



Moose Habitat Selection in Managed Forests: A Comparison Between *Pinus contorta* and *Pinus sylvestris*

Master thesis

Maria Bodlund

Independent project • 30 credits

Swedish University of Agricultural Sciences, SLU

Department of Wildlife, Fish and Environmental studies

Examensarbete / SLU, Institutionen för vilt, fisk och miljö

2025:18

Umeå 2025



Moose Habitat Selection in Managed Forests: A Comparison Between *Pinus contorta* and *Pinus sylvestris*

Älgens val av habitat i brukade skogar: En jämförelse mellan Pinus contorta och Pinus sylvestris

Maria Bodlund

Supervisor:	Wiebke Neumann, Swedish University of Agricultural Sciences, Department of Wildlife, Fish and Environmental Studies
Assistant supervisor:	Fredrik Stenbacka, Swedish University of Agricultural Sciences, Department of Wildlife, Fish and Environmental Studies
Examiner:	Fredrik Widemo, Swedish University of Agricultural Sciences, Department of Wildlife, Fish and Environmental Studies.
Credits:	30 credits
Level:	(A2E)
Course title:	Masterarbete i skogsvetenskap, A2E - Vilt, fisk och miljö
Course code:	EX0968
Programme/education:	Jägmästarprogrammet
Course coordinating dept:	Department of Wildlife, Fish and Environmental studies
Place of publication:	Umeå
Year of publication:	2025
Title of series:	Examensarbete / SLU, Institutionen för vilt, fisk och miljö
Part number:	2025:18
Keywords:	Moose (<i>Alces alces</i>), habitat choice, habitat selection, <i>Pinus contorta</i> , lodgepole pine, exotic species, forestry, step selection function

Swedish University of Agricultural Sciences

Faculty of Forest Sciences

Department of Wildlife, Fish and Environmental Studies

Abstract

The species *P. contorta* was introduced to Sweden for production purposes in forestry in 1920 and has been planted since 1970 within forestry because of its beneficial properties in terms of damage resistance and growth capacity. Introducing exotic species can however influence ecosystem features and other species, and forests based on exotic species are not always a preferred habitat by wildlife. Pine forest is an important habitat for moose (*Alces alces*) and especially during winter when moose's primary diet is pine. There is a lack of studies on habitat selection between these pine species, and this study was conducted to evaluate how moose respond to the *P. contorta* forest, and if the habitat use differs between seasons: the study was conducted on GPS data from 29 moose located in Västernorrland county in Sweden was performed using step selection function (SSF) and conditional logistic regression. The study showed that clearcut/ young forest was the most used habitat by moose during all seasons, especially during winter, probably due to forage availability, as moose during winter primarily feed on pine. My result showed that moose during winter avoided the habitat clearcut/young forest with a higher proportion of *P. contorta*, which could be a result of foraging preferences. During summer and autumn, moose habitat selection varied more. Previous studies have shown that this behavior is probably an effect of thermoregulation and their forage choice. During summer and autumn, my results showed that moose selected mature *Pinus contorta* forest compared to mature *Pinus sylvestris*, which could be due to the characteristic denser canopy of *Pinus contorta* resulting in lower temperatures in this forest.

Keywords: Moose (*Alces alces*), seasonal habitat selection, *Pinus contorta*, lodgepole pine, exotic species, forestry, step selection function

Sammanfattning

I Sverige introducerades tallarten *Pinus contorta* från Nordamerika under 1920 talet på grund av en oro för en framtida virkesbrist i Sverige. Sedan 1970 har arten använts inom skogsbruket på grund av fördelar i produktions syfte. Egenskaperna hos de två olika tallarterna skiljer sig däremot och kan påverka arters val av till exempel föda och habitat. Studier har visat på att tallskogen är ett väldigt viktigt habitat för älg, speciellt under vintern när älgens huvudföda är tall. För att se hur älg påverkas av *Pinus contorta* och om habitatvalet skiljer sig under de olika årstiderna utfördes denna studie. I studien användes GPS data från 29 älgar i Junsele i Västernorrland med metoden step selection function (SSF) och villkorlig logistisk regression. Studien visade att hyggen/ungskog var de mest använda habitatet hos älg under alla årstider, speciellt under vintern, mest troligt på grund av fodertillgångarna då älgens viktigaste föda under vintern är tall. Mitt resultat visade även på en skillnad i älgens användande av de olika tallarterna i hygge/ungskog under vintern, då älg undvek habitatet med större andel *P. contorta* jämfört med de andra hygge/ungskog habitaterna. Då tidigare studier visat på att älg äter mindre av *Pinus contorta* jämfört med *Pinus sylvestris*, skulle det kunna vara ett resultat av födoval. Under sommaren varierade älgens habitatval mer och äldre skogar blev mer viktiga, troligen på grund av födoval och skydd från värmen. Under sommaren och hösten kunde man även se att älg föredrog vuxen *Pinus contorta* skogar framför vuxen *Pinus sylvestris* skogar, vilket skulle kunna vara ett resultat av att contortan har en tätare krona, vilket skulle kunna resultera i lägre temperatur i skogen.

Table of contents

1. Introduction	7
1.1 Background	7
1.1.1 Introduction of <i>Pinus contorta</i> in Sweden	7
1.1.2 Difference between <i>Pinus contorta</i> and <i>Pinus sylvestris</i>	7
1.1.3 Moose habitat use	8
1.2 Previous studies on <i>Pinus contorta</i> and moose.....	10
1.3 Aim	10
2. Method	12
2.1 Study Area	12
2.2 Moose GPS data.....	13
2.3 Environmental variables.....	14
2.4 Statistical analyses	16
2.5 Seasons	16
3. Results	17
4. Discussion	20
5. Conclusion.....	25
Abbreviations	26
References	27
Acknowledgements.....	30
Popular science summary.....	31
Appendix 1	32
Appendix 2	35

List of tables:

Table 1, maps used for habitat classification with information, year, resolution, coordinate system and source.....	14
Table 2 Reclassified habitat from NMD map (Pine, Spruce, Deciduous, Mixed, Clear cut, Wetland and Other), including definition, code NMD (Naturvårdsverket 2023).	32
Table 3. Start and ending of the seasons of the study period, from Arrival maps (SMHI 2024).....	35

List of figures:

- Figure 1, Map representing Sweden. The light gray areas represent counties in all of Sweden and the dark green areas represent the counties in Sweden that belong to Norrland (a region in Sweden). The green highlighted indicates the study area. 13
- Figure 2. Estimates of the Relative Selection Strength on habitat selection of adult moose (*Alces alces*) over the entire annual cycle as given by a conditional logistic regression, Junsele 2022-2024. *Pinus sylvestris* forest is 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 indicate lower selection. The black horizontal bars represent the confidence intervals. If the confidence intervals do not cross the reference line, the selection is significant different from the reference habitat. 17
- Figure 3. Estimates of the Relative Selection Strength on the habitat selection of adult moose (*Alces alces*) in each season Winter, Spring, Summer and Autumn as given by the conditional logistic regression, Junsele 2022-2024. *Pinus sylvestris* forest is 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 indicate lower selection. The black horizontal bars represent the confidence intervals. If the confidence intervals do not cross the reference line, the selection is significant different from the reference habitat. 19

1. Introduction

1.1 Background

1.1.1 Introduction of *Pinus contorta* in Sweden

In the year 1920, the North American Lodgepole pine *Pinus contorta* was first introduced to Sweden (Elfving et al. 2001; Engelmark et al. 2001). The species introduction to Sweden was due to a prediction of a timber shortage in the future (Hagner 2005), and *P. contorta* was considered to have similar characteristics as the native Scots pine *Pinus sylvestris*, but with greater growth (Elfving et al. 2001; Hagner 2005). In 1970, *P. contorta* became more used in the Swedish forestry and has been used for production purposes since. However, the introduction of *P. contorta* did not go as expected, resulting in damaged trees, due to wind and snow instability (Elfving et al. 2001), and *Gremmeniella* fungus (*Gremmeniella abietina*) affected trees (Elfving et al. 2001; Hagner 2005). Due to environmental and political reasons, as well as tree damage, the Swedish Forest Agency (Skogsstyrelsen) decided to limit the total area allowed planting *P. contorta* each year from 26,000 ha in 1980 to 14,000 ha today (Elfving et al. 2001).

