For the camera: In a wild range of forages, what do you choose to eat, my deer?

Use of video collars to study foraging behaviour in wild deer.

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Monica Eriksson

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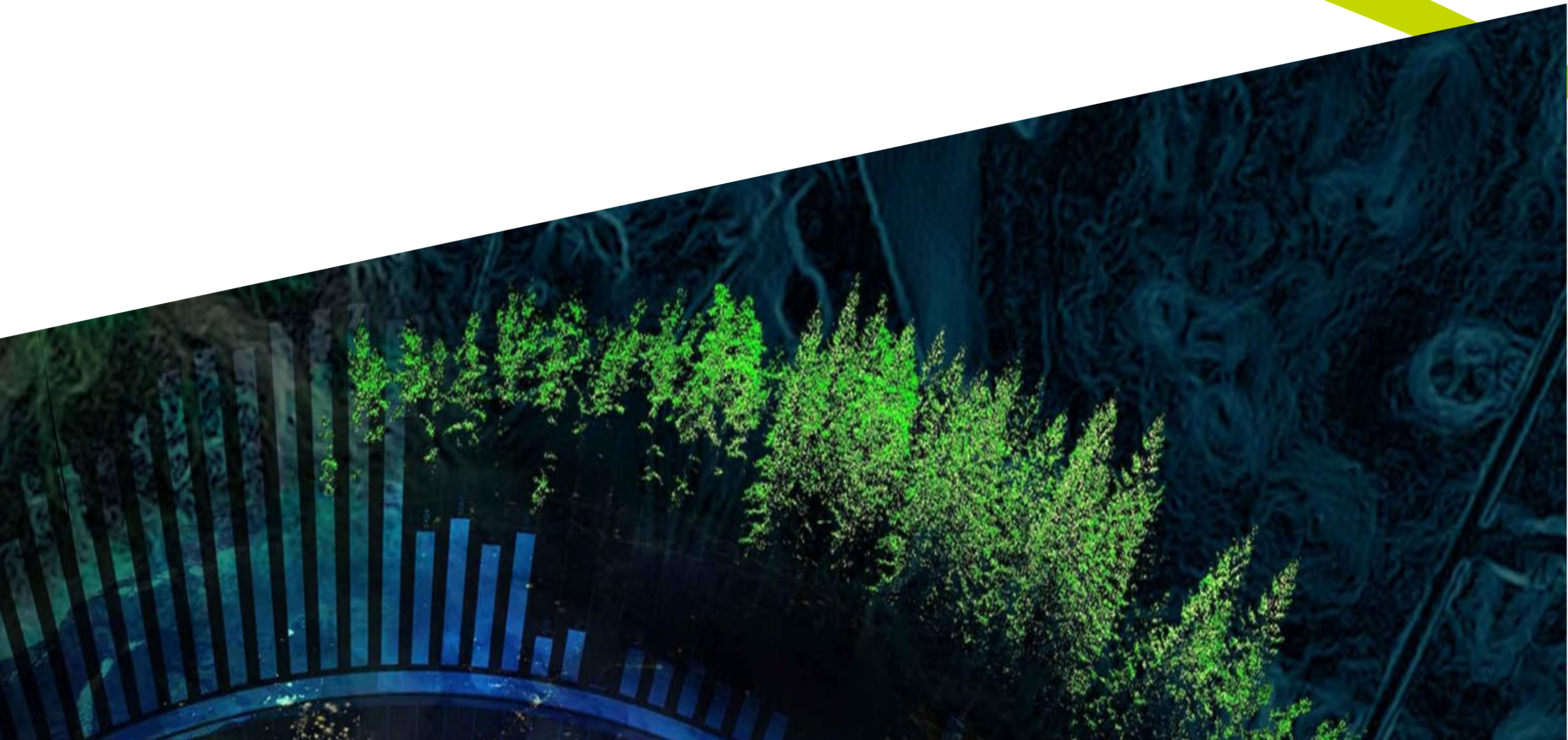

For the camera: In a wild range of forages, what do you choose to eat, my deer?
Use of video collars to study forage behaviour in wild deer.

Vilka födoval har du hjort i det vilda? Användning av kamerahalsband vid studier av hjortdjurs födoval och -beteende.

Monica Eriksson

Supervisor:	**Dr. Robert Spitzer, SLU, Department of Wildlife, Fish and Environmental Studies**
Assistant supervisor:	Dr. Annika Felton, SLU, Southern Forest Research Centre
Assistant supervisor:	Dr. Navinder Singh, SLU, Department of Wildlife, Fish and Environmental Studies
Examiner:	Therese Löfroth, Department of Wildlife, Fish and Environmental Studies

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Swedish University of Agricultural Sciences
Faculty of Forest Science
Department of Wildlife, Fish and Environmental Studies

Abstract

Animal-borne video collars are a developing technology with increasing picture quality and battery length. This study has investigated its use when studying foraging behaviours of the two largest deer species on the Scandinavian peninsula: moose (*Alces alces*) and red deer (*Cervus elaphus*). In the first of two studies included in this thesis, I compared the foraging choice of moose and red deer on both the inter- and intraspecific level. The data were collected from short, spread-out recordings (20 seconds every third hour per 24 hours over a period of several months). The second study, with a near-continuous recording (25 seconds every 3 minutes during 24 hours for a period of five days in July) focuses on the moose' selection for browse on the island of Vega, Norway. I have also compared the foraging frequency of browsers (the Vega moose) with that of grazers (dairy cows, using published data). An overall question throughout the projects has been whether video collars are a technology suitable for foraging studies of deer species and to what taxonomic resolution the cameras are able to capture the plant species. Study one was successful in showing that the camera collars are capable of showing that moose are browsers, with a low percentage of graminoids in their diet. It also managed to capture the difference in foraging choice of both moose and red deer, as well as the low diet overlap between the species during the summer months. Study two showed the moose' clear selection for browse even during the summer, despite the rather low abundance of browse compared to non-browse in their home range. It also showed that browsers indeed have more foraging bouts (6) per 24 hours than grazers (3). The overall conclusion is that video collars are indeed suitable for studying foraging behaviour in deer and that even the short recordings are able to show intraspecific differences – at least when it comes to common behaviour. Near-continuous recording is, however, more useful for capturing individual differences, both when it comes to foraging choices, foraging frequency and level of socialising behaviour.

Keywords: moose, *Alces alces*, red deer, *Cervus elaphus*, video collars, camera collars, forage, herbivore, browsing, grazing

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Abbreviations

AROW	Aspen, Rowan, Oak, Willow
NIBIO	Norwegian Institute of Bioeconomy Research
NIJOS	Norsk Institutt for jord- og skogkartlegging
NINA	Norwegian Institute for Nature research
SLU	Swedish University of Agricultural Sciences

1. Introduction

The foraging behaviour of moose (*Alces alces*) and red deer (*Cervus elaphus*) is of great interest from both an ecological and economic point of view. In a perfect world it would be possible to continuously observe wild animals in the field. With prey animals, such as deer, this is of course a challenge since they are normally very shy. The limitations are, however, not only due to the animal's shyness but also very often in resources (time and monetary) as well as the risk of bias with researchers only "seeing" what they already expect to see. The bias that comes from intrusiveness might also affect what behaviours we are actually able to observe (Beringer et al., 2004; Moll, 2008). Video collars offers us the possibility to observe foraging and other behaviours of animals without disturbing them (Egan, 2019; Beringer et al., 2004). The advantage of video collars as opposed to single images is that the video recordings are more likely to show a behaviour taking place (Moll, 2009). The disadvantage on the other hand is that analysing the recordings takes time and the analysing itself, as pointed out by Lavelle et al. (2012), also comes with observer bias as well as limitations in the field of view.

Video collaring is a fast-developing technology that is proving to be increasingly valuable for research. Egan (2019) and Moll (2009) described how it has been used globally on all kinds of species since the 1980s. A pilot study on bears in Yellowstone, USA described how video collars were useful when studying not only foraging, but also other behaviours, of three male bears (Bowersock et al., 2015). Beringer et al. (2004) described that they tranquillised and blindfolded white tail deer (*Odocoileus virginianus*) when investigating the use of animal-borne cameras on them. However, since this thesis is focused on deer species on the Scandinavian peninsula, the following description is how the procedure of equipping large mammals is done on Vega, Norway, where the tranquillisation and equipping moose with radio collars have been done since 1992 (Solberg et al., 2011). Here, equipping deer with video collars is preferably done in the winter, where tracks and the animals themselves are easily spotted against the snow. Solberg et al. (2011) describe the procedure: By following the animals from a helicopter, researchers push the animals out in the open on, for example, a mire where the animals can easily be shot with a tranquiliser dart. The tranquillising is done by a veterinarian who also ensures that the animal is physically monitored during the sedation and collaring process. When equipping the moose with GPS collars the added weight of a camera is negligible on an animal of this size. In the process of collaring the animals, blood and faeces samples can be taken and the animals are often weighted. This data can later be compared to data collected in case of re-collaring and from those individual shot during hunting season (ibid.)

Recent developments of video collars include improved battery length which has given us the opportunity to collect video material for longer periods than before. In addition, the improvements of picture quality provide us with video images of high enough resolution to identify the plant species the animals are foraging from. In other words: we are increasingly able to see the food choice and foraging behaviour almost as through the eyes of the deer itself. This is a great opportunity, because although there is a large amount of information collected about ungulate foraging, there are still substantial gaps in our understanding of how wild deer balance their diet. Recent analyses of video collars on moose in Sør-Trøndelag and Finnmark (Norway) by Åström (2022) has given us an insight into how the diets appear to differ between sexes, offspring/no offspring and of course location (i.e., availability of certain food species).

The proportion of protein, fibre and water in deciduous and evergreens varies between seasons (Capoani, 2019), which influences the deer foraging choices as they try to reach what appears to be a specific nutritional goal. The work of Felton et al. (2016) shows that the foraging of moose kept in captivity does not appear to aim at maximising energy intake, but rather to balance their diet towards a specific goal. This is known as the “nutrient balancing hypothesis” (Raubenheimer, 2011) and is confirmed to be the case also in wild moose in China (Ma et al., 2019) and in Sweden (Felton et al., 2021). This means that moose, when given the possibility, select and adjust their intake of different forages in proportion to reach a balance of carbohydrates and protein (Felton et al., 2021). As noted by Renecker and Hudson (1989) the number of feeding bouts is positively correlated to cell wall intake. Their study also showed that higher intake of dietary fibre increased the rumination time and thus decreased the number of feeding bouts. And that the digestion of graminoids (with their thicker cell walls) seems to require longer rumination and resting time between feeding bouts than browse. The thinner cell walls of browse (dicots), as described by Shipley et al. (1999), contain more sugar and protein than graminoids (monocots). This suggests that when comparing the number of feeding bouts, a species foraging from mainly browse (such as moose) should have more feeding bouts than a species foraging more frequently, or even mainly, on cell wall rich forages (graminoids) such as dairy cows.

To test the suitability of camera collars I will evaluate how well the data collected by the moose and red deer investigated in this thesis (below referred to as "focal individuals" or "focal moose") compared to already well researched and established foraging behaviours. I will provide an evaluation on how well differences in foraging choice between moose and red deer can be captured by these camera collars. I will also evaluate how the shorter, more spread-out recordings capture the diet of moose compared to a more continuous recording, by comparing the data sets from both types of recording during the same time of year. And lastly, I will compare how the feeding patterns differ between browsers (moose) and grazers (dairy cows), since the more continuous recording makes it possible to investigate the number of feeding bouts and feeding time of (wild) deer compared to (domesticated) cattle.

In order to advance towards a prediction, I have focused this thesis on how well camera collars can help us determine the activity pattern as well as how wild deer choose their food. Can camera collars placed on moose and red deer give us the missing pieces of the puzzle by showing us how and when the animals select different kinds of macronutrients? And is the quality of the recordings high enough to make it possible to determine any inter and intra specific differences in moose and red deer?

1.1 Browsers, grazers and those in between

Ruminants are all foregut fermenters, but their digestive system still differs. The work of Hofman (1989) is well-known and used in the research on large herbivores with its classification of ruminants into three classes: concentrate selectors; roe deer (*Capreolus capreolus*) and moose (*Alces alces*), intermediate feeders; red deer (*Cervus elaphus*) and goats (*Capra sp.*) and grass/roughage eaters; cows *(Bos taurus*) and sheep (*Ovis sp.*) based on their digestive systems. Clauss (2010) describe ruminants with moose-type (browsers, such as roe deer and moose) and cattle-type (cows and sheep) as extremes on more of a gliding scale, with intermediate/mixed feeders (red deer and fallow deer) as the base and centre. The classification done by Clauss et al. (2010) is also based on the ruminant's digestive system and by their capability to digest different kinds of cell-wall structure. In this thesis I refer to the moose-types and cattle-types classified by Clauss as "browsers" and "grazers".

Browsers, such as moose, are not designed to digest graminoids to any larger extent. Their ability to stratify monocots into gas and fluids is low (Clauss et al.,

2010) compared to intermediate feeders or grazers. Instead, they feed on more fibrous material, such as leaves, buds, twigs and bark from deciduous trees and shrubs, as well as lichens and needles from coniferous trees. The mixed feeders, such as red deer, are designed to digest a wider range of forages. During vegetation season their diet contains graminoids and forbs as well as browse but during non-vegetation season they can switch to a more browse rich diet, much like that of moose (Spitzer et al., 2020).

And lastly the grazers, such as cattle, that to a much larger extent feed on monocots (graminoids); a diet where the forage has thicker cell walls and higher content of (hemi-)cellulose (Shipley, 1999). Today most cattle are being fed fully, or partially, by humans and thus their feeding patterns are adjusted to time slots selected by the individual farmer. The forage quality and number of feeding bouts, as well as time of day, therefore varies a lot. Studies by Mattachini et al. (2019) shows that dairy cows require on average of 12,2 hours of lying down time per 24 hours and that they tend to eat in larger bouts rather than nibble here and there. Munksgaard et al. (2005) even conclude that cows choose lying over feeding and social behaviour when being on time constraint. Gibb et al. (1998), Mattachini et al. (2005) and DeVries (2005) have found that cows tend to have their major intake during the late evening hours. Most likely to be able to lie down and digest it during the nocturnal hours.

