Hedmark University College

Faculty of Applied Ecology and Agricultural Sciences

Floris Smeets

Master thesis

Moose *(Alces alces)* foraging decisions and habitat use during winter, at five spatial scales.

Master in Applied Ecology

2014

15.05.2014	Evenstad, Norway	Floris Smeets
Date	Place	Signature

I agree that this thesis is for loan in the library YES ☒ NO ☐

I agree that this thesis is open accessible in Brage YES ☒ NO ☐

Abstract

1. Forage availability is a strong tool for predicting large herbivore distribution and habitat use throughout different spatial scales. Yet, no large scale study has been executed where real biomass availability of palatable tree species was used as tool to explain moose browsing decisions and habitat use through different spatial scales.

2. In the boreal forest of southern Norway, I measured moose habitat use as the number of moose pellet groups, moose browsing as the quantity and proportion of biomass consumed and habitat characteristics at five spatial scales i.e. regional (N=1), landscape (N=3), large community (N=61), small community (N=976) and individual tree level (N=8038). I used quantity of biomass available, altitude, tree density, number of moose pellet groups, Feeding Site Attractiveness Value, intensity of old browsing, cutting classes and tree species as variables to explain moose browsing decisions and habitat selection through the different spatial scales.

3. The data, for the two largest spatial scales, were compared. Statistical analyses were run for the three smallest scales. I compared the change in the estimates of the variables in the full models between large community and small community scale. Additionally, for the three smallest scales, the best models were selected based on lowest AIC values. For the two smallest spatial scales, the best models predicting whether browsing occurred or not were also selected on lowest AIC values.

4. During the winter of 2011-2012, I found that moose selected cutting class 2 forest stands for foraging, which accounted for 53.35% of the available biomass. Here they consumed 80.47% of the measured browsed biomass. Cutting class 3, which accounted for 28.09% of the available biomass, was mainly selected for cover but minimally for foraging. Further, habitat use decreased with an increase in altitude. Moose increased usage of large patches with an increase in quantity of biomass available and increase in tree densities. For small communities, previous browsing was also a significant predictor, i.e. moose selected for small patches with higher quantity of biomass available which had been browsed in previous years, within the selected large patches.

5. Species which were rare on regional and landscape scale, suffered higher browsing pressure than those which were abundant. Scots pine was the main food source, accounting for 84.74% of the measured consumed biomass. Quantity and proportion of biomass browsed from small and large patches containing rare species, did not significantly differ from those without rare species. With an increase in previous browsing in small patches and on individual trees, the chance of being browsed increased. Both large and small communities showed an increase in quantity and proportion of biomass browsed with an increase in previous browsing. Yet, on individual tree level, previous browsing failed to explain quantity and proportion of biomass browsed.

6. To be able to reduce moose browsing pressure on young Scots pine stands, I advise increasing the forage availability in cutting class 2 stands and reducing the wintering moose densities. Creating disturbance by increasing predation risk could be an effective tool in reducing browsing pressure on young forest stands, as has been proven in Yellowstone National Park. However, as large carnivores and their existence in Norway are the base of ongoing conflicts, this potential solution may not be considered at the present time.

Key-words: moose, biomass, browsing, forage, spatial scale, landscape, community

Table of content

1. Introduction

In Fennoscandia moose is the largest herbivore, is found in great numbers, is the cause for severe damage on young Scots pine forest stands (Cederlung et al., 1980; Lavsund, 1987; Fremming, 1999) and is capable of suppressing highly favoured palatable tree species by browsing (Heikkilä and Härkönen, 1993, 1996; Solbraa, 2008; van Beest et al., 2010). In winter time the diet of a moose in Fennoscandia consists for the major part out of the woody shoots of Scots pine, birch species, Salix species, Willow, Aspen and Rowan (Wam and Hjeljord, 2010). With a daily average intake between eight and sixteen kilogram of wet biomass per day per moose (Sæther et al., 1992), parts of winter habitats are heavily negative affected (Cederlung et al., 1980; Lavsund, 1987; Fremming, 1999; Gundersen et al., 2004; Franzmann and Schwartz, 2007). One of the main effects is the loss of potential timber by browsing of the leading stem and the majority of lateral shoots of young trees (Gill, 1992; Fremming, 1999). This conflict has been the base of decennia of research, yet no major solutions have been found. Several studies pointed out that forage availability is a strong tool for predicting large herbivore distribution and habitat use throughout different spatial scales (Senft et al., 1987; Ward and Saltz, 1994; Morellet and Guibert, 1999; Månsson et al., 2007; Månsson, 2009; Månsson et al., 2012). Still no large scale study has been executed where real biomass availability of palatable tree species was used as tool to explain moose browsing decisions through different spatial scales. Often commercial Scots pine stands were the centre of these studies since they are supposedly the main source of winter food for moose and here the damage on commercial timber is the greatest (Fremming, 1999). However, moose winter home ranges, without supplementary winter feeding (van Beest et al., 2010), are spread over a much larger area (van Beest et al., 2011). By only sampling the favored feeding sites, one can hardly say anything about the rest of the habitat of large herbivores (Senft et al., 1987; Ward and Saltz, 1994; Månsson et al., 2007).

The study of Senft et al. (1987) on large herbivore foraging, is used in many large herbivore studies as a foundation to explain foraging behavior and decisions. The study showed large herbivore foraging mechanisms to be different from the optimal foraging theory. Optimal foraging theory assumes that animals learn about the forage availability distribution and use this optimally by distributing equally or proportionally over the available food resources (Pyke, 1984). This theory is based on studies on species which use different strategies, compared to herbivores, to find and consume food such as predators which feed on prey distributed in discreet patches and rich of nutrients (Belovsky, 1984; Senft et al., 1987). Food resources for large herbivores are generally distributed less patchy, more widely through over the landscape and vary in nutrition richness (Westoby, 1974; Senft et al., 1987). In order to study foraging behavior and foraging decisions of large herbivores, the influence of the composition of the landscape, from small scale patches up to large scale habitat types, has to be taken into account, i.e. the importance of hierarchy theory. Meaning, different foraging decisions can be explained by taking spatial scaling into account.

1.1 Herbivory and spatial scaling

Belovsky (1978), Senft et al. (1987) , Andersen and Saether (1992), Månsson et al. (2007) and Månsson (2009), pointed out that spatial scaling plays a key role when trying to explain large herbivore foraging patterns and habitat choices. Senft et al. (1987) has divided the different spatial scales into individual plants, plant communities (patches of plants), landscape systems and regional systems. This study follows these spatial scales almost identically, but divides communities into large communities (large patches) and small communities (large patches). Large communities are large patches within a landscape, such as forest stands. Small communities are small patches within large communities, such as a group of trees.

1.1.1 Regions

On regional scale, foraging decisions are made is a very low frequency. These decisions are coming from large differences in the animals habitat, such as seasonal changes which causes long term drought or snow coverage, decreasing forage availability, forcing animals to move to areas. Senft et al. (1987) described this as landscape-departure rather than landscape selection.

Seasonal migration is observed in many wild ranging animal species (Berger, 2004). Often it is the movement between a distinct summer and winter home range and is induced by the spatiotemporal variation in resource abundance during the different seasons (Fryxell et al., 1988; Lundberg, 1988; Hebblewhite et al., 2008; Bischof et al., 2012). Contrary to Senft et al. (1987), these studies do not describe the seasonal migration as habitat departure but as a strategy to maximize fitness by selecting areas with high food quality and quantity. Large herbivores are thought to follow the available forage quantity and quality through the seasons. This behavior is described in the Forage Maturation hypothesis (FMH), which proposes that ungulate migration is driven by the tradeoff between high forage quality and quantity (McNaughton, 1985; Fryxell et al., 1988; Hebblewhite et al., 2008). The tradeoff is induced by the decline in forage quality during the growth of plants i.e. during growing biomass, and on the other hand forage quantity available declines at low biomass after maturation of plants. Therefore, ungulates select for areas with intermediate forage quantity and quality, considering that areas with highest forage quantity lag in quality and areas with highest forage quality lag in quantity. Areas with intermediate forage quality and quantity are found in growing plant communities. Since growth of plants has a temporal and spatial difference, ungulates are thought to follow the growth stage which has an adequate mixture of forage quantity and quality, leading to the movement within the selected home range (Hebblewhite et al., 2008; Bischof et al., 2012). Contrary to this, moose in Scandinavia select during winter young commercial Scots pine forest stands which contain extremely high quantities of forage (Lavsund, 1987; Andren and Angelstam, 1993; Heikkilä and Härkönen, 1996; Fremming, 1999; Ball and Dahlgren, 2002; Månsson et al., 2007; Solbraa, 2008). These forests have timber production as primarily goal, which results in large stands with high quantities of young trees producing easy moose food (Löyttyniemi, 1985; Andren and Angelstam, 1993; Heikkilä and Härkönen, 1993, 1996; Ball and Dahlgren, 2002; Bergqvist et al., 2003).

Many migratory species, parallel to the seasonal migration, have to switch their diet because the spatial and temporal variation affects the composition of the available palatable forage (Belovsky, 1981; Augustine and McNaughton, 1998; Kielland, 2001). Many large ungulate herbivores forage on leaves, buds, parts of green shrubs, berries, grasses and other green plant tissue during the summer (Peterson, 1955; Dahlberg and Guettinger, 1956; Belovsky, 1981; Wam and Hjeljord, 2010), but switch their diet to woody shoots during winter (Augustine and McNaughton, 1998). Because of the seasonal migration, this means that there is a large difference in how herbivores affect the plant community in the two chosen seasonal home ranges. Especially when there is a large difference between summer and winter home range size, i.e. herbivore densities will differ between the different seasons. Due to the increase in herbivore density in the smaller home range, browsing pressure increases on the palatable plant species. The season where food quantity is less abundant, of lower quality and harder to reach, animal densities increase since smaller suitable living space is available (Mysterud et al., 1999; Lesage, 2000).

1.1.2 Landscapes

On landscape scale large herbivores match their forage selection to forage availability in the landscape. There is a linear relation between the food preference and the relative abundance of that food source. This has been found for a broad selection of herbivore species, such as domestic sheep and cattle, mule deer, wapiti, feral horses, North American bison, eastern grey kangaroos and wallaroos (Hunter, 1962; Taylor, 1982; Coppock et al., 1983; Duncan, 1983; Hanley, 1984; Senft et al., 1987). The home range boundaries of large herbivores are often set by features of the landscape they live in (Senft et al., 1987). Home range size of large herbivores is depending on the body size of the species and the demand of an adequate quantity and quality of forage for the individual (McNab, 1963; Harestad and Bunnell, 1979; Swihart et al., 1988; van Beest et al., 2011), i.e. with an increase in body size, home range size increases. Additionally, latitude, habitat productivity, social organization, behavior and seasonal timing play important roles in determining home range size (Lindstedt et al., 1986). van Beest et al. (2011) pointed out that there is variation in home range size with spatiotemporal scale, where climate stochasticity and variation in forage availability play an important role.

1.1.3 Large communities

On large community scale (large patches in the landscape), forage selection by large herbivores is explained to be the consumption of maximal quantity and adequate quality of forage. Selecting for quality is time consuming, leading to a decrease in quantity of food consumed. With a decrease in forage quality in the habitat, large herbivores can momentary maximize quantitative consumption (Senft et al., 1987). Meaning, they have to eat food items of low quality in order to maintain fitness (Westoby, 1974). Foraging selectivity and the degree of biomass consumed per plant species by ungulate herbivores, is thereby influenced by the relative and absolute abundance of that plant species in the home range (Augustine and McNaughton, 1998).

Abundance of high quality forage and shelter from predators are rarely found on the same place (Hebblewhite et al., 2008), therefor ungulates move between different habitat types (large patches) on a daily bases (Demarchi and Bunnell, 1995; Godvik et al., 2009). The highest quality of forage is often found in large open patches, which do not provide cover from predation or human disturbance (Hebblewhite et al., 2008; Godvik et al., 2009). In Norway during winter, moose forage in large young forest stands which provide high quantities of forage (Löyttyniemi, 1985; Andren and Angelstam, 1993; Heikkilä and Härkönen, 1993; Fremming, 1999; Ball and Dahlgren, 2002; Solbraa, 2008), yet these stands do not provide much cover from large predators and human disturbance (Demarchi and Bunnell, 1995; Hebblewhite et al., 2008; Godvik et al., 2009). Therefor moose also select for large patches which do not provide high quality or quantity of forage, but cover (Herfindal et al., 2009), i.e. habitat use and selection is not only explained by the distribution of forage quality and quantity.

Additionally, selection of large patches can be due to environmental factors such as snow cover and plant production (Poole and Stuart-Smith, 2006; Godvik et al., 2009). Young forest stands are used more early in the growing season due to the temporal higher nutrient quality (Hjeljord et al., 1990; Boyce et al., 2003) and higher density of forage (Hjeljord et al., 1990; Månsson, 2009). Contrary, older forest stands are used more intensely during winter because of the lower snow depth. Here animals use less energy moving and have better access to dwarf shrubs as food resource (Parker et al., 1984). Moose in Fennoscandia move during winter down to lower altitudes where snow depths are lower (Gundersen et al., 2004; Franzmann and Schwartz, 2007) and still utilize open young forest stands for foraging (Löyttyniemi, 1985; Andren and Angelstam, 1993; Heikkilä and Härkönen, 1993; Fremming, 1999; Ball and Dahlgren, 2002; Solbraa, 2008).

1.1.4 Small communities

On small community scale (small patches in the landscape), large herbivores select forage with the goal to maximize nutrient intake(Belovsky, 1984; Senft et al., 1987). In this case the forage selection is nonlinear related to the abundance of the available forage(Senft et al., 1987), i.e. large herbivores maximize nutrient intake by selecting small patches with high quantity of forage available and maximize utilization of these patches. However, a study on moose browsing patterns in Sweden showed underutilization of small patches with high quantity of available forage (Månsson et al., 2007).

Machida (1979), Danell et al. (1985), Löyttyniemi (1985) and Bergqvist et al. (2003) described feeding loops for browsing herbivores, where the animals return to the same small patches which were browsed in previous years and re-browse these. The browsing from the previous years, results in an increase in nutrient values in the affected plants in the patch (Löyttyniemi, 1985; Augustine and McNaughton, 1998; Ball et al., 2000; Kielland, 2001), making them more palatable for the resulting years.

1.1.5 Individual trees

On individual tree scale, large herbivores select forage in a similar way as in small patches, they ty to maximize nutrient intake by selecting plants with high quantities of forage and utilize these maximally (Belovsky, 1984; Senft et al., 1987). Trees which have been browsed, are exposed to an increase in chance to be re-selected for browsing in following years (Machida, 1979; Danell et al., 1985; Löyttyniemi, 1985; Bergqvist et al., 2003). The intensity of herbivory on individual plants, depends for a large part on how palatable the species is (Augustine and McNaughton, 1998; Ball et al., 2000; Solbraa, 2008). Trees of highly palatable species can be heavily suppressed by browsing with death as possible result (Heikkilä and Härkönen, 1996; Augustine and McNaughton, 1998; Solbraa, 2008). So are moose in Fennoscandia known to be able to suppress Rowan, Aspen and Willow species since these species are highly preferred for forage (Heikkilä and Härkönen, 1996; Solbraa, 2008). The relative abundance of a species within the landscape is a very important factor explaining foraging intensity on individual plants, since rare palatable species will suffer high foraging pressure (Augustine and McNaughton, 1998). This is further explained in the following section.

1.2 Effects of herbivory on forage.

Ungulate herbivores can influence plant species within the selected home range by changing quantity, quality and composition of the foraged plant species (Bryant et al., 1991; Hobbs, 1996; Augustine and McNaughton, 1998). The intensity of influence on the plant species within a selected home range, depends on the degree of tissue loss, resource availability, the growing stage of the plant when being foraged by herbivores and the species specific responses to tissue loss. Plants respond in two different ways; regrowth from residual tissue or death of residual tissue (Crawley, 1983; Augustine and McNaughton, 1998). The response of the foraged plant depends on the tolerance of the specific specie's ability to use stored nutrient resources for regrowth (Haukioja et al., 1990; Honkanen et al., 1999; Millard et al., 2001). Evergreen trees species store during winter nitrogen in needles, whereas deciduous tree species store it in the roots. This makes evergreen species more vulnerable to winter browsing by large herbivores since larger quantities of nutrition are removed from the individual plants (Millard et al., 2001). So shows Scots pine a decrease in growth after being exposed to browsing (Långström and Hellqvist, 1991; Solbraa, 2008).

The composition of plant species within the home range, rather than the composition of plant species in small patches, affects the selectivity by limiting the options of forage available (Heikkilä and Härkönen, 1996). White-tailed deer for example, are capable to lower the abundance of palatable plant species which are found in low densities within the home range. However, when these same palatable plant species are existing in high abundance within the home range, the deer don't decrease the plant population (Augustine and McNaughton, 1998). Acknowledging this, one can say that selectivity for non-abundant palatable plant species is higher than selectivity for abundant palatable plant species when looking at home range scale. When looking at unpalatable plants species, a similar pattern is observed. Brandner et al. (1990) and Heikkilä and Härkönen (1996), observed large generalist herbivores avoiding patches in the landscape with an high abundance of unpalatable plant species. However, in landscapes where this unpalatable plant species was rare, the ungulate herbivores managed to suppress these plant species by selecting these species for forage in order to acquire the needed nutrients.

