

**Diet composition and variation in winter of supplementarily fed  
moose**

**Rosemary Ogwe Nanji**

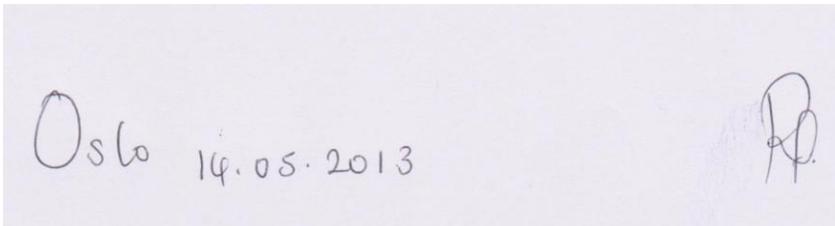


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## Abstract

Supplementary feeding of ungulates during winter is a common practice in Europe and North America. Amongst species that are fed with a diversionary purpose is the moose *Alces alces*. Winter supplementary feeding of moose has been practiced for over 20 years in Hedmark County, Norway. However, the goal of diverting moose from young pine stands remains questionable as there is still substantial browsing around the feeding stations. Little is known of the composition of browse species and the relative amounts eaten by the moose using feeding stations. Using microhistological technique, I identified the different plant species in the faeces of moose using feeding stations. I also investigated the ratio of browse to silage faecal fragments, the variation in diet composition through the winter and how diet composition related to feeding station use. I collected a total of 51 faecal samples around feeding stations between January and March 2011 and 17 from GPS collared moose in March 2010. Data were treated using logistic regression with a quasibinomial error structure. The results in this study indicate that moose using feeding stations still browse on natural forage and they have a different diet composition from moose not using feeding stations. Of the 13 plant species identified in the faecal samples, spruce and pine were the dominant natural forage, followed by bilberry. There was no significant difference in browse to silage ratio between the months. However, pine and spruce consumption were affected by month with pine decreasing through the winter due to depletion. There was a strong negative correlation between pine and silage and a weak positive but significant correlation between pine and spruce as well as pine and birch. Feeding stations were strategically put in spruce dense areas with the notion that it is a species avoided by moose which is however contrary in this study, especially in areas with long feeding history, I recommend the forest managers to redress the costs and benefits of using supplementary winter feeding to divert moose from commercially important browse species.

Key words: *Alces alces*, browsing, faecal sample, feeding, feeding station use, microhistology, supplementary winter

## CHAPTER ONE

### 1.0. INTRODUCTION

Large herbivore populations have been expanding and increasing in density across Europe and North America in recent decades (Côté et al. 2004; Milner et al. 2006). This has consequences for natural ecosystems and biodiversity. Heavy browsing in the forest by cervids can reduce plant cover and diversity, with cascading effects on other taxa, extending to insects, birds and mammals (Côté et al. 2004). For example, persistent negative impacts on the quantity and quality of vegetation have been documented for the white-tailed deer (*Odocoileus virginianus*) on the George Reserve in Michigan (McCullough 1979). Increasing elephant (*Loxodonta africana*) and ungulate populations has profoundly changed an ecosystem in Northern Botswana (Skarpe et al. 2004). Reported changes in vegetation structure and composition along the Chobe river front due to increasing elephant populations has caused a decline in habitat quality for some species like bushbuck (*Tragelaphus scriptus*) and an improved habitat for others, such as buffalo (*Syncerus caffer*) and impala (*Aepyceros melampus*) (Skarpe et al. 2004; Skarpe unpublished). Plant cover, which large herbivores reduce, is important for small mammal populations (Bowland and Perrin 1989). Bergström (2004) reported a positive correlation between small mammal densities and species richness on the one hand, and plant cover and reduced grazing pressure on the other in the Kalahari in Western Botswana. Smaller populations of small mammals have also been reported in areas with large herbivores in Southeastern Botswana (Saetnan and Skarpe 2006). When a plant is being browsed by large a herbivore, this influences either positively or negatively, the choice of this plant by other herbivores due to plant response. For example the choice of food for voles is influenced by moose browsing with subsequent consequences on vole population dynamics in Fennoscandia (Pedersen et al. 2011).

Recurrent browsing on commercially valuable young Scots pine (*Pinus sylvestris*) stands during winter (Bergquist et al. 2003; Kalen and Bergquist 2004) causes conflict between forestry and hunting interests throughout Scandinavia. The impact by browsing on pine regeneration is severe where moose (*Alces alces*) densities are high (Lavsund 1987; Andren and Angelstam 1993;

Heikkilä and Härkönen 2000), with high costs for the landowners (Storaas et al. 2001). A common practice to reduce this browsing pressure on commercial forests is the use of supplementary feeding (Smith 2001; Peek et al. 2002; Putman and Staines 2004). Supplementary feeding of cervids in the winter is also used to increase their survival (Boyce 1989), to maintain high densities of animals for hunting, to improve trophy quality (Raesfeld and Reulecke 1988; Sackl 1992; Wieselmann 1994), to reduce crop damage, and to promote game viewing and trapping (Smith 2001; Peek et al. 2002; Putman and Staines 2004; van Beest et al. 2010b). Species fed include white-tailed deer, red deer / North American elk (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and moose, amongst which it has been documented that space use patterns may be restricted to the vicinity of the feeding stations (e.g. white-tailed deer: Kilpatrick and Stober 2002, roe deer: Guillet et al. 1996, moose: van Beest et al. 2010a). Feeding cervids during winter is practiced in North America (Smith 2001) and some parts of Europe including Hungary, Austria, Germany, Denmark, Sweden and Norway (Gill 1990).

Several studies have investigated different aspects of moose and forest management in Stor-Elvdal municipality, Hedmark County in south eastern Norway. They include the economic value of moose hunting (Storaas et al. 2001), long-term impacts of moose browsing around feeding stations (van Beest et al. 2010b), the cascading effect of moose management on birds (Mathisen and Skarpe 2011), the effects of moose density on reproduction, growth and species composition in field-layer vegetation (Mathisen et al. 2010), the role of winter body mass in reproductive allocation in Norwegian moose (Milner et al. 2012a) and gastrointestinal nematodes of moose in relation to supplementary feeding (Milner et al. 2013), just to name a few. Landowners in Stor-Elvdal municipality have fed moose with silage during winter since the early 1990s to reduce moose movements and involvement in traffic accidents, as well as in an attempt to reduce intense browsing on young pine (Gundersen et al. 2004; Andreassen et al. 2005, Milner et al. 2012b). The silage is a mixture of graminoids and forbs, predominantly timothy (*Phleum pratense*). It also included oats (*Avena sativa*) and rape (*Brassica napus*) in the early years of the feeding programme. However, despite the large quantities of silage fed to moose (up to 2000 tons per winter (Milner et al. 2012b)), moose still eat considerable amounts of natural browse in addition, and with time and increasing numbers of moose at the feeding stations, the radius of

heavy browsing is increasing (Tange 2007; van Beest et al. 2010b). Leader stem browsing on most species is common up to 1km from feeding stations and browse species usually avoided, like Norway spruce (*Picea abies*), are also eaten close to the feeding stations (Van Beest et al. 2010b).

The intense browsing observed, in spite of the ample supply of readily available silage, implies that the silage alone may not fulfill all dietary requirements. There may be a need for additional resources, for example fiber, minerals (such as sodium and calcium), proteins and pectin. Milner et al. (2012a) also reported that reproductive success in Norwegian moose is limited by winter nutritional condition. Alternatively, the intense browsing around the feeding stations could be to avoid intra-specific competition between individuals. Intensified social strife and conflicts have been demonstrated amongst white-tailed deer (Ozoga 1972) and red deer (Veiberg et al. 2004) sharing a confined winter feeding area, as well as amongst moose at mineral licks during summer (Couturier and Barrette 1988). If this intense browsing around the feeding stations is because of the need for additional nutrient resources, then the ratio of browse to silage in the diet should be reasonably constant between individuals and throughout winter even as the availability of natural browse decreases. On the other hand, from the high quality diet (low in defense compounds such as tannins and phenolics) provided by the silage may allow moose to tolerate browse from plant species having high concentrations of chemical defenses which would otherwise be unpalatable (Bryant et al. 1991; Epple et al. 1996; Edlich and Stolter 2012). A better knowledge of browsing patterns by moose at feeding stations and the differences from moose not using feeding stations would be valuable for the management of moose in winter.

The aim of this research is to increase the knowledge of the winter diet of moose using feeding stations in comparison with naturally foraging moose. Two null hypotheses will be tested.