1.2 The investigated deer species

In this thesis I investigate the botanical diet composition of moose and red deer as well as how well the usage of collar cams can capture their choice of forage and the difference on both the inter- and intraspecific level. An overall question in this thesis was if camera collars are useful for monitoring/investigating the diet of deer species and if a continuous recording is needed to catch any differences in foraging choice of moose.

Moose are known to be mainly solitary animals; except for females followed by a calf or yearling and (mainly) young males and females that gather in small groups (Olsson, 2021). Red deer gather in small same-sex groups, save for during the rut when an adult male can gather a group of females (a harem) (Christoffersson, 2017). None of the species are territorial, save for during the rut, when male deer are prepared to fight off competitors.

The moose is the largest of the deer species. In Scandinavia, they can have a shoulder height of 2 m and with a weight span between 250 and 650 kg (Christoffersson, 2017). The moose are well adapted to a harsh northern climate with their insulating fur, long legs and large hooves that makes it easier to move through deep snow. Moose do not take density of their species into consideration but select their home range solely on the amount of protection and available forage (Herfindal et al. 2009). A high intake of energy and low mortality risk is therefore their priority when selecting their home range (ibid.). They are defined as concentrate selectors by Hofman (1989) and moose-type by Clauss (2010) with a main diet composed of deciduous trees and shrubs. Especially the AROW species: aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), oak (*Quercus robur*) and willow (*Salix spp.*), are considered the staple in their diet. Other known forages are bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*) (Spitzer, 2019; Felton et al., 2020). During winter moose are known to eat large amounts of pine trees (*Pinus sylvestris*) (Spitzer, 2019).

The red deer is the second largest deer species in Scandinavia. The males can reach a height of 1.4 m and their weight is normally between 110 and 250 kg (Christoffersson, 2017). Red deer are classified as intermediate or mixed-feeders (Hofman, 1989; Clauss, 2010), with the summer diet containing more graminoids (< 38%, Spitzer et al., 2020), legumes (Spitzer, 2019) and forb and the winter diet more like that of moose consisting of more browse from deciduous shrubs, trees and lichens (Christoffersson, 2017). Red deer are also known to strip the bark from spruces in plantations (ibid.). Their flexible digestive system is more similar to that of grazers, meaning that they are better adapted to digest monocots (graminoids) than moose.

1.3 The two studies

This thesis is divided into two studies. In the first one I extended the work of Åström (2022) to also include red deer. I investigated the diet composition and niche overlap for five moose and two red deer in northern Norway using video collar data recorded over a period of several months.

In the second study I studied moose foraging choice and selectivity of plant species on a finer scale, using near-continuous recording of three video collared moose on the island of Vega, in Norway. The recording schedule made it possible to compare individual meals as well as each individual's forage preference and selectivity. The near-continuous recording also opened for the possibility to compare the feeding pattern of browsers (moose) with that of grazers (dairy cows) to test if the camera collars can confirm the feeding patterns suggested by Hofman (1989) and Clauss (2010).

1.4 Hypotheses - both studies

1.4.1 Study one: Foraging differences between moose and red deer.

In this study I have performed the analysis on videos recorded during 2018 and 2019 by of camera collars worn by moose and red deer in central and northern Norway. I have focused on the interspecific difference regarding choice of forage to see if the camera data is able to confirm the hypothesis that moose are browsers, with a diet that contains a percentage of graminoids close to the 5%-threshold for a browser, as suggested by van Vieren (1996) and findings of Spitzer et al. (2020). And if the recordings have caught the mixed feeding pattern of red deer. An overall question of the study is whether the short video recordings can capture both the interspecific and intraspecific foraging difference of moose and red deer.

Hypothesis 1a: The proportion of graminoids in the moose diet is less than 5%.

I expect the recordings to show that moose are browsers, as suggested by Hofman (1989) and Clauss (2010). And thus, that graminoids (*Poaceae spp., Juncaceae spp., and Cyperaceae spp.)* are a minority in their diet.

Hypothesis 1b: The red deer eat significantly more graminoids than moose.

This is since the red deer, as mixed feeders, have a digestion closer to grazers and thus are better adapted to digest a wider range of forage than browsers, such as moose (Hofman, 1989; Clauss 2010).

Hypothesis 1c: Forage diversity is higher for red deer than for moose during the summer months.

With the red deer’s ability to digest a larger variety of food species (Clauss, 2010) a wider range of forage should be captured by the camera collars during the summer months, when the diversity of available forage plants is in its prime.

Hypothesis 1d: The intraspecific diet overlap is higher in moose than in red deer during the summer months.

The more limited digestion of moose should mean that the diet between individual moose is more similar than the diet between individual red deer.

1.4.2 Study 2: Moose food choice and foraging frequency

In this study I compared how well data from the near-continuous recording scheme match with the result from already published studies regarding choice of forage as well as number of feeding bouts per 24 hours. The feeding bouts of foraging moose were compared to that of grazers of approximately the same body mass: dairy cows. For the dairy cows I used data from Gekara (2005) and Kismul et al. (2019) to confirm that graminoids require a longer retention and digestion time than browse.

Hypothesis 2a: Moose on Vega will select for browse.

I expected the near-continuous recording of moose, together with food availability measurements in their home ranges on the island of Vega, to show that although non-browse might be more abundant, the moose will still mainly forage browse. I also expected to see that most of the browse selected for would be AROW species.

Hypothesis 2b: As browsers, moose have more foraging bouts per day than grazers (cows).

I expected to see a difference in the number of foraging bouts between grazers (dairy cows) and browsers (moose). Moose were expected to forage more browse; a diet with more easily digested cell-wall structure, but richer in proteins, lipids and sugar (Shipley et al., 1999) than graminoid. Thus, the foraging pattern of moose was expected to be more frequent and for shorter time per bout than that of dairy cows – who's diet of more cell wall rich food (i.e., monocots/graminoids) requires longer digestion time and thus fewer feeding bouts per day. Thus, I expected that moose would forage more times/day, but that each event would be for a shorter time period compared to the fewer and further in between foraging bouts of dairy cows.

2. Method

2.1 Study one: Foraging differences between moose and red deer.

2.1.1 The study areas

The deer in this study (Fig. 1) were distributed over the northern half of Norway, from the middle (Møre og Romsdal (62°30′N 7°10′E), Sør-Trøndelag (63^0 10^0N, 10^0 20’E)) to the most northern part Finnmark (70^0N, 29^0E). This results in a difference in habitats, precipitation, snow cover and anthropogenic presence. All which can gain - or restrict - abundance of food species.

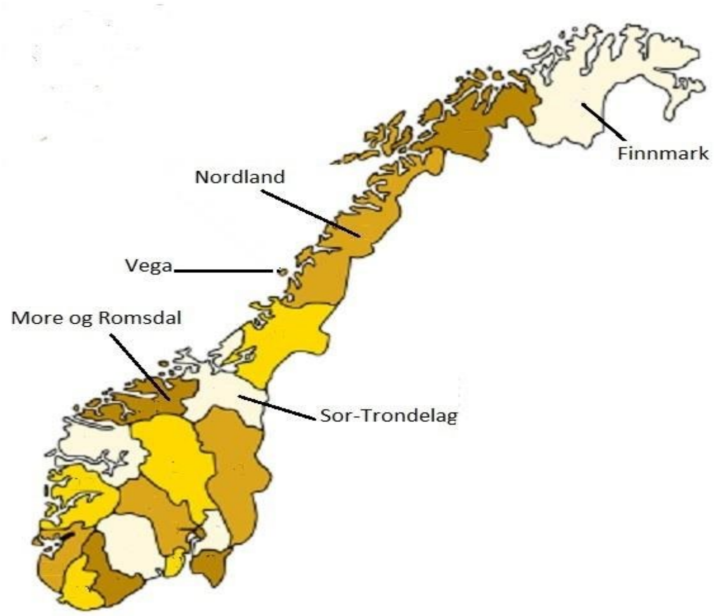

Figure 1. Map of Norway with its counties. The relevant ones from the most southern to the most northern are: Møre og Romsdal (62°30'N 7°10'E), Sør-Trøndelag (63^0 10’N, 10^0 20’E), the island of Vega (65°37'N 11°45'E) in Nordland and Finnmark (70^0N, 29^0E). Map modified from https://sv.wikipedia.org/wiki/Norges_fylken#/media/Fil:Norway_counties_(1972%E2%80%932017).svg

With its location on the west coast of Norway, bordering to the North Sea, the county Møre og Romsdal (62°30′N 7°10′E) has a maritime climate. The low coast landscape rapidly changes into mountains and an alpine landscape although many fjords cut through the landscape.

Sør-Trøndelag fylke (63^0 10'N, 10^0 20'E)). The county consists of 23 % forest and 5% is agricultural land (Norwegian Institute of Bioeconomy Research (NIBIO), 2017). Through the centre of the county cuts the Trondheim fjord and parts of the county border on the North Sea. This makes the weather condition vary between maritime climates in the west to a more stable inland climate (Lieng et al., 2005). The vegetation goes over the whole gradient with marshlands, deciduous forests and dry pine forests (ibid.).

Finnmark (70^0N, 29^0E) is the most northern part of Norway, bordering Finland and Russia in the east and Sweden in the south. In Finnmark the landscape is a mixture of agricultural land, wetlands (bogs and lakes) and an open alpine landscape. The mean temperature in July is 8-12^0 C (Iversen et al., 2009, see Moen, 1998). and common plant species are *Betula pubescens*, *Empetrum nigrum*, *Vaccinium myrtillus* and *Betula nana* (Iversen et al., 2009, see Lid & Lid, 2005).

2.1.2 Collared individuals and dates of observation

For study one I performed analyses on video material collected by NINA (Norwegian Institute for Nature Research) between the years 2017 and 2019. Five moose and three red deer, in different parts of northern Norway, had been equipped with collars and wore them between seven and twelve months (Table 1). This study includes the five moose but only two of the red deer due to time shortage. For four of the moose (deer ID 2209, 2219, 1922 and 1933) I used the data from Åström (2022).

Study one was only focused on video analysis and my contribution to the data set contains a female moose with twin calves (moose 1930) and two red deer: one female (Lilla 8) with calf and one male (Lilla 6). The moose was collared and spent all her time in Finnmark in northern Norway and the red deer were collared in Møre og Romsdal and Trøndelag respectively. Their locations made it possible to keep the same seasonal classification as Åström (2022), where the vegetation period in Finnmark is June to September and in Trøndelag and Møre og Romsdal - being further south –May to October.

Table 1: The animals that were compared and analysed in study one: 5 moose and 2 red deer. Animals in bold are uniquely analysed for this thesis whereas the data for the others were contributed by Åström (2022) and used for analysis in this thesis.

Area	Species	DeerID	CollarID	Sex	First recording	Last recording
Trøndelag	Moose	2209	1129	Female	01/03/2018	17/10/2018
Trøndelag	Moose	2213	1139	Male	02/03/2018	20/02/2019
Finnmark	Moose	1922	21762	Female	01/05/2017	09/09/2017
Finnmark	Moose	1933	21763	Female	01/05/2017	22/08/2017
Finnmark	**Moose**	**1930**	**21764**	**Female**	**10/03/2017**	**16/09/2017**
Trøndelag	**Red deer**	**Lilla 6**	**29470**	**Male**	**15/04/2018**	**28/10/2018**
Møre og Romsdal	**Red deer**	**Lilla 8**	**29533**	**Female**	**15/04/2019**	**23/10/2019**

2.1.3 Data analysis and hypothesis testing

For efficient use of time, and to standardise the analysis, I decided to set the number of times each video was watched to three: Once to decide average quality of the video, light condition and habitat; once to determine the weather, behaviour and time spent on each behaviour (if it changed during the video); and once to decide for certain what plant species the deer was foraging from (if foraging was happening in the video). The fact that the video clips only show us 20 seconds during a three-hour period makes it difficult to draw any conclusion regarding the amount of time the animals spend foraging, ruminating and resting. Using the actual observation time they spend foraging on something could lead to misinterpretations since the camera in some cases might only record the first or last seconds of an in reality much longer foraging event. At other times, we might have a full 20 second foraging event from a certain species, although the foraging of this particular plant species might be a one-time event, lasting for only these 20 seconds. To counter this I have chosen to draw my conclusions from the number of times each behaviour occurs in the videos.

I used the same protocol (appendix 1) as Åström (2022) for classification of the foraging. This meant that the classification of browsing vs. grazing follows the same logic i.e., that in the video analysis browse is considered to be twigs, buds and leaves from deciduous and coniferous trees and shrubs, as well as lichens. Foraging of forbs, graminoids (*Poaceae spp.*), sedges (*Cyperaceae spp.*) and rushes (*Juncaceae spp.*) are categorised as "grazing". In the statistical analysis, however, I have categorised only foraging of graminoids, sedges and rushes as "grazing". All dicots (including forb) are categorised as "browse". For consistency's sake is all analysis regarding forage species done on genus level since not all plants visible in the videos could be identified to species level.

I decided to use only data from the four common months for further analysis (Fig. 5) for the following reasons: i) it made it possible to compare the species on both inter- and intraspecific level, ii) these months were during vegetation period for all areas which made it possible to compare any differences in foraging choices when the range of forages were in its prime, and thus the selection for each growth form and/or food species were much more clear, iii) The fact that not all individuals - and species - had camera collars recording during the winter months heightens the risk on drawing conclusion from a too small dataset and sample size.