The positive characteristics of the exotic species that are presented for *P. contorta* today, are the faster growth (i.e. 40%) (Elfving et al. 2001; Unbeck 2011) that leads to economic benefits, less browsing damage by moose and higher survival rates compared to *P. sylvestris* (Elfving et al. 2001; Hagner 2005; Unbeck 2011; Sjöberg & Danell 2001). Today, *P. contorta* represents about two percent of the productive forest in Sweden, which is approximately 560,000 hectares of productive forest, primarily in the northern part of Sweden, including the counties Norrbotten, Västerbotten, Jämtland, Västernorrland and Gävleborg (Skogsdata 2024; Sjöberg & Danell 2001; Jacobson & Hannerz 2020).

1.1.2 Difference between *Pinus contorta* and *Pinus sylvestris*

The two pine species differ in characteristics, which leads to differences in the habitats they provide, which could lead to differences in habitat selection between the forests by wildlife (Sjöberg & Danell 2001; Roberge & Stenbacka 2014; Horstkotte et al. 2023). *P. contorta* and *P. sylvestris* are both pine species (*Pinus spp*), however, the structural characteristics of these two tree species differ, resulting in pine forests with different features. For example, *P. contorta* has a denser canopy, which results in reduced light entering through the crown, which may lead to different conditions for species living in the field layer (Bäcklund et al. 2018; Sjöberg & Danell 2001). The denser canopy of the *P. contorta* is a result of thicker, lower and longer branches which also results in more needles on the tree and therefore also more litter on the ground, which could influence the

species in the understorey (Bäcklund et al. 2018; Nilsson et al. 2008; Sjöberg & Danell 2001). However, although *P. contorta* has shown a denser canopy allowing less light passing through to the forest understory, *P. contorta* has shown to have a higher mortality in older mature forest than *P. sylvestris*, which could lead to more gaps in the forest and allowing more light into the forest (Elfving et al. 2001). As a result of the different characteristics of *P. contorta* compared to *P. sylvestris*, the *P. contorta* forest has also been shown to also have more dead lying wood in the forest and less scrubs (*Vaccinium spp*) (Roberge & Stenbacka 2014). These structural differences between the pine forests (*Pinus SPP*) may influence the habitat selection of animal species using the forest as habitat or for forage (Sjöberg & Danell 2001; Roberge & Stenbacka 2014; Horstkotte et al. 2023).

A study using GPS-marked semi-domesticated reindeer (*Rangifer tarandus*) Horstkotte et al. (2023) studied the habitat use of reindeer in *P. contorta* and *P. sylvestris* forests during winter. In the study, they found that the proportion and the height of the *P. contorta* forest stands seemed to influence the reindeer's choice of habitat. More specifically, they found that the reindeer avoid mature *P. contorta* forests (over 3 m height) compared to mature *P. sylvestris* forests. In older forests, the percentage of *P. contorta* seemed to influence the habitat selection as the reindeer tended to be less willing to use the habitat with a higher proportion of *P. contorta* (>60%) than forests with less proportion of *P. contorta* (20-60%). The authors discussed that one reason of this selective choice could be because of the difference in forage availability between *P. sylvestris* and *P. contorta* in mature forest, as the forest with a higher proportion of *P. contorta* had a lower lichen cover (Horstkotte et al. 2023). However, the study did not find any significant difference in the habitat choice of reindeer for forests that were below three meter high, suggesting that the younger trees did not seem to prevent the reindeer physically from movement, or it could be because their main food source during winter (lichen) has not yet been affected by the environment of the denser stands of the *P. contorta* in young stands (Horstkotte et al. 2023).

1.1.3 Moose habitat use

Moose adapt their habitat choice to factors as forage and water availability, thermoregulation, predators, and humans (Allen et al. 2016; Björneraas et al. 2011; Johnson & Rea 2024). Moose are partial migratory animals, which means that some individuals in the population migrate between seasonal areas (migrants that move varying distances) whereas others stay in the same area year-round, stationary moose, (Singh et al. 2012; Van Moorter et al. 2021).

Moose in Sweden migrate from the winter area to the summer area from the end of April to beginning of June and from winter sites in end of November until the middle of January (Allen et al. 2016; Singh et al. 2012). However, there are

several factors that can impact migration in a moose population, such as latitude, snow depth, age, and sex of moose (Allen et al. 2016; Singh et al. 2012).

Studies show that moose need different types of habitats, and that moose use different habitats in different ways, young stands for food and older forests for shelter are important for moose (Johnson & Rea 2024).

The moose's primary diet also changes throughout the year (Spitzer 2019; Spitzer et al. 2023). Overall, the three most important forage for moose is pine, shrubs (*Vaccinium* spp) and deciduous trees (Spitzer 2019). However, during winter moose primarily feed on woody browse like pine and towards the spring, the composition of shrubs forage increases. In summer, the moose consumes mostly broadleaf followed by shrubs, and towards the autumn, the use of shrubs increases (Spitzer 2019; Spitzer et al. 2023).

The selection of habitats is often regulated by the choice of food for the moose (Björneraas et al. 2011). The habitat choice also varies during the year and the different seasons. In Sweden during the summer moose mostly spends their time in habitats of pine forest, mixed forest, and wetlands. When migrating during winter and spring the moose prefer pine forest, clearcuts and mixed forest (Allen et al. 2016; Neumann et al. 2023).

The structure of trees could also be a factor that can influence the habitat choice of moose, as the amount of snow has shown to influence moose habitat selection, i.e. snow depth (Telfer 1970; Baskin & Danell 2003). In a study, Telfer (1970) found that the clear-cut areas had deeper snow than older forest with denser canopies, especially later in winter (Telfer 1970). Baskin & Danell (2003) also mentioned that moose is influenced by the snow depth when the snow is 70-80 cm or deeper.

In a review by Johnson & Rea (2024) on the habitat choice of moose, some of the studies showed that moose avoided clearcuts, while some studies showed that the moose selected for clearcuts, especially during winter. A study found that the moose preferred clearcut/young forest during the night for food and mature forest during the day as shelter (Björneraas et al. 2011). Temperatures has also been shown to influence the habitat choice by moose, especially during summer when its warmer, moose selected for older habitat (Van Beest et al. 2012). The influence of temperature was also observed in another study by Melin et al (2014), where it showed that the moose changed habitat when temperatures over 20 °C to higher, denser forest. As *P. contorta* has found to have denser canopies than *P. sylvestris* and studies have shown that denser canopies can affect moose' habitat choice in terms of snow amount on mobility and in terms of temperature, we expect that it could lead to less snow on the ground and therefore could be a suitable habitat during winters with lot of snow.

1.2 Previous studies on *Pinus contorta* and moose

Pine is the primary food source for moose during winter (Spitzer 2019, Spitzer et al. 2020). Not many studies have been performed between moose browsing between *P. contorta* and *P. sylvestris*, however some studies suggest a slight difference in moose browsing of *P. contorta* and *P. sylvestris*, where *P. contorta* is not as attractive food source as *P. sylvestris* (Sjöberg & Danell 2001; Rea et al. 2014). There is also one study showing that stem breakage due to browsing caused mainly by moose is higher on *P. sylvestris* than on *P. contorta* (Nilsson & Cory 2010). However, there are also studies indicating no differences and that moose browsing on *P. contorta* is similar to *P. sylvestris* (Ball & Dahlgren 2002; Niemela & Danell 1988), which suggests that *P. contorta* should not affect moose habitat choice for feeding purposes. Interestingly, one study by Niemela & Danell (1988) shows that *P. contorta* is more prone to browsing damage on the stem than *P. sylvestris* (Niemela & Danell 1988), which could indicate that moose prefer foraging on the *P. contorta* bark.