- 1) The proportion of browse in the diet of moose at feeding stations is relatively constant throughout the winter
- 2) Moose diet selectivity is unaffected by feeding station use

The specific objectives include:

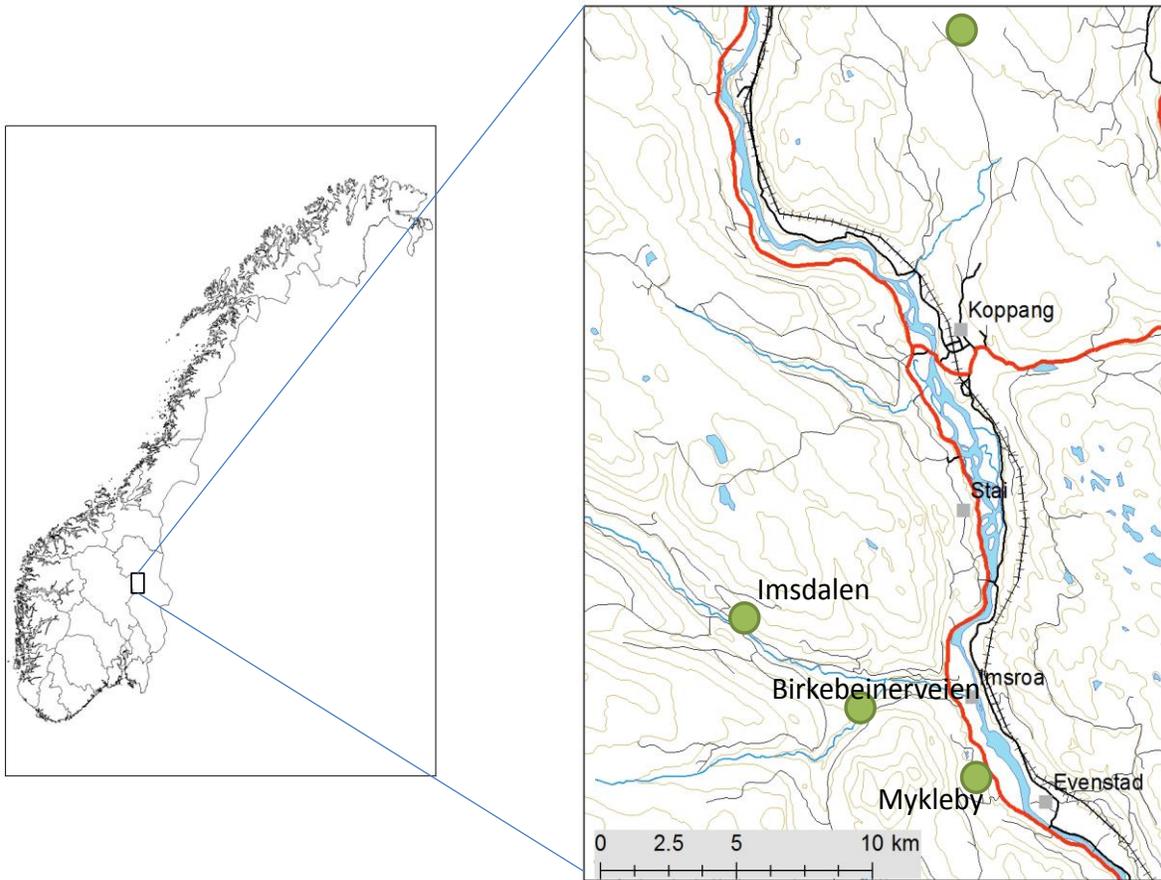
1. To identify the different plant species eaten by moose that use feeding stations and determine the ratio of browse to silage in the diet
2. To investigate how diet composition changes through the winter season
3. To investigate the composition of the diet of moose in relation to use of feeding stations

## CHAPTER TWO

### 2.0. MATERIALS AND METHODS

#### 2.1. Study area

This study was carried out in Stor-Elvdal municipality, Hedmark county in southeast Norway (61°24' 11°7'E; Fig. 1). The elevation ranges from 250 m to 1,100 m. The forested area is dominated by commercially managed pure or mixed stands of Scots pine and Norway spruce with low densities of deciduous species such as rowan (*Sorbus aucuparia* L.), willow (*Salix* spp.), birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth.) and aspen (*Populus tremula* L.). The mean temperature during January to March 2011 were -7.8 °C, -9.7°C and - 3.7 °C respectively and the snow depth, 257 m (Evenstad Forestry School weather station; Norwegian Meteorological Institute; [www.yr.no](http://www.yr.no)). Moose dominates the cervid community in this municipality with very low densities of roe deer and red deer (Gundersen et al. 2008). The current winter density of moose in this municipality is approximately 1.3 moose/km<sup>2</sup> and even higher at the local wintering areas (Milner et al. 2012). The supplementary feed here, silage, is provided ad libitum from November to April depending on annual snow conditions. The silage, which is in bales weighing 600-800 kg (fresh weight), is distributed at feeding stations which are located at permanent sites along snow-cleared forest roads with low human activity (van Beest et al. 2010b).



**Fig. 1** Map showing study area. The green circles represent the four feeding station areas (Koppang, Imsdalen, Birkebeinerveien and Mykleby) within which faecal samples were collected.



**Fig. 2. Picture of a feeding station in Stor-Elvdal municipality**

## **2.2. The Moose – a selective browser**

The moose is the largest member of the deer family (Cervidae). Moose inhabit boreal conifer and mixed deciduous forests of the northern hemisphere in temperate to subarctic climates. The moose range in North America includes almost all of Canada (excluding the arctic), Alaska, northern New England and upstate New York, northeastern Minnesota, Michigan's Upper

Peninsula, the upper Rocky Mountains, and Isle Royale (Bergström and Hjeljord 1987, Baskin and Danell 2003). The last strongholds of the European moose appeared to be in Scandinavian countries and patchy tracts of Russia by the early 20th century (Henttonen et al. 2008). Some of the features that have enabled moose to become adapted to areas with cold winters and deep snow and variation in availability of quality and quantity of food include large body size with long legs, substantial flexibility in digestive processes and tolerance to low temperatures (Bubenik 1998).

There has been a considerable growth in moose population sizes in Scandinavia since the mid 1900s with wintering areas having densities of up to 5-6 moose/km<sup>2</sup> (Lavsund et al. 2003). This increase has been favored by regulated and selective moose hunting, a decline in natural predators, decreased competition from free ranging livestock and changes in forest management with positive effects of clear cutting on forage availability (Cederlund and Markgren 1987). This is particularly important for moose as they are an early successional forest species.

Mammalian herbivores forage in response to variation in food conditions such as availability (Renecker and Hudson 1986; Lundberg 1988) and structural, morphological and chemical properties of the vegetation (Belovsky 1981; Spalinger, Robbins and Hanley 1986). The moose is a typical browser (Cederlund et al. 1980; Bergström and Hjeljord 1987) and needs approximately 10 kg of food (dry weight) per summer day and 5 kg of food (dry weight) per winter day to meet its nutritional requirements (Hjeljord et al. 1982, Persson et al. 2000). This is derived from vegetation consisting of forbs and leaves and young shoots from trees such as willow, rowan, aspen, juniper (*Juniperus communis*), birch, spruce and pine. Moose diet is very diverse during the summer but more uniform in the winter (Wam and Hjeljord 2010). Moose strip the leaves of deciduous trees and forage on shrubs and herbs during the summer with a high preference for birch, bilberry (*Vaccinium myrtillus*) and rowan (Wam and Hjeljord 2010). During the winter, moose feed predominantly on the twigs, barks and needles of coniferous trees with the probability of plant secondary metabolites influencing their food selection (Stolter 2005; Edlich and Stolter 2012). The quality of food resources is low during the winter by senescence of

plant tissues and the concentration of nutrients in non-accessible parts of the plants (Chapin, Johnson and McKendrick 1980), and can be successively reduced by depletion of the best food.

Empirically derived averages of proportions of grass and browse in the diet are often a primary characteristic used in herbivore classification (Hofmann 1989). Grazing entails eating graminoids, while browsing entails eating woody and non-woody dicotyledonous plants. Grasses predominate open landscapes, generally grow close to the ground, have low protein content (Codron et al. 2007) but high fiber content (Sanson 1989) and an overall high digestibility (van Weiren 1996, Hummel et al. 2006). Browse on the other hand predominates in forests or more spatially structured landscapes. Generally, with the exception of forbs, browse grows at heights above ground-level and has high protein but less fiber content and overall low digestibility (Sanson 1989; van Weiren 1996; Hummel et al. 2006; Codron et al. 2007). Although foraging strategies are often dichotomized between grazing and browsing, which are functionally very different and each have unique constraints and nutritional consequences (Ngugi et al. 1995; Clauss et al. 2003), foraging behavior of ungulates in reality occurs along a browser-grazer continuum. Although intraspecific variation in the balance of grazing and browsing (and its causes) has received less attention, diet shifts along the grazer–browser continuum may have important consequences for nutrition, competitive interactions and trophic cascades. Particularly, factors causing individuals to oscillate between the grazing and browsing guild may provide novel insight into herbivore evolution (Christianson and Creel 2007). Though a typical browser, the moose falls within the browser-grazer continuum, which is relevant to this study as moose are being fed with the forage typical of grazers.