Herbivore selective foraging behavior is able to change the competitive ability between different plant species since different species differ in tolerance to herbivory, have different capabilities for regrowth and are differently affected in reproductive capability after being attacked by herbivores (McNaughton, 1985). This can lead to a change in plant species composition within plant communities. Van Hees et al. (1996) studied roe deer and red deer and Manseau et al. (1996) studied caribou. Both found that foraging behavior of the species, altered the plant species composition within the home range. Roe deer and red deer fed on

Pedunculate oak (Quercus robur), Silver birch (*Betula pendula*) and Beech (*Fagus sylvatica*). Due to the high tolerance to browsing by beech and the lower tolerance of the oak and silver birch, the roe deer and red deer decreased the species with low browsing tolerance and increased the species with high browsing tolerance. A similar result was found with caribou. They managed to decrease the abundance of slow growing lichens dramatically, however palatable shrubs and graminoids remained more constant or even increased in abundance. The speed and intensity in which species composition is altered is not only depending on ungulate density but also on selectivity. Augustine and McNaughton (1998) wrote:

"*Understanding the effect of ungulate density on plant communities is critical from a management perspective because setting animal density is 1 of the main tools wildlife managers can use to manipulate ecosystems. Changes in ungulate numbers alone cannot alter the relative abundance of a plant species if foraging selectivity and plant tolerance remain constant. In such a situation, herbivores will continue to have the same relative effect on the competitive abilities of different species at all levels of herbivore abundance. The only exception is when a particular species is never eaten by ungulates (e.g., spruce in boreal forests), in which case increasing herbivore density will increasingly favor the uneaten species*."

Selective foraging on young small individual trees determines the composition of the future mature stand, and is described as the strongest effect of large herbivores on tree vegetation (Vourc'h et al., 2002; Danell et al., 2003).

Acknowledging that herbivores can change the forage availability (Bryant et al., 1991; Hobbs, 1996; Augustine and McNaughton, 1998) one can conclude that forage selectivity can be changed by herbivore density due to changes in available forage quantity and quality. I.e. if herbivore densities increase, selectivity will decrease because of the decrease in forage quantity of preferred palatable species available per animal. However, on low herbivore densities, selectivity for preferred palatable species is highest, yet the low animal density may not affect the plant species significantly negative. At intermediate herbivore densities, selectivity for preferred palatable species can remain high, however it is likely that total amount of forage quantity foraged by the animals will have a significant effect on the species composition by changing competition between the present plant species (Marquis, 1974; Tilghman, 1989; Brown and Stuth, 1993; Augustine and McNaughton, 1998). High ungulate herbivore densities can potentially completely change the species composition within a community by selective foraging if all species in a given community are edible (Marquis, 1974; Healy, 1997; Augustine and McNaughton, 1998).

1.3 This study

The aim of this study is to point out how certain habitat characteristics on different spatial scales affect moose browsing decisions and habitat selection, with forage biomass playing a key role. I measured moose habitat use in number of moose pellet groups, moose browsing as quantity and proportion of biomass consumed and habitat characteristics on five different spatial scales i.e. regional, landscape, large community, small community and individual tree level. I used quantity of biomass available, altitude, tree density, number of moose pellet groups, Feeding Site Attractiveness Value, intensity of old browsing, cutting classes and tree species as explainer variables to explain moose browsing decisions and habitat selection through the different spatial scales.

I expect:

1. on landscape level moose densities to be higher in landscapes with a higher quantity of palatable biomass available and to be lower in landscapes with low quantity of palatable biomass available.

2. moose to use cutting class 2 forest stands for foraging, cutting class 3 forest stands for cover and foraging and to find minimum use of the other cutting class forest stands.

3. to find with an increase in altitude a decrease in habitat use, quantity of biomass browsed and proportion of biomass browsed.

4. moose to maximize nutrient intake by browsing larger quantities and proportions from individual trees and small patches which; a. have higher quantities of palatable biomass available, b. have been exposed to browsing in previous years.

5. species which are rare on regional and landscape scale to be heavily browsed and have the highest proportional loss of biomass on individual tree scale.

6. small communities, and in lesser extend large communities, containing rare tree species to be used more intensively and suffer higher browsing pressure compared to those without rare species.

2. Methods

2.1 Study area

The study was conducted during the summer of 2012 in the boreal forest of south-eastern Hedmark (Norway) in the surroundings of Trysil. Three study areas (Plassen, Ljørdalen and Gravberget) were selected, owned by separate private land owners and state-owned forest. All three study areas have timber and pulp production as objective and are intensively used by moose through the whole year. Moose is an important game species and hunted creating income for the land owners in issue. The forest consists mainly out coniferous tree species Scots Pine (Pinus sylvestris) and Norway Spruce (Picea abies) and deciduous tree species Silver birch (Betula pendula) and Downy birch (Betula pubescens). Additionally Aspen (Populous tremula), Rowan (Sorbus aucuparia), Willow (Salix spec.), Juniper (Juniperus communis), Alder (Alnus incana) are present, mainly in shrub form. Undergrowth is dominated by Bilberry (Vaccinium myrtillus), Cowberry (Vaccinium vitis-idaea), Heather (Calluna vulgaris) and Lichen.

2.2 Data collection

From the beginning of May until the end of June 2012, a group of eight persons collected the field data for eight consecutive weeks. In each study area, twenty quadrats of 500 x 500 meter were placed with maximum distance between each quadrat. Lakes and infrastructure were avoided when selecting the placement of the quadrats. Study area Ljørdalen had more ground surface, which made it possible to place twenty-one quadrats. Each quadrat consisted out of sixteen plots, which were placed with one hundred meter distance from each other along the outer ribs of the quadrat.

With the use of GPS devices, we approached each plot center as close as possible. If the plot would end up on a forest road, a building or into a lake or stream, the plot was moved twenty up to one-hundred meter into the quadrat. If the plot had to be moved more than one-hundred meter inside, we moved it twenty up to one hundred meter outside of the quadrat. Relocating of plots was done in the perpendicular direction of the rib of the quadrat where the plot was located on.

From each plot center, one-hundred squire meter circular plots were sampled for moose winter pellet groups (from here after referred to as moose pellet groups). Moose pellet groups from the preceding winter period, consisting out of a minimum of ten pellets, were counted and removed from the plot to avoid recounting.

From the same plot centers, fifty squire meter circular plots were sampled intensively to obtain forest features and details of the trees in the plot. Per plot the following data were collected: Cutting class of the stand where the plot was located in and counts of number of trees per tree species within the plot.

Cutting classes were:

0 = Non- forest (bog, meadow, rocks etc.)
1 = Cutting class 1 (clear cut; no regeneration yet)
2 = Cutting class 2 (tree height < 10 m)
3 = Cutting class 3 (tree height > 10 m)
4 = Cutting class 4 (forest mature for logging)
5 = Cutting class 5 (old growth forest)

Of each species the ten trees (with a minimum height of 0.5m) closest to the plot center the height was measured, accumulated browsing was estimated (see next page for accumulated browsing classes), number of un-browsed shoots and number of browsed shoots were counted and five bite diameters were measured in millimeter with one decimal accuracy. To avoid bias selections towards specific bite diameters by the fieldworkers, for trees with more than five bites the selection for measurements was done by randomly grabbing a branch of the tree and measuring the bites on this branch. If the branch did not count five bites, another branch was randomly selected and bites were measured. This was repeated until five bite diameters were measured.

Accumulated browsing is a measure of how the growth form of the tree has been affected by browsing during its life time. New browsing from this year does not count in this measure, only old browsing. Accumulated browsing classes were:

0 = no old browsing
1 = old browsing visible but growth form not changed
2 = old browsing visible and growth form of tree changed
3 = old browsing visible and growth form strongly changed (topiary)

To indicate the intensiveness of previous browsing on plot and quadrat level, I calculated the mean accumulated browsing for each plot and quadrat.

The altitude, in meters elevation, for each plot was taken from a Digital Elevation Map in ArcGIS10.1, with the use of GPS locations of the plot centers.

2.3 Spatial scales

For this study I used five different spatial scales, following similar scale sizes described in (Senft et al., 1987). The scales used, ranked from largest to smallest are;

- Region scale (N=1), consisting out of all data combined
- Landscape scale (N=3), consisting out of the data from each study area
- Large community / large patch scale (N=61), consisting out of the data from each quadrat
- Small community / small patch scale (N=976), consisting out of the data from each plot
- Individual plant scale (N=5448), consisting out of the data from each individual tree

2.4 Moose density

Moose densities for the landscape and study areas were calculated based on moose pellet group counts, number of moose pellet groups produced per moose per day and the length of the 2011-2012 winter. A moose is thought to produce a mean of 14 pellet groups per day during winter (Persson et al., 2000) and the winter we estimated to be 180 days. The densities were calculated with the following formula:

*Moose density (N/km²) = Mean number of moose pellet groups per plot / 14 / 180 * 10000*

2.5 Calculating biomass

To calculate biomass weights available and browsed, a second group of students collected a separate data set in the same three study areas. Since Picea abies and Alnus incana are rarely eaten by moose in our studied areas, these species were not included in this data collection. Tree species Pinus sylvestris, Betula pubescens, Betula pendula, Salix, Populus tremula, Sorbus aucuparia and Juniperus communis were sampled. Sampling was done by driving along forest roads, stopping each 500 meter, going 50 meter to the left and right from the road, chose the closest three trees of each species to sample. At each tree, they measured shoots at three height classes (0,3-1m, 1.1m-1.5m, 1.51m – 2m). At each height they measured the diameter (mm) and length (cm) of three random twigs at the bottom of the yearly shoot. If the closest trees did not have twigs below 2m height, more trees were measured until they had three times three observations at each height. They clipped one shoot from each height, from each tree and cut them at different diameters (1mm up to 12mm). Of each clipped shoot, the length and diameter was measured and collected from the field. For Pinus sylvestris the needles remained on the collected twigs, however for deciduous species leaves were removed. The twigs were dried at 105 degrees Celsius, for 48 hours and weighed individually. With this data, dry biomass weight to twig diameter regression curves were made for each sampled species (see appendix).

Dry biomass available in grams (from here after referred to as biomass available) was calculated by taking from each species from each study area 90% of the smallest bite diameters. The largest bite diameter of this selection was set to be the diameter of an available shoot of that species for that study area (Palo et al., 1992; Jia et al., 1995). Biomass available per tree was calculated by fitting the shoot diameters into the regression models and multiplying the outcome with the sum of N un-browsed shoots and N browsed shoots per tree.

Biomass browsed per tree was calculated by using the mean of the measured bite diameters on that individual tree and fitting them into associating regressions. If a tree measured more than five bites, the mean biomass of the five bites was multiplied with the total number of bites counted on that tree. Biomass available per plot was calculated by taking the sum of available biomass of the trees in the plot. If the number of trees of a species succeeded ten, the mean biomass available on the ten measured trees was multiplied with the total abundance of that species in the plot. Biomass available per quadrat was calculated by taking the sum of the biomass of the total biomasses calculated for the plots within that quadrat.

Proportion of biomass browsed was calculated on each spatial level by dividing the quantity of browsed biomass by the quantity of biomass available.

2.6 Feeding Site Attractiveness Value (FSAV)

Since not all tree species are equally preferred by moose for forage (Heikkilä and Härkönen, 1996; Solbraa, 2008), I calculated the Feeding Site Attractiveness Value (from here after referred to as FSAV) (Stokke, 1999) for each plot and quadrat. In order to calculate the FSAV values, a forage preference index (FPI) was calculated. To account for the difference in biomass composition between the three study areas, which influences the forage selectivity, the FPI values were calculated for each study area separately.

$$\text{FPI species } X = \frac{\text{Biomass browsed species } X \,/\, \text{Total biomass browsed}}{\text{Biomass available species } X \,/\, \text{Total biomass available}}$$

The FSAV for plot and quadrat scale consisted out of the sum of the products of the FPI of each species with its abundance within the plot or quadrat.

$$\text{FSAV plot } X = (\text{FPI species } 1 * \text{N trees species 1 in plot } X) + (\ldots\text{species } 2 * \ldots\text{species } 2) + \ldots$$

2.7 Statistical analyses and modeling

Since regional scale (N=1) and landscape scale (N=3) are low in sample size, data from these scales were compared. I run t-tests for moose density, quantity of biomass available, quantity of biomass browsed and proportion of biomass browsed, to control for any statistical differences between the three studied landscapes. Quadrat (N=61), plot (N=976) and tree (N=8038) scale were included for statistical modeling. To explain moose browsing decisions, I used number of moose pellet groups, quantity of biomass browsed and proportion of biomass browsed as response variables. I used mixed models, with for each scale the larger scales as random variables, i.g. on tree scale, plot, quadrat and study area were random variables. On plot and tree level, there was a large amount of zero values in the response variables quantity and proportion of biomass browsed. To account for this, the data sets were split up for two separate analyses. The first analyses explained whether a plot or tree was browsed or not browsed. The second analyses only include plots (N=301) and trees (N=798) which were selected for browsing and predicted the quantity and proportion of biomass which was browsed. For each response variable the full additive model was stepwise reduced with one variable in order to create the possible models. All models were run in R ‘stats’.

2.7.1 Number of moose pellet groups

Only on plot and quadrat scale the number of moose pellet groups was used, since there are no moose pellet groups per tree. In order to explain number of moose pellet groups, variables; biomass available, altitude, tree density, FSAV, accumulated browsing and cutting class were used. I used mixed glmer models with a poisson family.

2.7.2 Quantity of biomass browsed

To explain quantity of biomass browsed on quadrat and plot scale, variables; altitude, tree density, FSAV, number of moose pellet groups, accumulated browsing and cutting class were used. Since not all variables could be applied on tree scale, different variables were included i.e. accumulated browsing, tree height (m) and tree species. On quadrat, plot and tree scale I used linear (lme) models to explain how much was browsed. Additionally, on plot and tree scale, glmer models with a binomial family and a logit link function were used to explain whether browsing occurred or not.

2.7.3 Proportion of biomass browsed

To explain proportion of biomass browsed on plot and quadrat level, the variable “quantity of biomass available” was added to the variables used to explain quantity of biomass browsed. Variables used on tree level were; accumulated browsing, tree height (m) and tree species. On quadrat, plot and tree scale I used linear (lme) models to explain the proportion of biomass which was browsed. Additionally, on plot and tree scale, glmer models with a binomial family and a logit link function were used to explain whether a proportion was browsed or not.

2.8 Transformations

The values for biomass available, on all spatial scales, included for the largest part lower values yet some large values. To account for this, I took the nature logarithm of biomass available to acquire a normal distribution of the data. Proportion of biomass browsed, showed a skewed distribution since most of the values were close to zero and therefor was ArcSine-square-root transformed. The presented results are back transformed, which resulted in non-symmetric standard-error values.

2.9 Comparing models

On plot and quadrat level, I used the same variables to be able to compare the change in slopes and significance between the two different spatial scales. For each response variable, I run the full models on both spatial scales and compared the estimates.

2.10 Selecting models based on AIC

In order to obtain the best fit models for each response variable on each spatial scale, I selected models based on Akaike’s information criterion (Burnham and Anderson, 2002). The model with the lowest AIC value was selected as best fit model. If models showed an ΔAIC value lower than 2.0, they were additionally selected. For each response variable, I compared the selected models for the different spatial scales. AIC model selection was applied to all of the created models.

2.11 Matching of biomass browsed to biomass available

To be able to test the hypothesis that moose overmatch quantity of biomass browsed on the smallest spatial scales (i.e. individual trees and plant communities), match quantity of biomass browsed on the large spatial scales (i.e. landscape and region), linear models with "quantity of biomass browsed" as response variable and "quantity of biomass available" as predictor variable were run for the three smallest spatial scales. Each model included the larger spatial scales as random variables.

3. Results

3.1 Regional scale.

In all 976 sampled plots combined, a total of 203 moose winter pellet groups were counted, with a mean of 0.21 (2SE=0.042) moose pellet groups per 100m² plot. Leading up to a mean moose density of 0.83 (2SE=0.166) moose per km².

The study included 8038 trees within browsing height. From this selection, 3344 (41.60%) trees had old browsing and 3387 trees (42.14%) had visible old and / or new browsing. For calculating biomass availability and biomass consumption, 5448 trees were included, of which 4024 had biomass available between 0.5m and 3.0m. Of all trees with biomass, 798 trees (19.83%) had fresh browsing. 3007 individual trees had old browsing and 3050 trees (75.80%) had visible old and / or new browsing. 43 trees (1.06%) had fresh browsing, but did not have any old browsing, i.e. they were browsed for the first time. Downy birch and Scots pine were dominant in abundance in the region and accounts for the largest numbers of browsed trees (table 1). Yet, the proportion of trees browsed, compared between all species, is the lowest for Scots pine with 42.94% . When only looking at fresh browsing, Downy birch and Scots pine still account for the largest number of browsed trees. However, the proportions of trees fresh browsing, compared between all species, is the lowest for Downy birch with 13.95%. Of all Scots pine trees, 24.32% had fresh browsing.