In a study conducted in North America, where *P. contorta* is native, moose browsed less on *P. contorta* than on *P. sylvestris*. However, in these systems, moose prefer to browse on spruce over all pine species (Rea et al. 2014) – which is different to observations made in Northern Europe (Spitzer 2019). This could also then reflect on the different moose habitat selection during winter in North America.

Whereas some studies have investigated browsing pressure on *P. contorta* by moose (Niemela & Danell 1988; Ball & Dahlgren 2002; Rea et al. 2014), so far, the habitat selection of moose of *P. contorta* in a landscape where *P. contorta* is exotic is understudied. Previous studies have shown that non-native forests can result in lower biodiversity (Stephens & Wagner, 2007), likely due to structural differences between *P. contorta* and *P. sylvestris* forests. An increased use and planting of *P. contorta* in Sweden could affect the habitat options of moose and could have consequences for both forestry and moose management. Considering the gap in research on moose and *P. contorta*, observing the habitat selection of the moose in areas with *P. contorta* would improve our understanding of the ecological impact of the non-native tree species.

1.3 Aim

The aim of this study is to investigate the habitat choice of moose and how the occurrence of the non-native tree species *P. contorta* within the Swedish forest

landscape affects the habitat selection of a large herbivore like moose throughout the year. Specifically, I will investigate the following research questions:

1. What is the habitat selection of moose when *P. contorta* is available in the area, and does the selection for forests dominated by *P. contorta* differ between seasons?
2. Does the habitat selection of moose for pine forests differ between *P. contorta* and *P. sylvestris* forests, and is there a seasonal effect?

2. Method

2.1 Study Area

To perform the study on habitat selection of moose in areas where forest stands of *P. contorta* occur more commonly in the Swedish forest landscape, position data from adult GPS-marked moose near the village Junsele in the municipality of Sollefteå were used (Fig 1). Junsele is located in the southern parts of Norrland, Sweden, and falls into the boreal biome. Southern Norrland contains the largest proportion of *P. contorta* in Sweden, 4,6% of the productive forest (SLU 2024). In southern Norrland, the Norway spruce (*Picea abies*) is the most common tree species, followed by the native pine *P. sylvestris* (SLU 2024). The conifers, *P. sylvestris* and *Picea abies* each represent around 40% of the standing timber volume in southern Norrland, representing 80% conifers, birch (*Betula spp*) 10%, *P. contorta* 4%, and the rest of the standing timber volume is other deciduous trees (SLU 2024). Coniferous forests are interspersed with mires.

The average ambient temperature of the study area is 2°C that changes with the season. In winter, the average ambient temperature is -8°C, increasing to 2°C in spring, 13°C in summer, and 2°C in autumn. Winter typically arrives around 25 October in the study area, followed by spring 10 April, summer 27 May, and autumn first of September (SMHI 2024). During most of the winter season, the study area is covered with snow with a depth of 50-100 cm (SMHI 2024). In Sweden, moose are managed through hunting with a three-year management plan decided for each moose management area, including considerations of different interests in land use (e.g., degree of browsing damage and moose-vehicle collisions), and with the plans being approved by the Administrative County Board (Länsstyrelsen Västernorrland 2025, Apollonio et al. 2010). In my study area Västernorrland, Northern Sweden, the moose hunt starts first of September and lasts until all animals of the decided quota are shot or until 31 of January (Länsstyrelsen 2025).

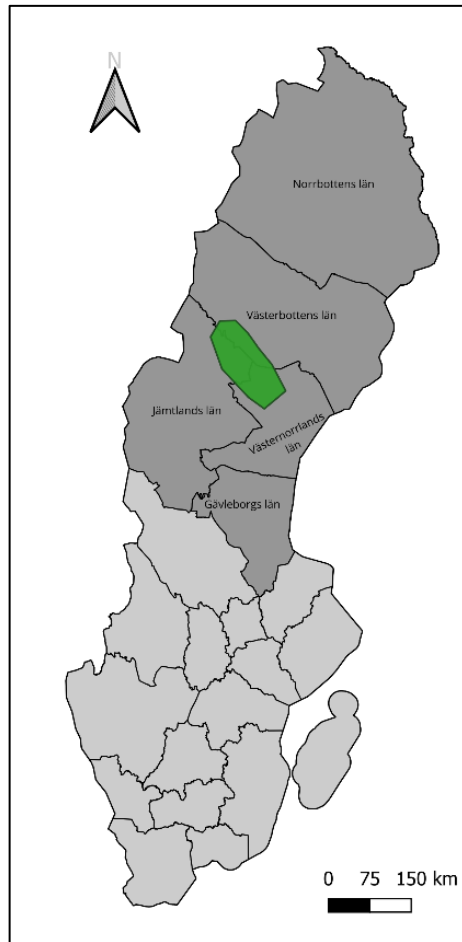


Figure 1, Map representing Sweden. The light gray areas represent counties in all of Sweden and the dark green areas represent the counties in Sweden that belong to Norrland (a region in Sweden). The green highlighted indicates the study area.

2.2 Moose GPS data

Many of the moose individuals in this study migrated long distances and their positions reached into counties nearby, like Västerbotten and Jämtland (Figure 1). The migration route resulted in positions of moose in elevation of 200-400 in summer areas and up to 700 in winter areas. For my study, I used position data collected between 01 April 2022 and 01 March 2024. My study included position data from a total of 29 different moose (21 females and 8 males), resulting in a total of 96 857 observations (2028 positions per moose \pm 248). Number of moose that could be followed a given year differed, and in total my analysis included 60 moose-year (year 2022: n=20, 2023: n=24, 2024: n=16). To apply the same time intervals for my analysis throughout the year, I sub-sampled the data set to 3-hours intervals.

2.3 Environmental variables

To classify and characterise different forest habitats and differentiate the forests dominated by two *Pinus* species, I used information given by four different maps: the national land cover map (NMD), the additional height cover map 0,5-5m, the additional height cover map 5-45m, and the contorta proportion map (Table 1).

Table 1, maps used for habitat classification with information, year, resolution, coordinate system and source.

Map	Information	Year	Resolution	Coordinate system	Source
National Land Cover Map	Different land cover types	2019	10x10	SWEREF99 TM (EPSG:3006)	Swedish Environmental Protection Agency
Contorta proportion	Percent contorta of standing volume	2017-2019	10x10	SWEREF99 TM (EPSG:3006)	SLU Forest map
Additional layer Object height 0,5-5m	Height of objects under 5 meters	2019	10x10	SWEREF99 TM (EPSG:3006)	Swedish Environmental Protection Agency
Additional layer Object height 5-45m	Height of objects over 5 meters	2019	10x10	SWEREF99 TM (EPSG:3006)	Swedish Environmental Protection Agency

The main data source to determine the different forest habitats was the NMD. I reclassified the 25 different land cover classes (Appendix 1) into the following 11 habitat classes meaningful for moose using information given by the four maps (Table 2).

First, I reclassified the land cover classes from the NMD map into seven different habitat classes: Pine, Spruce, Deciduous, Mixed Forest, Clearcut/young forest (tree height <5m), Wetland and Others. The NMD map did not include

specific information about *P. contorta*. Therefore, the habitat Contorta was based on the contorta proportion map provided by SLU tree species map. To include the *P. contorta* as a habitat, considering different shares of *P. contorta*, I created two new habitats, Contorta 20-40% and Contorta >40%. These were restricted to forest habitats (Pine, Spruce, Deciduous, Mixed Forest or Clearcut with a tree height <5m), to ensure that they reflected forest habitat. The threshold of the *P. contorta* proportion was based on a prior study on reindeer habitat selection that used the proportion 20-60% and >60% (Horstkotte et al. 2023). Due to lack of data in my study area where proportion on *P. contorta* were above 60%, I used a threshold of 40% instead. Next to proportion, also height of *P. contorta* can impact the habitat selection of ungulates (threshold 3 m tree height (Horstkotte et al. 2023)). Since I was interested in moose selection of Pine forests (with a tree height ≥ 5 m), clearcut/young forest (tree height < 5 m), I divided my contorta habitats into two height classes: less than 5 m (<5m) and more than 5 m. The first named represented forests that included the height classes 0,5-3 m from NMD height map 0,5-5m and clearcut habitat as given by the NMD. This resulted in 4 different *P. contorta* habitats (Table 2).