### **2.3. Sample collection**

This study is based on microhistological analysis of faecal samples. There were three independent faecal sample collections:

1. Faecal samples picked up from the ground around feeding stations (with the assumption that these samples were deposited by moose which had been using the feeding stations).

2. Faecal samples from GPS collared moose (with knowledge of where they have been and which habitats they have been using).
3. Faecal samples from captive moose fed known diets for the purpose of calibrating analyses of other samples.

Faecal samples were collected from multiple feeding stations in Bikerbeinervejen, Insdalen, Mykleby and Koppang (Fig. 1) during the winter of 2011. These samples represented moose using feeding stations. The distance between the feeding stations within each area reduced the probability of sampling the same individual more than once. At each station, approximately eight pellets were collected from a pellet group and put into a plastic bag. Pellet selection was based on freshness and size. I chose recent, average to large pellet sizes corresponding to adult moose. The sex of the moose was unknown. At the end of January, February and March 2011, 20, 13 and 19 samples were collected respectively. The inconsistency in sample size was due to fluctuations in the number of active feeding sites at the time of collection, as well as accessibility constraints. Samples were frozen after each collection, prior to laboratory analysis.



**Fig. 3. Faecal sample collection at a feeding station.**

Faecal samples from 17 individually-marked moose were collected from GPS collared moose during capture in March 2010 (Milner et al. 2013). The spatial location of these moose, including use of feeding stations, had been monitored throughout the winter and the proportion of time spent within 100m of a feeding station during the last 72 hours before sampling was known for each individual except one. Faecal samples were collected by the capture team from the rectum of immobilized moose and frozen prior to analysis.

In order to calibrate the composition of samples from the feeding stations, Christina Skarpe set up a feeding experiment in a moose farm in Sweden. Two captive adult female moose (named Elvira and Philippa) were fed known quantities of browse and silage between March 28<sup>th</sup> and April 4<sup>th</sup> 2010. The browse consisted of pine, spruce, grey alder (*Alnus incana*) and birch which was freshly cut from the nearby forest. Two to four saplings, between about 2 and 3 m high and with ample shoots from last growing season per species were given to the moose each evening during the trial. The silage was similar in composition to that being fed to moose in Norway. Faecal samples were collected twice daily for 6 days and frozen prior to analysis. We do not know the exact gut retention time. However, previous studies have documented a shorter retention time of food in the digestive tract of browsing ruminants than in grazing ruminants with less selective retention of particles (Hummel et al 2005; Clauss et al. 2006; Hummel et al. 2006). How fast and efficient the browse and grass species are decomposed by bacterial is influenced by the cell wall thickness (Wilson and Mertens 1995). Cellulose levels have been documented to be similar in grasses and twigs and significantly higher than in browse leaves and herbs (Hummel et al. 2006). Moreover, browsing wild ruminants have been observed to have lower proportions of cellulolytic bacteria in their rumen fluid than grazing species (Prins and Geelen 1971). This lack of cellulolytic efficiency should therefore make browsing wild ruminants like moose less efficient in digesting high fiber grass material (Ward 1971; Clemente et al. 2005). Grazing ruminants are more efficient in digesting fiber than browsing ruminants (Perez-Barberia et al. 2004).

All the frozen faecal samples were sent to Barbro Dahlberg at Ås, an expert in the identification of plant epidermal fragments using microhistological methods. She prepared the samples following procedures of Garcia-Gonzalez (1984). After thawing each sample, about 5 faecal pellets were lightly ground in a mortar. About 1ml of the homogenous mixture was then placed in a test tube containing 4ml of concentrated Nitric acid. The tube was placed in a boiling water bath for 1 minute. The sample was then diluted with 200ml water and boiled for another 4 minutes. The suspension was passed through 1.00mm and 0.20mm sieves and rinsed with water. The 0.20mm fraction of the sample was conserved in a mixture of 85% ethanol (of 70% solution), 10% formalin (of 40% solution), and 5% glacial acetic acid. The fragments were dispersed on microscope slides in a 50% aqueous solution of glycerin. Cover slips (20\*40mm) were then fixed to the slides and sealed with nail varnish. Two slides were made from each sample.

#### **2.4. Fragment Identification**

In order to identify plant fragments in the faecal sample slides, previous knowledge from the identification of reference material (shoots, bark and leaves of trees, forbs and grasses that are common around Hedmark county) was used. With directions from Christina Skarpe, I prepared the reference material for spruce, pine and birch species which I cut in the vicinity of one of the feeding stations at Imsdalen in January 2009. I carefully peeled off the bark of the stem of each species with a razor. I also cut out the shoots, buds and leaves. Each specimen was put in a foil dish, labeled and put in the oven to dry at 60°C for 72 hours. The samples were then ground with a blender. Barbro Dahlberg had a collection of other shrubs and grass species that are common in Norway.

Using the prepared slides, transects were placed 3mm apart and fragments dissecting the 40 x 1 mm long transects were counted. The identified fragments were recorded for each slide. Epidermal cell structure, presence/absence of hairs, shape of hairs and shape of stomata were some of the features used in distinguishing the tree species as well as identification of forbs and

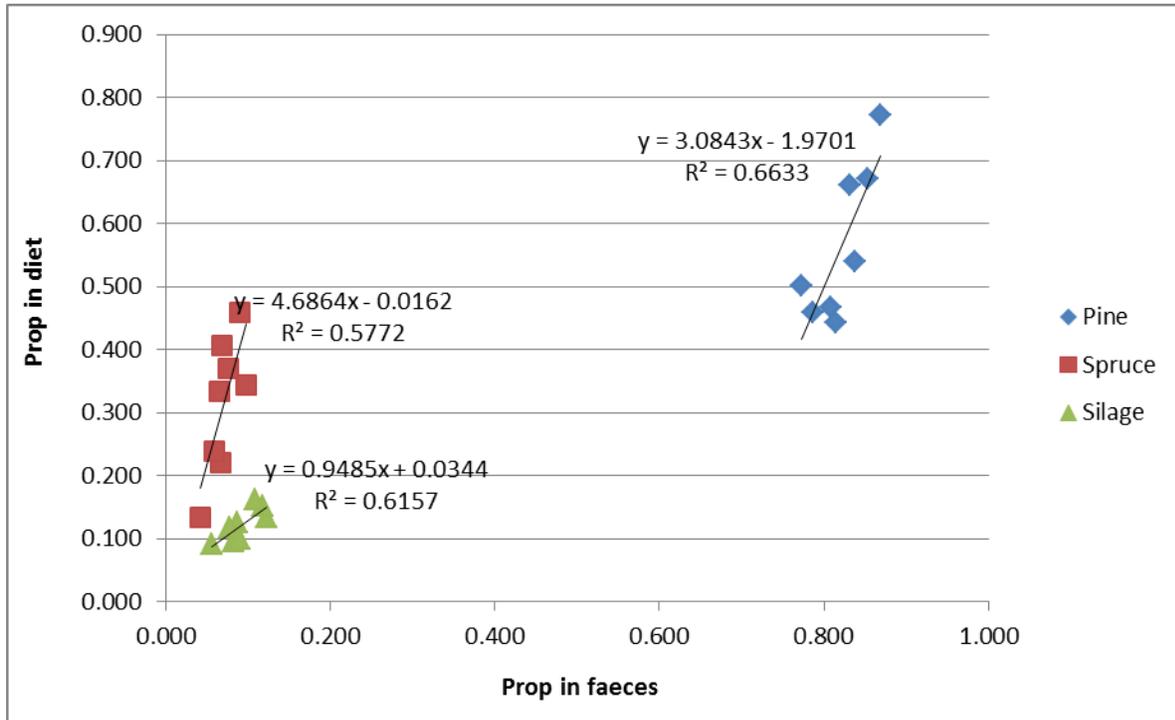
grasses. Fragments were identified to species or genus, with an average of 462 (minimum of 390 and maximum of 563) epidermal fragments in total per slide. When I report percent fragments of browse or silage as found in the faeces, this value is the species proportions calculated among identified fragments only.

## **2.5. Calibration**

From the calibration data, the number of bites taken from the provided browse was counted every day before the saplings were removed and fresh ones provided. Ten bite diameters were measured for each tree sapling. The biomass corresponding to each of these diameters was calculated using regression equations for the appropriate species which had been calculated by Christina Skarpe. She recorded the dry masses of 20 twigs with a basal diameter of 1 mm, 2 mm, 3 mm, etc covering all diameters within the range bitten by the moose for each tree species. The average biomass of the bites measured in the feeding experiment was multiplied by the number of bites taken to estimate the total biomass consumed per day. The sum of the total biomass of each browse species eaten per day was then calculated for each moose. The amount of silage eaten each day was calculated from weighing the silage put in at the beginning of each day and the remaining silage taken out the next day. In order to calculate the actual amount eaten, a correction factor calculated from a control sample was used. This allowed for natural drying of the silage over the sample period or any rain water that soaked up in the silage. The amount of silage eaten was the fresh weight. The dry weight was calculated by multiplying by 0.3 since the dry matter content is assumed to be approximately 30%.