All statistical analysis has been done in R version 4.2.1 (R Core Team, 2022) using RStudio (version 2022.02.3+492) with 0,05 as level of significance.

Hypothesis 1a: The proportion of graminoids in the moose diet is less than 5%.

Since the data was not normally distributed, based on visual inspection, I used a one-tailed Wilcoxon-Mann-Whitney test to test if the proportion of graminoids in the moose diet was higher than 5% and a two tailed test to see whether it was significantly different than the 5% threshold.

Hypothesis 1b: The red deer are expected to eat significantly more graminoids than moose.

Here, too, a preview in the form of a histogram ruled out a normal distribution. The proportions of graminoids in the two deer species diet were instead compared with a Wilcoxon-Mann-Whitney test.

Hypothesis 1c: Forage diversity is higher for red deer than for moose during the summer months.

To compare the interspecific differences in number of food items I first visualised the data by plotting them as bar graphs to get a better overview of the collected data (Fig. 4). Due to the large number of forages (especially for red deer Lilla_6) which could not be identified, I kept “unidentified” as a food category. I also decided to keep “soil” since the deer were seen eating this on several occasions. Analyses were then performed on genus level due to the uncertainties of many graminoid species and willow species. I decided on the Shannon-Wiener index to compare the evenness (or possible lack thereof) in the species diet and - with the data close to normally distributed - a two tailed T-test to test if the difference was significant. The Shannon entropy could be calculated to Hillnumber, as described in Spitzer (2019) and used to calculate the significance via a Welch's T-test, since it does not require equality in variances.

Hypothesis 1d: The intraspecific diet overlap in forage is higher in moose than in red deer during the summer months.

For the investigated months (May to August), I used Pianka's index (Pianka, E.R., 1988) to compare dietary niche overlap on the inter- and intraspecific level. Since Pianka's index reaches from 0 (no overlap) to 1 (full overlap) it is an easy way to compare similarities in the diets. To test for any differences in the diets I used permutational analysis for variances (perManova). To visualise the result, I decided to use non-metric multidimensional scaling (NMDS). Calculations were done on growth form level, since I concluded that this still was a fine enough scale to compare any dietary overlap.

2.2 Study two: Moose food choice and foraging frequency

With the data regarding foraging choices of moose in northern Norway from study one I wanted to do some deeper testing and analysis of food choice over a shorter time period, as well as with a more continuous recording. Three adult, male moose on the island of Vega in Nordland, Norway, were equipped with video collars in February 2022. The collars recorded for 25 sec every 3 minutes during the first week of July 2022 (1st – 5th July; below referred to as "continuous recording"). The limited area of the island made it possible to retrace their movements from the GPS collars, and the recordings analysed - once the collars had been dropped off and collected – to collect samples of their food items for nutritional analysis. This thesis will only cover the foraged species and foraging activity during the five days of recording comparing the moose selectivity for AROW species during the vegetation period. It will also compare how their foraging time and pattern deviates from that of a grazer of approximately the same size – in this study dairy cows.

Field work was performed between 4th and 22nd of July. During this period I spent the time on the island of Vega in Norway together with my main supervisor, collecting collars, conducting the inventory and analysing the videos to see which food species that had been recorded.

2.2.1 The study area

Figure 2: Map with the island of Vega (65°37'N 11°45'E), modified from norgeskart.no, with area containing the home ranges for the three focal moose in July 2022 (orange line). The waypoint marks the largest settlement on the island; Gladstad.

The continuous recording of three moose bulls took place on the island of Vega in Norway (65°37′N 11°45′E). The island is accessible with a ferry from the mainland. In the south lies the mountain Trollvasstinden with its highest peak reaching 800 metres above sea level. On the northern part of the island the landscape is flatter with wetlands together with arable land and settlements. The largest settlement on the island is Gladstad, and the rest of the inhabited spots on the island are mainly farms and smaller settlements. The first moose most likely arrived at Vega by swimming from the mainland from island to island in the archipelago, something that still happens with some regularity, bringing new blood to the population. The number of moose is maintained by hunting, since there are no large predators present. Before winter the moose population is culled down to 50 individuals. The animals are regularly checked upon (easy to do when almost all individuals wear radio tracking devices!) and an employee from NINA is daily checking in and registering any new calves during calving season. The relatively small area that the three investigated moose used for this study gives an interesting insight into the habitat choice of moose (Fig. 2).

2.2.2 Collared individuals

The moose that were equipped with camera collars for continuous recording of the first week of July (1st – 5th July) were all adult males. This, to be able to rule out possible differences due to age and sex (and thus calf/no calf). In Norway, at this latitude during the summer, the midnight sun makes it possible to record the animals 24 hours per day.

Although Vega is a rather small island the fact that the recording took place during summer when there is a high abundance of food available, the camera collars were placed to three adult male moose and that moose are solitary animals the expectation of seeing many conspecifics captured by the video collars was rather low.

2.2.3 Methods in the field

To create a field protocol suitable for the vegetation and landscape on Vega I used the vegetation overview from Vegetasjon og skog på Vega (Angehoff, et al., 2021) complemented with information on vegetation type from NIBIO (Norwegian Institute of Bioeconomy Research) as a base and created a spreadsheet (in English and Swedish) with short descriptions of each habitat type as well as signature plant species for that habitat type (appendix 2).

Since we had been able to follow the moose' movement online (at dyreposisjoner.no) in advance we knew roughly in what area and how far the moose walked per day (Fig. 2). This made it possible to retrace their movements on a day-to-day basis during the days the recording took place - even before we went out to collect the collars. This allowed for planning the transects from which we would calculate the food abundance. We released and collected the collars on the 6th of July.

2.2.4 Calculating food availability and selectivity

To measure food availability along the transects corresponding to the daily movements of each moose, we used the step-point method (Evans & Love, 1957; Coulloudon et al., 1999). On average the length of the transects ended up being 7 km/day and due to experience from earlier projects we decided that 25 m between the measured spots were of a realistic and high enough resolution. To execute the measuring, we walked the determined number of metres along the transects, put the stick down and while one person identified all plant species touching the stick the other wrote down the identified species. To avoid bias and/or inconsistency in species determination it was always the same person making the species determination. This also made sure that the distances and steps were always the same. The species found touching the stick at each point were noted in the food availability protocol. The noted species were then transferred into an excel sheet containing all available species. From this the abundances could be calculated into proportions, which allows for directly relating food availability to the observed diet compositions. I calculated selectivity by comparing the availability of plants with the ones that we actually saw them eating in the videos. This was also transformed to proportions in order to calculate how much of the available forage that the moose actually utilised.

2.2.5 Video analysis

Since study two consisted of near-continuous recordings over a five-day period, the videos were screened for foraging events by the moose. Just like in study one, we recorded the plant species and the part eaten for each feeding event (i.e. meal). (No records were kept over the time foraging on each species, only the numbers of times were noted.) We also collected samples of all plant species that were foraged in the videos for future analysis of macronutrients, but the result of these is not included in this study.

2.2.6 Hypotheses testing

The focus in study two was to deepen the knowledge of foraging behaviour (food choice and number of feeding bouts) of moose, with particular emphasis on investigating selectivity. It was also to investigate the difference in forage frequency between browsers (moose) and grazers (dairy cows). The main testing was therefore done by comparisons between already known data (from study one and literature) and the data collected by continuous recording and field work. The moose on Vega was expected to show the same choice of forage as the moose in study one and have browse (especially AROW species) as their main forage. As for AROW species, I already knew that oak was not present on the island due to its northern location. Instead, I included species I knew were present on the island from Vegetasjon og skog på Vega (Angeloff et al., 2021). These species were: birch (*Betula pubescens*), bog bean (*Menyanthes trifoliata*), meadowsweet (*Filipendula ulmaria*), clover (*Trifolium spp.*), dooryard dock (*Rumex spp.*), bilberry and lingonberry (*Vaccinium myrtillus* and *V. vitis-idaea*) and spruce (*Picea spp.*).

Hypothesis 2a: Moose on Vega will select for browse.

Here I compared the number of times moose choose to forage from browse instead of graminoids. Just like in study one, I identified most plants to species level, but for consistency I only did the analysis on a genus level, since it was not possible to identify many of the willow or graminoid species to a finer taxonomic resolution. I used Jacob’s diet selectivity index to calculate the selectivity of the plants found in the habitats utilised by my three focal individuals. The choice of Jacob's D was since it made it possible to calculate utilisation of the plant species in relation to availability. The range from (-1) to (+1), makes it easy to determine preference (positive value) where use is higher than availability, neutral (0), meaning they utilize the resource to the extent it is available, or avoidance (negative value) where use is below availability of the plant species found in the moose' home range.

Hypothesis 2b: Browsers (moose) have more foraging bouts per day than grazers (cows).

I compared the feeding bouts on the near-continuous-recordings of the moose on Vega with data from studies on dairy cows by Kismul et al. (2019) and Gekara (2005), whose data and figures have been the source for my figures in the result section.

3. Results

3.1 Study one: Foraging difference between moose and red deer

In study one a total of 9546 unique videos were used for analysis. Out of these 1201 (12,6%) were deemed unusable, due to being “too dark” (93,1%) caused by poor light condition or body parts obscuring, lens in snow (6,3%), snow or water droplets on lens (0,3%) or vegetation (0,2%). The rest of the videos were usable and either deemed good – which meant nothing was obscuring or limiting the recording, or medium or poor (criteria in appendix 3).

The most frequently recorded behaviours were ruminating_lying (29,7 %), foraging (29,6 %), resting_lying (28,2 %), resting_standing (5,5 %) and walking (4,0 %). Other behaviours, such as for example grooming calf, drinking, interacting conspecific etc. were all < 1% each and were therefore categorised as “other” in the comparisons below (Fig. 3).

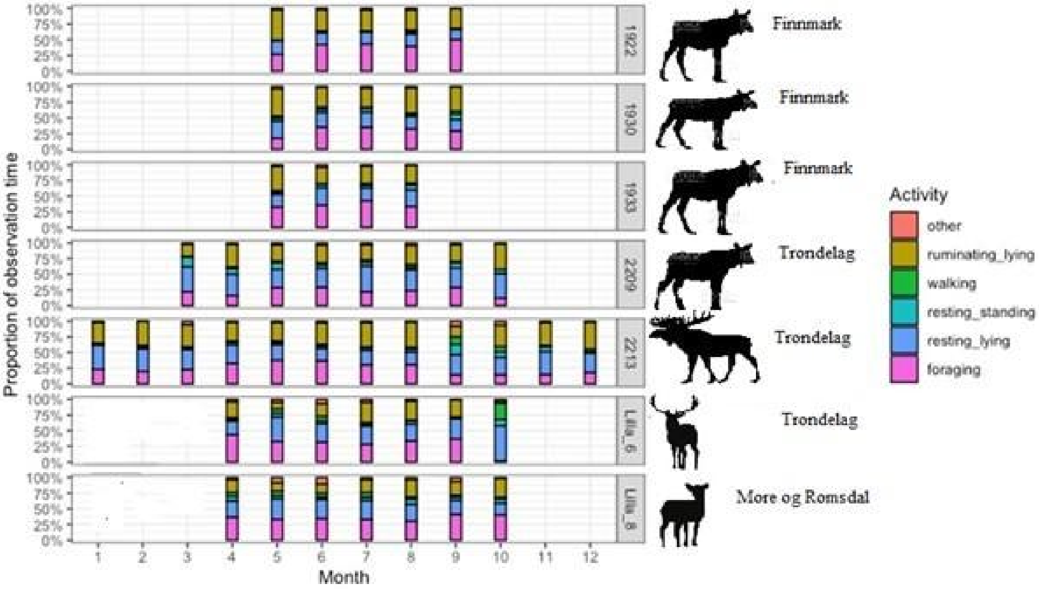

***Figure 3:** Recorded activities of the focal individuals (n=7) in this study together with their species, sex and geographical origin. Activities are presented as proportion of observation time and include six categories indicated in colour. "Other" behaviours include, for example, drinking, grooming a calf, and interacting with conspecifics. On average the two deer species were seen foraging in almost 1/3 (29,6%) of the videos over the whole period.*

As seen in figure 4 not many animals wore the camera collars during what I defined as winter months in their respective location. The months where data were accessible for all individuals were during the vegetation season, specifically May, June, July and August (below referred to as "summer months").

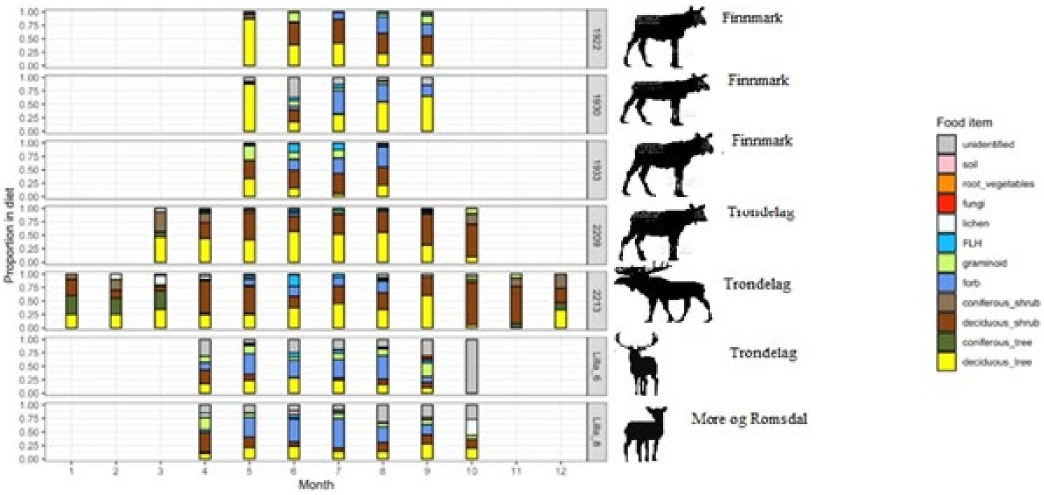

***Figure 4:** The monthly foraging choices for each of the seven focal individuals together with each individual's species, sex and geographical origin. Forages are presented on growth form level indicated by colour.*

Between the two deer species over 60 different plant species were foraged (Fig. 5). About 38% of these they had in common, whereas the rest was only foraged by one of the species. Most plant species were identified to species level when I analysed the videos, but since not all of them were - and the fact that *Salix spp.* (which made up such a large percent of the diet for both species) was only identified at genus level - I choose to only present the statistical results on a genus level. When analysed to genus level, *Betula spp*., *Salix spp., Vaccinium* (*myrtillus* and *vitis-idaea*) and *Epilobium spp.* were the most frequently eaten by moose, while red deer mainly foraged from *Betula spp., Anemone nemorosa, Vaccinium (V. myrtillus and V. vitis-idaea) and Sorbus aucuparia*. Although it can be argued that *V. vitis-idaea* should be classified as an evergreen, since it does not lose its leaves during winter, it is in this thesis classified as a deciduous shrub together with the other *Vaccinium* species (*V. myrtillus and V. uliginosum*).