Table 2, Habitat classes with definition within this study to test for moose habitat selection of different forest types, Junele 2022-2024.

Habitats	Definition
Pine	Minimum crown cover of 10%, crown cover of at least 70% of pine.
Spruce	Minimum crown cover of 10%, crown cover of at least 70% of spruce.
Deciduous	Minimum crown cover of 10%, crown cover of at least 70% of deciduous species.
Mixed Forest	Minimum crown cover of 10%
Clearcut <5m	Temporary non-forest land with a height below 5 m expected to grow into a forest, for example, clearcuts, fire/wind-damaged forests.
Wetlands	Open land, with wetland.
Others	Not forest related habitat: Arable land, Inland/marine water, open land, roads and buildings.
Contorta 20-40%	Forestland with the proportion of 20-40% <i>Pinus contorta</i> . More than 5 meters.
Clearcut/young Contorta 20-40%, <5m	Forestland with the proportion of 20-40% <i>Pinus contorta</i> . Forest less than 5 meters. The height classes 0,5-1 and 1-3 m from height map 0,5-5m
Contorta >40%	Forestland with a proportion of more than 40% <i>Pinus contorta</i> . More than 5 meters.

Clearcut/young Contorta >40%, <5m	Forestland with the proportion of 20-40% <i>Pinus contorta</i> . Forest less than 5 meters. The height classes 0,5-1 and 1-3 m from height map 0,5-5m
--------------------------------------	---

2.4 Statistical analyses

To test both overall and seasonal selection of different forest habitats by moose in an area where *P. contorta* is relatively common, I applied step selection functions (SSF) (R package ‘amt’, Signer et al. 2019). The SSF compares a given observed step with a set of random steps to quantify animals’ selection in relation to the reference habitat (in my case: *P. sylvestris* forest) and all habitats’ availability in the surrounding (Thurfjell et al. 2014). The random steps are generated by fitting parametric distribution of the observed steps length and angle of rotation of the observed animal using the gamma distribution and von Mises distribution, respectively (Thurfjell et al. 2014; Signer et al. 2019). For each observed step, I created 10 random steps with a tolerance of 1 hour (Thurfjell et al. 2014). I spatially linked the end of each random and observed step of a given moose with my final habitat classification map (Signer et al. 2019).

I used a conditional logistic regression with a significance level of 0.05 to test for habitat selection of moose in areas with *P. contorta* present and the difference in habitat selection between the two types of pine forests.

All spatial data including processing of maps and habitat classification was performed using R, version. 4.4.1.

2.4.1 Seasons

As the Swedish climate changes throughout the year, this study also aims to examine seasonal variation in moose habitat selection. Therefore, the data was divided and categorised in four seasons: winter, spring, summer, and autumn (Appendix 2). I sub-divided my dataset following the time intervals of the seasons each year that were determined from maps providing the mean arrival date of given season in a given region and year (SMHI 2024).

3. Results

Considering the entire year, moose primarily selected the habitat clearcut/young forests with a tree height under 5 m followed by clearcut/young *P. contorta* forests with a proportion of 20-40% (Contorta 20-40%, <5m). Moose also preferred deciduous forests over mixed forest and spruce, mature *P. contorta* 20-40% and the two contorta forests with higher proportion of contorta (i.e. with proportion over 40%). It can be observed that the moose never significantly selected less for *P. contorta* forests than for *P. sylvestris* forests, across all the seasons. Overall and during all season, moose avoided wetlands, which was the least selected habitat (Figure 2).

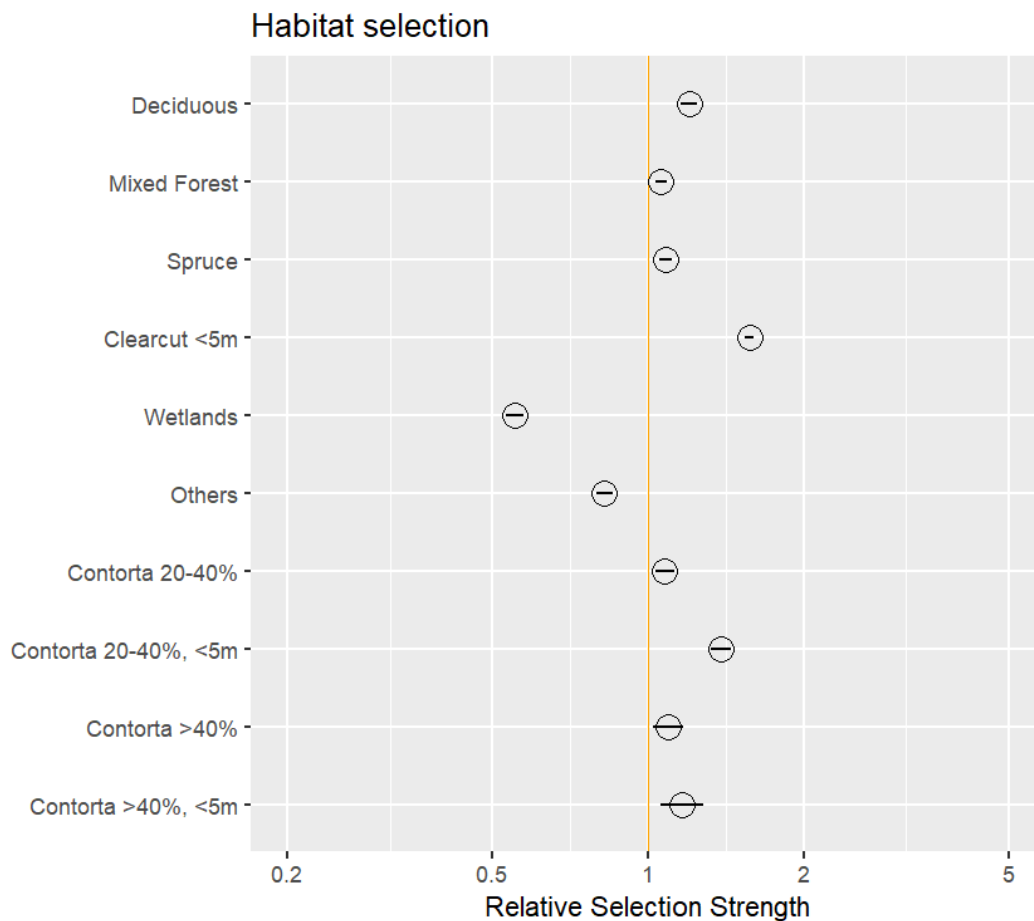


Figure 2. Estimates of the Relative Selection Strength on habitat selection of adult moose (*Alces alces*) over the entire annual cycle as given by a conditional logistic regression, Junsele 2022-2024. *Pinus sylvestris* forest is the reference habitat (orange line). Values larger than one indicate selection for a given habitat in relation to the reference habitat and in relation to habitats availability, values smaller than one indicate lower selection. The black horizontal bars represent the confidence intervals. If the confidence intervals do not cross the reference line, the selection is significant different from the reference habitat.

The habitat selection of moose varied between seasons, yet some habitats were always selected (Figure 3). For example, clearcuts/young habitat was the most selected habitat by moose in all the seasons, whereas moose always selected against wetlands. In all seasons except winter, moose selected against the habitat Others (i.e. representing roads, buildings, fields etc.).

During winter, moose selected for a reduced number of habitats when compared to other seasons. During winter season, moose selected three types of forests more than pine forests: clearcut/young forest, the clearcut/young *P. contorta* habitat with the proportion of 20-40%, and deciduous forests. There was a difference in selection between the two clearcut/young *P. contorta* habitats (< 5m), where Contorta forests with a lower proportion of *P. contorta* (20-40%) were selected more than those with a higher proportion of *P. contorta* (>40%). There was no significant difference in habitat selection between the habitats Spruce, Others, or the other Contorta habitats from the selection for *P. sylvestris* forests.

In spring, the Clearcut/young forest habitat remained the most selected habitat next to a selection for Deciduous forests, whereas moose selected against Spruce forests and Wetlands.