Using the sum of the total biomass of pine, spruce, birch, alder and silage eaten per day, I estimated the proportional composition of the diet. The proportion of each species eaten was plotted against the corresponding proportion of the species in the faecal sample (value from microhistology analysis) for Philippa and Elvira and a linear relationship was fitted (Fig. 4). This was plotted for several different gut retention times (24 hours, 36 hours, and 48 hours) and the trial with the best  $R^2$  values for all three species was adopted, assuming it corresponded to the appropriate retention time. In this case it was 24 hours. Using the corresponding equations for

each species, the proportion of the species in the diet was calculated from  $y = ax + b$  where  $y$  is the proportion in the diet and  $x$  is the proportion in faeces.



**Fig. 4. Regression of proportions of pine, spruce and silage fragments in faeces vs. their corresponding proportions in the diet 24 hr earlier. It shows the calibration equations for pine, spruce and silage from the captive moose feeding trials.**

Unfortunately, the relationships in the calibration material were not as easy to apply to the samples collected from free-ranging moose as hoped. This may be because the diet that the captive moose were eating was not sufficiently similar to the diet of the free-living moose to allow a robust calibration. Furthermore, the gradient in the relationship between percentage fragments in faeces and percentage in the diet was so steep, especially for pine and spruce, that a tiny change in the faeces gave a massive change in the proportion estimated in the diet. When applied to free-ranging moose, the sum of the percentage in the diet was therefore often considerably greater than 100. Furthermore, alder and birch which were consumed by the captive

moose did not appear in the lab results of the faecal analysis. Thus using these calibration factors would be introducing a lot of error. It was therefore more appropriate to use the faecal fragment data as an index of the diet to compare differences in diet between the months.

## **2.6. Data Analysis**

Of all the different plant species fragments present in the faeces, I was most interested in pine, spruce and silage (which in this case was a combination of grasses, sedges and herbs). I used generalized linear models using logit link function (i.e. logistic regression) with quasibinomial error to determine how the proportion of pine, spruce and silage fragments in the faeces varied between the months. A quasibinomial error structure was used to account for over dispersion which was identified after first using binomial errors. The response variable was the number of silage fragments (1)/the number of non-silage fragments (0). From the lab results from Babro Dahlberg, I had the total number of fragments counted for each sample, and the percentage of fragments for each dietary component. I calculated the number of silage fragments present by multiplying the percentage of silage fragments present by the total number of fragments for each sample. It was rounded up to the nearest whole number. The non-silage fragment in each sample was therefore the total number of fragments minus the number of silage fragments. The same calculations were done for pine and spruce. The explanatory variables were month (three-level factor), area (four-level factor) and their interaction. Although I was not really interested in the area, it was added to the model in case it was an important source of variation. The browse to silage ratio was calculated and differences were tested for using a binomial proportions test. I also tested for any correlation between the proportions of species using Spearman's rank correlation. A regression of time spent within 100 m of feeding stations versus the amount of silage consumed was plotted for the GPS collared moose to test the relationship between moose spending time around feeding station and its consumption of silage while at the feeding station.

## CHAPTER THREE

### 3.0. RESULTS

#### 3.1. Diet composition

13 different species were identified in the diet of the feeding station moose. All except for lichen were also identified in the diet of the GPS collared moose (Table 1).

**Table 1. List of the different species identified in the 52 faecal samples of the moose using feeding stations and the 16 faecal samples of the GPS collared moose**

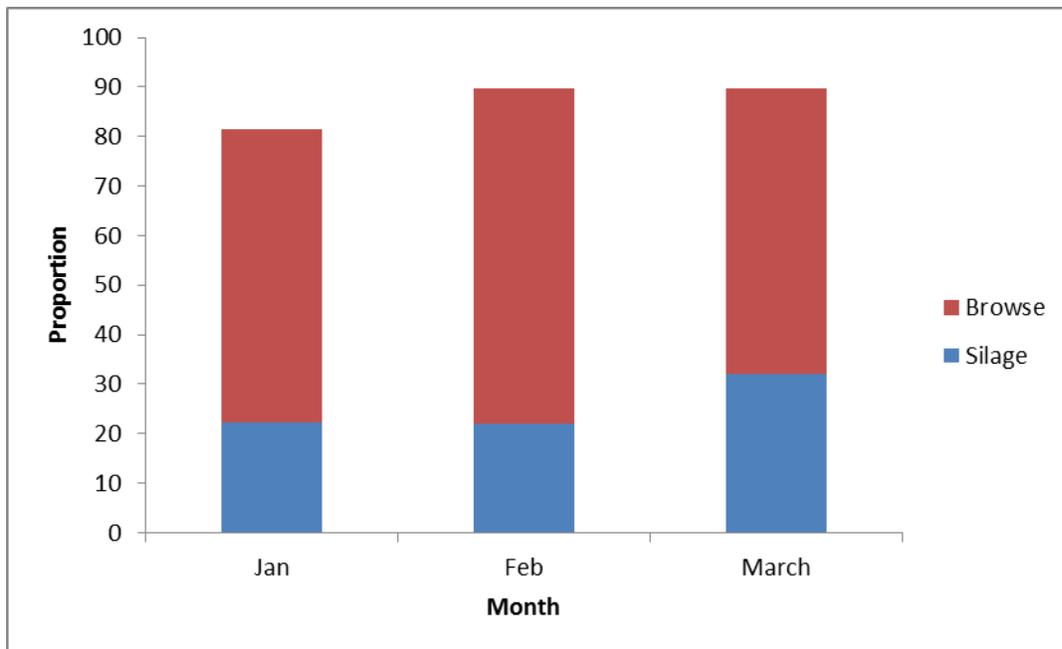
<b>Plant fragments in the faeces of Feeding Station moose</b>	<b>Plant species in the faeces of GPS collared moose</b>
Scots pine <i>Pinus sylvestris</i>	Scots pine <i>Pinus sylvestris</i>
Norway spruce <i>Picea abies</i>	Norway spruce <i>Picea abies</i>
Juniper <i>Juniperus communis</i>	Juniper <i>Juniperus communis</i>
Birch <i>Betula spp.</i>	Birch <i>Betula spp.</i>
Bilberry <i>Vaccinium myrtillus</i>	Bilberry <i>Vaccinium myrtillus</i>
Rowan <i>Sorbus aucuparia</i>	Rowan <i>Sorbus aucuparia</i>
Heather <i>Calluna vulgaris</i>	Heather <i>Calluna vulgaris</i>
Willow <i>Salix spp.</i>	<i>Salix spp.</i>
Grasses Poaceae	Poaceae
Sedges e.g <i>Carex spp.</i>	<i>Carex spp.</i>
Forbs	Herbs
Mosses	Mosses
Lichens	

**Table 2. Grouping of the species identified into browse (6 species groups), silage (3 species groups) and dwarf shrubs (2 species).**

<b>Browse</b>	<b>Silage</b>	<b>Dwarf shrubs</b>	<b>Others</b>
Pine	Grasses	Bilberry	Mosses
Spruce	Sedges	Heather	Lichens
Birch	Herbs		
Juniper			
Rowan			
Willow			

### 3.2. Browse to silage ratio in the diet

The ratio of browse to silage (Table 2) faecal fragments was 2.66:1 in January, 3.08:1 in February and 1.80:1 in March (Fig. 5). There was however no significant difference between the months for the browse to silage ratio ( $X^2 = 2.963$ ,  $df = 2$ ,  $p = 0.227$ ).