Table 1. Trees browsed on region level. The left section of the table represents all trees which were sampled, also including trees without biomass available within browsing height (0.5m – 3.0m). The number of browsed trees are trees which showed old and –or new browsing, these same trees are represented in the percentage of trees browsed. The right section of the table represents all trees with biomass available within browsing height. The number of trees with fresh browsing are the trees which were browsed during the 2011-2012 winter period. These same trees are represented in the percentage of trees with fresh browsing. Species are: Bpe = Silver birch, Bpu = Downy birch, Jco = Juniper, Psy = Scots Pine, Ptr = Aspen, Sal = Willow species, Sau = Rowan.

Species	N trees measured	N trees browsed	% trees browsed	N trees with biomass available	N trees freshly browsed	% trees freshly browsed
Bpe	122	95	77.87	107	41	38.32
Bpu	2379	1693	71.16	2057	287	13.95
Jco	135	109	80.74	135	39	28.89
Psy	2520	1082	42.94	1480	360	24.32
Ptr	42	32	76.19	28	8	28.57
Sal	116	110	94.83	99	41	41.41
Sau	134	123	91.79	118	22	18.64

The available biomass in the region is composed for the largest part out of Juniper and Scots pine, with 49.60% and 39.65% of all biomass available respectively (table 2). Downy birch comes on the third place with 10.03%. Comparing Scots pine with downy birch, the mean quantity of biomass available from Scots pine is much higher (4152.00 kg/km² 2SE=1124.79 compared to 1050.38 2SE=251.65, N=976). Most of the measured browsed biomass has been consumed from pine (a total 7.55kg, with 154.81 kg/km², SE=60.73), making up

3.73% of the available pine biomass and contributing up to 84.74% of the browse diet of moose in the region. Juniper is the second largest part of the browse diet with 7.97% of the consumed biomass, with a mean consumption of 15.05kg/km^2 (2SE=18.35). Downy birch comes on the third place with 4.51% of the moose browse diet, with a mean consumption of 8.23kg/km^2 (2SE=2.78). Moose browsed a total mean of 182.69kg/km^2 (2SE=68.32), from the 10472.81kg/km^2 (2SE=4928.82) biomass available in the region, which is 1.74%.

Table 2. Biomass available and browsed per species in the region. Biomass available is described with; biomass composition in %, total measured quantity of biomass available in grams and the calculated mean biomass available in kilograms per square kilometer. Biomass browsed is described with; total measured biomass browsed in grams, the calculated mean biomass browsed in kilograms per square kilometer, the proportion of the available biomass browsed and the composition of the browsed biomass in %. Means are with 2SE in parentheses. Species as in table 1.

Species	Biomass composition in %	Biomass available (g)	Biomass available (kg/km^2)	Biomass browsed (g)	Biomass browsed (kg/km^2)	% of biomass browsed	Browsed biomass composition in %
Bpe	0.48	2454.50	51.13 (29.94)	104.46	2.18 (2.08)	4.26	1.17
Bpu	10.03	51258.47	1050.38 (251.65)	401.68	8.23 (2.78)	0.78	4.51
Jco	49.60	253498.11	5370.72 (4761.82)	710.28	15.05 (18.38)	0.28	7.97
Psy	39.65	202617.37	4152.00 (1124.79)	7554.79	154.81 (60.73)	3.73	84.74
Ptr	0.06	293.17	6.32 (5.38)	24.69	0.53 (0.79)	8.42	0.28
Sal	0.11	544.66	11.54 (8.02)	71.49	1.51 (1.44)	13.13	0.80
Sau	0.08	406.89	8.48 (4.62)	48.04	1.00 (1.43)	11.81	0.54
Total	100	511073.16	10472.81 (4928.82)	8915.43	182.69 (68.32)	1.74	100

Note: Means and standard errors were calculated from plot level, giving a sample size of 976 for each species.

The largest proportion of biomass in the region was found in cutting class two stands (N=299), accounting for 53.50% of the measured biomass with 182.88kg/ha (2SE=99.82) (table 3). Secondly, cutting class three (N=347) holds 28.09% of the available biomass, with 82.75 kg/ha (2SE=35.91). Quantity of biomass browsed was the highest in cutting class 2 and contributed to 80.47% of the measured browsed biomass with 4.80 kg/ha (2SE=1.67) browsed. From cutting class 3, 7.85% of the browsed biomass was taken, with 0.40 kg/ha (2SE=0.23) browsed. Fifty percent of the registered moose pellet groups were found in cutting class 2 stands and 24.78% in cutting class 3 stands. Furthermore, the highest density of moose pellet groups (34.45 per hectare (2SE=9.70)) was found in cutting class 2.

Table 3. Quantity of biomass available and browsed (in kilograms), percentage of total measured biomass available and browsed, mean quantity (kilograms) of biomass available and browsed per hectare, number of moose pellet groups counted, percentage of total counted moose pellet groups and moose pellet group density in counts per hectare, for each cutting class, on region scale. 2SE between parenthesis. Cut class = cutting class

Cut class	N	Biomass available (kg)	% of available biomass	Biomass available (kg/ha)	Biomass browsed (kg)	% of browsed biomass	Biomass browsed (kg/ha)	N moose pellet groups	% of moose pellet groups	Moose pellet groups (N/ha)
0	51	23.02	4.50	90.28 (100.16)	0.09	1.00	0.35 (0.46)	0	0	0
1	75	2.71	0.53	7.24 (10.26)	0.39	4.40	1.05 (3.75)	15	7.39	20.00 (13.69)
2	299	273.40	53.50	182.88 (99.82)	7.17	80.47	4.80 (1.67)	103	50.74	34.45 (9.70)
3	347	143.57	28.09	82.75 (35.91)	0.70	7.85	0.40 (0.23)	49	24.14	14.12 (4.69)
4	157	49.36	9.66	62.88 (44.19)	0.52	5.80	0.66 (0.80)	30	14.78	19.11 (12.41)
5	47	19.00	3.72	80.86 (72.15)	0.04	0.48	0.18 (0.36)	6	2.96	12.77 (13.07)

Note: N is the number of plots sampled within each cutting class type, not number of forest stands.

3.2 Landscape scale

In Gravberget the highest total number of moose pellet groups was counted (N=91), compared to 57 in Plassen and 55 in Ljørdalen. Gravberget had a significant higher moose density than Ljørdalen (t= 2.18, DF=556, p=0.014) and Plassen (t=1,93, DF=546, p=0.027), yet the standard errors do overlap (figure 1). Ljørdalen and Plassen did not significantly differ from each other in moose density (t= -0.34 , DF=654, p=0.367).

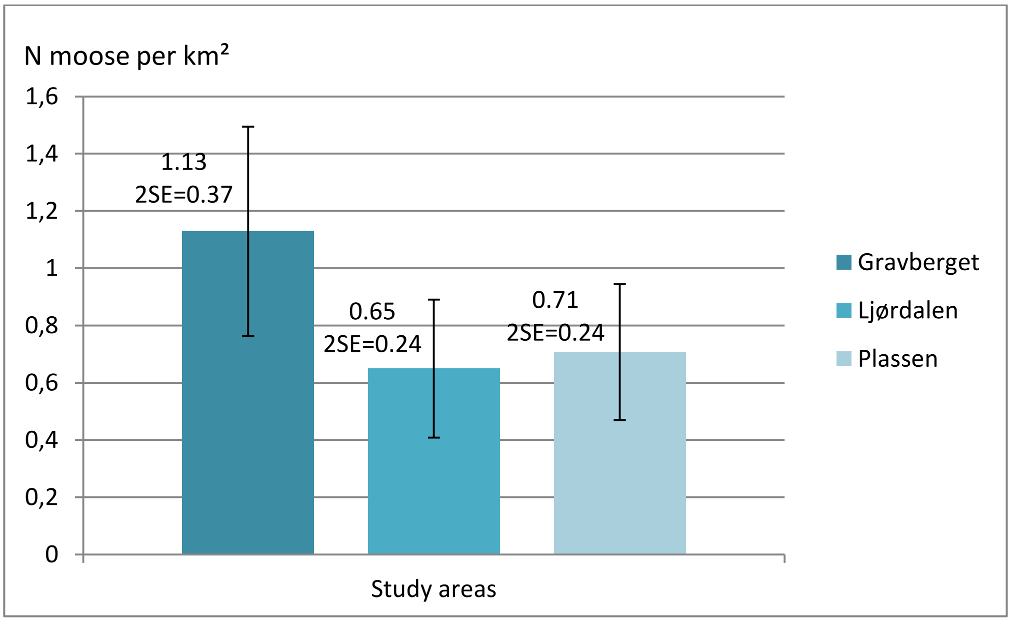


Figure 1. Mean moose winter densities (N moose per km²) in the three study areas with 2SE.

Gravberget had a significant lower quantity of biomass available (t=-2.55, DF=27, p=0,008) than Ljørdalen and the lowest measured quantity of biomass available of all three study areas, yet the highest quantity of browsed biomass was recorded here, resulting in a 3.92% loss of biomass (table 4). However, the standard errors from Plassen, overlap with the two other study areas. Ljørdalen had more Scots pine biomass available as Plassen with 6502.74 kg/km² (2SE=2641.98) compared to 2597.92 (2SE=1084.10) and Gravberget with 3237.79kg/km² (2SE=1178.74), however the standard errors of Gravberget and Ljørdalen do overlap. Total quantity and proportion of biomass browsed was the highest in Gravberget, but there was no significant difference (p values 0.21, 0.27 and 0.38) in quantities of biomass browsed between the three areas and also here the standard errors overlaped. The proportion of biomass browsed in Gravberget was significantly higher than Ljørdalen (t=2.04, DF=26, p=0.025) but there was no significant difference between the other areas (p=0.100 and p=0.230).

Table 4. Mean quantity of biomass available and browsed in kilograms per square kilometer, with 2SE. Species as in table 1.

Site	Species	Biomass available (kg/km²)	2SE	Biomass browsed (kg/km²)	2SE	% browsed (%/km²)	2SE
Gravberget	Bpe	116.54	80.13	5.17	5.70	12.03	10.30
Ljørdalen	Bpe	28.94	23.49	1.21	2.13	2.92	2.81
Plassen	Bpe	3.58	5.31	0.07	0.14	1.36	2.50
Gravberget	Bpu	949.06	365.99	11.28	6.14	3.11	1.54
Ljørdalen	Bpu	1102.36	434.25	6.98	4.57	1.58	0.74
Plassen	Bpu	1012.77	521.40	5.87	3.29	1.93	1.49
Gravberget	Jco	1612.44	1561.71	2.04	2.81	10.83	13.74
Ljørdalen	Jco	5128.25	4701.13	12.70	21.85	2.32	2.90
Plassen	Jco	8846.53	13391.29	29.02	50.35	5.57	9.97
Gravberget	Psy	3237.79	1178.74	201.14	135.62	11.43	4.69
Ljørdalen	Psy	6502.74	2641.98	150.14	95.60	5.96	4.74
Plassen	Psy	2597.92	1084.10	113.38	78.81	7.68	3.51
Gravberget	Ptr	2.12	2.03	0.08	0.11	5.50	6.88
Ljørdalen	Ptr	8.21	8.33	0.30	0.61	1.23	2.46
Plassen	Ptr	7.58	13.43	1.14	2.27	2.81	3.97
Gravberget	Sal	14.15	16.03	2.66	3.89	10.51	9.21
Ljørdalen	Sal	6.69	10.41	0.96	1.32	7.59	9.98
Plassen	Sal	12.87	14.74	0.80	1.32	21.58	15.74
Gravberget	Sau	7.60	7.13	0.30	0.58	5.52	10.00
Ljørdalen	Sau	5.55	4.01	2.42	4.06	10.53	7.04
Plassen	Sau	12.00	11.38	0.16	0.19	3.78	4.05
Gravberget	Total	6026.95	2085.69	223.32	140.12	3.92	2.07
Ljørdalen	Total	12782.74	4863.29	174.72	99.91	1.60	0.93
Plassen	Total	12493.24	14046.03	150.45	117.09	2.25	1.47

Note: Means and standard errors were calculated using data from quadrat level, giving a sample size of 20 for Gravberget and Plassen and a sample size of 21 for Ljørdalen.

In all three study areas cutting class two and three stands were dominant in abundance in the terrain (table 5). Cutting class two contained the highest mean quantities of biomass available, biomass browsed and the highest mean number of moose pellet groups per ha. In Ljørdalen and Plassen, about 70% of the browsed biomass came from cutting class two. In Gravberget this was 92.86%, were moose browsed 6.26kg/ha (2SE=3.08) compared to 4.13 kg/ha (2SE=2.61) and 3.84 kg/ha (2SE=2.98) in Ljørdalen and Gravberget respectively. Accordingly, the moose pellet group density in cutting class two in Gravberget, was higher than those in the same cutting class in the other two study areas. In none of the study areas moose pellet groups were found in cutting class 0.

Table 5. Percentage of total measured biomass available and browsed, mean quantity (in kilograms) of biomass available and browsed per hectare, number of moose pellet groups counted, percentage of total counted moose pellet groups and moose pellet group density in counts per hectare, per cutting class for each study area. 2SE between parenthesis. Area: Gr = Gravberget, Lj = Ljørdalen and Pl = Plassen. Cut class = cutting class

Area	Cut class	N *	% of available biomass	Biomass available (kg/ha)	% of browsed biomass	Biomass browsed (kg/ha)	N moose pellet groups	% of moose pellet groups	Moose pellet groups (N/ha)
Gr	**0**	24	20.99	168.65 (195.44)	1.99	0.59 (0.88)	0	0.00	0
Gr	**1**	43	0.22	0.97 (1.05)	0.53	0.09 (0.12)	11	12.09	25.58 (21.14)
Gr	**2**	106	59.91	109.01 (29.45)	92.86	6.26 (3.08)	44	48.35	41.51 (19.12)
Gr	**3**	105	18.09	33.22 (14.39)	4.50	0.31 (0.29)	22	24.18	20.95 (10.72)
Gr	**4**	39	0.80	3.94 (2.20)	0.12	0.02 (0.04)	14	15.38	35.90 (39.90)
Gr	**5**	3	0.00	0	0.00	0	0	0.00	0
Lj	**0**	14	0.62	19.10 (15.98)	0.61	0.25 (0.38)	0	0.00	0
Lj	**1**	12	0.44	15.60 (16.36)	0.00	0	0	0.00	0
Lj	**2**	104	44.46	183.60 (56.78)	73.13	4.13 (2.61)	31	56.36	29.81 (14.17)
Lj	**3**	125	29.02	99.72 (40.37)	12.17	0.57 (0.50)	11	20.00	8.80 (6.02)
Lj	**4**	41	16.67	174.65 (154.81)	12.71	1.82 (2.55)	9	16.36	21.95 (25.67)
Lj	**5**	40	8.79	94.38 (84.53)	1.38	0.20 (0.41)	4	7.27	10.00 (11.98)
Pl	**0**	13	0.72	22.26 (24.92)	0.00	0	0	0.00	0
Pl	**1**	20	0.79	15.71 (40.51)	15.51	3.73 (14.93)	4	7.02	20.00 (23.40)
Pl	**2**	89	60.11	270.01 (328.06)	71.02	3.84 (2.98)	28	49.12	31.46 (16.48)
Pl	**3**	117	31.92	109.06 (95.92)	7.56	0.31 (0.27)	16	28.07	13.68 (7.64)
Pl	**4**	77	6.40	33.22 (28.23)	5.83	0.36 (0.47)	7	12.28	9.09 (6.60)
Pl	**5**	4	0.06	6.33 (11.96)	0.09	0.11 (0.30)	2	3.51	50.00 (100.00)

* N is the number of plots sampled within each cutting class type, not number of forest stands.

3.3 Quadrat, plot and tree scale

3.3.1 Moose pellet groups

On plot scale, number of moose pellet groups increased with an increase in available biomass and an increase in accumulated browsing. Additionally, cutting class was a significant predictor yet there was no significant difference between the different cutting classes (p values varied between 0.98 and 0.99). The number of moose pellet groups had a tendency to decrease with an increase in altitude, however tree density and Feeding Site Attractiveness Value (FSAV) were not significant predictors in the full model. On quadrat scale, number of moose pellet groups increased with an increase in available biomass and an increase in tree density, but decreased with an increase in altitude. FSAV, accumulated browsing and cutting class were not significant (table 6).

Table 6. Estimates, standard errors and p-values for the full models predicting number of moose pellet groups on plot and quadrat scale. Bold values are significant and the italic values have a tendency towards significance.