In summer and autumn, the habitat selection of the moose became more diverse by including more habitats. Whereas animals selected for all forest habitats, including all *P. contorta* forests (except Contorta > 40%, < 5m in autumn), they selected against Wetlands. During summer and autumn, moose selected mature *P. contorta* forest (>5m) more than *P. sylvestris*.

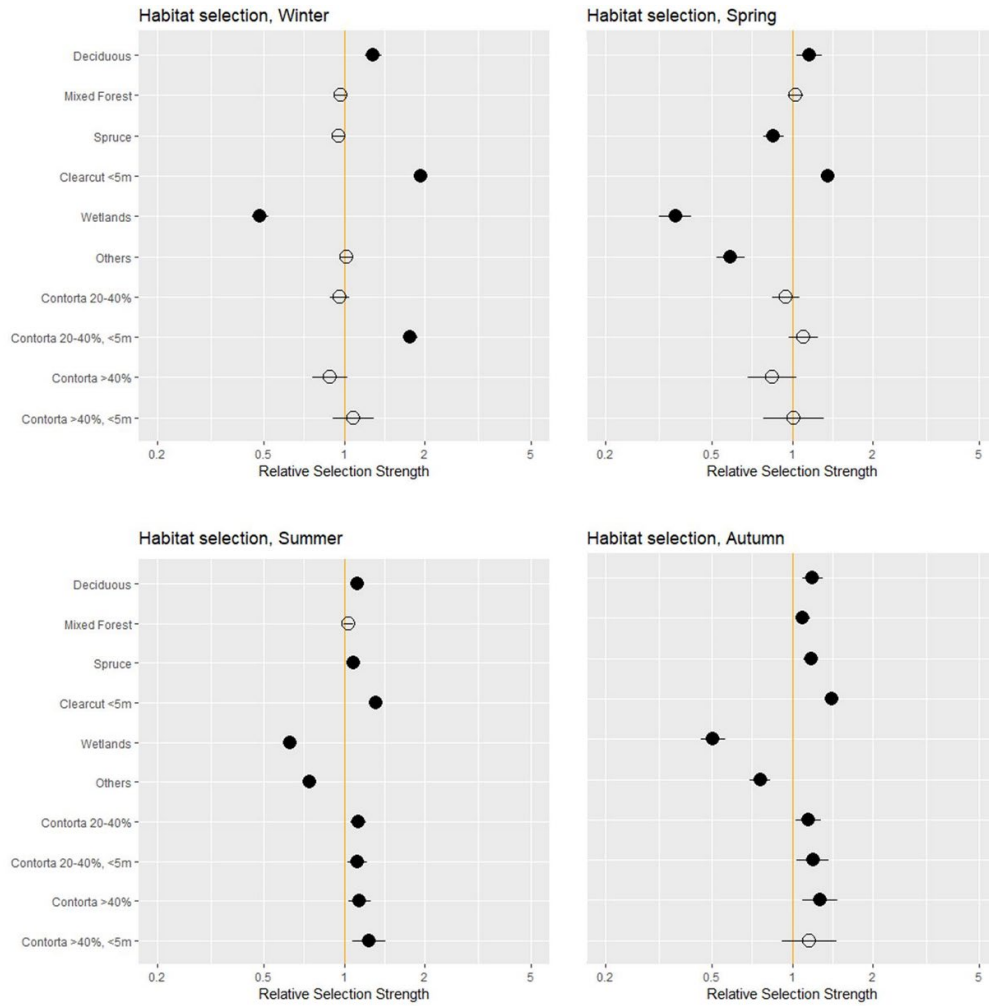


Figure 3. Estimates of the Relative Selection Strength on the habitat selection of adult moose (*Alces alces*) in each season Winter, Spring, Summer and Autumn as given by the conditional logistic regression, Junsele 2022-2024. *Pinus sylvestris* forest is the reference habitat (orange line). Values 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 indicate lower selection. The black horizontal bars represent the confidence intervals. If the confidence intervals do not cross the reference line, the selection is significant different from the reference habitat.

4. Discussion

Using position data of GPS-marked adult moose, I have examined moose habitat selection in areas with *P. contorta* forests on an annual and seasonal basis, with special focus on whether moose habitat selection differed between pine forests based on *P. contorta* (exotic) and the *P. sylvestris* (native).

My study suggests three main findings. First, Clearcuts/young forests are preferred habitat for moose year-round. Second, habitat selection included more forest habitats in summer and autumn. Third, moose selected for *P. contorta* forests, yet the selection differed between the proportion of *P. contorta*, depending on season.

Clearcut/young forests are preferred habitat for moose year-round

Throughout all seasons, the most important habitat for moose was Clearcuts/young forests in my study area. Previous studies have also shown that young successional forests are a habitat that is used a lot by moose within managed forest landscapes and especially during the winter months (Johnson & Rea 2024). The reason for this habitat choice is probably due to moose' food preferences during winter (Björneraas et al. 2011; Borowik et al. 2024) as animals mainly feed on young pine as woody browse during winter/spring (Allen et al 2016; Spitzer 2019). This aligns with previous studies where moose use coniferous forests during winter, most likely due to the forage choice during winter (Borowik et al. 2024). In my study, I only included clearcuts as a category representing the Swedish forest below 5 m in height and therefore could not examine habitat choice by moose between any tree species except two *P. contorta* habitats of Clearcut/young forest (height below 5 m). Therefore, I could not compare the habitat use between species in young successional forest, which could be very interesting, as the habitat clearcuts are a primary habitat during winter. Also, some studies show slight different results in foraging between the pine species, and comparing the habitat selection in younger successional forest could align with that. From the result, it can be observed that Clearcut/younger forests (below 5 m) are most popular (as both clearcut and one of the *P. contorta* habitats below 5 m were most used during winter). This finding suggests that forest in young successional stages is a very important habitat for moose during the year, but especially during winter.

In spring, Clearcut/young forests became less important in my study area, and even less during summer and autumn. The use of more mature forests aligns with the moose's food choice changes, and during spring, as they start to eat more deciduous and shrub species (Björneraas et al. 2011; Spitzer 2019)

Habitat selection included more forest habitats in summer and autumn

My results show that moose during summer and autumn have a more varied choice of habitat but still select for Clearcut/young forest the most. In a previous study, it was shown that moose preferred deciduous forest during summer and autumn (Borowik et al. 2024), and also that during summer the moose vary their habitat more than in winter (Nikula et al. 2004). In previous studies, it has been shown that the moose's habitat choice is influenced by ambient temperature, making moose willing to use older forests as protection from the sun and warmth when temperatures rise during the summer and warmer days (Van Beest et al. 2012; Melin et al. 2014). My results show that moose seem to select more mature forest during summer than during winter, which could be a result of moose using thermological shelter in older forest. The habitat selection from my results is also shown to be consistent with the moose forage choice during summer and autumn, as moose use more mature forest and deciduous trees during summer and autumn, as the forage is dominated by deciduous trees and shrubs during summer and towards the autumn more shrubs (Spitzer 2019).

*Moose selection for *P. contorta* forests in relation to the proportion of *P. contorta* and season.*

In my study, when comparing *P. sylvestris* and *P. contorta*, it can be observed that the moose' selection for *P. contorta* forests was never less than for *P. sylvestris*. However, the moose habitat use of *P. contorta* did differ some between the seasons.