**Fig. 5. Proportion of browse to silage fragments in the faeces of moose using feeding stations through the winter.**

### 3.3. Variation in diet composition through winter

The proportion of pine in the faeces differed significantly between the months dropping significantly ( $p = 0.001$ ) from  $38 \pm 0.08$  % in January to  $15 \pm 0.04$  % in mid February and even down to  $11 \pm 0.02$  % in March. Moreover, there was a significant difference in the proportion of pine fragments in the faeces across the sampling areas. However, month had more effect on the proportion of pine consumed than area (Table 3, Fig. 6). The proportion of silage was fairly constant at  $22 \pm 0.04$  % from January to mid February with a non significant increase to  $32 \pm 0.07$  % in March. However, the proportion differed significantly between the different areas (Table 3, Fig. 6). Moreover, the logistic model on area alone showed that silage intake was significantly influenced by Imsdalen and Koppang but not by Mykleby

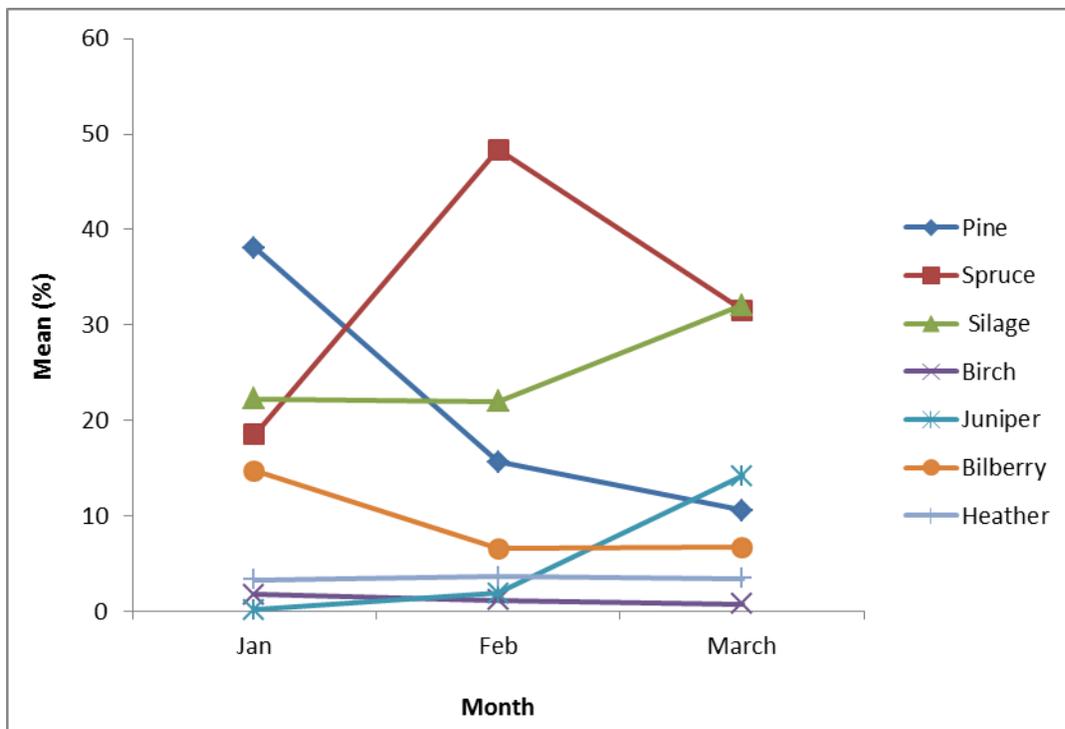
As for Spruce, there was a very significant ( $p = 0.001$ ) increase in its proportion from  $18 \pm 0.05$  % in January to  $48 \pm 0.1$  % in February with a marginally significant ( $p = 0.051$ ) drop to  $32 \pm 0.07$  % in March. The proportion of spruce however did not differ between the different areas (Table 3, Fig. 6).

A drop in the proportion of bilberry from  $15 \pm 0.03$  % in January to  $7 \pm 0.02$  % by mid February was evident which then remained constant through to March. A steady but slight increase in the proportion of juniper was observed with values of 0 in January to  $2 \pm 0.05$  % in mid February and a sharp increase to  $15 \pm 0.03$  % through March. Heather with a proportion of  $4 \pm 0$  % was fairly constant from January through March. Birch was the least represented, with a proportion of  $2 \pm 0$  % in January which dropped to  $1 \pm 0$  % by mid March (Fig. 6).

**Table 3. Summary of logistic regression model for pine, silage and spruce showing variation in their proportions in the diet between the months and areas**

Model species	Parametric coefficient	Df	Deviance	F	P
Pine	Month	2	- 2133.9	19.758	6.404e-07 ***
	Area	3	- 1016.8	6.276	0.001 **
	Month*Area	5	- 588.01	2.474	0.048*
Silage	Area	3	1167.2	5.837	0.0018 **
	Month	2	- 360.55	2.765	0.073
	Month*Area	5	- 215.00	0.612	0.691
Spruce	Month	2	1607.9	8.070	0.001 **
	Area	3	- 595.29	2.176	0.104
	Month*Area	5	- 488.31	1.099	0.376

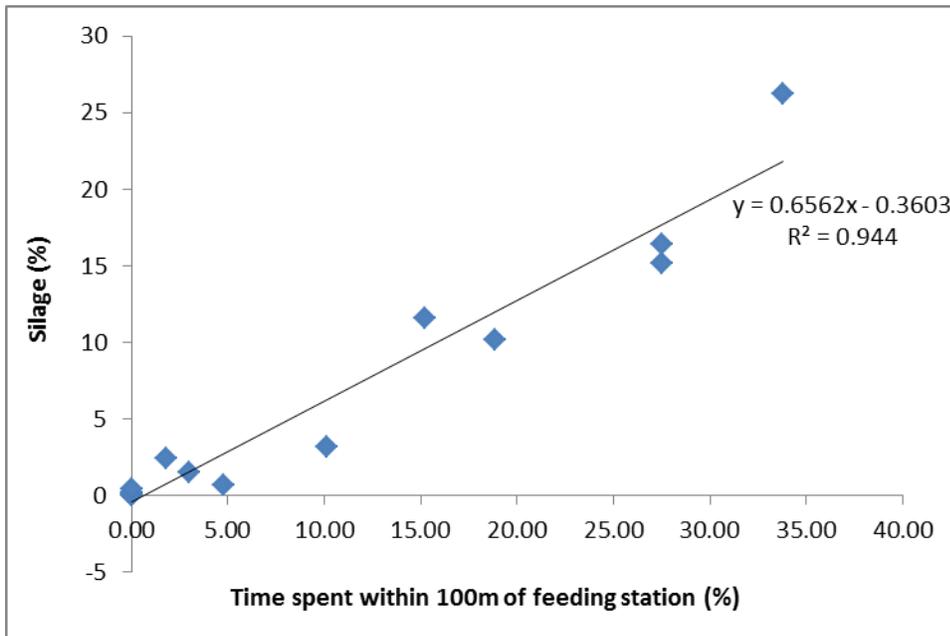
Significant codes: \*\*\*  $\leq 0.001$ , \*\*  $\leq 0.01$ , \*  $\leq 0.05$



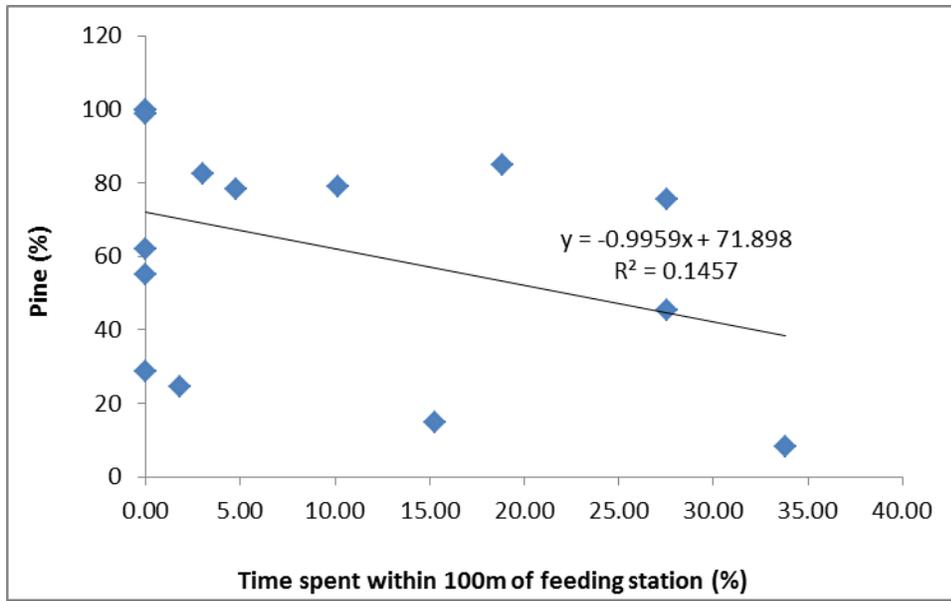
**Fig.6. Variation in the mean (%) of the different plant fragments in the faeces collected at feeding stations from January to March.**

