweden – a review. – *For. Ecol. Manage.* 141: 15–29.
- Engelmark, O. et al. 2001. Ecological effects and management aspects of an exotic tree species: the case of lodgepole pine in Sweden. – *For. Ecol. Manage.* 141: 3–13.
- Felton, A. M., Holmström, E., Malmsten, J., Felton, A., Croomsigt, J. P. G. M., Edenius, L., Ericsson, G., Widemo, F. and Wam, H. K. 2020. Varied diets, including broadleaf forage, are important for a large herbivore species inhabiting highly modified landscapes. – *Sci. Rep.* 10: 1904.
- Felton, A. M., Wam, H. K., Borowski, Z., Granhus, A., Jvany, L., Matala, J., Melin, M., Wallgren, M. and Mårell, A. 2024. Climate change and deer in boreal and temperate regions: from physiology to population dynamics and species distributions. – *Global Change Biol.* 30: e17505. <https://doi.org/10.1007/s10980-020-01018-4>.
- Felton, A. M., Juvany, L., Hedwall, P.-O., Felton, A., Erbrech, J., Sayn, A., Morel, J., Wallgren, M., Jarnemo, A., Schönbeck, L. and Spitzer, R. 2026. Forest stand characteristics drive the macronutrient composition of *Vaccinium* winter forage for cervids. – *Ecol. Appl.* 36: e70182.
- Gill, R. M. A. 1992. A review of damage by mammals in north temperate forests: 1. Deer. – *Forestry* 65: 145–169.
- Græslis, A. R., Thiel, A., Fuchs, B., Singh, N. J., Stenbacka, F., Ericsson, G., Neumann, W., Arnemo, J. M. and Evans, A. L. 2020. Seasonal hypometabolism in female moose. – *Front. Ecol. Evol.* 8: 00107.
- Graf, L., Bohlin, I., Hedwall, P.-O., Dahlgren, J. and Felton, A. M. 2025. Mapping cervid forage in Sweden using remote sensing and national forest inventory data. – *Int. J. Appl. Earth Obs. Geoinf.* 144: 104850.
- Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Var-on, Y. M., Moran, U., Antman, T., Meiri, S., Roll, U., Noor, E. and

- Milo, R. 2023. The global biomass of wild mammals. – Proc. Natl Acad. Sci. USA 120: e2204892120.
- Gren, I. M., Haggmark-Svensson, T., Elofsson, K. and Engelmann, M. 2018. Economics of wildlife management – an overview. – Eur. J. Wildl. Res. 64: 22.
- Guidobaldi Stenbacka, D., Bastianelli, M. L., Singh, N. J., Heurich, M., Ericsson, G. and Neumann, W. 2025. Influence of landscape composition and structure on habitat selection of a large herbivore in managed forests along a latitudinal environmental gradient. – For. Ecol. Manage. 597: 123167.
- Hambeson, E., Orlikowska, E. H. and Wallgren, M. 2025. Winter browsing by moose (*Alces alces*) in a forested mountainous landscape of west-central Sweden. – Wildl. Biol. 2025: e01338.
- Hedwall, P.-O., Brunet, J., Nordin, A. and Bergh, J. 2013. Changes in the abundance of keystone forest floor species in response to changes of forest structure. – J. Veg. Sci. 24: 296–306.
- Hodder, D. P., Rea, R. V. and Crowley, S. 2013. Diet content and overlap of sympatric mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and elk (*Cervus elaphus*) during a deep snow winter in north-central British Columbia, Canada. – Can. Wildl. Biol. Manage. 2: 43–50.
- Holbrook, J. D., Olson, L. E., DeCesare, N. J., Hebblewhite, M., Squires, J. R. and Steenweg, R. 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. – Ecol. Appl. 29: e01852.
- Horstkotte, T., Sandström, P., Neumann, W., Skarin, A., Adler, S., Roos, U. and Sjögren, J. 2023. Semi-domesticated reindeer avoid winter habitats with exotic tree species *Pinus contorta*. – For. Ecol. Manage. 540: 121062.
- Jensen, W. F. et al. 2020. A review of circumpolar moose populations with emphasis on Eurasian moose distributions and densities. – Alces 56: 63–78.
- Johnson, C. J. and Rea, R. V. 2024. Response of moose to forest harvest and management: a literature review. – Can. J. For. Res. 54: 366–388.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – Ecology 61: 65–71.
- Kardell, L. and Eriksson, L. 2011. Blåbärs- och lingonrisets återhämtning 30 år efter kalavverkning och markberedning 1977–2010, vol. 112. – SLU, in Swedish.
- Karlsson, A., Albrektson, A., Elfving, B. and Fries, C. 2010. Development of *Pinus sylvestris* main stems following three different precommercial thinning methods in a mixed stand. – Scand. J. For. Res. 17: 256–262.
- Kreeger, T. J. and Arnemo, J. M. 2007. Handbook of wildlife chemical immobilization, 3rd edn. – Terry J. Kreeger.