During the winter, the clearcut/younger habitats (ie. Clearcut/young forest, two *contorta* habitats <5m) were most used by moose. In my study, however, I had only divided the clearcut/young forest habitats (>5m) into "clearcut, <5m" and two *contorta* habitats with different proportions ("20-40%", ">40%"). From my results, it can be observed that there was not a notable difference between the habitat selection of clearcut/young forest and the clearcut/young *P. contorta* habitat with a lower proportion. However, the *contorta* habitat with a higher proportion was avoided compared to the other two clearcut/young forest habitats. This suggests that the moose's habitat choice of the Clearcut/younger forests seems to be affected by the proportion of *P. contorta* and that during winter, moose prefer Clearcut/young forests but seem to avoid habitats with a higher proportion of *P. contorta*. The habitat selection of clearcut/young forest aligns with the forage preferences of moose during winter (Spitzer 2019; Spitzer et al. 2020) and their habitat choice could reflect on differences in foraging choice for *P. contorta* and *P. sylvestris* as previous studies have shown that moose browse slight more on *P. sylvestris* than *P. contorta* (Sjöberg & Danell 2001; Nilsson &

Cory 2010; Rea et al. 2014) or that moose browse equally on both pine species (Niemela & Danell 1988; Ball et al. 2001). Whereas the higher proportion of *P. sylvestris* could mean more forage availability for moose, forests containing a higher proportion of *P. contorta* likely contain less *P. sylvestris* trees, which could indicate that moose prefer browsing of *P. sylvestris* over *P. contorta* during winter. Yet, investigating browsing levels on *P. contorta* and *P. sylvestris* was beyond the scope of my study, and I suggest further research to examine that in moose management purpose.

In a study conducted on semidomesticated reindeer, there was no clear difference in selection between clearcut/young forests of *P. contorta* and *P. sylvestris* in winter; however, their forage availability (lichens) showed no difference (Horstkotte et al. 2024). This difference could be explained by the species' (moose and reindeer) different diets as reindeer primarily feed on lichen and moose primarily feed on pine during winter, as Clearcut/young forests did not differ in the lichen coverage (primarily food source for reindeer during winter) in *P. contorta* and *P. sylvestris*, respectively, forests (Horstkotte et al. 2024). The tendency of moose to avoid *P. contorta* habitats with a higher proportion of *P. contorta* in clearcut/young forest compared to reindeer could indicate food and habitat preferences between the pine species.

Planting *P. contorta* instead of *P. sylvestris* could lead to more browsing pressure on *P. sylvestris* in the broader landscape (e.g., in *P. sylvestris* dominated stands) as a result of a reduction in the forage availability of *P. sylvestris*, which could lead to more conflicts in forestry and management (Spitzer 2019). However, there could be other factors that affected the observed patterns in moose' habitat selection.

In winter, my study did not show a difference in moose habitat selection between the two mature pine species (i.e. *P. contorta*, and *p. sylvestris*). The moose could favor using the *P. contorta* due to snow and mobility. As studies show that the amount of snow affects the moose's habitat choice (Telfer 1970; Baskin & Danell 2003), where it can be seen that during the winter, there is less snow in forests than in open clearcuts (Telfer 1970). Moose could be favored by using the mature *P. contorta* since the denser canopies (Bäcklund et al. 2018; Sjöberg & Danell 2001) could result in lesser snow depth.

In a previous study on semidomesticated reindeer (*Rangifer tarandus*) it was discussed that one reason why reindeer avoided the older *P. contorta* forest in winter could be because of movement due to the lower growing branches of the *P. contorta* (Horstkotte et al. 2024) and mature forests of *P. contorta* have also been found to have more dead lying wood (Roberge & Stenbacka 2014). However, this argument seems unlikely for the moose habitat selection in my study, as my results show that the moose used the mature *P. contorta* forests more likely than the mature *P. sylvestris* forest during all seasons and does not seem to affect the

moose habitat selection due to mobility. It would be interesting to investigate why the moose's habitat choice was not affected by the different mature pine tree species during winter compared to semidomesticated reindeer.

During the summer, all *P. contorta* habitats were used more than *P. sylvestris*. The reason could align with previous studies showing that moose use older, denser forest during warm summer days (Van Beest et al. 2012; Melin et al. 2014), as *P. contorta* has a denser canopy than *P. sylvestris* (Bäcklund et al. 2018; Sjöberg & Danell 2001), and therefore could be beneficial for thermoregulation and cover as less sunlight is passing through *P. contorta* canopies. Moose could therefore benefit from the denser canopy of the *P. contorta* during for example, warmer days. The moose's habitat choice does not seem to be negatively affected by the denser canopy and the reduction of light, neither in terms of possible changes in species in the understory (Roberge & Stenbacka 2014; Bäcklund et al. 2018), or the moose's mobility due to tree structural characteristics.

In the autumn, habitat selection by moose was similar to summer, and all mature *P. contorta* habitats significantly higher use than *P. sylvestris*. This indicates that in this case the *P. contorta* is not negatively affecting the moose; instead, a preferable habitat during summer and autumn. The mature *P. contorta* forests are a preferable habitat for moose than *P. sylvestris* during autumn and could be because of the denser canopies of *P. contorta* forests or as thermological shelter.

If moose prefer foraging on *P. sylvestris*, it could lead to forestry planting more *P. contorta* in areas with moose browsing problems, leading to an advantage for forestry. However, it could potentially lead to more problems with foraging on *P. sylvestris* nearby, leading to an economic problem for forest owners. The moose could also be affected by the forage availability during winter if the *P. contorta* is less preferred than *P. sylvestris*. The fact that moose prefer mature *P. contorta* during summer and autumn could be an advantage for moose. Further studies could investigate what affects this habitat choice, could it be the temperature or food availability.

Methodological limitations

A weakness in my study is that the Clearcut/younger forest habitats are only divided into clearcut/young forest and two different *P. contorta* habitats. To get a better result, the Clearcut/young forest habitat could have been divided into different tree species to have the chance to study the difference between *P. contorta* and *P. sylvestris* use in Clearcut/young forests. To be able to answer my questions even better, the habitats could have been divided into more habitat classes, such as dividing the habitat Clearcut/young forest not only into different tree species, but as well as into different age classes, to see if the moose use different ages of forest at different times.

Future research

Future research could therefore perform further studies of how different *P. contorta* compositions can influence moose habitat selection and foraging behavior in clearcut/young forests to make management strategies. It would also be interesting to study night or day use of *P. contorta* to see if there is any pattern of habitat choice and if moose use the older *P. contorta* forest habitat during the daytime in the summer to avoid the heat as one study showed that moose move into denser canopies during hot summer days (Van Beest et al. 2012; Melin et al. 2014). These findings can impact the forest management and moose management.

5. Conclusion

This study found that moose overall preferred the habitats Clearcut/young forests, of all habitats, during all seasons. However, the Clearcut/young forests habitats were highly selected during winter, probably due to forage availability, as moose during winter primarily feed on pine. During the summer and autumn, moose had a more varied habitat selection, which suggests that the old forest became more preferred. This finding may be due to the thermoregulation and the diet changes between the seasons. When comparing the habitat selection between *P. contorta* and *P. sylvestris*, the results show that moose during summer and autumn prefer *P. contorta* compared to *P. sylvestris* in mature forests. This could be due to the two pine species structural differences. In previous studies, it has been shown that moose use older, denser forests during summer for thermal shelter, and *P. contorta* has a denser canopy, which could lead to a more preferred habitat during warm summer days.

With my result, I could not define if there was a difference in habitat selection between *P. contorta* and *P. sylvestris* in Clearcut/young forest during winter, however, moose avoided habitats with a higher proportion of *P. contorta*, which could indicate that moose prefer habitats with less *P. contorta*. This aligns with studies showing that moose prefer *P. sylvestris* as forage compared to *P. contorta*.