### **3.4. Diet composition in relation to use of feeding station**

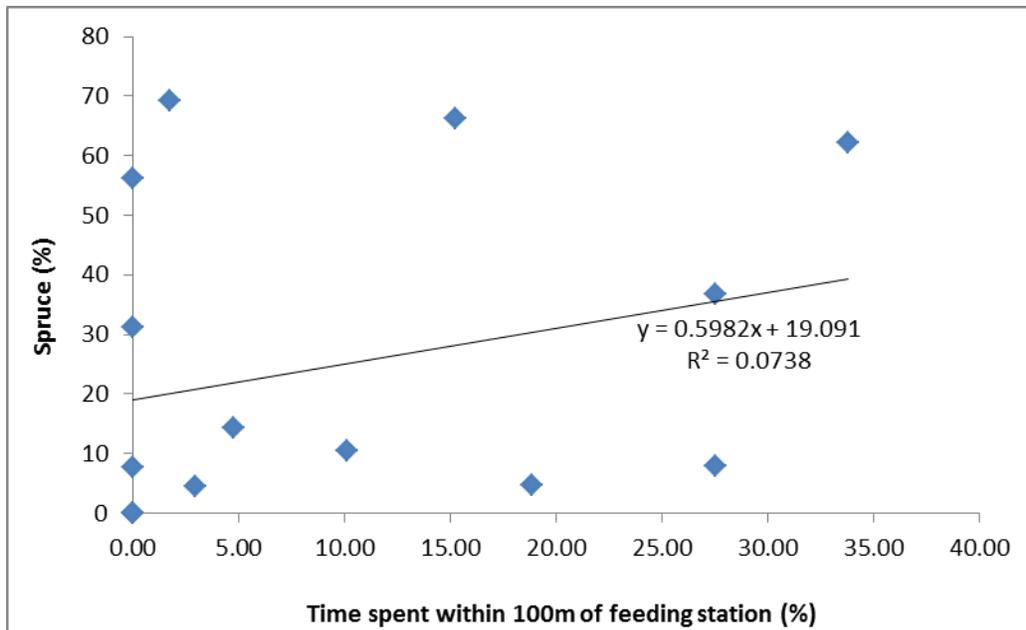
A linear regression of the silage fragments in the faeces and the time spent (15-72 hours before sampling) within 100m around the feeding station revealed a strong positive linear relationship ( $R^2 = 0.944$ ) (Fig.7a). Although it was not possible to determine the proportion of silage in the diet from this, this result implies there is a relationship between time spent at the feeding station and the amount of silage eaten. There was also a negative linear relationship for pine (Fig. 7b) and a positive relationship for spruce (Fig. 7c) in relation to time spent at the feeding station.



**Fig. 7a. The proportion of silage present in the faeces of GPS collared moose (n=16) in relation to their use of feeding stations during the period 15-72 h prior to sampling. Feeding station use was measured by percentage of time spent by moose within 100 m of feeding stations.**



**Fig. 7b.** The proportion of pine present in the faeces of GPS collared moose (n=16) in relation to their use of feeding stations during the period 15-72 h prior to sampling. Feeding station use was measured by percentage of time spent by moose within 100 m of feeding stations.



**Fig. 7c.** The proportion of spruce present in the faeces of GPS collared moose (n=16) in relation to their use of feeding stations during the period 15-72 h prior to sampling. Feeding station use was measured by percentage of time spent by moose within 100 m of feeding stations.

### 3.5. Correlation between species in the diet of feeding station moose

There was a strong negative correlation between pine and silage fragments in the faeces (Table 5). Although the negative correlations between silage and birch and also silage and bilberry were not strong, they were statistically significant. Pine and spruce as well as pine and birch were both weakly positively but significantly correlated. Spruce on the other hand had a very weak negative and non significant correlation with silage (this result corresponds with the non-significant-looking regression in Fig. 7c), but however a strong negative correlation with juniper. The strongest correlation was found between bilberry and heather, which were positively correlated.

**Table 5. Summary of the correlation for all the combinations of pine, spruce and silage and only the other plant combinations that were significant. Df was 50.**

Species combination	Correlation coefficient r	P value
Silage/Birch	- 0.38	0.005**
Silage/Bilberry	- 0.35	0.012**
Silage/Pine	- 0.54	0.001***
Silage/Spruce	- 0.03	0.827
Silage/Juniper	- 0.07	0.624
Silage/Heather	- 0.09	0.514
Silage/Willow	+ 0.23	0.107
Pine/Spruce	+ 0.29	0.033*
Pine/Birch	+ 0.30	0.033*
Pine/Juniper	+ 0.03	0.807
Pine/Bilberry	+ 0.20	0.157
Pine/Heather	+ 0.02	0.884
Pine/Willow	+ 0.13	0.342
Spruce/Juniper	- 0.51	0.001***
Spruce/Birch	- 0.15	0.29

Spruce/Bilberry	- 0.16	0.26
Spruce/Heather	- 0.19	0.18
Spruce/Willow	- 0.05	0.703
Birch/Bilberry	+ 0.31	0.03*
Bilberry/Heather	+ 0.74	0.001***

## CHAPTER FOUR

### DISCUSSION

The results in this study indicate that moose using feeding stations still browse on natural forage, which has implications for forest damage (van Beest et al. 2010b). The browse to silage ratio was relatively constant throughout the winter, thus supporting my first hypothesis. This suggests that the silage did not fulfill all the moose's requirements. Of the natural browse species present, spruce and pine were dominant, followed by bilberry. This result is partially consistent with the findings of Bergström and Hjeljord (1987) and Hjeljord et al. (1990) that moose feed predominantly on twigs of deciduous trees and Scots pine during the winter. However, Norway spruce is generally not eaten by moose (Cederlund et al. 1980; Bergstrom and Hjeljord, 1987; Hornberg, 2001; Kalen and Bergquist, 2004) so the result of high spruce intake in this study is really different from normal. This therefore implies that the diet selectivity of moose using feeding stations differs from the usual winter diet. This is contrary to my second hypothesis that moose diet selectivity is unaffected by feeding station use.

Norway spruce, a species generally avoided by moose because of its high content of defense chemicals (Edlich and Stolter 2012), was more represented in the faeces than pine. The amount of spruce eaten was unusually high, possibly due to long-term resource depletion of preferred forage species around the feeding stations (van Beest et al. 2010b). In addition, feeding station users may be able to tolerate an unusually high content of spruce in the diet due to the relatively high quality of silage available to them. However, the very weak negative and non significant

correlation between spruce and silage (Table 5.) shows that there is no evidence from our data to suggest that heavy users of feeding stations are more able to tolerate spruce. Proportions of pine changed through the winter. A reduction in the proportion of pine was likely due to seasonal resource depletion of preferred species as has been shown in moose elsewhere in Norway (van Beest et al. 2010c). Resource depletion through the winter is a result of snow cover, absence of new vegetation growth and natural browsing (Edenius 1991).

Pine was highly represented compared to birch. Thomas and Taylor (2006) have documented that Scots pine is considered to be of higher quality and also have a much higher biomass than birch during the winter (although both species are classified as low quality browse during the summer), and browsers select for the best quality forage at small spatial scales (van Beest et al. 2010c). In this study, birch was present in very low proportions and rowan almost absent (1.1 % amount present only in one faecal sample). This finding is not in line with expectations from Wam and Hjeljord (2010) who documented birch, rowan and bilberry as the dominant species in the moose diet both in the winter and summer in southern Norway. The availability of bilberry is very much dependent on snow depth as it is a field layer species. It is therefore important in the winter diet only in the early winter or in areas with little snow cover. This is true for this study as the highest proportion of bilberry (15 %) was in January and then dropped in February (8 %) as snow depth increased and then remained relatively constant through March. The very low representation of birch as well as rowan in the faeces could be because of a lack of availability since the proportions of birch, rowan and bilberry in the moose winter and summer diets are positively related to their availability (Wam and Hjeljord 2010). However, it may also have arisen as a result of a methodological bias. The microhistological method is based on the identification of plant epidermal fragments in the faeces and, as such, may under-represent deciduous woody browse species if epidermal cells account for a low proportion of their biomass (Hummel et al. 2006). The fact that the captive moose were known to have eaten birch and alder yet these species were not recorded in their faeces strongly points to such a bias. Furthermore, the relative proportions of plant fragments present in the faeces are influenced by differences in the degradation of the different plant species present and the combination of plant species present in the diet. Large errors in estimates of diet composition have been recorded for herbivore diets

in which the components' physical characteristics differed widely (McInnis et al. 1983; Gill et al. 1983). It has been recognized that there are limitations to the quantitative accuracy of species composition of ingested forage (Holechek et al. 1982). Our attempt to calibrate the samples using individuals of known diet was largely unsuccessful in counteracting the bias.

Month had a significant effect on the amount of pine and spruce intake, but not on silage. It is no doubt month had an effect on the amount of pine consumed as pine is an important part of moose winter diet and its consumption which is significantly positively correlated with its availability (Wam and Hjeljord 2010), reduces through the winter. The young Scots pine is buried in the snow and the moose has difficulty browsing on the tops of matured pine trees; where chemical defenses are lowest (Danell et al. 1983; Nordengren et al. 2003). Scots pine was found to be predominant in the rumen of moose during January-February (Cerdelund et al. 1980). This is in line with this study as the highest proportion of pine fragments were consumed in January, and then dropped in February and March. Spruce intake on the other hand peaked in February but was still however consumed more than the pine in March. This again can be attributed to the negative correlation between spruce and pine with the availability of pine twigs and dwarf shrubs in January being reduced in February and March.