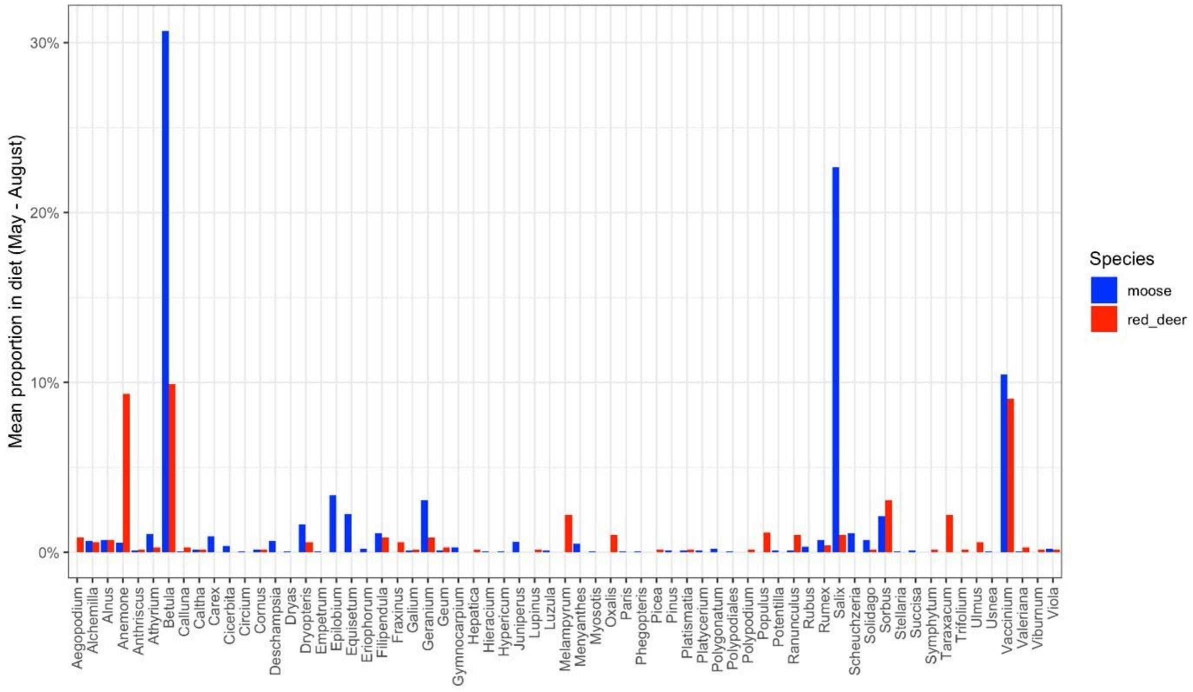

Figure 5: *All forages that were observed to be utilised by moose (n=5) and red deer (n=2) included in this study during the period from May to August. Plants are presented at genus level.*

3.1.1 Hypothesis 1a: Proportion of graminoids in moose diet is less than 5%.

The proportion of graminoids proved to vary quite a lot between the individuals. With the highest (14%) in the female moose (1933) in Finnmark and lowest (1%) in the male Trøndelag moose (2213) (Fig. 6). On average the proportion was 5,8 %, which is slightly higher than the findings of van Vieren (1996).

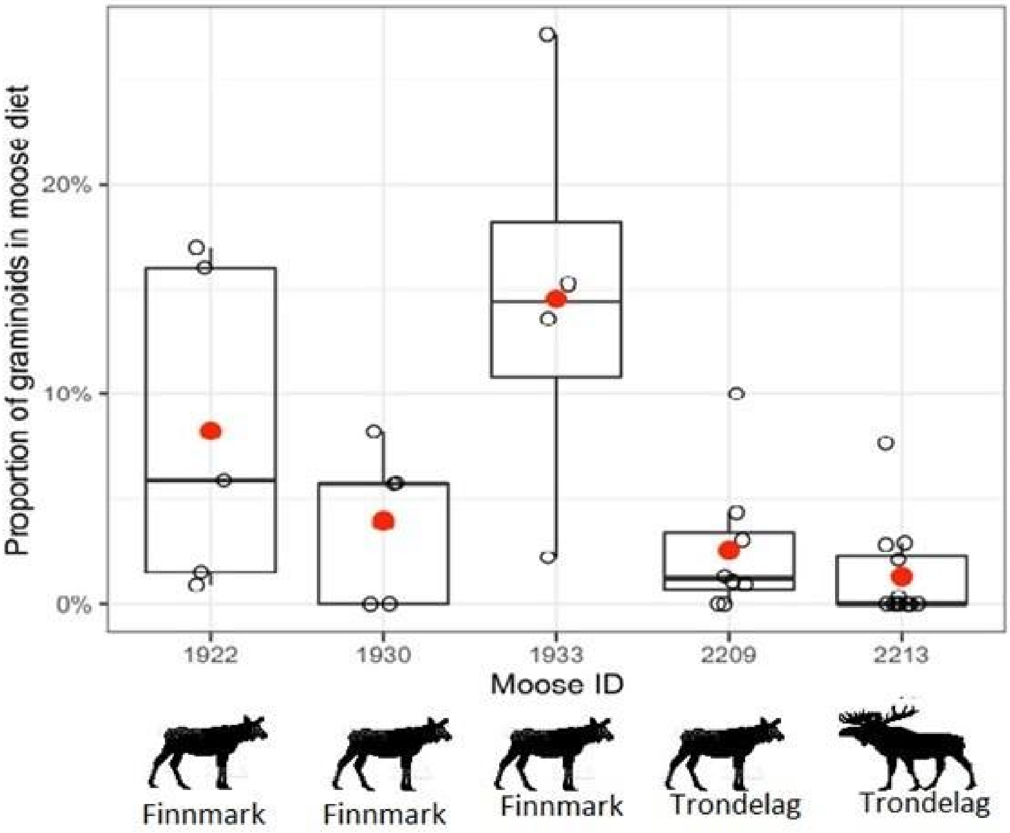

Figure 6: Proportional intake of graminoids by five camera collared moose in Norway during the months they were recording. Average monthly intake (hollow circles), indicating the mean (red dot) and the median (black horizontal line).

3.1.2 Hypothesis 1b: Prop. of graminoids in red deer diet is significantly higher than moose.

As shown in figure 7 moose diets contain on average 5,8% graminoids during the vegetation period, whereas for red deer the proportion of graminoids is 9,2%, which is significantly higher (Wilcoxon-Mann-Whitney Test, $p = 0.039$). The two red deer are rather similar in their foraging choice throughout all months. The same goes for moose 2209 and 2213, both located in Trøndelag. Moose 1930 - who had 14% graminoids in her diet ¬ is the one most similar to the red deer.

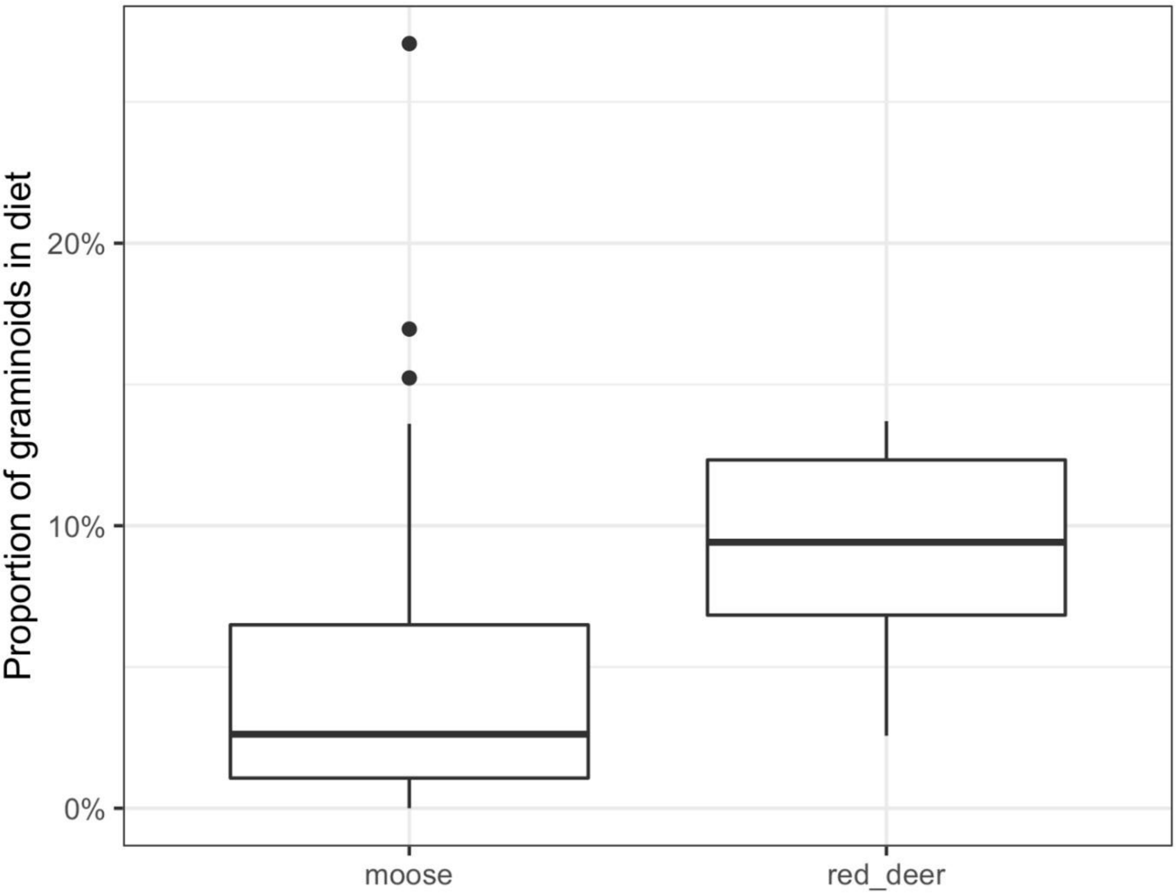

Figure 7: The proportions of the amount of graminoid on an intraspecific level of the focal individuals of deer in northern Norway for the years 2017 to 2019. Mean intake (black line) of the five moose is 5,8 % and the two red deer 9,2 %.

3.1.3 Hypothesis 1c: The forage diversity is higher for red deer than for moose.

When comparing the deer species foraging during the summer months moose (n=5) appear to have a much more diverse diet than red deer (n=2), at least on growth form level (Fig. 8 and 9). However, when zooming in on species level, Hills number is significantly higher for red deer than for moose (Welch's T-test, t = -3,64, p= 0,002), showing that the intermediate feeder red deer - despite moose having a higher number of investigated individuals and a wider geographical spread - has a higher diet diversity.

3.1.4 Hypothesis 1d: The intraspecific diet overlap in moose is higher than in red deer.

Both species had a high degree of intraspecific overlap. Pianka's index gives us 0,84 for moose. For the red deer the overlap was even higher with a Pianka index of 0,97. The result is that from the collected data there's nothing suggesting that the diet overlap in moose is higher than in red deer, but rather the opposite.

The perManova gives us a p-value of 0,001 on species level so there's a significant difference between the deer species diets. The moose 1930 (Finnmark) has a higher dietary overlap with the red deer (0,7) according to Pianka's index, whereas the overlap between red deer and moose in Trøndelag is 0,5.