Abbreviations

Abbreviation	Description
P. contorta	Pinus contorta
P. sylvestris	Pinus sylvestris

References

- Allen, A.M., Månsson, J., Sand, H., Malmsten, J., Ericsson, G. & Singh, N.J. (2016). Scaling up movements: from individual space use to population patterns. *Ecosphere*, 7 (10), e01524. <https://doi.org/10.1002/ecs2.1524>
- Apollonio, M., Andersen, R. & Putman, R. (red.) (2010). *European ungulates and their management in the 21st century*. Cambridge University Press.
- Ball, J.P. & 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. *Scandinavian Journal of Forest Research*, 17 (5), 427–435. <https://doi.org/10.1080/028275802320435441>
- Ball, J.P., Nordengren, C. & Wallin, K. (2001). Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology*, 7 (1), 39–47. <https://doi.org/10.2981/wlb.2001.007>
- Baskin, L.M. & Danell, K. (2003). *Ecology of ungulates: a handbook of species in Eastern Europe and Northern and Central Asia*. Springer.
- Borowik, T., Kowalczyk, R., Ratkiewicz, M., Maślanko, W., Duda, N. & Żmihorski, M. (2024). A highly variable habitat selection in moose across diel and seasonal scales. *Movement Ecology*, 12 (1), 69. <https://doi.org/10.1186/s40462-024-00508-3>
- Bäcklund, S., Jönsson, M., Strengbom, J. & 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. *Scandinavian Journal of Forest Research*, 33 (3), 245–254. <https://doi.org/10.1080/02827581.2017.1364785>
- Van Beest, F.M., Van Moorter, B. & Milner, J.M. (2012). Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour*, 84 (3), 723–735. <https://doi.org/10.1016/j.anbehav.2012.06.032>
- Björneraas, K., Solberg, E.J., Herfindal, I., Moorter, B.V., Rolandsen, C.M., Tremblay, J., Skarpe, C., Sæther, B., Eriksen, R. & Astrup, R. (2011). Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology*, 17 (1), 44–54. <https://doi.org/10.2981/10-073>
- Bäcklund, S., Jönsson, M., Strengbom, J. & 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. *Scandinavian Journal of Forest Research*, 33 (3), 245–254. <https://doi.org/10.1080/02827581.2017.1364785>
- Elfving, B., Ericsson, T. & Rosvall, O. (2001). The introduction of lodgepole pine for wood production in Sweden — a review. *Forest Ecology and Management*, 141 (1–2), 15–29. [https://doi.org/10.1016/S0378-1127\(00\)00485-0](https://doi.org/10.1016/S0378-1127(00)00485-0)
- Engelmark, O., Sjöberg, K., Andersson, B., Rosvall, O., Ågren, G.I., Baker, W.L., Barklund, P., Björkman, C., Despain, D.G., Elfving, B., Ennos, R.A., Karlman, M., Knecht, M.F., Knight, D.H., Ledgard, N.J., Lindelöw, Å., Nilsson, C., Peterken, G.F., Sörlin, S. & Sykes, M.T. (2001). Ecological effects and management aspects of an exotic tree species: the case of lodgepole pine in Sweden. *Forest Ecology and Management*, 141 (1–2), 3–13. [https://doi.org/10.1016/S0378-1127\(00\)00498-9](https://doi.org/10.1016/S0378-1127(00)00498-9)
- Hagner, S. (2005). *Skog i förändring: vägen mot ett rationellt och hållbart skogsbruk i Norrland ca 1940-1990*. Kungl. Skogs- och lantbruksakademien.
- Horstkotte, T., Sandström, P., Neumann, Skarin, A., Adler, S., Ullrika, R. & Sjögren, J. (2024). Semi-domesticated reindeer avoid winter habitats with exotic tree species *Pinus contorta* - ScienceDirect. <https://www.sciencedirect.com/science/article/pii/S0378112723002967> [2024-12-01]
- Horstkotte, T., Sandström, P., Neumann, W., Skarin, A., Adler, S., Roos, U. & Sjögren, J. (2023). Semi-domesticated reindeer avoid winter habitats with exotic tree species

- Pinus contorta*. *Forest Ecology and Management*, 540, 121062.
<https://doi.org/10.1016/j.foreco.2023.121062>
- Jacobson, S. & Hannerz, M. (2020). Natural regeneration of lodgepole pine in boreal Sweden. *Biological Invasions*, 22 (8), 2461–2471.
<https://doi.org/10.1007/s10530-020-02262-0>
- Johnson, C.J. & Rea, R.V. (2024). Response of moose to forest harvest and management: a literature review. *Canadian Journal of Forest Research*, 54 (4), 366–388.
<https://doi.org/10.1139/cjfr-2023-0158>
- Länsstyrelsen Västernorrland (2025). *Älgjakt. Länsstyrelsen*. [text].
<https://www.lansstyrelsen.se/vasternorrland/djur/jakt-och-vilt/algjakt.html> [2025-04-14]
- Länsstyrelsen (2025). *Älgjakt. Länsstyrelsen*.
<https://www.lansstyrelsen.se/vasternorrland/djur/jakt-och-vilt/algjakt.html> [2025-04-14]
- Melin, M., Matala, J., Mehtätalo, L., Tiilikainen, R., Tikkanen, O., Maltamo, M., Pusenius, J. & Packalen, 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 Biology*, 20 (4), 1115–1125. <https://doi.org/10.1111/gcb.12405>
- Naturvårdsverket (2023). *Nationella marktäckedata 2018 basskikt*. (Produktbeskrivning, Utgåva 2.3)
- Neumann, W., Stenbacka, F., Jatko, M. & Ericsson, G. (2023). *Slutrapport GPS-märkta älgar i Haradsområde 2020-2023*. (Rapport (Sveriges lantbruksuniversitet, Institutionen för vilt, fisk och miljö), 2023:3). Sveriges lantbruksuniversitet, Institutionen för vilt, fisk och miljö.
- Niemela, P. & Danell, K. (1988). Comparison of Moose Browsing on Scots Pine (*Pinus sylvestris*) and Lodgepole Pine (*P. contorta*). *The Journal of Applied Ecology*, 25 (3), 761. <https://doi.org/10.2307/2403744>
- Nikula, A., Heikkinen, S. & Helle, E. (2004). Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. *Wildlife Biology*, 10 (2), 121–135.
<https://doi.org/10.2981/wlb.2004.017>
- Nilsson, P. & Cory, N. (2010). Skogsdata 2010: aktuella uppgifter om de svenska skogarna från Riksskogstaxeringen: tema: contortatall i Sverige. Institutionen för skoglig resurshushållning, Sveriges lantbruksuniversitet. *Skogsdata*, (2010).
<https://res.slu.se/id/publ/30712> [2025-03-04]
- Rea, R.V., Hjeljord, O. & Härkönen, S. (2014). Differential selection of North American and Scandinavian conifer browse by northwestern moose (*Alces alces andersoni*) in winter. *Acta Theriologica*, 59 (2), 353–360. <https://doi.org/10.1007/s13364-013-0170-9>
- Roberge, J.-M. & Stenbacka, F. (2014). Assemblages of epigaeic beetles and understory vegetation differ between stands of an introduced pine and its native congener in boreal forest. *Forest Ecology and Management*, 318.
<https://doi.org/10.1016/j.foreco.2014.01.026>
- Telfer, E. (1970). Winter Habitat Selection by Moose and White-Tailed Deer. *The Journal of Wildlife Management*, (34(3)), 553–559. <https://doi.org/Available at: https://www.jstor.org/stable/379886>
- Signer, J., Fieberg, J. & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution*, 9 (2), 880–890. <https://doi.org/10.1002/ece3.4823>
- Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N. & Ericsson, G. (2012). From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, 22 (7), 2007–2020. <https://doi.org/10.1890/12-0245.1>

- Sjöberg, K. & Danell, K. (2001). Introduction of lodgepole pine in Sweden — ecological relevance for vertebrates. *Forest Ecology and Management*, 141 (1–2), 143–153. [https://doi.org/10.1016/S0378-1127\(00\)00497-7](https://doi.org/10.1016/S0378-1127(00)00497-7)
- SLU (2024). *Skogsdata 2024*: aktuella uppgifter om de svenska skogarna från SLU Riksskogstaxeringen. Umeå: Sveriges lantbruksuniversitet,.
- SMHI (2024). *Månads-, årstids- och årskartor | SMHI. SMHI.* <https://www.smhi.se/data/meteorologi/kartor/normal/arstid-start/var> [2024-12-13]
- Spitzer, R. (2019). *Trophic resource use and partitioning in multispecies ungulate communities*. Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies. <https://publications.slu.se/?file=publ/show&id=30712> [2024-11-10]
- 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. & Widemo, F. (2023). Macro-nutritional balancing in a circumpolar boreal ruminant under winter conditions. *Functional Ecology*, 37 (5), 1256–1268. <https://doi.org/10.1111/1365-2435.14296>
- Spitzer, R., Felton, A., Landman, M., Singh, N.J., Widemo, F. & Cromsigt, J.P.G.M. (2020). Fifty years of European ungulate dietary studies: a synthesis. *Oikos*, 129 (11), 1668–1680. <https://doi.org/10.1111/oik.07435>
- Stephens, S.S. & Wagner, M.R. (2007). Forest Plantations and Biodiversity: A Fresh Perspective. *Journal of Forestry*, 105 (6), 307–313. <https://doi.org/10.1093/jof/105.6.307>
- Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, 2 (1), 4. <https://doi.org/10.1186/2051-3933-2-4>
- Van Moorter, B., Singh, N.J., Rolandsen, C.M., Solberg, E.J., Dettki, H., Pusenius, J., Månsson, J., Sand, H., Milner, J.M., Roer, O., Tallian, A., Neumann, W., Ericsson, G. & Myrsterud, A. (2021). Seasonal release from competition explains partial migration in European moose. *Oikos*, 130 (9), 1548–1561. <https://doi.org/10.1111/oik.07875>

Acknowledgements

I would like to thank my supervisor Wiebke Neumann for all the guidance and help during my writing on my master thesis, and especially for guidance in R Studio. I would also like to thank both Wiebke Neuman and Fredrik Stenbacka for discussing ideas and coming up with this interesting thesis idea!