In this study, feeding station area had a significant effect on the amount of silage and pine consumed, but not spruce. The accessibility of the feeding stations determined whether or not silage bails were constantly available and may have meant that the use of each area was not constant throughout the study. Differences in the availability of natural forage between areas and in the history of feeding stations in each area could also have affected the amount of silage and pine eaten. For example, Imsdalen has a very big feeding area with a long history of moose feeding while Birkebeinerveien is a much smaller area and has been less intensively fed so its natural forage is less damaged. Also, there could be lesser use of feeding stations in areas with shorter history of feeding owing to the assumption that some of the moose have not yet learnt to feed on the supplied food or they have not discovered the feeding stations if they have not visited all parts of their winter range (Van Beest et al. 2010a). On the other hand, logging activity in an

area could also have influenced the availability and therefore consumption of pine. Higher consumption of twigs made available by felled old Scots pine compared to that browsed on growing young pine trees has been documented by Bergström et al. (1995). I observed logging activities during the time of sample collection at Koppang area. Results of model ran for area alone reported that Koppang area affected the amount of pine intake (higher) while the other three areas did not. Månsson et al. (2010) acknowledged that pine trees felled during winter can make a considerable additional contribution to winter moose forage availability.

## **Conclusion**

In this paper I looked at the species composition in the faeces of moose using feeding stations during winter. The results show that feeding station users still browse on natural forage in the vicinity of the feeding stations and that Scots pine is an important part of its diet. The use of supplementary feeding to divert moose from commercially valuable stands (in this case Scots pine) is therefore not fully effective. Moose using feeding stations have a different diet composition from moose not using feeding stations. They eat an abnormally high amount of spruce around feeding stations with a long history (van Beest 2010b). It is therefore important for forest managers to evaluate the costs and benefits of supplementary feeding and its impact on commercially valuable forest stands around the feeding areas. This will allow the landowners to know the cost effectiveness of the programme. Also, it might be worth finding out any long term effect of the high intake of spruce on the feeding station users. Creating feeding stations around the areas where logging would be done might help reduce destruction of valuable stands in that vicinity. I could not estimate the diet of the feeding station users from the species proportions in the faeces due to the limitations of the calibration trials. The use of calibration data and/or an alternative surveillance technique to quantify the amount of browse consumed would be important to quantify the diet of moose using feeding stations. I suggest the feeding trial experiment may be improved by feeding the tamed moose browse from the same vicinity and at the same time as the study in question.

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## References:

Andreassen HP, Gundersen H, Storaas T (2005) The effect of scent-marking, forest clearing, and supplemental feeding on moose-train collisions. *Journal of Wildlife Management* 69:1125–1132

Andren H, Angelstam P (1993) Moose browsing on Scots pine in relation to stand size and distance to forest edge. *Journal of Applied Ecology* 30:133–142

Baskin L, Danell K (2003) Ecology of ungulates. A handbook of species in eastern Europe and northern and central Asia. Berlin: Springer

Belovsky GE (1981) Food plant selection by a generalist herbivore: the moose. *Ecology* 62:1020-1030

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

Bergström A (2004) Small mammal diversity in Kalahari – impact of land-use and pans in a semi-arid savanna, southwestern Botswana. M.Sc. thesis, Uppsala University

Bergström R, Hjeljord O (1987) Moose and vegetation interactions in northwestern Europe and Poland. *Swedish Wildlife Research S* 1:213–228

- Bowland AE, Perrin MR (1989) The effect of overgrazing on the small mammals in Umfolozi Game Reserve. *Zeitschrift für Säugetierkunde* 54:251–260
- Boyce MS (1989) *The Jackson elk herd: intensive wildlife management in North America.* – Cambridge University Press, Cambridge, 306 pp
- Bryant JP, Provenza FD, Pastor J, Reichardt PB, Clausen TP, Du Toit JT (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* 22:431–446
- Bubenik AB (1998) Ecology and Management of the North American Moose. *Behavior*. Pages 173–222 in Franzmann AW, Schwartz CC editors. Smithsonian Institution Press, Washington D.C., USA
- Cederlund G, Markgren G (1987) The development of the Swedish moose population, 1970–1983. *Swedish Wildlife Research*, Part 1:55–62
- Cederlund G, Ljunqvist H, Markgren G, Stålfelt F (1980) Foods of moose and roe deer at Grimso in central Sweden. Results of rumen content analyzes. *Swedish Wildlife Research* 11:169–247
- Chapin FS, Johnson DA, McKendrick JD (1980) Seasonal movement of nutrients in plants of different growth form in an Alaskan tundra ecosystem: implications for herbivory. *Journal of Ecology* 68:189–209
- Christianson DA, Creel S (2007) A review of environmental factors affecting elk winter diets. *Journal of Wildlife Management* 71:164–176
- Clauss M, Castell JC, Kienzle E, Dierenfeld ES, Flach EJ, Behlert O, Ortman S, Streich WJ, Hummel J, Hatt JM (2006) Digestion coefficients achieved by the black rhinoceros (*Diceros bicornis*), a large browsing hindgut fermenter. *Journal of Animal Physiology and Animal Nutrition* 90:325–334
- Clauss M, Frey R, Kiefer B, Lechner-Doll M, Loehlein W, Polster C, Rössner GE, Streich WJ (2003) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* 136:14–27
- Clemente F, Riquelme E, Mendoza GD, Bàrcena R, Gonzàalez S, Ricalde R (2005) Digestibility of forage diets of white-tailed deer (*Odocoileus virginianus*) using different ruminal fluid inocula. *Journal of Applied Animal Research* 25:71–76
- Codron D, Lee-Thorp JA, Sponheimer M, Codron J (2007) Nutritional content of savanna plant foods: implications for browser/grazer models of ungulate diversification. *European Journal of Wildlife Research* 53:100–111

- Côté SD, Rooney TP, Trembley J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics* 35:113-147
- Couturier S, Barrette DC (1988) The behavior of moose at natural mineral springs in Quebec, Canada. *Canadian Journal of Zoology* 66:522-528
- Danell K, Bergström R, Dirke K (1983) Moose browsing on juvenile and adult birches (*Betula pendula* and *B. pubescens*): Test of hypothesis on chemical defense. In P. Hell, P. (Ed.), *International Union of Game Biologists XVI Czechoslovakia*. pp. 400-406
- Edenius L (1991) The effect of resource depletion on the feeding behaviour of a browser—winter foraging by moose on Scots pine. *Journal of Applied Ecology* 28:318–328
- Edlich S, Stolter C (2012) The effect of essential oils on the feeding choice by moose. *Alces* 48:17-25
- Epple G, Niblick H, Lewis S, Nolte LD, Campell DL, Mason JR (1996) Pine needle oil causes avoidance behaviors in pocket gopher *Geomys bursarius*. *Journal of Chemical Ecology* 22:1013-1025
- Garcia-Gonzalez R (1984) L'emploi des epidermis vegetaux dans la determination du regime alimentaire de l'Isard dans les Pyrenees occidentales. *Ecologic des milieux montagnards et de haute altitude. Documents d'Ecologie Pyreneenne. III-IV*:307-313
- Gill RMA (1990) Monitoring the status of European and North American Cervids. *GEMS Information Series, 8*; Global Environment Monitoring Systems, United Nations Environment Programme, Nairobi
- Gill RB, Carpenter LH, Bartmann RM, Baker DL, Schoonveld GG (1983) Fecal analysis to estimate mule deer diets. *Journal of Wildlife Management* 47:902-915
- Guillet C, Bergström R, Cederlund G (1996) Size of winter home range of roe deer (*Capreolus capreolus*) in two forest areas with artificial feeding in Sweden. *Wildlife Biology* 2:107-111
- Gundersen H, Andreassen HP, Storaas T (2004) Supplemental feeding of migratory moose (*Alces alces*): forest damage at two spatial scales. *Wildlife Biology* 10:213–223
- Gundersen H, Solberg E, Wabakken P, Storaas T, Zimmermann B, Andreassen HP (2008) Three approaches to estimate wolf *Canis lupus* predation rates on moose (*Alces alces*) populations. *European Journal of Wildlife Research* 54:335-346
- Heikkilä R and Härkönen S (2000) Thinning residues as a source of browse for moose in managed forests in Finland. *Alces* 36:85-92