	Plot			**Quadrat**		
	Estimate	SE	p-value	Estimate	SE	p-value
Intercept	-17.05	900.40	0.985	-0.35	0.63	0.572
logBiomass available (g)	**0.09**	**0.05**	**0.045**	**0.22**	**0.08**	**0.006**
Altitude (m)	*-0.002*	*0.001*	*0.085*	**-0.003**	**0.001**	**0.009**
Tree density	-0.001	0.10	0.989	**0.003**	**0.0007**	**<0.001**
FSAV	-0.29	0.31	0.353	0.50	0.40	0.209
Accumulated browsing	**0.34**	**0.14**	**0.013**	-0.29	0.39	0.456
Cutting class	-	-	**<0.001**	-	-	0.841

Based on AIC selection, three best fit models were selected for both plot and quadrat scale. On both scales, number of moose pellet groups increased with an increase of biomass. On plot scale mean accumulated browsing and cutting class were included in all of the three selected models. On quadrat scale tree density was included in all of the three selected models (table 7).

Table 7. AIC selected models for predicting number of moose pellet groups on plot and quadrat level. The title row shows the variables which were included in the full model. For each variable which was selected for each model, the estimates are given with SE between parenthesis. Bold values are significant italic values have a tendency towards significance. Mean Acc = Mean accumulated browsing.

Spatial scale and model	**Biomass available (g)**	**Altitude (m)**	**Tree density**	**FSAV**	**Mean Acc**	**Cut Class**	**Δ AIC**	**Δ next model**	**AIC best**
Plot m1	**0.09 (0.04)**	*-0.003 (0.001)*	-	-	**0.30 (0.13)**	**p< 0.001**	0		1
Plot m2	**0.09 (0.04)**	*-0.002 (0.001)*	-	-0.31 (0.30)	**0.33 (0.14)**	**P< 0.001**	1		1.2
Plot m3	**0.08 (0.04)**	-	-	-	**0.32 (0.13)**	**P< 0.001**	1.2		2
Quadrat m1	**0.15 (0.06)**	-	**0.003 (0.0006)**	-	-	-	0		0.8
Quadrat m2	**0.18 (0.07)**	-	**0.003 (0.0007)**	-	-0.24 (0.35)	-	1.5		1.9
Quadrat m3	**0.15 (0.06)**	-	**0.003 (0.0006)**	0.15 (0.36)	-	-	1.9		3.1

3.3.2 Quantity of biomass browsed

On plot scale, the full model for predicting quantity of biomass browsed, altitude, log sum of trees, number of moose pellet groups, mean accumulated browsing and cutting class came out as significant predictors (table 8). On quadrat scale, the number of moose pellet groups, mean accumulated browsing and cutting class come out as significant predictors. Moose pellet groups is a stronger predictor on plot scale, although mean accumulated browsing is a stronger predictor on quadrat scale. On quadrat scale there was no significant difference between the different cutting classes. On plot scale, cutting class two is predicted to have larger quantities of biomass browsed as cutting class three (Figure 2).

Table 8. Estimates, standard errors and p-values for the full models predicting quantity of biomass browsed on plot and quadrat scale. Bold values are significant.

Quantity of biomass browsed	**Plot**			**Quadrat**		
	Estimate	-SE, +SE	p-value	Estimate	-SE, +SE	p-value
Intercept	-0.71	0.04, 0.32	0.099	-0.48	0.37, 0.28	0.5949
Altitude (m)	**0.002**	**0.001, 0.001**	**0.0339**	0.002	0.002, 0.003	0.3872
Log tree density	**0.46**	**0.15, 0.17**	**0.0005**	0.003	0.002, 0.002	0.1294
Log FSAV	-0.10	0.05, 0.06	0.1014	-0.58	0.27, 0.40	0.4058
N moose pellet groups	**0.59**	**0.14, 0.16**	**<.0001**	**0.20**	**0.07, 0.07**	**0.0034**
Mean Acc	**1.18**	**0.30, 0.36**	**<.0001**	**11.46**	**6.83, 15.10**	**0.0026**
Cutting Class	**-**	**-**	**0.0002**	**-**	-	**0.0151**

3.3.3 Browsing occurrence (quantity of biomass browsed)

The binomial models, for predicting if any quantity of biomass was browsed or not on tree and plot scale, are shown in table 9. On the smallest scale, the full model was selected, which includes the variables tree species, accumulated browsing and tree height. On plot scale, two models were selected. The top model included the variables tree density, number of moose pellet groups, FSAV and mean accumulated browsing. The second best model (Δ AIC 1.9) also included the variable altitude.

Table 9. AIC selected binomial models, predicting if any quantity of biomass was browsed or not. The title row shows the variables which were included in the model selection. For each variable which was selected for each model, the estimates are given with SE within parenthesis. Bold values are significant. NAs were placed for the variables which were not included on that specific spatial scale.

Spatial scale	**Alti-tude (m)**	**Tree density**	**N moose pellet groups**	**FSAV**	**Cut Class**	**Mean Acc / Acc**	**Height (m)**	**Species**	**Δ AIC**	**Δ AIC next best model**
Tree	NA	NA	NA	NA	NA	**p< 0.001**	**0.45 (0.20)**	**p< 0.001**	0	3
Plot m1	-	**0.93 (0.12)**	**0.56 (0.17)**	0.07 (0.07)	-	**1.43 (0.17)**	NA	NA	0	1.9
Plot m2	0.0003 (0.001)	**0.94 (0.13)**	**0.56 (0.17)**	0.07 (0.07)	-	**1.44 (0.17)**	NA	NA	1.9	4.6

On tree scale, Downy birch had a significantly lower chance of being browsed than Scots pine, Juniper, Silver birch and Salix species (Figure 3). Salix species had a significant higher chance of being browsed than rowan.

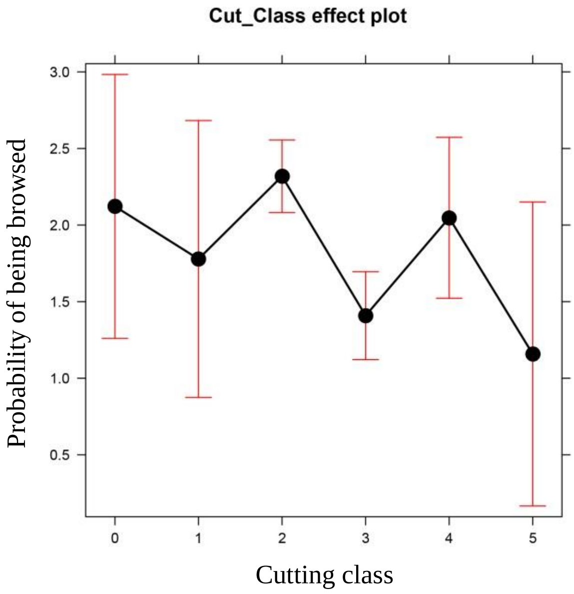


Figure 2. Effect of cutting class in the full model explaining quantity of biomass browsed on plot level

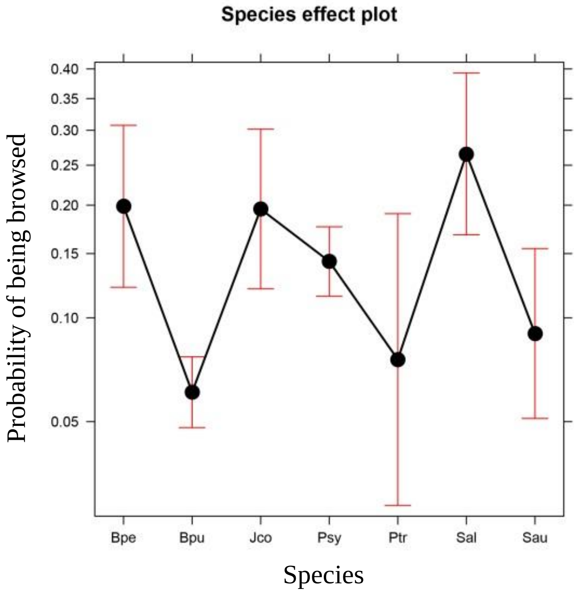


Figure 3. Effect of species in the AIC selected model, predicting if a tree would be browsed or not. Species as in table 1.

3.3.4 AIC model selection for quantity of biomass browsed

The AIC based selected models, explaining the quantity of biomass is browsed on tree, plot and quadrat scale, are shown in table 10. On the tree scale, the full model was selected, which includes variables tree species, accumulated browsing and height. On plot scale, the variables tree density, number of moose pellet groups, FSAV, mean accumulated browsing and cutting class were selected, with a Δ AIC 5.15 of the next best model. On quadrat scale two models were selected. The first model includes variables number of moose pellet groups, mean accumulated browsing and cutting class. The second best model, with a Δ AIC of 0.04, adds FSAV as explainer variable to the model.

Table 10. Best fit models for explaining quantity of biomass browsed on tree, plot and quadrat scale, based on AIC selection. The title row shows the variables which were included in the model selection. For each variable which was selected for each model, the estimates are given with SE between parenthesis. Bold values are significant and italic values have a tendency towards significance.

Spatial scale	**Altitude (m)**	**Tree density**	**N moose pellet groups**	**FSAV**	**Cut Class**	**Mean Acc / Acc**	**Height (m)**	**Species**	**Δ AIC**	**Δ AIC next best model**
Tree	NA	NA	NA	NA	NA	**P<0.001**	**0.58 (0.26-0.93)**	**P< 0.001**	0	2.19
Plot	-	**0.41 (0.27-0.56)**	**0.58 (0.44-0.74)**	-0.09 (-0.14--0.03)	**p< 0.001**	**1.15 (0.85-1.50)**	NA	NA	0	5.15
Quadrat m1	-	**-**	**0.22 (0.15-0.28)**	-	**p= 0.050**	**15.15 (6.62-33.22)**	NA	NA	0	0.04
Quadrat m2	-	-	**0.22 (0.16-0.29)**	-0.37 (-0.76-0.61)	*p= 0.074*	**16.31 (7.02-36.34)**	NA	NA	0.04	5.7

3.3.5 Proportion of biomass browsed

On plot scale, the full model for predicting proportion of biomass browsed, the intercept, log biomass available, number of moose pellet groups, mean accumulated browsing and cutting class came out as significant predictors (table 11). There was no significant difference between the different cutting classes. On quadrat scale only the intercept was significant in the full model and number of moose pellet groups had a tendency towards significance.

Table 11. Estimates, standard errors and p-values for the full models predicting proportion of biomass browsed on plot and quadrat scale. Bold values are significant and italic values have a tendency towards significance.

Proportion of biomass browsed	**Plot**			**Quadrat**		
	Estimate	-SE, +SE	p-value	Estimate	-SE, +SE	p-value
Intercept	**0.04**	**0.03, 0.07**	**0.003**	**0.04**	**0.01, 0.004**	**0.038**
Log Biomass available (g)	**0.64**	**0.05, 0.05**	**<0.001**	0.0003	0.00003, 0.0003	0.161
Altitude (m)	1.00	0.001, 0.002	0.745	9.26E-09	4.03E-09, 3.63E-08	0.550
Log tree density	1.17	0.18, 0.21	0.339	1.61E-08	0.01E-08, 3.25E-08	0.325
Log FSAV	0.98	0.08, 0.10	0.868	4.38E-05	4.39E-05, 4.38E-05	0.917
N moose pellet groups	**1.47**	**0.19, 0.22**	**0.007**	*3.9E-05*	0.72E-05, 1.82E-05	*0.086*
Mean Acc	**1.97**	**0.41, 0.52**	**0.004**	0.006	0.0004, 0.004	0.183
Cutting class	-	-	**<0.001**	-	-	0.223

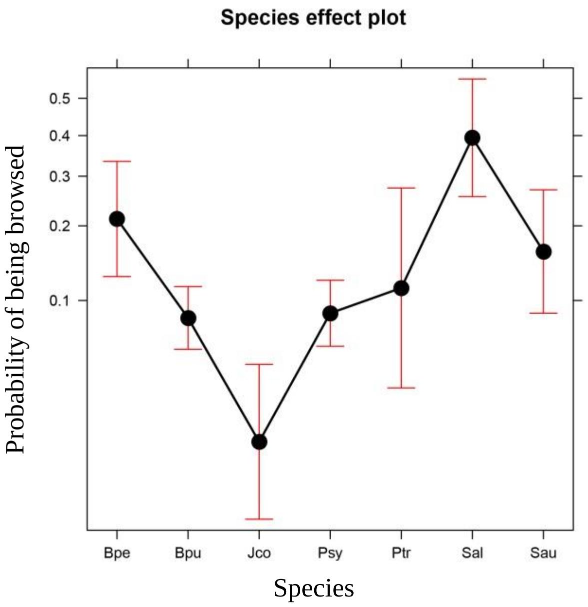
3.3.6 Browsing occurrence (proportion of biomass browsed)

The binomial models, for predicting if any proportion of biomass was browsed on tree and plot scale, are shown in table 12. On tree scale, the full model was selected, which includes variables quantity of biomass available, tree species, accumulated browsing and height. On plot scale three models had a Δ AIC smaller than two. The top model includes variables quantity of biomass available, tree density, number of moose pellet groups, FSAV and mean accumulated browsing. Biomass available, number of trees, number of moose pellet groups and mean accumulated browsing were selected in all three of the models.

Table 12. AIC selected binomial models, predicting if any proportion of biomass was browsed or not. The title row shows the variables which were included in the model selection. For each variable which was selected for each model, the estimates are given with SE between parenthesis. Bold values are significant

Spatial scale	**Alti-tude (m)**	**Tree density**	**N moose pellet groups**	**FSAV**	**Cut Class**	**Log Biomass available (g)**	**Mean Acc / Acc**	**Height (m)**	**Species**	**Δ AIC**	**Δ AIC next best model**
Tree	NA	NA	NA	NA	NA	**1.20 (0.14)**	**p< 0.001**	**-0,89 (0.28)**	**P< 0.001**	0	9
Plot m1	-	**0.79 (0.13)**	**0.54 (0.18)**	**0.10 (0.07)**	-	**0.22 (0.05)**	**1.25 (0.18)**	NA	NA	0	1.8
Plot m2	**-0.0005 (0.001)**	**0.77 (0.14)**	**0.54 (0.18)**	**0.10 (0.07)**	-	**0.22 (0.06)**	**1.24 (0.18)**	NA	NA	1.8	1.9
Plot m3	**-0.0004 (0.001)**	**0.80 (0.13)**	**0.52 (0.17)**	-	-	**0.21 (0.06)**	**1.33 (0.18)**	NA	NA	1.9	4.6

The effect of species and accumulated browsing showed significant difference between the different classes. Juniper had significant lower probability of being browsed as both birch species, Scots pine, Salix species and Rowan (Figure 4). Salix species had a significant higher chance of being browsed than Downy birch, Juniper and Scots pine. Downy birch and Scots pine had approximately similar chances of being browsed. Trees with accumulated browsing of zero, had a significant lower probability of being browsed compared to trees with higher accumulated browsing (Figure 5). Trees with accumulated browsing of three, had significant highest probability of being browsed.



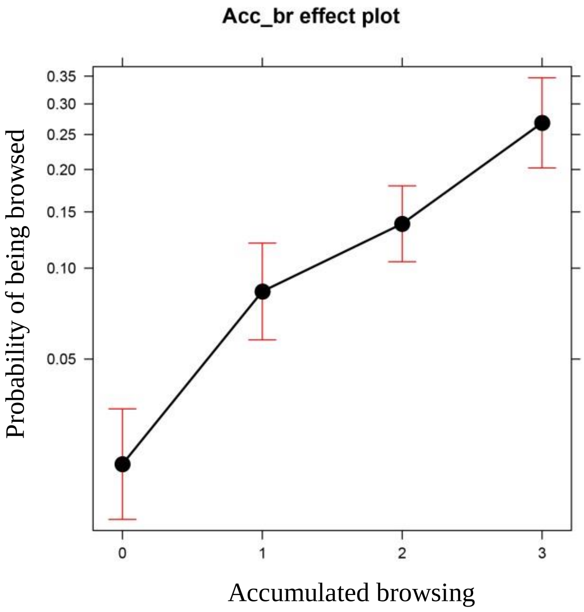


Figure 4. Effect of species within the AIC based selected model (x axis), predicting the probability of a proportion of biomass being browsed or not (y-axis). Species as in table 1.

Figure 5. Effect of accumulated browsing within the AIC based selected model, predicting the probability of a proportion of biomass being browsed or not (y-axis).

The AIC based selected models, which predict the proportion of biomass is browsed on tree, plot and quadrat scale, are shown in table 13. On tree scale, the best model consists out of variables quantity biomass available and species.

Table 13. Best fit models for explaining proportion of biomass browsed on tree, plot and quadrat scale, based on AIC selection. The title row shows the variables which were included in the model selection. For each variable which was selected for each model, the estimates are given with SE between parenthesis. Bold values are significant.