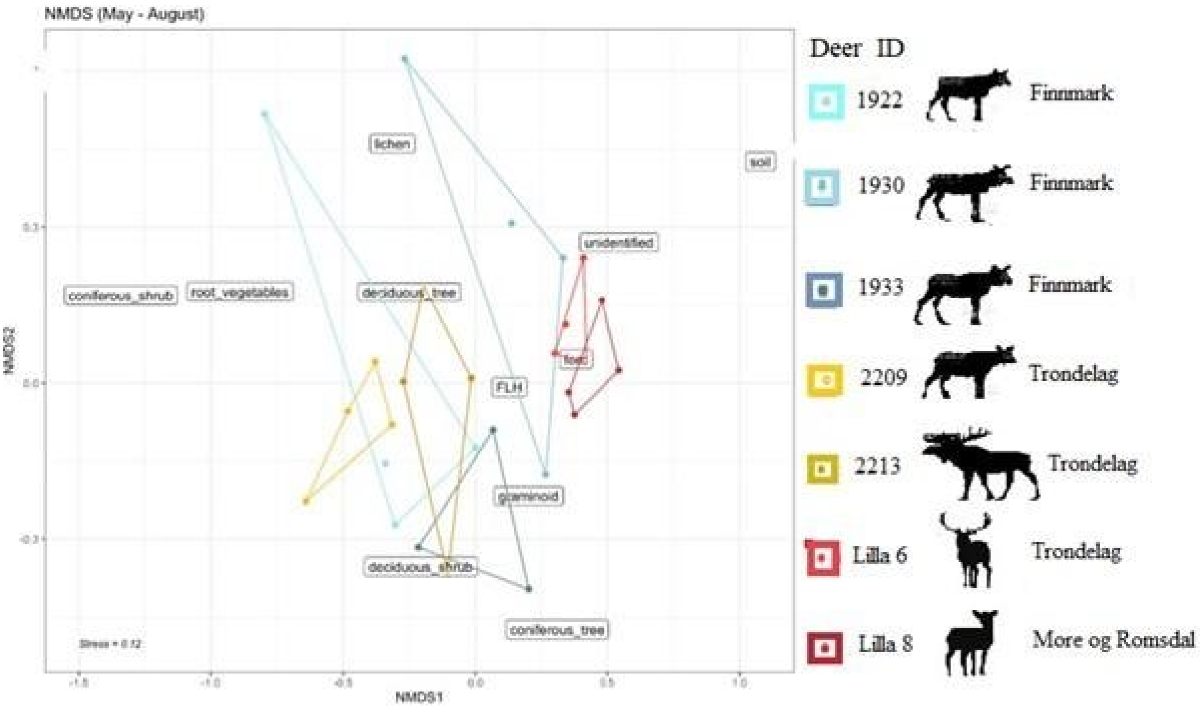

Figure 8: Presented on growth form level, each dot represents a diet/month and each polygon the diet of an individual during the summer months in Norway. The colour representing each individual is presented next to said individual's sex, species and geographical origin. (FLH = ferns, lichens and horse tail.)

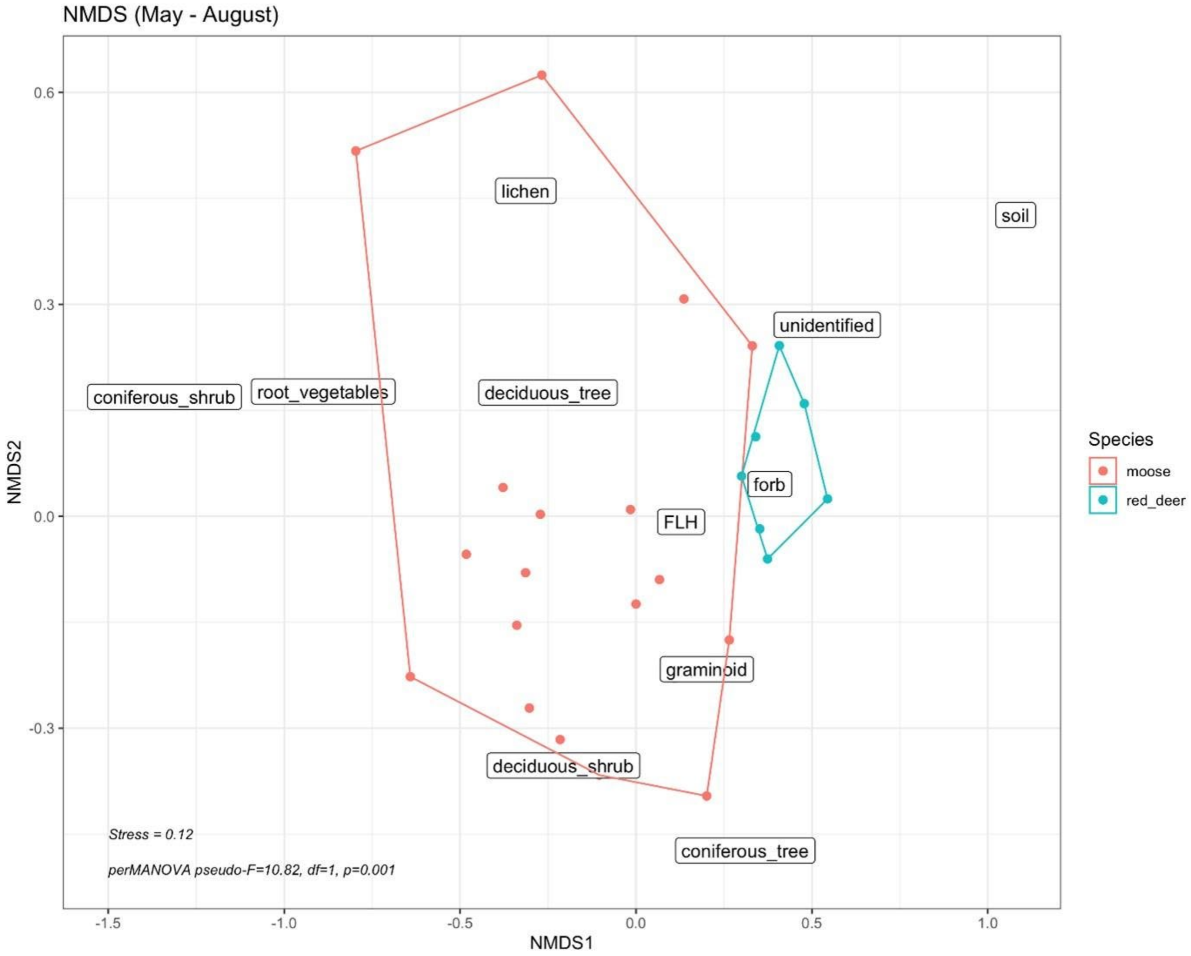

Figure 9: NMDS ordination of diet compositions at growth form resolution. The red polygon represents the food space of moose (n=5) during the months of May to October in Norway. And the same period is represented in blue for red deer (n=2). Each dot represents the average diet for each individual at each month. The major food items are also projected onto the data.

When summarising the results in study one, it is clear that video collars are able to show us the feeding pattern of both moose and red deer and that even short, spread-out recordings can show the difference in diet between browsers and intermediate feeders.

3.2 Moose food choice and foraging frequency

Graminoids were the most abundantly available growth form in the home ranges of "our" moose (Fig. 10), since they spent most of their time on wetlands or on cultivated land. "Other forb" are species that either could not be identified, are known to not be eaten by moose and/or that were so few that presenting each of them simply would not be possible. When comparing the available forages (Fig. 10) with the forages the Vega moose are recorded to ingest (Fig. 12) it leaves us with the result that moose only forage from 35 % of the plants in their home range.

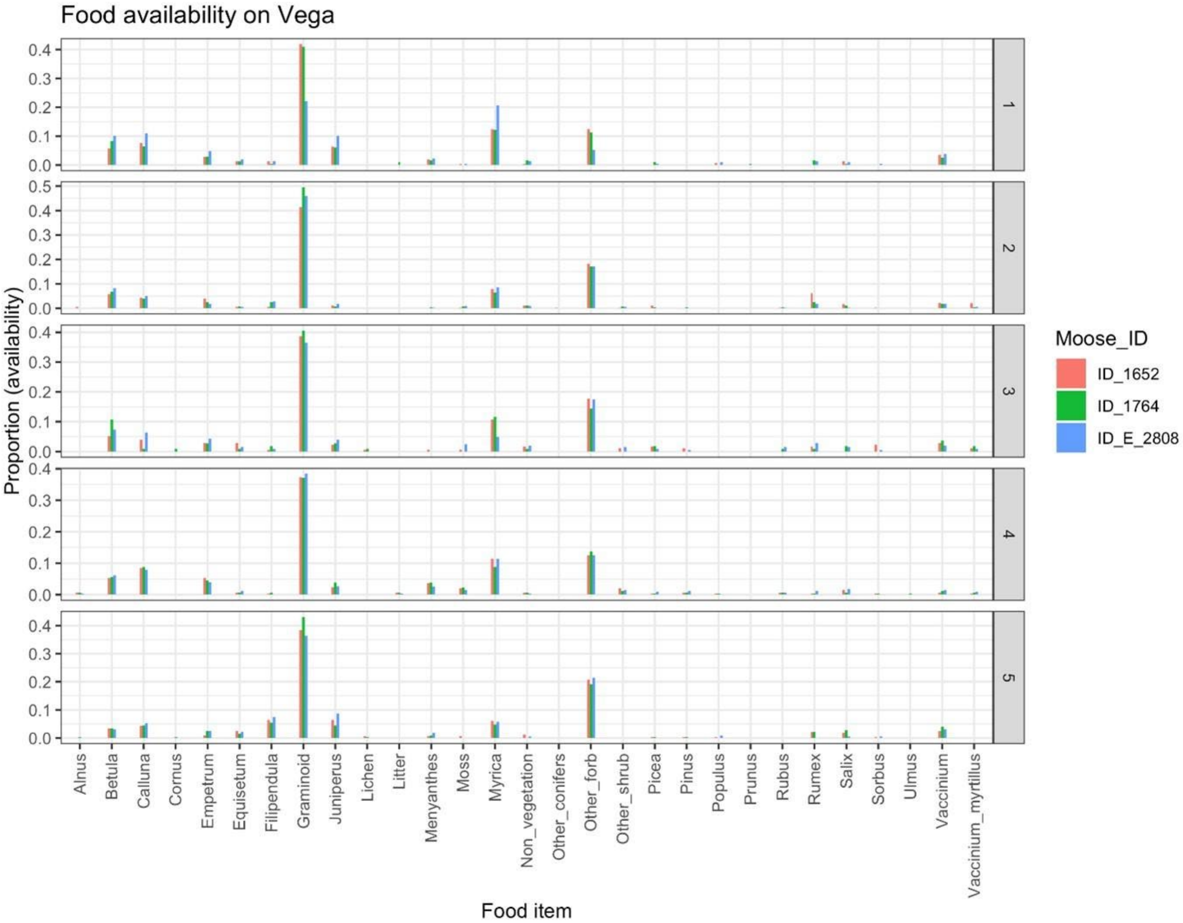

Figure 10: Food availability (as proportion of plants) in the areas used by three individual moose (indicated by colours) during the period from 1st-5th July on Vega, Norway. Plants are presented (mostly) on genus level.

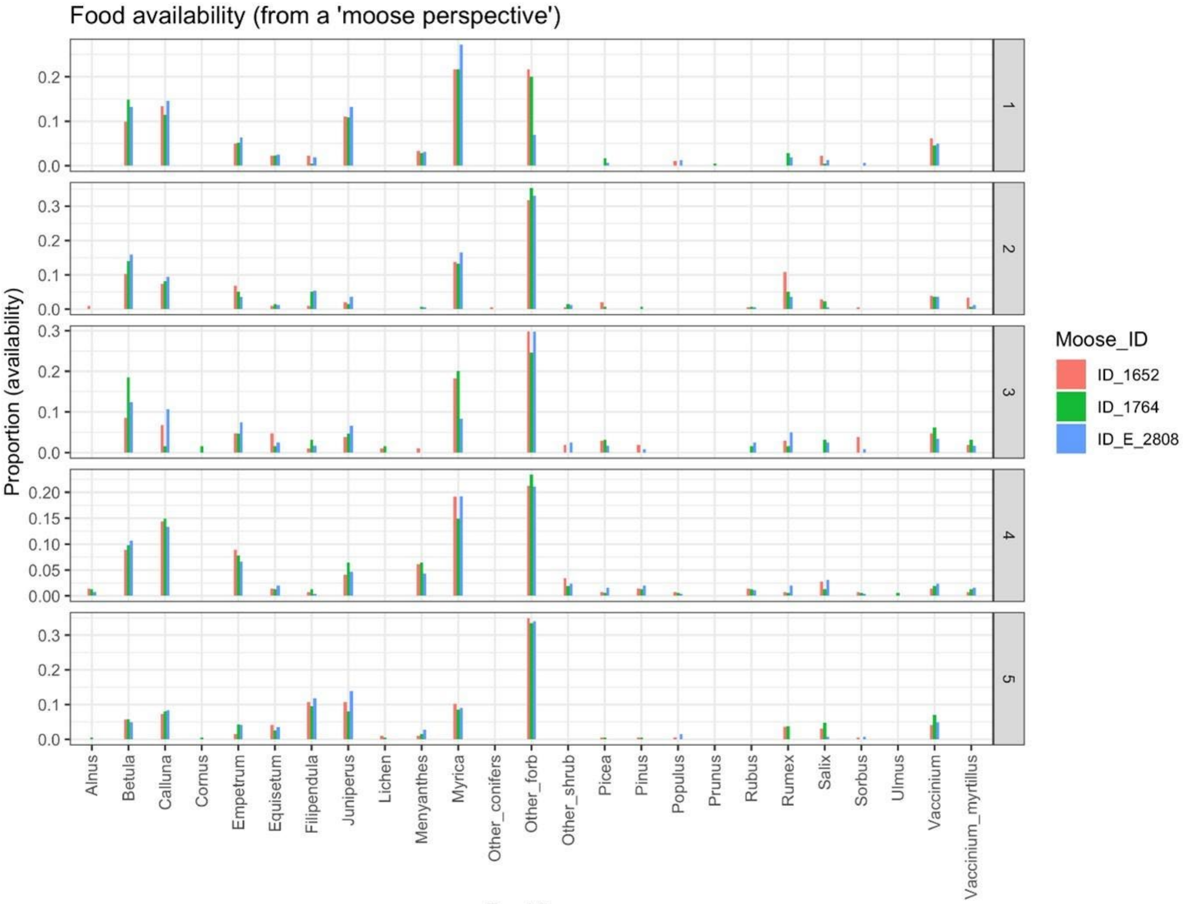

*Figure 11***:** *Availability of plants moose are known to forage from, presented on genus level. The focal moose (n=3) represented by colour.*

The moose diets were generally dominated by two food items: *Salix spp.* and *Betula pubescens*. *Filipendula ulmaria* and *Rumex longifolius* were utilised to lesser extent, but still high in proportion. Both *Salix spp.* and *Sorbus aucuparia* were highest in proportions during day 3, whereas *Betula pubescens* peaked on day 4 and *Filipendula ulmaria* on day 5 (for 1652 and 1764, at least – for E2808 the proportion is slightly higher on day 1).