Finally, I want to thank all my good friends who supported me and shared ideas with me when I was stuck in my work.

Popular science summary

For many years, the *Pinus contorta* pine has been a discussed tree species. It grows fast and are robust, but how does it affect wildlife. In Sweden, the species was introduced in the 1920s in order to compensate for a potential shortage of future hours. Since the 1970s, *Pinus contorta* has been planted and used for production purposes in Swedish forestry due to its favorable production characteristics. However, the pine species *Pinus contorta* is an exotic species in the Swedish landscape and has characteristics that differ from the native *Pinus sylvestris*, which could affect wildlife habitat selection and food choice, as previous studies have shown that there are some species that have shown a difference in use between these pine species. Since the pine forest is a key habitat for moose all year round, and especially as a food source during the winter, it is essential to study how moose are affected by *Pinus contorta* habitat. To check how the moose's habitat choice is affected in forests with *Pinus contorta*, a study was conducted on 29 GPS tagged moose in Västerbotten county, located in Sweden. It was performed with a statistical model, step selection function (SSF) and conditional regression to analyse the habitat selection from GPS data.

The study showed that moose generally used mostly clearcut/young forest, and that it was the most used habitat over all seasons. The clearcut/young forest habitat was found to be most important for moose during the winter. This is consistent with the moose's food choice during the winter, as moose mostly feed on young pine and there are studies showing that moose prefer *Pinus sylvestris* to *Pinus contorta* as forage.

My study showed that moose avoided Clearcut/young forest with a higher proportion of *Pinus contorta* compared to Clearcut/young forests with a lower proportion of *Pinus contorta*, which might suggest that food selection is a factor. Potentially, this could lead to increased grazing pressure on nearby pine forests if an area contains a lot of *Pinus contorta*, which would be an economic advantage. However, moose avoiding *Pinus contorta* plantation might be beneficial for forest owners in areas with a lot of moose damage in young pine stands, to be able to plant *Pinus contorta* instead.

However, during summer and fall, older forests became more important, the moose preferred the older *Pinus contorta* forests in contrary to the native *Pinus sylvestris* forests. which could be a result of the *Pinus contorta*'s different characteristics with a denser canopy than *p. sylvestris*, possibly resulting in thermal cover.

This study showed that *Pinus contorta* can both be rejected and preferred as a habitat depending on the season.

Appendix 1

Table 2 Reclassified habitat from NMD map (Pine, Spruce, Deciduous, Mixed, Clear cut, Wetland and Other), including definition, code NMD (Naturvårdsverket 2023).

	Definition	NMD code
Pine		
Pine forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of the crown cover consists of pine. Trees are higher than 5 meters.	111
Pine forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where >70% of the crown cover consists of pine. Trees are higher than 5 meters.	121
Spruce		
Spruce forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of the crown cover consists of spruce. Trees are higher than 5 meters.	112
Spruce forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where >70% of the crown cover consists of spruce. Trees are higher than 5 meters.	122
Decidius		
Deciduous forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of the crown cover consists of deciduous trees (primarily birch, alder and/or aspen). Trees are higher than 5 meters.	115
Deciduous hardwood forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which >50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.	116
Deciduous forest with deciduous hardwood forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which 20 - 50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.	117
Deciduous forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where >70% of the crown cover consists of deciduous trees (primarily birch, alder and/or aspen). Trees are higher than 5 meters.	125
Deciduous hardwood forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which >50% is broad leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.	126

Deciduous forest with deciduous hardwood forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which 20 - 50% is broad leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.	127
Mixed		
Mixed coniferous not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of consists of pine or spruce, but none of these species are >70%. Trees are higher than 5 meters.	113
Mixed forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where neither coniferous nor deciduous crown cover reaches >70%. Trees are higher than 5 meters.	114
Mixed coniferous on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where >70% of consists of pine or spruce, but none of these species are >70%. Trees are higher than 5 meters.	123
Mixed forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where neither coniferous nor deciduous crown cover reaches >70%. Trees are higher than 5 meters.	124
clear-cut		
Temporarily non-forest not on wetland	Open and re-growing clear-felled, storm-felled or burnt areas outside of wetlands. Trees are less than 5 meters.	118
Temporarily non-forest on wetland	Open and re-growing clear-felled, storm-felled or burnt areas on wetlands. Trees are less than 5 meters.	128
Wetland		
Open wetland	Open land where the water for a large part of the year is close by, in or just above the ground surface.	2
Other		
Arable land	Agricultural land used for plant cultivation or kept in such a condition that it can be used for plant cultivation. The land should be able to be used without any special preparatory action other than the use of conventional farming methods and agricultural machinery. The soil can be used for plant cultivation every year. Exceptions can be made for an individual year if special circumstances exist.	3
Non-vegetated other open land	Other open land that is not wetland, arable land or exploited vegetation-free surfaces and has less than 10% vegetation coverage during the current vegetation period. The ground can be covered by moss and lichen.	41
Vegetated other open land	Other open land that is not wetland, arable land or exploited vegetation-free surfaces and has more than 10% vegetation coverage during the current vegetation period.	42
Artificial surfaces, building	A durable construction consisting of roofs or roofs and walls and which is permanently placed on the ground or	51

	partly or wholly below ground or is permanently placed in a certain place in water and is intended to be designed so that people can stay in it.	
Artificial surfaces, not building or road/railway	Artificial open and vegetation-free surfaces that are not building or road/railway.	52
Artificial surfaces, road/railway	Road or railway.	53
Inland water	Lakes or watercourses.	61
Marine water	Sea, ocean, estuaries or coastal lagoons.	62
Outside mapping area	Outside the borders of Sweden and the Exclusive Economic (EEZ) Zone	0

Appendix 2

Table 3. Start and ending of the seasons of the study period, from Arrival maps (SMHI 2024)

Seasons	Start	End
Winter	2021-10-12	2022-04-16
Spring	2022-04-17	2022-05-20
Summer	2022-05-21	2022-08-27
Autumn	2022-08-28	2022-11-11
Winter	2022-11-12	2023-04-10
Spring	2023-04-11	2023-05-18
Summer	2023-05-19	2023-09-13
Autumn	2023-09-14	2023-10-17
Winter	2023-10-18	2024-04-08

Publishing and archiving

Approved students' theses at SLU can be published online. As a student you own the copyright to your work and in such cases, you need to approve the publication. In connection with your approval of publication, SLU will process your personal data (name) to make the work searchable on the internet. You can revoke your consent at any time by contacting the library.

Even if you choose not to publish the work or if you revoke your approval, the thesis will be archived digitally according to archive legislation.

You will find links to SLU's publication agreement and SLU's processing of personal data and your rights on this page:

- <https://libanswers.slu.se/en/faq/228318>

☒ YES, I, Maria Bodlund, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this.

☐ NO, I/we do not give my/our permission to publish the full text of this work. However, the work will be uploaded for archiving and the metadata and summary will be visible and searchable.