- Linnell, J. D. C., Cretois, B., Nilsen, E. B., Rolandsen, C. M., Solberg, E. J., Veiberg, V., Kaczensky, P., Van Moorter, B., Panzacchi, M., Rauset, G. R. and Kaltenborn, B. 2020. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. – Biol. Conserv. 244: 108500.
- Melin, M., Packalén, P., Matala, J., Mehtätalo, L. and Pusenius, J. 2013. Assessing and modeling moose (*Alces alces*) habitats with airborne laser scanning data. – Int. J. Appl. Earth Obs. Geoinf. 23: 389–396.
- Melin, M., Matala, J., Mehtätalo, L., Tiilikainen, R., Tikkanen, O., Maltamo, M., Pusenius, J. and Packalén, P. 2014. Moose reacts to high summer temperatures by utilizing thermal shelters in boreal forests – an analysis based on airborne laser scanning of the canopy structure at moose locations. – Global Change Biol. 20: 1115–1125.
- Neumann, W., Levers, C., Widemo, F., Singh, N. J., Croomsigt, J. P. G. M. and Kuemmerle, T. 2022. Hunting as land use – understanding the spatial associations of hunting, agriculture and forestry. – Ecol. Soc. 27: 2.
- Neumann, W., Stenbacka, F., Widemo, F., Ball, J. P., Bodlund, M. and Ericsson, G. 2026. Data from: Habitat selection of moose in Sweden in managed boreal forests with *Pinus contorta* and *Pinus sylvestris*. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.6djh9w1gt>.
- Niedzialkowska, M., Neumann, W., Borowik, T., Kołodziej-Sobocińska, M., Malmsten, J., Arnemo, J. M. and Ericsson, G. 2022. Moose *Alces alces* (Linnaeus, 1758). – In: Hackländer, K. and Zacos, F. E. (eds), Handbook of the mammals of Europe. Terrestrial Cetartiodactyla. Springer, pp. 215–245.
- Niemela, P. and Danell, K. 1988. Comparison of moose browsing on Scots pine (*Pinus sylvestris*) and lodgepole pine (*P. contorta*). – J. Appl. Ecol. 25: 761.
- Nikula, A., Heikkinen, S. and Helle, E. 2004. Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. – Wildl. Biol. 10: 121–135.
- Nilsson, P. and Cory, N. 2010. Skogsdata: current data on Swedish forests from the National Forest Inventory. Theme: lodgepole pine in Sweden. – Swedish Univ. of Agricultural Sciences, in Swedish.
- Northrup, J. M., Vander Wal, E., Bonar, M., Fieberg, J., Laforge, M. P., Leclerc, M., Prokopenko, C. M. and Gerber, B. D. 2022. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. – Ecol. Appl. 32: e02470.
- Pascual-Rico, R., Morales-Reyes, Z., Aguilera-Alcalá, N., Olszańska, A., Sebastián-González, E., Naidoo, R., Moleón, M., Lozano, J., Botella, F., von Wehrden, H., Martín-López, B. and Sánchez-Zapata, J. A. 2021. Usually hated, sometimes loved: a review of wild ungulates' contributions to people. – Sci. Tot. Environ. 801: 149652.
- Persson, I.-L., Danell, K. and Bergström, R. 2005. Different moose densities and accompanied changes in tree morphology and browse production. – Ecol. Appl. 15: 1296–1305.
- Pfeffer, S. E., Singh, N. J., Croomsigt, J. P. G. M., Kalén, C. and Widemo, F. 2021. Predictors of browsing damage on commercial forests – a study linking nationwide management data. – For. Ecol. Manage. 479: 118597.
- Pringle, R. M., Abraham, J. O., Anderson, T. M., Coverdale, T. C., Davies, A. B., Dutton, C. L., Gaylard, A., Gohee, J. R., Holdo, R. M., Hutchinson, M. C., Kimuyu, D. M., Long, R. A., Subalusky, A. L. and Veldhuis, M. P. 2023. Impacts of large herbivores on terrestrial ecosystems. – Curr. Biol. 33: R584–R610.
- Raudsepp-Hearne, C., Peterson, G. D. and Bennet, E. M. 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. – Proc. Natl Acad. Sci. USA 107: 5242–5247.
- Rea, R. V., Hjeljord, O. and Härkönen, S. 2014. Differential selection of North American and Scandinavian conifer browse by northwestern moose (*Alces alces andersoni*) in winter. – Acta Theriol. 59: 353–360.
- Roberge, C., Dahlgren, J., Nilsson, P., Wikberg, P.-E. and Fridman, J. 2024. Skogsdata: current data on Swedish forests from the National Forest Inventory. Theme: species. – Swedish Univ. of Agricultural Sciences, in Swedish.
- Roberge, J.-M. and Stenbacka, F. 2014. Assemblages of epigeic beetles and understory vegetation differ between stands of an introduced pine and its native congener in boreal forest. – For. Ecol. Manage. 318: 026.

- Roos, U., Lidestav, G., Sandström, S. and Sandström, P. 2022. Samråd: an institutional arrangement in the context of forestry and reindeer husbandry in northern Sweden. – *Int. For. Rev.* 24: 441–457.