Although *Filipendula spp.* and *Rumex spp.* make up a large proportion of individual moose diet on some days, they do select for AROW species – especially willow (*Salix spp.)* which is the AROW that has the highest abundance on the island.

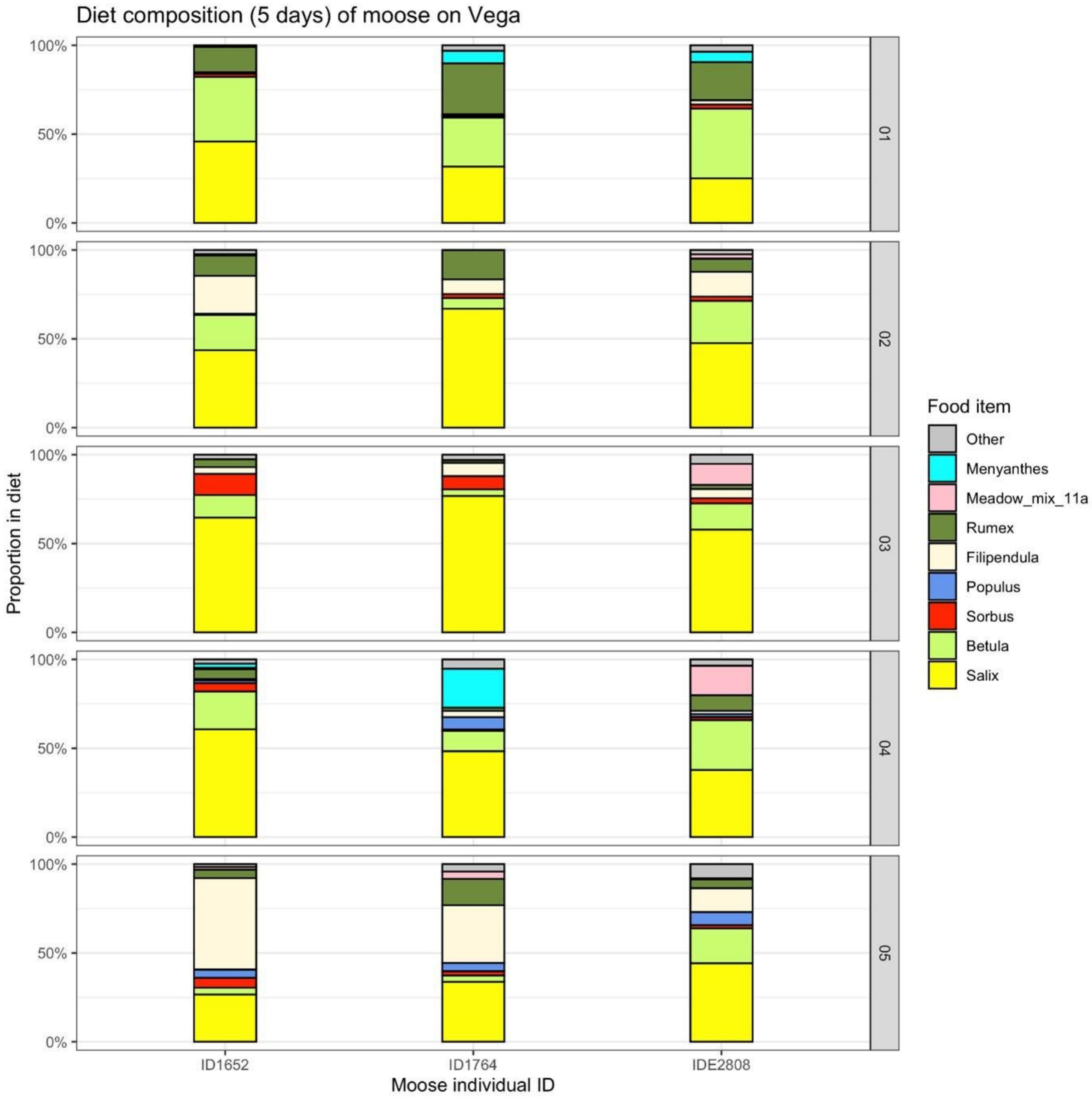

Figure 12: The proportions of forage in each focal moose diet on a daily level. Each facet represents one recording day, with the number corresponding to the date of recording. Food items are presented by colour.

3.2.1 Hypothesis 2a: Moose on Vega will select for browse.

The camera collars showed how moose have a clear preference for browse even during summer. As we can see in figure 13, even though the individual differences were noticeable, the average selection for browse is higher than for non-browse.

The (male) moose on Vega showed some differences in foraging choice, both in number of times selecting for the species and how the selection varied over the five days. The selection for *Salix spp.* is however clear for all moose during the whole period, both on average (Fig. 13) and individual (Fig. 12 and 14) levels. The selectivity for browse and especially the AROW species present at Vega is clear in figure 13 with *Salix spp.* as a total dominator albeit it is relatively low in abundance. With *Betula pubescens* making the second largest proportion (18%) and only individual moose on individual days is driving up the amount of forb (*Filipendula spp.* 11 % and *Rumex spp.* 10 %) the hypothesis holds that (male) moose (on Vega) ingest more browse, than what can be predicted from its availability in their habitat. For example, there are few occasions in the recordings that the moose forage from *Sorbus aucuparia, Populus tremula* and *Menyanthes trifoliata* – which are common in moose diet – but these are only sparsely found in their home range on Vega. The high ingestion of *Filipendula ulmaria* and *Rumex longifolius* shows on the other hand that the summer diet of moose contains a rather high proportion of forb. *Picea spp.* was only eaten once during the recording. Although they appear to be low in abundance according to our measurements, Sitka spruce (*Picea sitchensis*) are actually high in abundance in plantations all over the island.

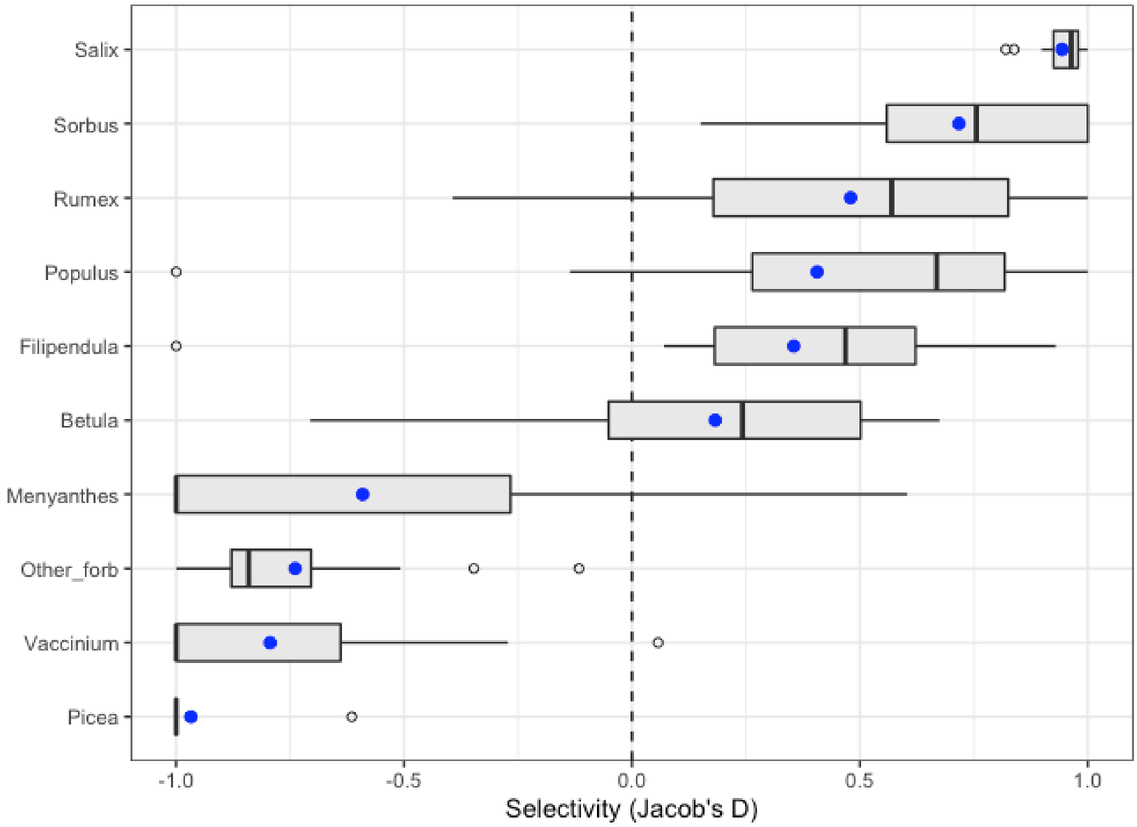

Figure 13: Relating selectivity (x-axis) for moose (n=3) to 10 typical forages (y-axis) on the island Vega, Norway, July 2022. Boxes indicate variation in selectivity together with the median (black line) and mean (blue dot). Dotted line marks the use: to the left is below availability ("avoidance"), and to the right is higher than availability ("preference").

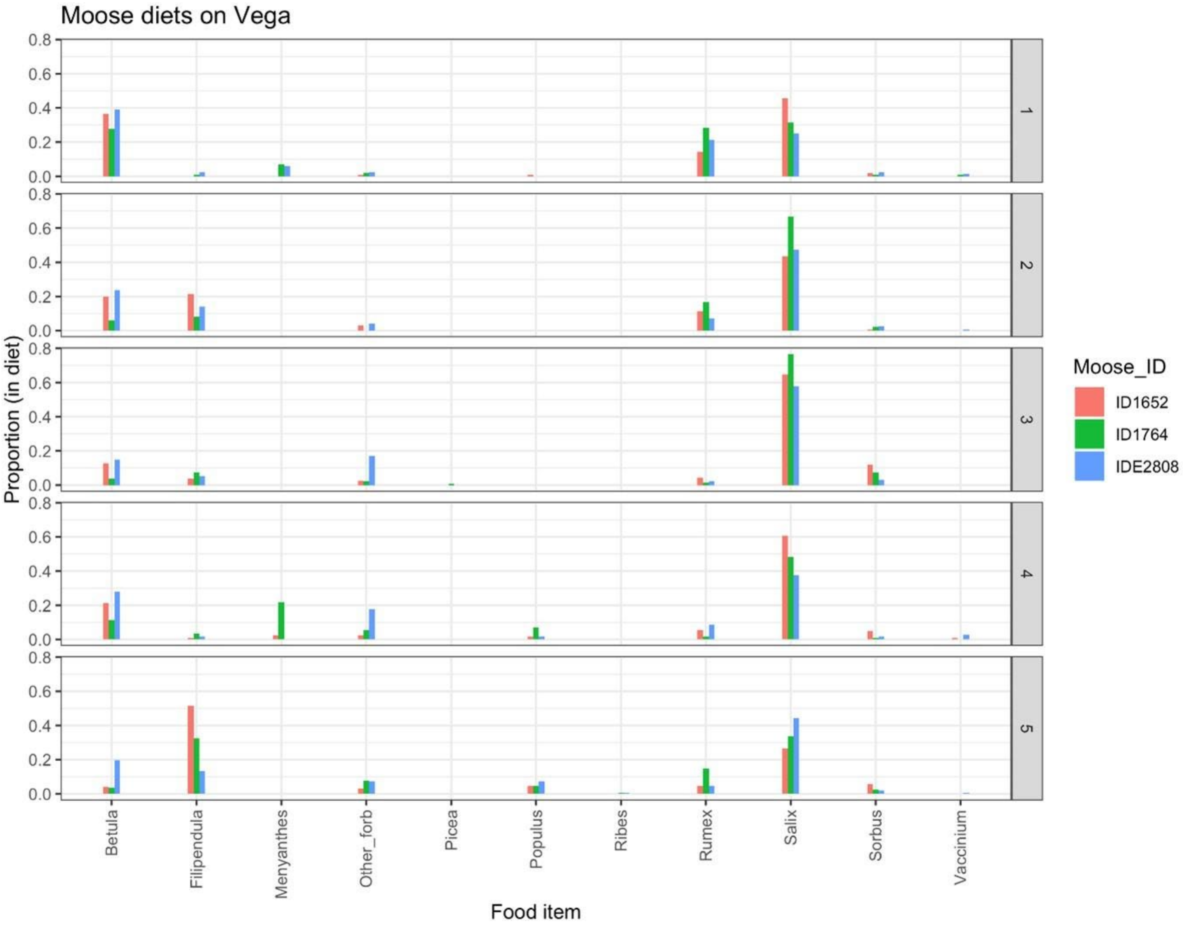

Figure 14: The recorded proportion of forage of the three focal moose bulls on Vega, Norway on a daily level during five days in July. Each facet represents one day, with the date corresponding to the number of the facet. Individuals represented by colour. Plants presented on genus level.

When I zoomed in on the individual moose's foraging choice during all five days it is clear that *Salix spp.* is high in proportion for all moose and all five days. Moose 1652 ingested a higher amount of *Filipendula ulmaria* during day two and day five. Moose E2808 is the most consistent in foraging *Betula pubescens*, in similar proportions, over all five days. 1764 seems to have the highest preference for *Rumex longifolius* but switched to *Menyanthes trifoliata* for day 4 and even more *Salix spp.* day 3.

3.2.2 Hypothesis 2b: As browsers, moose have more foraging events per day than grazers (dairy cows).

The continuous recording gives an insight into the activity pattern of moose over a 24-hour period. Our data suggest that moose on average have 5-6 major foraging bouts per day interspersed with periods of less food intakes (Fig. 15 and 16). The duration of the feeding bouts varies.