Spatial Scale	**Altitude (m)**	**Tree density**	**N moose pellet groups**	**FSAV**	**Cut Class**	**Biomass available (g)**	**Mean Acc / Acc**	**Height (m)**	**Species**	**Δ AIC**	**Δ AIC next best model**
Tree	NA	NA	NA	NA	NA	**0.05 (0.04-0.06)**	-	-	**p< 0.001**	0	4.2
Plot m1	-	-	**1.46 (1.27-1.68)**	-	**p<0.001**	**0.65 (0.61-0.70)**	**1.91 (1.53-2.39)**	NA	NA	0	1.5
Plot m2	-	-	-	-	**p<0.001**	**0.05 (0.02-0.10)**	**2.02 (1.62-2.53)**	NA	NA	1.5	4.75
Quadrat	-	-	-	-	-	-	**0.01 (0.004-0.025)**	NA	NA	0	4.3

Within the variable species, Juniper and Scots pine had significant higher proportions browsed than the two birch species (table 14). On plot scale two best models were selected, with both including biomass available, mean accumulated browsing and cutting class predictors with number of moose pellet groups added in the first model. With the effect of cutting class, only cutting class two and three significantly differed from each other (figure 6). On quadrat scale only the variable mean accumulated browsing was selected as best model for explaining proportion of biomass browsed.

Table 14. Effect of species within AIC based selected model on proportion of biomass browsed on tree scale. Species as in table 1.

Species	Estimate	Lower limit	Upper limit	p-value
Bpe	**0.26**	**0.22**	**0.31**	**<0.001**
Bpu	0.26	0.26	0.27	0.233
Jco	**0.32**	**0.29**	**0.36**	**<0.001**
Psy	**0.38**	**0.36**	**0.40**	**<0.001**
Ptr	0.39	0.38	0.42	0.245
Sal	0.39	0.39	0.40	0.906
Sau	0.40	0.39	0.41	0.228

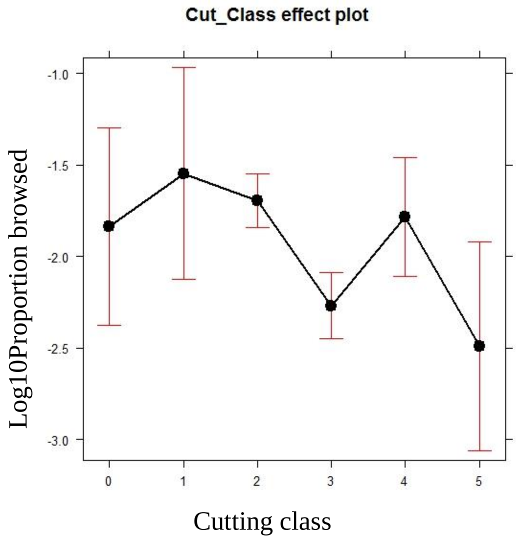


Figure 6. Effect of cutting class within the AIC based selected model, predicting the proportion of biomass browsed on plot scale

3.4 Matching of biomass browsed to biomass available.

Because of the low sample size of the two largest spatial scales, i.e. region scale (N=1) and local scale (N=3), these two scales were excluded for testing the hypothesis that moose overmatch quantity of biomass browsed on the smallest scales, match quantity of biomass browsed on the intermediate scale and under-match the quantity of biomass browsed on the largest scales. The intermediate scale is represented by the quadrats (N=61), the second smallest scale is represented by the plots (N=976) and the smallest scale is represented by the individual trees which have been browsed (N=798). Figure 7 clearly shows that on all three tested spatial scales, moose under-match their biomass consumption in relation to biomass availability(i.e. slope < 1). The tree scale shows this the strongest (slope =0.3997, SE=0,0209, p<0,001), secondly the plot scale (slope=0.5014, SE=0.04610, p=0.0014) and the quadrat scale the weakest (slope= 0.8395, SE=0.1802, p<0.001) with a tendency towards matching.

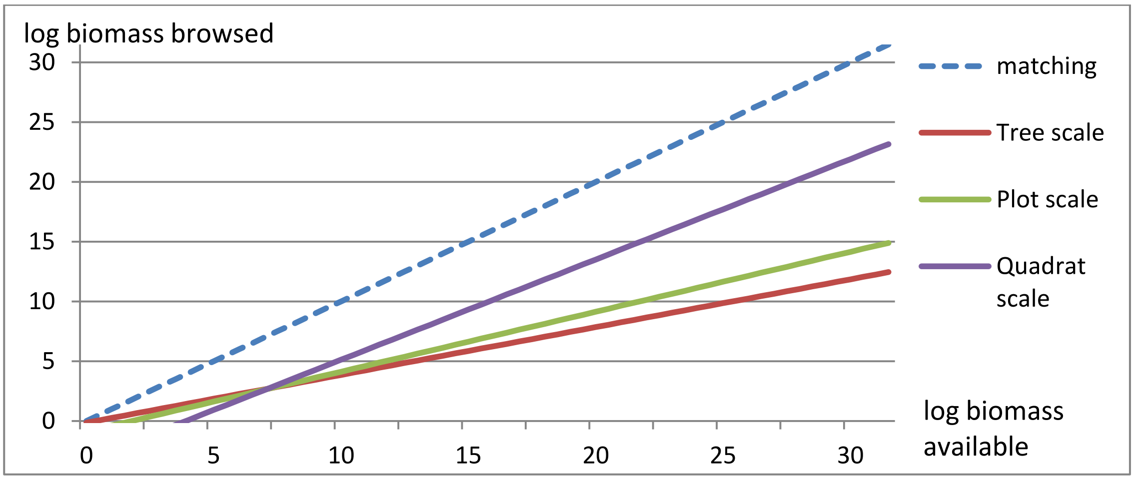


Figure 7. The blue dotted line indicates how the linear regression would look like if moose would match their biomass consumption to biomass availability, i.e. slope = 1.00.

Tree scale: logBiomass browsed = -0.1463+0.3997*logBiomass available (SE slope =0.0209, p<0.001)

Plot scale: logBiomass browsed =-0.8938+0.5014*logBiomass available (SE slope =0.0461, p<0.001)

Quadrat scale: logBiomass browsed =-3.2800+0.8395*logBiomass available (SE slope =0.1802, p<0.001)

4. Discussion

4.1 Moose pellet groups

4.1.1 Regional scale

Based on the pellet group counts on regional level, our study area had a moose density of 0.83 (2SE=0.1660) moose per km² during the winter of 2011-2012. The method used for estimating the moose density is inaccurate, since moose can also produce pellets before and after the winter period and some moose pellet groups could have been determined fresh, even though they were old. However, since the same method was used through the whole study, the counts of moose pellet groups can be used as an index for indicating usage of the terrain or time spent per terrain unit. Half of the moose pellet groups counted, were located in cutting class 2 stands, i.e. moose spent about 50% of the time in these stands. Additionally, moose spent 24.14% of their time in cutting class 3. The quantities of biomass consumed in these two cutting classes explains for what they were selected. Cutting class two provided 80.47% of the consumed forage biomass and cutting class 3 just 7.85%. This means that cutting class 2 stands were selected for foraging and cutting class 3 most likely for avoidance of disturbance since this forest stage provides most cover (Demarchi and Bunnell, 1995; Hebblewhite et al., 2008).

4.1.2 Landscape scale

Our estimated moose densities for the three studied landscapes, based on moose pellet group counts, did not significantly differ between Ljørdalen and Plassen. Gravberget did experience a significant higher moose density than Ljørdalen and Plassen.

4.1.3 Large and small community scale

On large community and small community scale, both the AIC based selected models and the full models for explaining number of moose pellet groups, pointed towards the same explainer variables, e.g. quantity of biomass available, tree density, altitude, accumulated browsing and cutting class (tables 7 and 8). When comparing the full models between the two spatial scales, biomass available is on both scales a significant predictor. Yet, much stronger for large communities (slope =0.22, SE=0.08, p<0.0001) than for small communities (slope =0.09, SE=0.05, p=0.045). Additionally, tree density was a significant predictor (slope=0.003, SE=0.0007, p<0.0001) on the large community scale in the full model and was selected with the AIC selection. This means, moose selected for large patches with high quantity of biomass available and high tree densities. For small communities, accumulated browsing was also a significant predictor, i.e. moose selected for small patches with higher quantity of biomass available which had been browsed before, within the selected large patches.

Cutting class did not come out as a significant predictor for large communities. This can be due to the fact that each quadrat covered multiple forest stands of different cutting classes. This made this predictor not accurate on this spatial scale. Acknowledging that cutting class two stands contained most of the available biomass, provided more than 80% of the browsed biomass, were selected on both regional and landscape scale and is known to be selected by moose for winter browsing (Cederlung et al., 1980; Lavsund, 1987; Fremming, 1999), one can assume that the selection for high quantity of biomass on large community level is in fact the selection for cutting class two stands. Additionally, the number of moose pellet groups was estimated to decrease with 0.3 (SE=0.07, p<0.0001) per quadrat, with an increase of 100 meter in altitude, i.e. lower areas were more used than higher areas. This behavior can be due to the increase of snow cover with an increase in altitude. Moose are known to descent in altitude to avoid deep snow (Gundersen et al., 2004; Franzmann and Schwartz, 2007; Månsson et al., 2012). This behavior follows the landscape departure theory from Senft et al. (1987).

If the increase in selectivity for quantity of biomass available from large- to small community scale would persist to larger spatial scales, as shown in Månsson et al. (2007), one can assume that landscapes with higher quantity of biomass available have higher probability to be selected by moose as winter habitat, i.e. moose selected their winter habitat based on favoring properties of the landscape, as described for other large ungulates by Fryxell et al. (1988), Lundberg (1988), Hebblewhite et al. (2008) and Bischof et al. (2012). This is contradictory to the habitat departure theory from Senft et al. (1987).

4.1.4 Why did Gravberget experience an higher moose density?

Gravberget had the lowest quantity of biomass available, yet still experienced the highest moose density. Machida (1979), Danell et al. (1985), Löyttyniemi (1985) and Bergqvist et al. (2003) described feeding loops for browsing herbivores, where the animals returned to the same patches to re-browse. Our data shows that this translates to the larger spatial scales. When it scales up to the level of winter habitat selection, it means that moose return to the same winter areas after they have selected a winter area. This reselection repeats itself year after year, by which the browsing pressure on the selected area results in loss in growth rate and starts to produce less biomass (Långström and Hellqvist, 1991; Persson et al., 2007; Solbraa, 2008). When the selection for previous browsed sites is stronger than the selection for biomass availability, it could explain why Gravberget was selected above the other two areas and has a lower quantity of biomass available. That means that Gravberget must have had a period when it was more likely to be selected in the first place.

When looking at the tree densities of the three sampled landscapes, Gravberget has the highest tree density, also in cutting class two (Gravberget: 29.61 trees per plot (2SE=4.82, N=106), Ljørdalen: 18.41 trees per plot (2SE=3.60, N=104) and Plassen: 20.15 trees per plot (2SE=4.77, N=89). Following the findings of Ball and Dahlgren (2002) and Heikkilä and Härkönen (1996), our data showed an increase in usage of large communities with an increase in stem density. Additionally, based on the higher stem density in cutting class 2 stands, I assume that there was a period where Gravberget had a superior quantity of biomass available compared to the other two areas (Fremming, 1999). This made Gravberget a more attractive wintering area. As a result of the yearly reselection and re-browsing, biomass availability lowered over the years ((Långström and Hellqvist, 1991; Persson et al., 2007; Solbraa, 2008). Regardless of the lower forage availability, the available quantity was more than sufficient (only 3.9% of the available biomass was browsed) to maintain the current wintering moose density. Moose densities in our studied landscapes are relatively low compared to other areas (Lavsund, 1987; Andren and Angelstam, 1993; Heikkilä and

Härkönen, 1993, 1996; van Beest et al., 2010), i.e. the populations were below maximum social caring capacity. Because of these factors there was no need for the moose to select a different wintering area

4.2 Quantity and proportion of biomass browsed

4.2.1 Regional scale

Large ungulates are assumed to consume only a small proportion from the net primary production in forest systems (Hobbs, 1996). The moose in our studied region followed this assumption and consumed 182.69 kg/km² (2SE=68.32) accounting for 1.74% of the available biomass.

Juniper, Scots pine and Downy birch were most abundant in biomass in the region, with 49.60%, 39.65% and 10.03% of the total biomass available respectively. When comparing this with the composition of the by moose browsed biomass (7.97% Juniper, 84.74% pine and 4.51% Downy birch), it gets clear that moose selected for pine as main food source. Further, moose selected for Rowan, Aspen and Salix species which are favored by moose (Heikkilä and Härkönen, 1996). Biomass consumption, from these species, was disproportional (factor seven higher) to their abundance in the region. However, there combined biomass summed up to only 0.25% of the available biomass in the region. Even though the largest quantity and proportion of biomass was consumed from pine, only 3.70% of the measured available pine biomass was consumed. This might not seem as much, but looking from the forestry point of view, 24.32% of all pine had fresh browsing and 42.94% had old and or fresh browsing. The relative low annual loss of biomass in the region, has a large effect on forestry, especially since the damage is inflected on young trees (Heikkilä and Härkönen, 1993, 1996).

The quantity of Juniper biomass available is most likely overestimated. The data which was used to make the regression curve for number of shoots per m³ of crown, included Junipers with a maximum crown content of 1.6m³. It did not include extremely large Juniper bushes, which have large openings between the different branches. However, in the sampled plots we encountered and measured extremely large Juniper bushes with crowns up to 7.15m³, which had large openings between the separate branches. This led to an overall overestimation of the available biomass.

4.2.2 Landscape scale

Comparing the three landscapes, Gravberget had the lowest quantity of biomass available, about half as much of the other study areas. Still moose browsed here the largest quantity of biomass, 223.32kg/km² (2SE=22.32) compared to 174.72kg/km² (2SE=99.91) and 150.45kg/km² (2SE=117.09). This resulted in a higher proportion of biomass browsed in Gravberget, 3,71% compared to 1,37% and 1,20%. The difference in quantity of available biomass between the study areas was due to the relative low abundance of Juniper in Gravberget but its high abundance in Plassen and the high abundance of Scots pine in Ljørdalen (table 5).

4.2.3 Large community and small community scale

Predicting quantity of biomass browsed on large community and small community scale, accumulated browsing was significant in the full models and was selected on base of lowest AICs, for both spatial scales. On quadrat level accumulated browsing was the strongest predictor with a slope of 11.46 compared to a slope of 1.18 on plot level. Moose pellet groups was a stronger explainer variable on plot scale with a slope of 0.59 compared to a slope of 0.20 (table 10). There was no significant difference between cutting classes on large community scale. However, similar to the results from predicting the number of moose pellet groups, I expect that this due to the fact that quadrats covered multiple cutting classes. From our measured browsed biomass, 80% came from cutting class 2 stands additionally, previous studies showed that moose select young forest stands for browsing (Lavsund, 1987; Heikkilä and Härkönen, 1993, 1996; Solbraa, 1998; Fremming, 1999). On small community level, plots located in cutting class two were predicted to have about 2.46 times higher quantities browsed as plots in cutting class three.

Feeding Site Attractiveness Value (FSAV), did not come out significant in any of the full models. Yet, it was selected based on lowest AIC value for the binomial model predicting whether browsing occurred or not at small community level. Small communities with highly palatable tree species, were more likely to be browsed than those without highly palatable species. But it failed to explain quantities and proportions of biomass browsed. Danell et al. (1991) showed that moose more heavily used stands where Scots pine was mixed with highly palatable species, such as Aspen. However, the browsing intensity on Scots pine did not differ to Scots pine stands without palatable species. The highly palatable species in our studied region summed up to just 0.25% of the available biomass. Considering the strong selection by moose for these species for forage, plots and stands containing these species, were ranked with an high FSAV. Since moose did not significantly increase browsing pressure on Scots pine, which accounted for the majority of the available biomass in the region, FSAV was neither capable to predict quantities nor proportion of biomass browsed. Because the increase of browsing on the rare palatable species was masked by the sheer quantity of browsed Scots pine biomass. These results are contrary to findings from Fremming (1999) and Heikkilä and Härkönen (1993), who found higher browsing intensities in stands which were mixed with broadleaved species compared to monoculture Scots pine stands. Yet, the difference was described as minimum.

4.2.4 Tree scale

On tree scale, the full model was selected based on lowest AIC. For trees which were browsed, the quantity of biomass browsed increased with an increase in height of the tree. Even though accumulated browsing and species were selected, there was no significant difference within these classes. From these results, I conclude that moose select foraging areas on intermediate scale, which were selected too in previous years for foraging. The higher quantity of biomass browsed from cutting class two stands above cutting class three stands, indicate that the selectivity for cutting class two stands is higher. Within the selected stands, there is a preference for patches which have been browsed before in previous years. Trees within the selected patches, experience an increase in biomass loss with an increase in height.