- Henttonen H, Stubbe M, Maran T, Tikhonov A (2008) *Alces alces*. In: IUCN 2010. IUCN Red List of Threatened Species. Journey to New England by Patricia Harris, David Lyon – Patricia Harris-David Lyon 1999 Page 398
- Hjeljord O, Sundstøl F, Haagenrud H (1982) The nutritional value of browse to moose. *Journal of Wildlife Management* 46:333–343
- Hjeljord O, Høvik N, Pedersen HB (1990) Choice of feeding sites by moose during summer: the influence of forest structure and plant phenology. *Holarctic Ecology* 13:281–292
- Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443–457
- Holechek JL, Vavra M, Pieper RD (1982) Botanical composition determination of range herbivore diets: A review. *Journal of Range Management* 35:309–315
- Hornberg S (2001) The relationship between moose (*Alces alces*) browsing utilization and the occurrence of different forage species in Sweden. *Forest Ecology and Management* 149:91–102
- Hummel J, Clauss M, Zimmermann W, Johanson K, Noergaard C, Pfeffer E (2005) Fluid and particle retention in captive okapi (*Okapia johnstoni*). *Comparative Biochemistry and Physiology A* 140:436–444
- Hummel J, Sudekum KH, Streich WJ, Clauss M (2006) Forage fermentation patterns and their implications for herbivore ingesta retention times. *Functional Ecology* 10:1365–2435
- Kalen C, Bergquist J (2004) Forage availability for moose of young silver birch and Scots pine. *Forest Ecology and Management* 187:149–158
- Kilpatrick HJ, Stober WA (2002) Effects of temporary bait sites on movements of suburban white-tailed deer. *Wildlife Society Bulletin* 30:760–766
- Lavsund S (1987) Moose relationships to forestry in Finland, Norway and Sweden. *Swedish Wildlife Research Supplement* 1:229–244
- Lavsund S, Nygren T, Solberg EJ (2003) Status of moose populations and challenges to moose management in Fennoscandia. *Alces* 39:109–130
- Lundberg P (1988) Functional response of a small mammalian herbivore: the disc equation revisited. *Journal of Animal Ecology* 57:999–1006
- Månsson J, Bergström R, Pehrson A, Skoglund M, Skarpe C (2010) Felled Scots pine (*Pinus sylvestris*) as supplemental forage for moose (*Alces alces*): Browse availability and utilization. *Scandinavian Journal of Forest Research* 25(1):21–31

- Mathisen KM, Skarpe C (2011) Cascading effects of moose (*Alces alces*) management on birds. *Ecological Research* 26(3):563-574
- Mathisen KM, Buhtz F, Danell K, Bergström R, Skarpe C, Suominen O, Persson IL (2010) Moose density and habitat productivity affects reproduction, growth and species composition in field-layer vegetation. *Journal of Vegetation Science* 21(4):705-716
- McCullough DR (1979) *The George Reserve Deer Herd*. Ann Arbor: Michigan University Press. 271pp
- McInnis ML, Vavra M, Krueger WC (1983) A comparison of four methods used to determine the diets of large herbivores. *Journal of Range Management* 36:302-306
- Milner JM, Bonenfant C, Mysterud A, Gaillard JM, Csanyi S, Stenseth NC (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology* 43:721-734
- Milner JM, van Beest FM, Solberg EJ, Storaas T (2012a) Reproductive success and failure: the role of winter body mass in reproductive allocation in Norwegian moose. *Oecologia*
- Milner JM, Storaas T, van Beest FM, Lien G (2012b) Sluttrapport for Elgføringsprosjektet. Oppdragsrapport nr. 1-2012. Research and Development Report, Hedmark University College, Norway, 89 pp. (In Norwegian with English summary.) [http://brage.bibsys.no/hhe/bitstream/URN:no-bibsys\\_brage\\_26766/1/opprapp01\\_2012.pdf](http://brage.bibsys.no/hhe/bitstream/URN:no-bibsys_brage_26766/1/opprapp01_2012.pdf).
- Milner JM, Wedul SJ, Laaksonen S, Oksanen A (2013) Gastrointestinal nematodes of moose (*Alces alces*) in relation to supplementary feeding. *Journal of Wildlife Diseases* 49(1):69-79
- Ngugi RK, Hinds FC, Powell J (1995) Mountain big sagebrush browse decreases dry-matter intake, digestibility, and nutritive quality of sheep diets. *Journal of Range Management* 48:487-492
- Nordengren C, Hofgaard A, Ball JP (2003) Availability and quality of herbivore winter browse in relation to tree height and snow depth. *Annales Zoologici Fennici* 40:305-314
- Ozoga JJ (1972) Aggressive behavior of white-tailed deer at winter cuttings. *Journal of Wildlife Management* 36:861-868
- Pedersen S, Andreassen HP, Persson IL, Julkunen-Tiitto R, Danell K, Skarpe C (2011) Vole preference of bilberry along gradients of simulated moose density and site productivity. *Integrative Zoology* 6:341-351
- Peek JM, Schmidt KT, Dorrance MJ, Smith BL (2002) Supplemental feeding and farming of elk. In: Toweill DE, Thomas JW (Eds.), *Elk of North America, Ecology and Management*. Smithsonian Institute Press, Washington, pp. 614-647

Pérez-Barbería FJ, Elston DA, Gordon IJ, Illius AW (2004) The evolution of phylogenetic differences in the efficiency of digestion in ruminants. *Proceedings Royal Society London B* 271:1081–1090

Prins RA, Geelen MJH (1971) Rumen characteristics of red deer, fallow deer, and roe deer. *Journal of Wildlife Management* 35:673-680

Persson IL, Danell K, Bergström R (2000) Disturbance by large herbivores in boreal forests with special reference to moose. *Animal Zoology Fennoscandia* 37:251–263

Putman RJ, Staines BW (2004) Supplementary winter feeding of wild red deer (*Cervus elaphus*) in Europe and North America: justifications, feeding practice and effectiveness. *Mammal Review* 34:285–306

Reasfeld F, Reulecke K (1988) *Das Rotwild*. Paul Parey, Hamburg/Berlin

Renecker LA, Hudson RJ (1986) Seasonal foraging rates of free-ranging moose. *Journal of Wildlife Management* 50:143-147

Sackl K (1992) Erfahrungen mit der Kommissionierung von Rotwildfütterungen und Rotwildwintergattern. Diploma Thesis, Agricultural University of Vienna

Saetnan ER, Skarpe C (2006) The effect of ungulate grazing on a small mammal community in southeastern Botswana. *African Zoology* 41(1):9–16

Sanson GD (1989) Morphological adaptations of teeth to diets and feeding in the Macropodoidea. In Grigg G, Jarman P, Hume I [eds.], *Kangaroos, wallabies and rat-kangaroos* 151-168 Surrey Beatty and Sons, Sydney, Australia

Skarpe C, Aarrestad PA, Andreassen HP, Dhillion SS, Dimakatso T, du Toit JT, Halley DJ, Hytteborn H, Makhabu S, Mari M, Marokane W, Masunga G, Modise D, Moe SR, Mojaphoko R, Mosugelo D, Motsumi S, Neo-Mahupeleng G, Ramotadima M, Rutina L, Sechele L, Sejoe TB, Stokke S, Swenson JE, Taolo C, Vandewalle M, Wegge P (2004) The Return of the Giants: Ecological Effects of an Increasing Elephant Population: *A Journal of the Human Environment* 33:(6)276-282

Smith BL (2001) Winter feeding of elk in western North America. *Journal of Wildlife Management* 65:173-190

Spalinger DE, Robbins CT, Hanley TA (1986) The assessment of handling time in ruminants: the effect of plant chemical and physical structure of breakdown of plant particles in the rumen of mule deer and elk. *Canadian Journal of Zoology* 64:312-321

Storaas T, Gundersen H, Henriksen H, Andreassen HP (2001) The economic value of moose in Norway - A review. *Alces* 37(1):97-107

Stolter C, Ball JP, Julkunen-Tiitto R, Lieberei R, Ganzhorn JU (2005) Winter browsing of moose on two different willow species: Food selection in relation to plant chemistry and plant response. *Canadian Journal of Zoology* 83:807-819

Tange AC (2007) Moose browsing on Scots pine in relation to feeding stations and forest stand characteristics. M.Sc. Thesis. Norwegian University of Science and Technology, Trondheim, Norway (in Norwegian)

Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management* 70:324-336

van Beest FM, Loe LE, Mysterud A, Milner JM (2010a) Comparative space use and habitat selection of moose around feeding stations. *Journal of Wildlife Management* 74:219–227

van Beest FM, Gundersen H, Mathisen KM, Milner JM, Skarpe C (2010b) Long-term browsing impact around diversionary feeding stations for moose in Southern Norway. *Forest Ecology Management* 259:1900-1911

van Beest FM, Mysterud A, Loe LE, Milner JM (2010c) Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology* 79:910-922

Van Wieren SE (1996) Browsers and grazers: foraging strategies in ruminants. *Digestive Strategies in Ruminants and Non ruminants*. Thesis Landbou, University of Wageningen, the Netherlands

Veiberg V, Loe LE, Mysterud A, Langvatn R, Stenseth NC (2004) Social rank feeding and winter weight loss in red deer: any evidence of interference competition? *Oecologia* 38:135-142

Wam HK, Hjeljord O (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

Ward A, (1971) In vitro digestibility of elk winter forage in southern Wyoming. *Journal of Wildlife Management* 35:681–688

Weiselmann H, (1994) *Rotwildfütterung: Kernsätze, Details, Empfehlungen*. Landesjagdverband, Vienna

Wilson JR, Mertens DR (1995) Cell wall accessibility and cell structure limitations to microbial digestion of forage. *Crop Science* 35:251–259