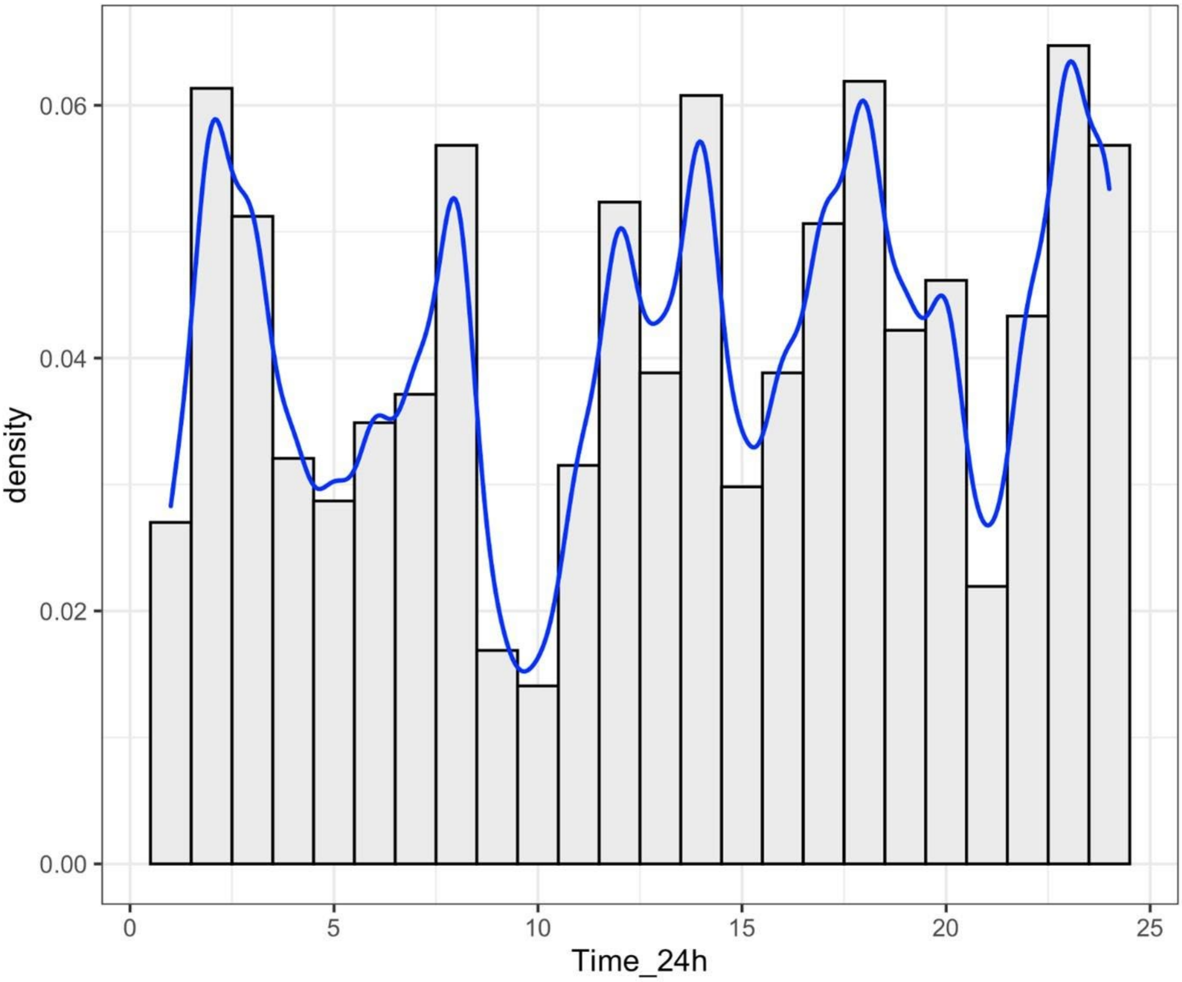

Figure 15: The averaged foraging pattern for the three focal moose over five days in July 2022 on Vega, Norway.

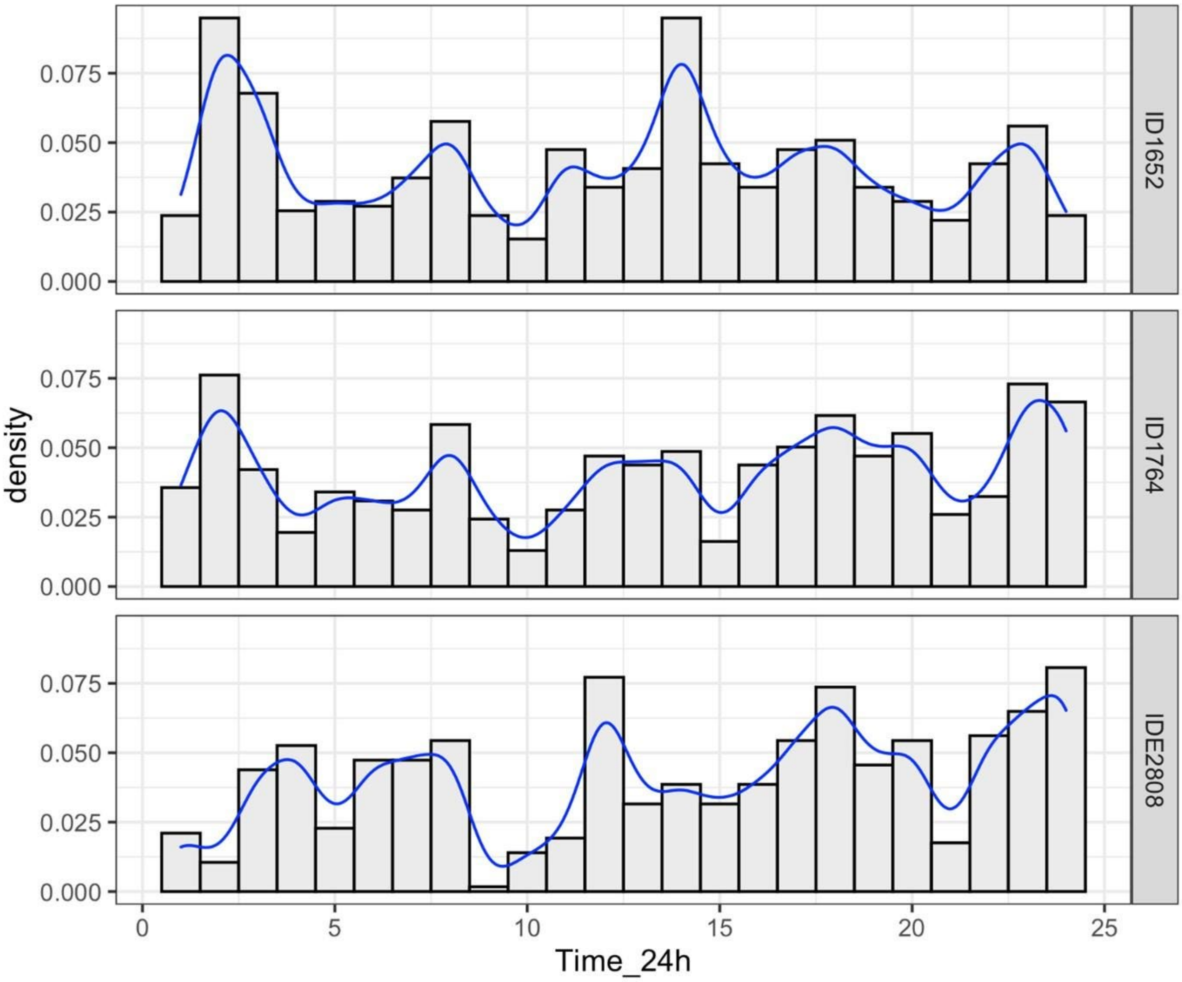

Figure 16: The average density of foraging events of the three focal individuals during the five days of recording of moose in July 2022 on Vega, Norway.

As a comparison to the moose foraging pattern, the data from Kismul et al (2019) (Fig.17) shows an example of how dairy cows with unrestricted access to grazing had three feeding bouts per 24 hours. The cows were kept in an open housing facility, giving them the possibility to choose when to eat or rest, and with access to pasture. The cows also foraged for longer time periods which means fewer high peaks, while the moose had less non-foraging time, but instead higher peaks.

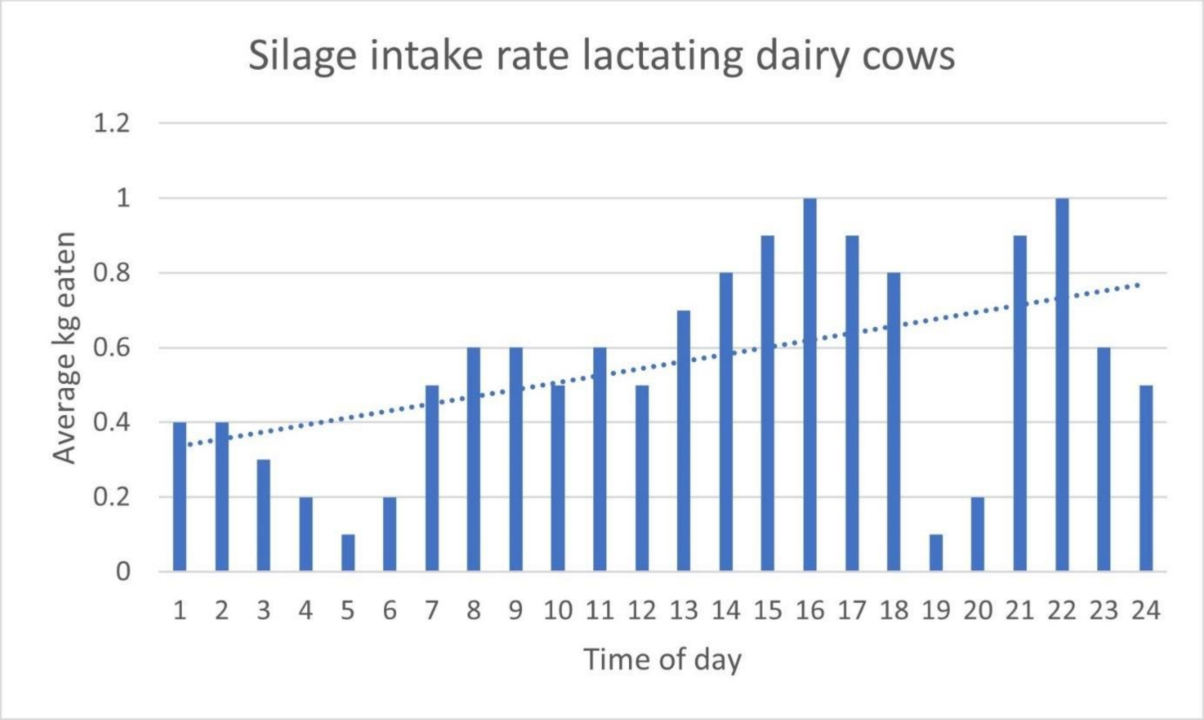

Figure 17: Re-draw from data collected from Kismul et al. (2019), figure 5a. Average amount (kg) of silage eaten by lactating dairy cows with access to exercise pens. Trend line show how the eating increase during the day (dotted line).

The study of Gekara (2005) compared the foraging patterns between cows with restricted and un-restricted grazing time. All cows had three feeding bouts with one peak during the morning but two longer feeding bouts during afternoon and evening (Fig. 18).

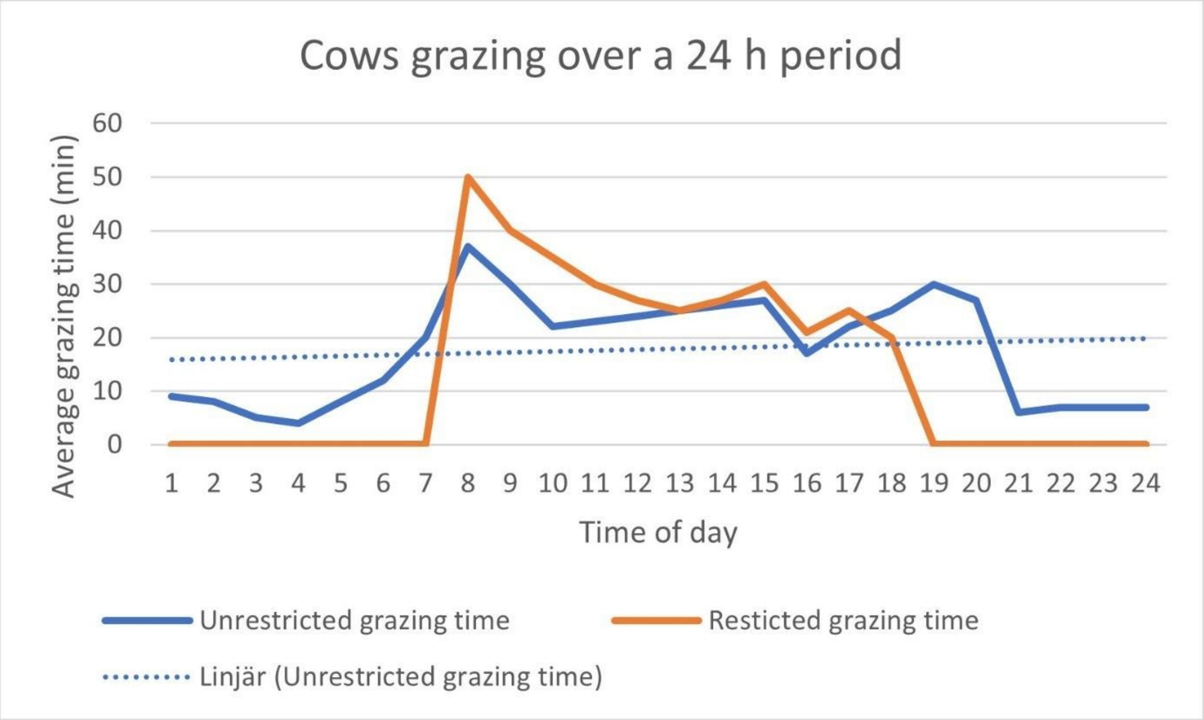

Figure 18: Re-draw from data collected by Gekara (2005). Average minutes feeding during each hour of the day for cows with unrestricted grazing time (blue) and cows with restricted grazing time (red). Trend line (dotted line) show a slight increase in grazing towards the evening for cows with unrestricted grazing time.