Salix species had the highest and Juniper the lowest probability of being browsed (plot 2). Downy birch and Scots pine had similar probability of being browsed and had a higher probability of being browsed than Juniper, but lower than Silver birch. Taking the abundance of the species into account, species which were rare on regional level, had the highest probabilities of being browsed on tree level (Heikkilä and Härkönen, 1993, 1996; Augustine and McNaughton, 1998; Solbraa, 2008). Biomass of Juniper was abundant over the region and, following the expectations, found a low probability of being browsed (Augustine and McNaughton, 1998). Scots pine however, was selected stronger than Juniper, even though the abundance of Scots pine biomass in the region was similar to Juniper. This clearly shows that Scots pine is a more valuable part of the moose’s diet.

Downy birch, which was also abundant in the region, had a similar probability to be browsed as pine. Yet, the quantity of biomass browsed of Downy birch was much lower than Scots pine, 4.51% and 84.74% respectively. The similar probability to be browsed for the two species is explained by the biomass composition on regional scale and the quantity of biomass available per tree per species. In the region, the quantity of biomass available of Downy birch was much lower as Scots pine, 10% and 40% of the total available biomass respectively. Additionally, in average Downy birch produced less forage biomass per tree than Scots pine. In order to acquire the needed biomass of Downy birch forage, moose had to browse from a high number of trees. This increased the probability of this species to be browsed (Heikkilä and Härkönen, 1993, 1996; Augustine and McNaughton, 1998).

The selection between trees, regardless of species, was partly explained by the extend of previous browsing, i.e. accumulated browsing (plot 4) and Bergqvist et al. (2003), Löyttyniemi (1985) and Bergstrom (1984). During the winter of 2011-2012, only 1% of the trees which did not show any old browsing, were selected for browsing. One should take into account that 74.80% of the trees which we registered, had old browsing. This means, by chance, trees with old browsing had a higher probability of being selected. Still, the probability of being selected significantly increased over the different scales of accumulated browsing, indicating the selectivity of moose on trees with old browsing. Individual trees which were heavily browsed in previous years (accumulated browsing 3), experienced a ten time higher chance of being browsed than trees which did not have any old browsing. Yet, in contradiction to quadrat and plot scale, on tree level there was no significant difference in quantity of biomass browsed neither proportion of biomass browsed, in the different accumulated browsing classes.

Including biomass availability per tree into the full model, the probability of being browsed increased with an increase of biomass (slope=1.20, SE=0.14, $p<0.001$), i.e. moose selected for trees with higher quantities of biomass. Yet, after they selected these trees with more biomass, they did not increase their biomass consumption proportionally. Moose only ate between four to six percent of the biomass increase between individual trees, e.g. if one tree would have 100 grams more biomass than the other, moose ate between 4 to 6 grams more of the tree with more biomass. Contrary to the predictions of Senft et al. (1987) but following the finding of Månsson et al. (2007). This might indicate that moose do not actively select for the feature of high quantity biomass on tree level. It can be assumed that the chance of encountering easy reachable shoots increases with an increase in biomass availability on a tree. By chance, trees with more biomass available will be selected above those with less. Since food was overabundant in the region, landscapes and selected large communities, moose mainly browsed easy reachable shoots and moved on to the next tree.

This does not count for the rare species, where moose browsed more than just easy reachable shoots (Heikkilä and Härkönen, 1996; Augustine and McNaughton, 1998; Solbraa, 2008).

4.3 Matching of biomass consumption to biomass availability.

Senft et al. (1987) hypothesized that on the smallest spatial scales, large ungulate herbivores overmatch biomass consumption to biomass availability, i.e. with a doubling of biomass available a browsing response with more than doubling of biomass consumption is to be expected. Resulting in high proportions of biomass consumption on trees with large quantity of biomass available and low proportions of biomass consumed from trees with low quantity of biomass available. This overmatching of biomass consumption should gradually change to matching with an increase of spatial scale to region and landscape level. However, our data shows undermatching of biomass consumption on the two smallest scales (slope=0.40 (SE=0.02) on tree scale and slope=0.50 (SE=0.05) on plot scale) and a tendency towards matching on an intermediate scale (slope=0.84 (SE=0.18) on quadrat scale), contradicting my hypothesis. Månsson et al. (2007), found the same results, however could not explain this with their data. Our data takes more variables into account, which could be used to explain this behavior.

It should be expected that moose overmatch biomass consumption to biomass availability to maximize nutrient intake, by eating larger proportions of biomass from trees and patches of trees with high quantity of biomass available. To be able to explain this contradiction, we have to look to the largest spatial scale. On regional level, we found a standard deviation of 19247,66 kg/km² in biomass available, with a mean of 10472,81 kg/km² (2SE=4928.82), i.e. food availability is unequal distributed over the region. While, he hierarchy theory assumes that food is distributed equally over the region (Senft et al., 1987). Intense forestry in our study area creates this large variation in biomass availability, by dividing the forested landscape into large monoculture patches of forest, i.e. forest stands (Wam et al., 2005; Wam and Hjeljord, 2010). Within each stand, the variance in biomass available and species composition is low. However, the variance between stands is high. Forest stands of cutting class two contain the highest quantity of forage available. These stands function as feeding sites for moose during winter. My results showed that during the winter of 2011-2012, moose spent half of their time in cutting class two stands and our models suggest that moose selected for these stands. These stands are packed with food. More than 80% of the measured consumed biomass came from these stands. This can explain why moose under-match their biomass consumption to biomass availability on the smallest spatial scales. In a cutting class two stand, the moose have a high quantity of trees with browse available. The trade-off between energy spent acquiring food and amount of food consumed seems to be more profitable by moving from tree to tree, only browsing the biomass which is easy reachable and which is favored (i.e. selecting for preferred species and trees with intense old browsing), than eating as much as possible from trees with a high quantity of biomass available.

4.4 Applications

This research project focused on biomass availability and biomass consumption. Something which is important from the moose's point of view. However, persons who are familiar with how young Scots pine stands in moose wintering areas, might be confused when reading that moose only consumed 1.74% of the total measured biomass and 3.73% of the available Scots pine biomass. The damage inflicted by the moose is hard to miss and seems to be much more intense as described in this thesis (Danell et al., 1985; Danell et al., 1991; Heikkilä and Härkönen, 1993, 1996; Solbraa, 1998; Fremming, 1999; Solbraa, 2008; van Beest et al., 2010). If I would have focused on shoots, instead of biomass, the numbers would have looked quite different. From all species together, on regional level, moose browsed 4.78% of the available shoots and for Scots pine 6.11% of all available shoots. When focusing on cutting class two stands, this increases up to 7.87%. This means that in our studied area moose did not take 100% of the available biomass of the selected shoots. They took roughly 50% of what was available per shoot, except the highly palatable species which were maximally browsed, as was expected (Hobbs, 1996; Augustine and McNaughton, 1998). Additionally for all species, 9.94% of all fresh bites measured, were leading shoots and for Scots pine this was10.30%. This selectivity affects the growth form of the trees severely (Solbraa, 1998). We showed with our study that moose select many trees to browse from. The 3.73% of the available Scots pine biomass which was browsed, affected 24.32% of all pine in our studied region. Adding to that, browsing damage accumulates over the years (Bergstrom, 1984; Löyttyniemi, 1985; Bergqvist et al., 2003). So had 42.94% of all Scots pine some kind of browsing damage. All these factors combined make the damage, inflicted by the moose in young Scots pine stands, prominent.

4.4.1 Change forage availability

When thinking about which measures to take to decrease moose browsing intensity on young Scots pine stands, increasing biomass availability might seem a solution. By doubling biomass availability, one can expect to reduce the proportion of biomass browsed by half, assuming the moose density does not change, which is contrary to our and other previous findings (Heikkilä and Härkönen, 1996; Ball and Dahlgren, 2002). In our studied area this would mean that measures have to be taken to increase the biomass with 10472,81 kg/km² (2SE=4928.82), which probably would be impossible. It is to be questioned if the proportion of undamaged young trees will increase by this measure. During winter, moose selected cutting class 2 forest stands for foraging, even though cutting class 3 also contained a high quantity of available forage. Acknowledging this and taking into account the low proportional consumption of biomass in the region (1.74% of the measured available biomass was browsed), I highly doubt it that measures to increase biomass availability on regional or landscape level in areas with high abundance of moose forage, will be able to reduce damage on young commercial forest stands effectively.

Currently it is being discussed if moose browsing damage on young Scots pine can be reduced by increasing the biomass availability of the highly palatable tree species, such as Rowan, Aspen and Willow species. van Beest et al. (2010) pointed out that these highly palatable species are eaten first and afterwards moose switch to Scots Pine. By increasing the availability of these species, it could be possible to postpone when moose start browsing on Scots pine, which will shorten the browsing intensity on this species. As in previous studies (Heikkilä and Härkönen, 1993, 1996; Solbraa, 2008), Rowan Aspen and Willow species were heavily browsed in our studied region, because of their relative rarity (Bryant et al., 1991; Heikkilä and Härkönen, 1996; Hobbs, 1996; Augustine and McNaughton, 1998). If measures will be taken to increase numbers of these species in areas with high moose winter densities, it will be a difficult task to maintain the forage availability of these species, considering that moose will inflict severe browsing pressure on these species. As Augustine and McNaughton (1998), Bryant et al. (1991) and Hobbs (1996) showed, moose are capable to suppress these highly favored species. Perhaps large plantations, consisting out of highly palatable species will be able to maintain a sustainable supply of forage. Although I doubt it that this can bring financial benefits to the landowners.

Actions to increase forage availability should be taken in cutting class two stands, since these stands are selected for foraging (Fremming, 1999; Ball and Dahlgren, 2002; Bergqvist et al., 2003). Foresters can increase the available biomass by increasing number of seedlings and maintaining high densities of trees (Fremming, 1999). Browsed trees should not be removed during pre-commercial thinnings, since moose prefer to re-browse these trees. When removing all badly damaged trees, moose are forced to eat from the remaining good trees. Instead of removing unwanted trees, trees can be topped in order to create more light and space for the undamaged trees and on the same time keep provide forage (Bergström and Bergqvist, 2009). Additionally, increasing the stem density will increase the quantity of undamaged and slightly damaged trees in the young stand (Heikkilä and Härkönen, 1993, 1996; Fremming, 1999). Stem densities can be increased by increasing the intensity of the soil scarification (Beland et al., 2000).

Based on my findings, I suggest to maintain low moose densities to be able to minimalize damage on young Scots pine stands (Lavsund et al., 2003). Since moose migrate from different areas to winter habitats (Ball and Dahlgren, 2002; van Beest et al., 2011), additional harvesting of moose during winter should be applied to reduce the wintering population effectively. Considering the large proportion of trees affected even with low proportions of biomass loss, these suggested measures will be most effective when combined.

4.4.2 Changing moose behavior and habitat selection

Moose select you Scots pine stands for browsing during winter (Belovsky, 1981; Bergstrom, 1984; Heikkilä and Härkönen, 1993, 1996; Fremming, 1999; Ball and Dahlgren, 2002; Bergqvist et al., 2003). These stands do not provide much cover for moose from predators and human disturbance (Demarchi and Bunnell, 1995; Godvik et al., 2009). Considering the low abundance of large predators in the studied area, moose could afford spending 50% of their time in cutting class 2 stands during the winter period of 2011-2012, acquiring 80% of the total browsed biomass. Cutting class 3 stands provide better cover from large predators and human disturbance. Adding to that, there 28% of the available biomass was found in this cutting class. Yet, moose in our studied region, spent 25% of their time here and acquired barely 8% of the browsed biomass. This indicates that moose selected cutting class 2 stands for foraging and cutting class 3 stands for resting, digesting, cover and to minimum extend foraging. If actions could be taken to force moose to select cutting class 3 stands more intensively for foraging, this could reduce the browsing damage on young Scots pine.

In Yellowstone national park, large numbers of elk were able to suppress the growth of woody plants (Ripple and Beschta, 2003), until the reintroduction of wolf (Ripple et al., 2001; Ripple and Beschta, 2003; Mao et al., 2005). By the presence of the wolf, elk were forced to change their habitat choice and especially time spent per habitat type. The change in the behavior of the elk, had great favorable consequences for the woody plant species in the area. The risk of predation effectively reduces browsing pressure and number of trees browsed (Ripple et al., 2001). It would be interesting to see how moose browsing patterns would change when the wolf density would be increased in our studied region. However, large carnivores and their existence in Norway are the base of ongoing conflicts (Vitterso et al., 1998; Kaltenborn et al., 1999; Linnell et al., 1999; Linnell et al., 2000; Skogen, 2001; Røskaft et al., 2003; Swenson and Andrén, 2005; May et al., 2008), which makes this probable solution not considerable for this time, but hopefully in the near future.

This study was conducted in a boreal forest system where timber production is a primary goal. This resulted in a patchy distribution of foraging sites through the landscape. Forage for moose was highly abundant and mainly consisted out of Scots pine. Salix species, Rowan and Aspen were rare species, accounting for only 0.25% of the available biomass, but were strongly selected as forage. The findings presented in this thesis might not apply for other areas with wild moose populations. Especially not for areas with different forage composition and forage distribution.

4.5 Future research

My assumption, that moose mainly browsed easy reachable shoots, cannot be statistically confirmed with our data set, since we did not include any variables which account for reachability of the browsed shoots. Future research projects can include observational data from observing moose browsing behavior in cutting class two Scots pine stands. Simply measuring the location of bites which have been taken, would not be sufficient. Since multiple moose can have browsed from the same tree during one winter. Shoots which are easy reachable for one moose, might not be easy reachable for another moose, if they approach the tree from a different direction or at different times during the winter.

We did not have any accurate data for estimating real moose densities. It would be interesting to include genetic analyses of the droppings to get a better indication of moose density in the areas. It would be interesting to look at the distribution and habitat use of individual moose to see if all individuals select for similar habitat types for foraging.

To get a broader perspective of moose browsing decisions on spatial scales, I would suggest a different study design. With the study design we used, the two largest spatial scales are too low of sample size and cover quite a lot more area than the next smallest scale. It would be of great value to have a spatial scale between quadrat and study area scale, to see how the different predictor variables change with an increase in scale. Additionally, it would be interesting to repeat the study in a different area where biomass availability, composition and distribution are different from our study area.

5. Acknowledgements

First of all I want to say many thanks to Professor Christina Skarpe, not only for being my supervisor but also for involving me in this research project and getting me back to Norway in the first place. It has been a great pleasure working together with you over the past four years! I thank Karen Marie Mathisen for being my second supervisor, advising me with the statistics and providing me with the data set with dry shoot biomass weights for the studied species. I thank the team of fieldworkers with who I in 2012 collected the data for this study, and the additional team of fieldworkers who collected the data on shoot weights.

Boris Fuchs, Martin Mayer, Torfinn Jahren, Cyril Milleret and Asuncion Semper Pascual, thank you for the occasional help during the master period.

References

Andersen, R., and B.-E. Saether. 1992. Functional response during winter of a herbivore, the moose, in relation to age and size. Ecology: 542-550.

Andren, H., and P. Angelstam. 1993. Moose browsing on Scots pine in relation to stand size and distance to forest edge. Journal of Applied Ecology: 133-142.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. The Journal of wildlife management: 1165-1183.

Ball, J. P., and J. Dahlgren. 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: 427-435.

Ball, J. P., K. Danell, and P. Sunesson. 2000. Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. Journal of Applied Ecology 37: 247-255.

Beland, M., E. Agestam, P. Ekö, P. Gemmel, and U. Nilsson. 2000. Scarification and seedfall affects natural regeneration of Scots pine under two shelterwood densities and a clear-cut in southern Sweden. Scandinavian Journal of Forest Research 15: 247-255.

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology 14: 105-134.

Belovsky, G. E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62: 1020-1030.

Belovsky, G. E. 1984. Herbivore optimal foraging: a comparative test of three models. American Naturalist: 97-115.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18: 320-331.

Bergqvist, G., R. Bergström, and L. Edenius. 2003. Effects of moose (< i> Alces alces</i>) rebrowsing on damage development in young stands of Scots pine (< i> Pinus sylvestris</i>). Forest Ecology and Management 176: 397-403.

Bergstrom, R. 1984. Rebrowsing on birch (Betula pendula and B. pubescens) stems by moose. In: Proceedings of the North American Moose Conference and Workshop. p 3-13.

Bergström, R., and G. Bergqvist. 2009. Viltvård I skogslandskapet. Weberyd Widemo & Mörner (Eds.)

Viltvårdsboken. Svenska Jägareförbundet.: Pp 237.

Bischof, R. et al. 2012. A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? The American Naturalist 180: 407-424.

Boyce, M. S. et al. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10: 421-431.

Brandner, T. A., R. O. Peterson, and K. L. Risenhoover. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. Ecology: 155-164.

Brown, J. R., and J. W. Stuth. 1993. How herbivory affects grazing tolerant and sensitive grasses in a central Texas grassland: integrating plant response across hierarchical levels. OIKOS-COPENHAGEN- 67: 291-291.

Bryant, J. P. et al. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annual Review of Ecology and Systematics 22: 431-446.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer.

Cederlung, C., H. Ljungqvist, G. Markgren, and F. Stalfelt. 1980. Foods of Moose and Roe-deer at Grimsö in Central Sweden. Results of Rumen Contents Analyses. Svenska Jägareförbundet.