- Sand, H., Jamieson, M., Andrén, H., Wikenros, C., Cromsigt, J. and Månsson, J. 2021. Behavioral effects of wolf presence on moose habitat selection: testing the landscape of fear hypothesis in an anthropogenic landscape. – *Oecologia* 197: 101–116.
- Sandström, P., Cory, N., Svensson, J., Hedenäs, H., Jougda, L. and Borchert, N. 2016. On the decline of ground lichen forests in the Swedish boreal landscape: implications for reindeer husbandry and sustainable forest management. – *Ambio* 45: 415–429.
- Signer, J., Fieberg, J. and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. – *Ecol. Evol.* 9: 880–890.
- Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N. and Ericsson, G. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. – *Ecol. Appl.* 22: 2007–2020.
- Sjöberg, K. and Danell, K. 2001. Introduction of lodgepole pine in Sweden – ecological relevance for vertebrates. – *For. Ecol. Manage.* 141: 143–153.
- SLU. 2022. Official forest statistics. Technical report of the National Forest Inventory. – Swedish Univ. of Agricultural Sciences, in Swedish.
- SMHI. 2024. Maps on seasonal arrival times. – Swedish Meteorological and Hydrological Institute, in Swedish.
- Speed, J. D. M., Austrheim, G., Hester, A. J., Solberg, E. J. and Tremblay, J.-P. 2013. Regional-scale alteration of clear-cut forest regeneration caused by moose browsing. – *For. Ecol. Manage.* 289: 289–299.
- Spitzer, R., Coissac, E., Felton, A., Fohringer, C., Juvany, L., Landman, M., Singh, N. J., Taberlet, P., Widemo, F. and Cromsigt, J. 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.
- Spitzer, R., Coissac, E., Cromsigt, J. P. G. M., Felton, A. M., Fohringer, C., Landman, M., Neumann, W., Raubenheimer, D., Singh, N. J., Taberlet, P. and Widemo, F. 2023. Macro-nutritional balancing in a circumpolar boreal ruminant under winter conditions. – *Funct. Ecol.* 37: 1256–1268.
- Spitzer, R., Coissac, E., Felton, A. M., Landman, M., Singh, N. J., Taberlet, P., Widemo, F. and Cromsigt, J. P. G. M. 2025. Metabarcoding reveals fine scale patterns of trophic resource use and partitioning along gradients of land use and deer density in a multi-species ungulate community. – *Ecol. Evol.* 15: e72365.
- Standen, M. P., Dittmer, M. A., Stoner, D. C., Hersey, K. R. and Carter, N. H. 2025. Differential effects of environmental predictability on ungulate movement behavior in disparate ecosystems. – *Wildl. Biol.* 2026: e01484, <https://doi.org/10.1002/wlb3.01484>.
- Stewart, K. M., Bowyer, R. T., Ruess, R. W., Dick, B. L. and Kie, J. G. 2006. Herbivore optimization by North American elk: consequences for theory and management. – *Wildl. Monogr.* 167: 1–24.
- Swedish EPA. 2019. Description of national land cover map 2018 base layer. – Swedish Environmental Protection Agency.
- Thurfjell, H., Ciuti, S. and Boyce, M. S. 2014. Applications of step-selection functions in ecology and conservation. – *Mov. Ecol.* 2: 4.
- Turner, K. G., Odgaard, M. V., Bøcher, P. K., Dalgaard, T. and Svenning, J. C. 2014. Bundling ecosystem services in Denmark: trade-offs and synergies in a cultural landscape. – *Landsc. Urban Plan.* 125: 89–104.
- Van Beest, F. M., Mysterud, A., Loe, L. E. and Milner, J. M. 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. – *J. Anim. Ecol.* 79: 910–922.
- Van Beest, F. M., Van Moorter, B. and Milner, J. M. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. – *Anim. Behav.* 84: 723–735.
- Verzuh, T. L., Rogers, S. A., Mathewson, P. D., May, A., Porter, W. P., Class, C., Knox, L., Cufau, T., Hall, L. E., Long, R. A. and Monteith, K. L. 2023. Behavioural responses of a large, heat-sensitive mammal to climatic variation at multiple spatial scales. – *J. Anim. Ecol.* 92: 619–634.
- Widemo, F., Elmhagen, B. and Liljebäck, N. 2019. Viltets ekosystemtjänster - en kunskapssammanställning. – Report 6889. Swedish Environmental Protection Agency, in Swedish.
- Widén, A., Cromsigt, J. P. G. M., Felton, A. M., Widemo, F., Graf, L., Ericsson, G. and Singh, N. J. 2025. Temperature mediated habitat selection in sympatric deer species with varying body size: thermal cover and forage availability as potential drivers. – *Mov. Ecol.* 13: 52.
- Youngentob, K. N., Felton, A. M., Lindenmayer, D. B. and Marsh, K. J. 2025. Managing nutritional landscapes as the next frontier in forest ecology and conservation. – *Front. Ecol. Environ.* 24: e70015.