Coppock, D. L., J. Ellis, J. Detling, and M. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia: 10-15.

Crawley, M. J. 1983. Herbivory: the dynamics of animal-plant interactions. Univ of California Press.

Dahlberg, B. L., and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin.

Danell, K., R. Bergström, L. Edenius, and G. Ericsson. 2003. Ungulates as drivers of tree population dynamics at module and genet levels. Forest Ecology and Management 181: 67-76.

Danell, K., L. Edenius, and P. Lundberg. 1991. Herbivory and tree stand composition: moose patch use in winter. Ecology: 1350-1357.

Danell, K., K. Huss-Danell, and R. Bergström. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology: 1867-1878.

Demarchi, M. W., and F. Bunnell. 1995. Forest cover selection and activity of cow moose in summer. Acta Theriologica 40.

Duncan, P. 1983. Determinants of the use of habitat by horses in a Mediterranean wetland [in France]. Journal of Animal Ecology.

Franzmann, A. W., and C. C. Schwartz. 2007. Ecology and management of the North American moose.

Fremming, O. R. 1999. Elgbeiting på furu: en kunnskapsoversikt.

Fryxell, J. M., J. Greever, and A. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist: 781-798.

Gill, R. 1992. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry 65: 363-388.

Godvik, I. M. R. et al. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90: 699-710.

Gundersen, H., H. P. Andreassen, and T. Storaas. 2004. Supplemental feeding of migratory moose Alces alces: forest damage at two spatial scales. Wildlife Biology 10: 213-223.

Hanley, T. A. 1984. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. Journal of applied ecology 21: 423-436.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight—a reevaluation. Ecology 60: 389-402.

Haukioja, E., K. Ruohomäki, J. Senn, J. Suomela, and M. Walls. 1990. Consequences of herbivory in the mountain birch (Betula pubescens ssp tortuosa): importance of the functional organization of the tree. Oecologia 82: 238-247.

Healy, W. M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts.

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological monographs 78: 141-166.

Heikkilä, R., and S. Härkönen. 1993. Moose (Alces alces L.) browsing in young Scots pine stands in relation to the characteristics of their winter habitats.

Heikkilä, R., and S. Härkönen. 1996. Moose browsing in young Scots pine stands in relation to forest management. Forest Ecology and Management 88: 179-186.

Herfindal, I. et al. 2009. Scale dependency and functional response in moose habitat selection. Ecography 32: 849-859.

Hjeljord, O., N. Hövik, and H. B. Pedersen. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Ecography 13: 281-292.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. The Journal of Wildlife Management: 695-713.

Honkanen, T., E. Haukioja, and V. Kitunen. 1999. Responses of Pinus sylvestris branches to simulated herbivory are modified by tree sink/source dynamics and by external resources. Functional Ecology 13: 126-140.

Hunter, R. 1962. Hill sheep and their pasture: a study of sheep-grazing in south-east Scotland. The Journal of Ecology: 651-680.

Jia, J.-B., P. Niemelä, and K. Danell. 1995. Moose Alces alces bite diameter selection in relation to twig quality on four phenotypes of Scots pine Pinus sylvestris. Wildlife Biology 1: 47-55.

Kaltenborn, B. P., T. Bjerke, Vitters, and J. oslash. 1999. Attitudes toward large carnivores among sheep farmers, wildlife managers, and research biologists in Norway. Human Dimensions of Wildlife 4: 57-73.

Kielland, K. 2001. Short-circuiting the nitrogen cycle: Ecophysiological strategies of nitrogen uptake in plants from marginal environments Plant Nutrient Acquisition. p 376-398. Springer.

Lavsund, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. Swedish Wildlife Research.

Lavsund, S., T. Nygrén, and E. J. Solberg. 2003. Status of moose populations and challenges to moose management in Fennoscandia. Alces 39.

Lesage, L. 2000. QUALITY OF PLANT SPECIES CONSUMED BY NORTHERN WHITE-TAILED OEER IN SUMMER ALONG A CLlMATlC GRADIENT. ÉCOLOGIE ESTIVALE DU CERF DE VIRGINIE Ala LIMITE NORD DE SON AIRE DE DISTRIBUTION: DE LA MÉTAPOPULATION Al'INDIVIDU.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology 67: 413-418.

Linnell, J. D., J. Odden, M. E. Smith, R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: do “problem individuals” really exist. Wildlife Society Bulletin 27: 698-705.

Linnell, J. D., J. E. Swenson, and R. Andersen. 2000. Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? Biodiversity & Conservation 9: 857-868.

Lundberg, P. 1988. The evolution of partial migration in birds. Trends in Ecology & Evolution 3: 172-175.

Löyttyniemi, K. 1985. On repeated browsing of Scots pine saplings by moose (Alces alces).

Långström, B., and C. Hellqvist. 1991. Effects of different pruning regimes on growth and sapwood area of Scots pine. Forest Ecology and Management 44: 239-254.

Machida, S. 1979. Differential use of willow species by moose in Alaska, University of Alaska, Fairbanks.

Manseau, M., J. Huot, and M. Crête. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. Journal of Ecology: 503-513.

Mao, J. S. et al. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69: 1691-1707.

Marquis, D. A. 1974. The impact of deer browsing on Allegheny hardwood regeneration.

May, R. et al. 2008. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. Journal of Applied Ecology 45: 1382-1391.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist: 133-140.

McNaughton, S. 1985. Ecology of a grazing ecosystem: the Serengeti. Ecological monographs 55: 259-294.

Millard, P., A. Hester, R. Wendler, and G. Baillie. 2001. Interspecific defoliation responses of trees depend on sites of winter nitrogen storage. Functional Ecology 15: 535-543.

Morellet, N., and B. t. Guibert. 1999. Spatial heterogeneity of winter forest resources used by deer. Forest ecology and management 123: 11-20.

Mysterud, A., P. K. Larsen, R. A. Ims, and E. Østbye. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Canadian Journal of Zoology 77: 776-783.

Månsson, J. 2009. Environmental variation and moose Alces alces density as determinants of spatio-temporal heterogeneity in browsing. Ecography 32: 601-612.

Månsson, J., H. Andrén, Å. Pehrson, and R. Bergström. 2007. Moose browsing and forage availability: a scale-dependent relationship? Canadian Journal of Zoology 85: 372-380.

Månsson, J., N. Bunnefeld, H. Andrén, and G. Ericsson. 2012. Spatial and temporal predictions of moose winter distribution. Oecologia 170: 411-419.

Palo, R., R. Bergström, and K. Danell. 1992. Digestibility, distribution of phenols, and fiber at different twig diameters of birch in winter. Implication for browsers. Oikos: 450-454.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. The Journal of Wildlife Management: 474-488.

Persson, I.-L., K. Danell, and R. Bergstrom. 2000. Disturbance by large herbivores in boreal forests with special reference to moose. In: Annales Zoologici Fennici. p 251-263.

Persson, I. L., R. Bergström, and K. Danell. 2007. Browse biomass production an. regrowth capacity after biomass loss in deciduous and coniferous trees: responses to moose browsing along a productivity gradient. Oikos 116: 1639-1650.

Peterson, R. L. 1955. North American moose. Univ. Toronto

Press, Ontari.

Poole, K. G., and K. Stuart-Smith. 2006. Winter habitat selection by female moose in western interior montane forests. Canadian Journal of Zoology 84: 1823-1832.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual review of ecology and systematics: 523-575.

Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184: 299-313.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. Biological Conservation 102: 227-234.

Røskaft, E., T. Bjerke, B. Kaltenborn, J. D. Linnell, and R. Andersen. 2003. Patterns of self-reported fear towards large carnivores among the Norwegian public. Evolution and human behavior 24: 184-198.

Senft, R. et al. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37: 789-795.

Skogen, K. 2001. Who's Afraid of the Big, Bad Wolf? Young People's Responses to the Conflicts Over Large Carnivores in Eastern Norway*. Rural Sociology 66: 203-226.

Solbraa, K. 1998. Elg og skogbruk; biologi, økonomi, beite, taksering, forvaltning. Red. Hårstad, Gunnar O. Skogbrukets Kursinstitutt, Biri.

Solbraa, K. 2008. Elg i Atndal og naboområder: forvaltning av elg og skog.

Stokke, S. 1999. Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. Canadian Journal of Zoology 77: 1723-1732.

Swenson, J., and H. Andrén. 2005. A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. CONSERVATION BIOLOGY SERIES-CAMBRIDGE- 9: 323.

Swihart, R. K., N. A. Slade, and B. J. Bergstrom. 1988. Relating body size to the rate of home range use in mammals. Ecology 69: 393-399.

Sæther, B.-E., K. Solbraa, D. P. Sødal, and O. Hjeljord. 1992. Sluttrapport elg-skog-samfunn. NINA forskningsrapport 28: 1-153.

Taylor, R. 1982. Group size in the eastern grey kangaroo, Macropus giganteus, and the wallaroo, Macropus robustus. Wildlife Research 9: 229-237.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. The Journal of Wildlife Management: 524-532.

van Beest, F. M., H. Gundersen, K. M. Mathisen, J. M. Milner, and C. Skarpe. 2010. Long-term browsing impact around diversionary feeding stations for moose in Southern Norway. Forest ecology and management 259: 1900-1911.

van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology 80: 771-785.

Van Hees, A., A. Kuiters, and P. Slim. 1996. Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. Forest Ecology and Management 88: 55-63.

Vitterso, J., B. P. Kaltenborn, and T. Bjerke. 1998. Attachment to livestock and attitudes toward large carnivores among sheep farmers in Norway. Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals 11: 210-217.

Vourc'h, G. et al. 2002. Monoterpene effect on feeding choice by deer. Journal of chemical ecology 28: 2411-2427.

Wam, H. K., and O. Hjeljord. 2010. Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. European journal of wildlife research 56: 745-755.

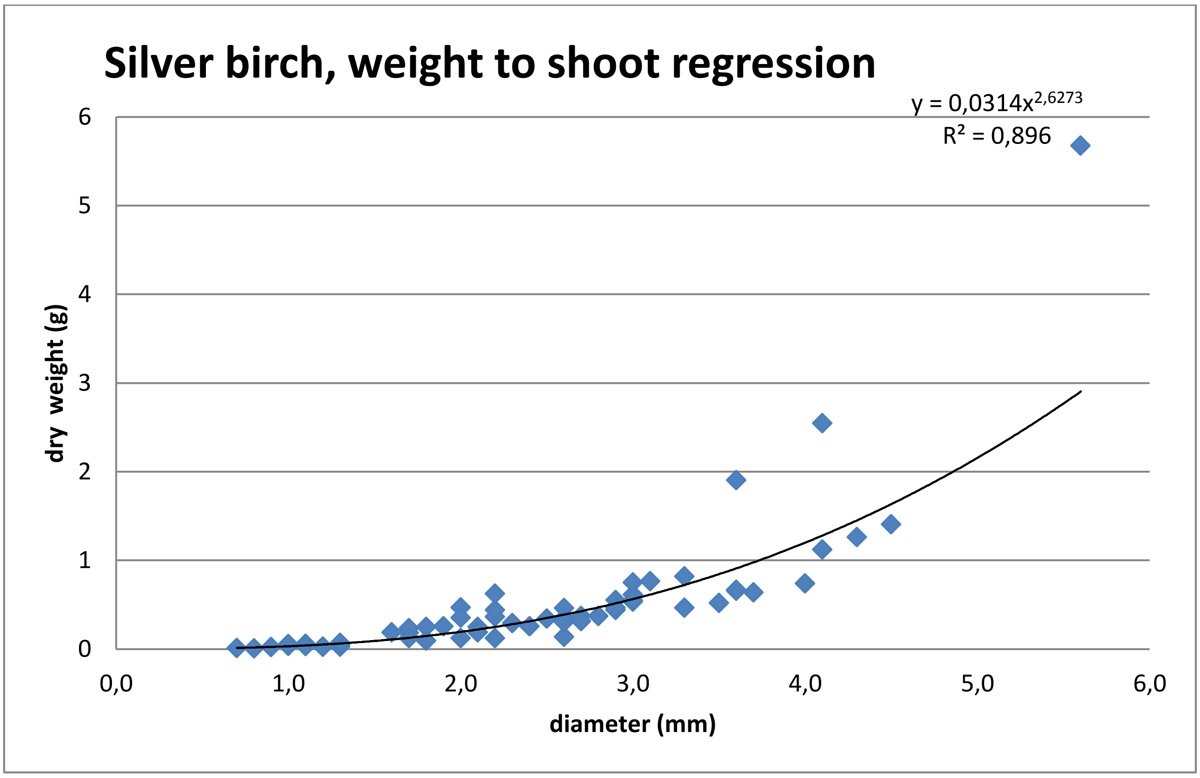
Wam, H. K., O. Hofstad, E. Nævdal, and P. Sankhayan. 2005. A bio-economic model for optimal harvest of timber and moose. Forest ecology and management 206: 207-219.

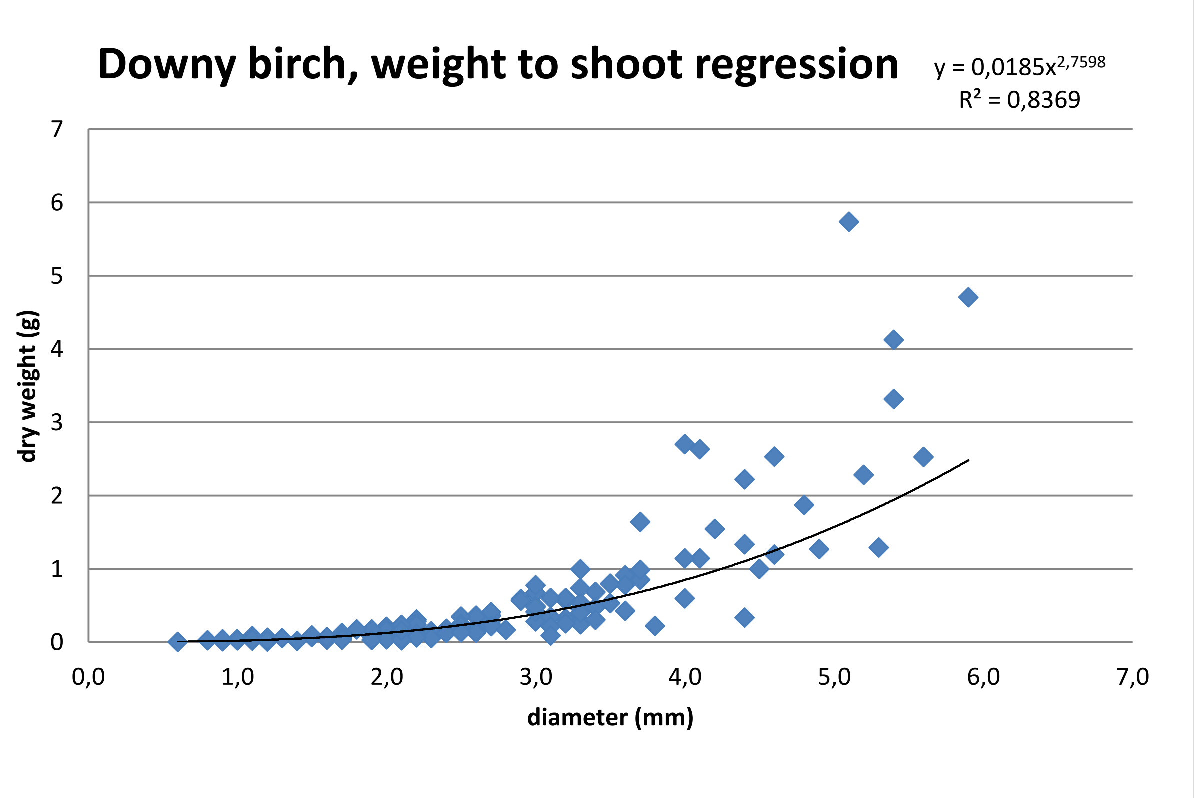
Ward, D., and D. Saltz. 1994. Forging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. Ecology: 48-58.

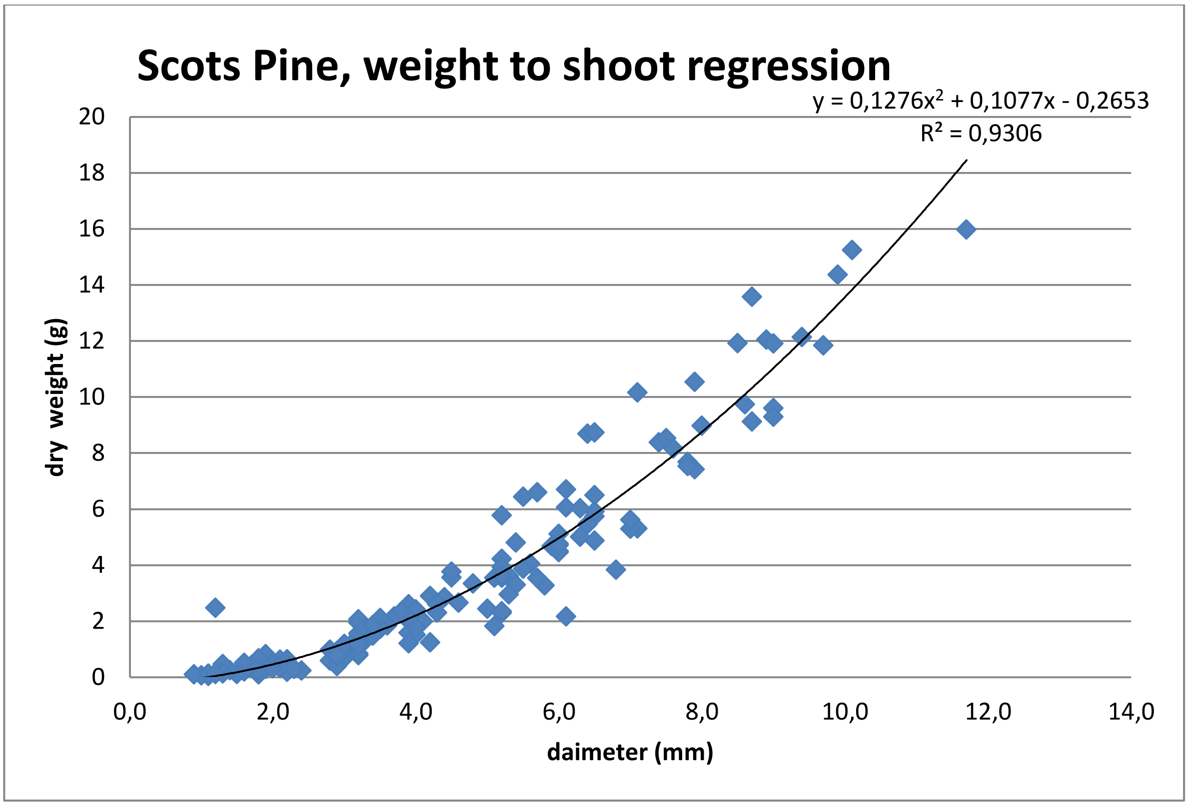
Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. American Naturalist: 290-304.

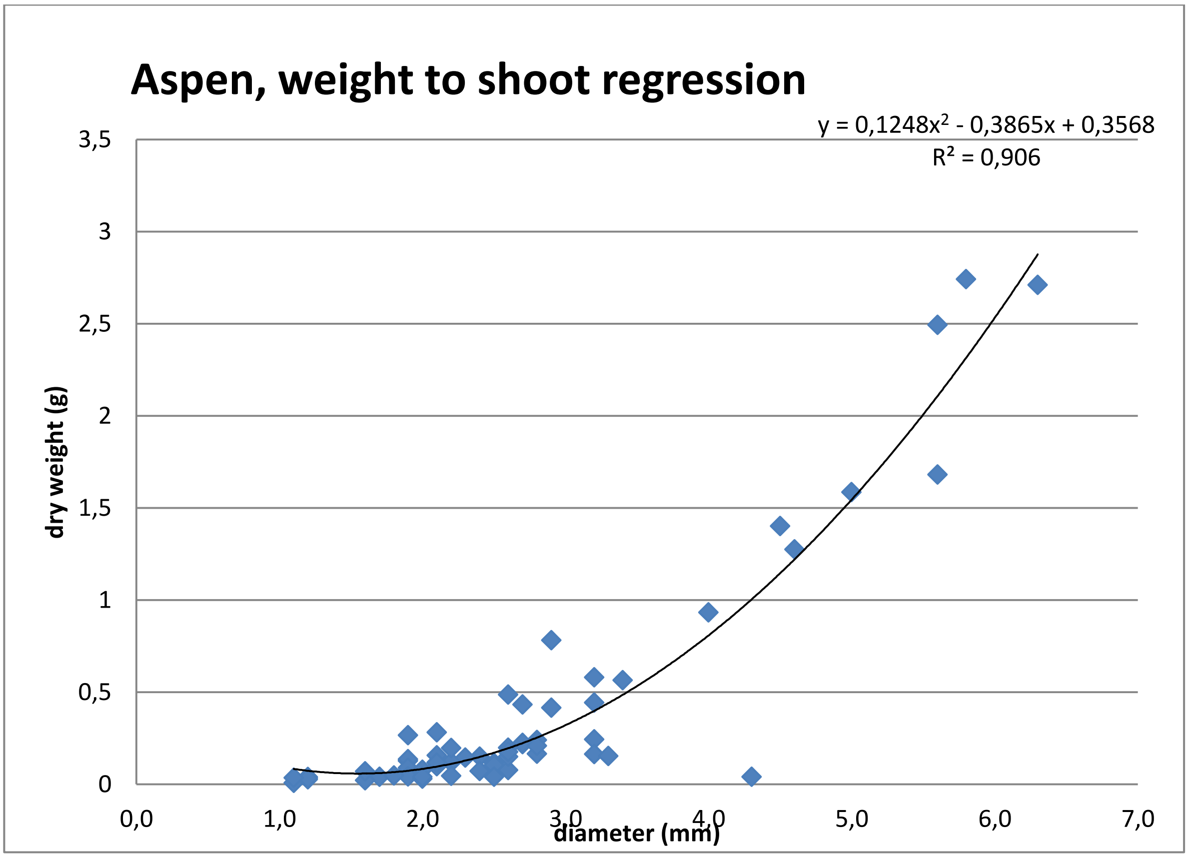
Appendix

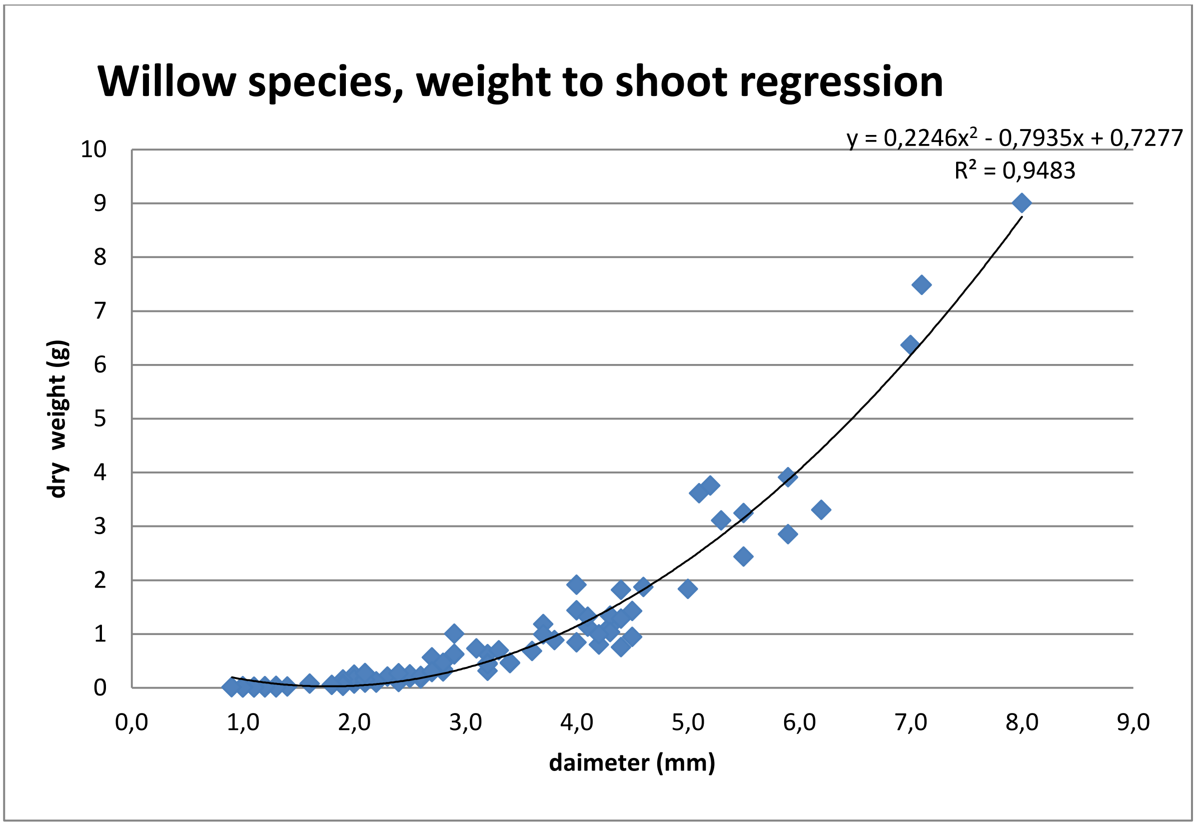
Regression curves of dry biomass weights to shoot diameters and number of shoots to crowns content for Juniper.



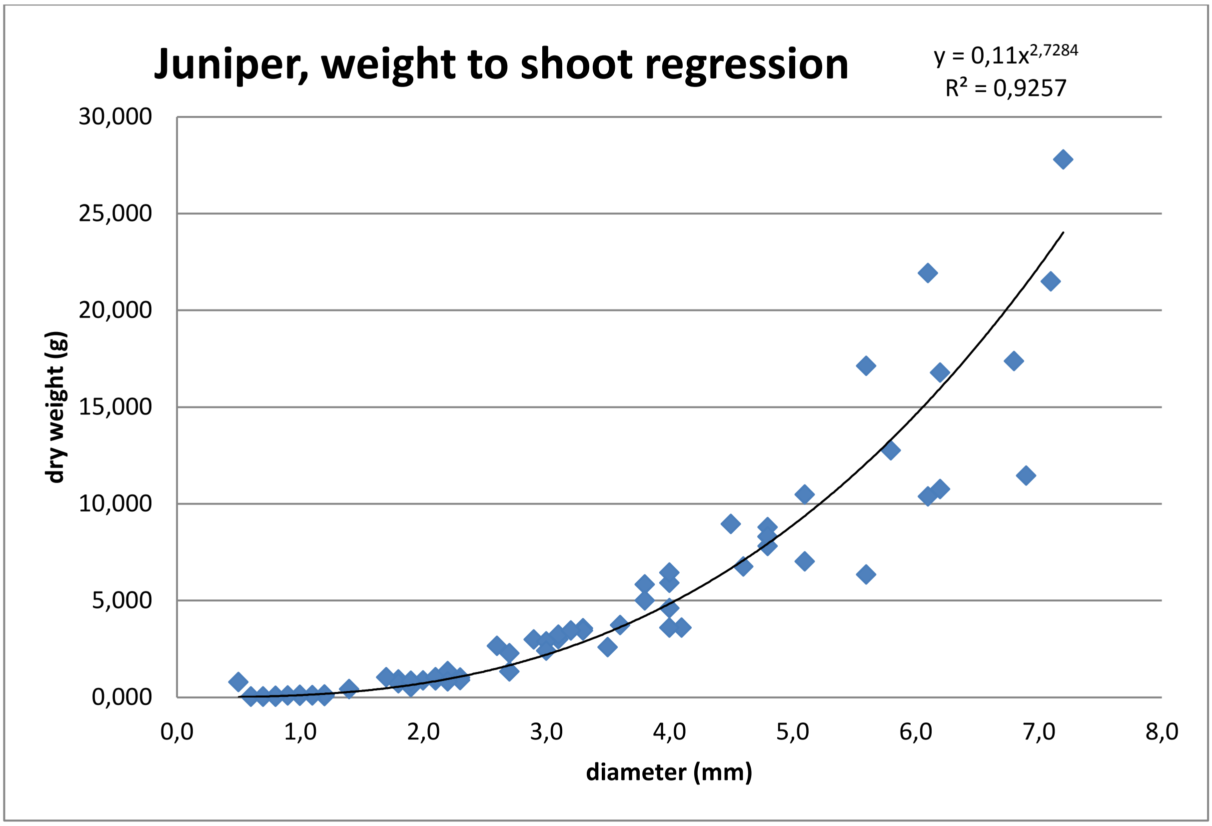


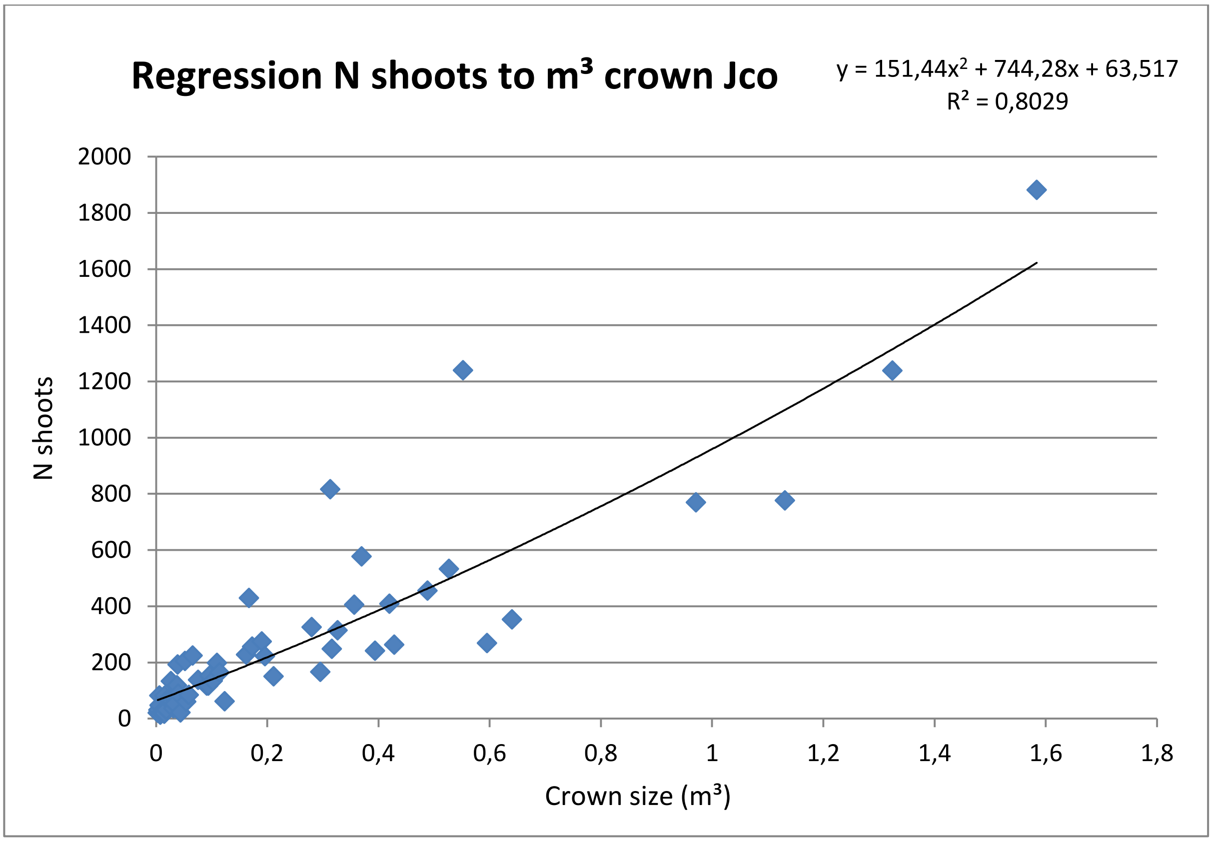

Scots Pine, weight to shoot regression
y = 0,1276x² + 0,1077x - 0,2653
R² = 0,9306
dry weight (g)
20
18
16
14
12
10
8
6
4
2
0
0,0
2,0
4,0
6,0
8,0
10,0
12,0
14,0
daimeter (mm)


Aspen, weight to shoot regression
y = 0,1248x² - 0,3865x + 0,3568
R² = 0,906
dry weight (g)
3,5
3
2,5
2
1,5
1
0,5
0
0,0
1,0
2,0
3,0
4,0
5,0
6,0
7,0
diameter (mm)


Willow species, weight to shoot regression
y = 0,2246x² - 0,7935x + 0,7277
R² = 0,9483
dry weight (g)
10
9
8
7
6
5
4
3
2
1
0
0,0
1,0
2,0
3,0
4,0
5,0
6,0
7,0
8,0
9,0
daimeter (mm)


Rowan, weight to shoot regression
y = 0,0085x^3,0386
R² = 0,8634
dry weight (g)
9
8
7
6
5
4
3
2
1
0
0,0
1,0
2,0
3,0
4,0
5,0
6,0
7,0
8,0
9,0
10,0
diameter (mm)


Juniper, weight to shoot regression
y = 0,11x^{2,7284}
R² = 0,9257
dry weight (g)
30,000
25,000
20,000
15,000
10,000
5,000
0,000
0,0
1,0
2,0
3,0
4,0
5,0
6,0
7,0
8,0
diameter (mm)


Regression N shoots to m³ crown Jco
y = 151,44x² + 744,28x + 63,517
R² = 0,8029
N shoots
2000
1800
1600
1400
1200
1000
800
600
400
200
0
0
0,2
0,4
0,6
0,8
1
1,2
1,4
1,6
1,8
Crown size (m³)