4. Discussion

Video collar recordings of foraging behaviour in our two largest deer species have shown to be useful. Although the expenses of the camera collars themselves together with the tranquilising and collaring procedure are high, I would still argue that video collars on deer are well worth the investment. The two studies in this thesis shows that the video quality in most cases is good enough to identify foraged species to at least genus level, but often even to species level.

The major difficulties with the camera collars are – as I see it - the following: i) they are capable of collecting a lot of data, which in turn have to be analysed, which requires time, ii) as mentioned above; switching the analysts of the video data is difficult. Even in my case – where I had a proper walk through of the data set and how to categorise film quality, snow cover etc. - the interpretations of weather, film quality, dominating vegetation etc. can still differ. It also heightens the risk of differentiating what the quality limiter is: for example, Åström (2022) categorised “body parts obscuring” as “too dark” – something I would have preferred to have as a category of its own. Both i) and ii) are pointed out by Lavelle et al (2012) as potential drawbacks of video recording collars, iii) As a continuation of ii); Quality limiters might only occur in a later stage of the analysis which forces the decision to either add it and skew the data or ignore it and miss certain information, iiii) the small sample size of moose - and even smaller of red deer – makes it difficult to draw any major conclusions. I couldn’t say for sure if the moose that ate much more graminoids than expected did this due to personal preference, calf/no calf or perhaps because she lived in Finnmark where other forage were scarcer than in the more southern Trøndelag or Møre og Romsdal. A small sample also makes the data set more vulnerable for technical difficulties. For example, a majority of the videos recorded in October 2019 by the male red deer Lilla 6 were of very poor and unusable quality. This means the loss of almost a whole month of data, which is costly when investing in collaring an animal with all the time and monetary resources that it brings. iiiii) the risk of trusting the timecode on the recordings completely. There were periods when they were off with several hours, showing a recording time of mid-day when it - according to the light condition - clearly was during the night. If this was due to a glitch in the programming or something that occurred when downloading and processing data I could not determine, but if one wishes to determine when activities occur during the day it is something to stay vigilant of.

4.1 Study one: Foraging differences between moose and red deer.

The four hypotheses in study one all aimed to evaluate the foraging differences between moose and red deer and if it was possible to capture them on video with short daily recording times, spread out over a long recording period of several months. The number of times each behaviour was observed was rather similar between the individuals across time as well as between the species. The only big difference was that the foraging frequency decreased, and the walking frequency increased, for the two male deer (moose 2213 and red deer Lilla_6) when the rutting season came (Fig. 3).

The hypothesis that moose, as browsers, would forage a proportion of graminoids less than the 5 % suggested by van Wieren (1996) was not fully true. Although the moose were found foraging mainly on browse, the average proportion of graminoids was slightly higher (5,8%). This difference might not be big enough to be significant, but does suggest that some moose, maybe due to the availability in their home range, eat more graminoids than what we would expect from a browser. That the proportion of graminoids in the red deer diet was significantly higher than moose (9,2% vs 5,8%) was in line with the hypothesis that red deer, as intermediate feeders, to higher extent forage monocots during the summer months, although they are capable to also digest a more browse rich diet (Christoffersson, 2017). This goes hand in hand with the third hypothesis, based on the findings of Spitzer et al. (2020) that red deer has a higher diet diversity than moose, a hypothesis that proved to be true when investigating the diversity on plant species level. That this is visible in a data set with few moose (n=5) and even fewer red deer (n=2) is remarkable, especially when considering that the home ranges of the two red deer were in geographical regions much closer to each other and thus more homogeneous than the moose who were geographically more dispersed. As for the fourth hypothesis, I could not find any evidence of moose having a higher intraspecific dietary overlap than red deer (Spitzer, 2019). Both species had a high degree of intraspecific overlap. Pianka's index gives us a high dietary overlap for moose (0,84), implying that although the home ranges differ in latitude - and thus forage availability varies between the sites - moose as a species select for a similar diet no matter where they are living. For the red deer the overlap was even higher (0,97). Worth to keep in mind here~~,~~ though, is that they were located in areas much closer - and thus more similar in almost all biotic and abiotic factors – than the moose. The low number of focal individuals should be considered. This might explain the difference from the findings of Spitzer (2019). But from the collected data there’s nothing suggesting that the diet overlap in moose is higher than in red deer, but rather the opposite.

4.2 Study two: Moose food choice and foraging frequency

When I compared the routes taken by the moose on Vega it was clear that they often walked in rather close proximity to each other. Over several days the routes were more or less the same, at least to some extent. (Samples of plants and faeces were collected but are not in the range of this thesis.) The variety of their forage intake is in line with the findings of Felton (2016): Their intake is chosen towards a nutritional balance that varies slightly between days, but that individuals chose their forage to compensate for a lack of some nutrients one day by eating more of a complementing forage the next. Thus keeping a rather similar balance over (at least a shorter period of) time.

As for the hypothesis that continuous filming can capture the differences in the individual’s activity pattern this seems to be correct. Although the moose on Vega appear to be more social and spending more time together with the rest of their conspecifics than what I expected there still are some differences in when and for how long they forage. The high amount of social behaviour on the recordings was somewhat surprising, due to all focal animals being adult males. A longer period of recording closer to the rut would be interesting to show any change in foraging as well as tendency to spend time in such close proximity with other (male) moose. With that high level of socialising behaviour, I wouldn’t be surprised if they are more synchronised than other populations. As for resting and walking I have had no time to analyse the data to that level of detail. The small differences in foraging pattern (Fig. 16) suggests that higher and shorter foraging peaks are followed by deeper dips of non-foraging. There seems to be no clear “feeding time” and “resting time”, but rather occasional feeding tops with smaller feeding bouts in between. Such as they grab a mouthful here and there when on the move. The small dips might be due to being on the move and/or resting. Naturally moose are free and thus likely to adjust their activity pattern depending on outer factors such as weather conditions and degree of disturbance. The recorded feeding pattern of the Vega moose compared to that of dairy cows shows that browsers have more feeding bouts than grazers. These results are in line with the findings of Renecker and Hudson (1989) that foraging of monocots requires longer digestion time.

Figure 16 implies that there are times during the day the moose are more prone to forage than others. As hypothesised by Hofman (1989) the activity pattern for browsers, such as moose, should be higher than for grazers, such as cattle. When comparing the data from my focal moose with data on the average number of feeding bouts of dairy cows the figures are redrawn from data collected by Kismul et al. (2019) and Gekara (2005). Taking into consideration that dairy cows are fed and thus restricted in both their choice of feeding time during the day as well as the quality and nutritional content of their food the data collected still shows/suggest that cows usually choose to feed an average of three to four bouts per day. This, together with the findings by Munksgaard et al. (2005) that shows that cows choose to rest over basically any other activity is an indication that foraging a more cell wall rich diet (graminoids) requires longer ruminating time than a more browse rich diet. This is in line with the suggestion of Renecker and Hudson (1989). The trend line in figures 18 and 19 show that dairy cows have a tendency to eat during the evening hours. This is somewhat on par with the average moose on Vega, suggesting that ruminators no matter where they are on the foraging scale tend to use the night for resting and ruminating.

An analysis on whether the chosen forage species has an impact on the length of the feeding occasion and/or time in between them is a suggestion for deeper understanding of the moose activity pattern.

5. Conclusion

This project has tested several hypotheses, as well as evaluated how well the technical advances can help researchers and if camera collars can capture the feeding and activity patterns of wild deer. It has also evaluated how well short recordings over a long time can show “the full picture” of the individuals' foraging choices (study one) compared to more continuous recording for a shorter time (study two). The limitations are mainly due to environmental factors, such as light conditions, water (lenses becoming blurry due to water drops or moisture) and/or snow as well as vegetation. All which are consistent with the findings of Åström (2022) and Egan (2019). The fact that the camera collars are of high enough quality for us observers to be able to identify the forages (often down to species level) is an indication that they can be of great advantage in future research.

5.1 Study one: Foraging differences between moose and red deer.

Judging from the result in study one the camera collars are able to capture the differences in forage choice in moose and red deer, as well as the fact that red deer have a more diverse diet than moose, but also appears to have a larger intraspecific dietary overlap. Of course, with such a small number of individuals no general conclusions can be drawn since the differences might be due to food availability, sex and/or calf/no calf. But it is possible to conclude that red deer are more prone to utilise more species, but still focus their diet on graminoids and forb during the vegetation period, whereas moose might forage from more growth forms, but the majority of their food is browse.

The average foraging choice of moose and red deer can be confirmed, but the short clips cannot be used to show the activity pattern and/or confirm the length of feeding, rumination and resting occasions for comparisons between the species. The trade-off is that we instead can follow an animal throughout many seasons which sometimes might be more valuable than behaviour on an individual level.

5.2 Study two: Moose food choice and foraging frequency

The moose on Vega showed a clear preference for browse in their foraging. Despite the low abundance of AROW species on the island *Salix spp.* made up on average 50% of their diet. The second most ingested browse was *Betula pubescens*. This was not remarkable since *Betula spp.* often are foraged due to their relatively high abundance on these longitudes, but it is normally not one of the, by moose, highest ranking forages. On the other hand might the limited area of the island have them ingest species that are higher in abundance despite them normally being lower on the preferred scale, simply because some (such as oak) are not present at all and others (such as rowan and aspen) are very low in abundance.

The near-continuous recording time proved to be excellent to study not only foraging behaviour, but also showed clear possibilities to be used for more in-depth behaviour studies such as resting time and behaviours that happen less frequently, for example social behaviour. It confirms the intraspecific differences in foraging choice of moose - even for such a short time during summer. It provides us with a deeper understanding of individual differences, since social behaviours are more likely to get caught on video. In this study it gave me the opportunity to compare the number of foraging bouts of the browsing moose with that of dairy cows, which proved to be in line with the suggestions of Hofman (1989) and Clauss (2010) in that that browsers forage in more bouts (6) per day than the grazing dairy cows (3).

The conclusion of these studies is that a recording schedule with even such a short glimpse (at maximum a total of 2,4 minutes per 24 hours) into the life of deer can not only provide us with enough information to tell the differences in foraging choice of two different species. It can help us determine their foraging choice in many cases down on plant species level. With increasing recording time we are able to study the behaviours of deer on an even finer scale: personalities, amount of resting time and pretty much any other behaviour we want to investigate. In short: The possibility this technology has makes the future research of foraging behaviour in wild deer look bright, indeed.

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Popular science summary

The two largest deer species in the Scandinavian peninsula are moose and red deer. Despite their similarity in size and home areas research has shown that they normally feed on very different plants and plant types. And this even though they, just like cows, are ruminants which mean that they chew their food several times. Moose are known to eat mostly browse, especially leaves and twigs from aspen, rowan, oak and willow – amongst scientists referred to as the AROW species. Although they can eat forbs and grass their digestive system is less adjusted to benefit from monocots (grass). The red deer on the other hand has a digestive system that extract the nutrition from a wider range of plant species and is known to eat more grass and forbs during the summer – which makes them more similar to cows - and to have a diet more similar to moose in the winter, when they eat more twigs, lichens and evergreens, such as lingonberry shrubs.

This project has been divided into two studies: The first one had eight short recordings (20 seconds every third hour) per 24 hours over several months. Here I investigated how well camera collars worn by five moose and two red deer, all living in the northern part of Norway, were able to capture their food choice and if the recordings showed the differences between the deer species - and between individuals of each species - regarding the amount of grass and browse as well as the variety in their diet.

In the second study the recordings were more or less continuous, with 25 seconds of recording every 3 minutes for a period of five days (i.e., 5 x 24h). The three collared moose lived on the island of Vega in northern Norway, and the recording took place in July which meant that the midnight sun made it possible to record the moose behaviour even during the night. This continuous recording also made it possible to investigate how many times per day the moose ate and compare it with how many times per day cows - that normally feed mainly on grass and forbs - eats. This is interesting since browse is usually considered to be faster to digest than grass.

The results are that moose do eat more browse than red deer, but the recordings showed that they eat slightly more grass than the 5% threshold that have been suggested in earlier studies. Red deer on the other hand eat almost twice as much grass than moose, which was expected. Red deer also had a more varied diet, with more plant species than moose. But I found no evidence of the two red deer having any huge difference in food choice between them. In fact, the five moose showed a much higher degree of difference in their choice of food species, where one ate a lot more grass than expected and the others also showed personal preferences towards different plants. It must be kept in mind, though, that the red deer lived in areas geographically closer and thus more similar to each other, whereas the moose had a wider geographical spread and therefore more variation in the amount and variation in food species.

The moose on the island of Vega did indeed choose to eat browse, despite browse being low in proportion of plant species on the island. Grass and forbs were much more frequent. The Vega moose ate between five and six times per 24 hours. This is twice as many times as the dairy cows I compared them with, although the dairy cows did have free access to their food all through the day. Which is an indication that browse is faster to digest and therefore requires more frequent feeding than grass.

The camera collars have proved to be a useful tool when researching the food choice and feeding pattern of deer species. It has proven many hypotheses correct and shown us that they are able to collect valuable data regarding not only what, when and how often deer species eat, but also other behaviours such as social interactions, resting and moving around in their home range.

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Appendix 1

Table A1: Classification of foraging and forages in the video analysis. Modified after the protocol developed by Åström (2022).

Factors	**Factor_levels**	**Remarks**
Foraging_type	Browsing	Consumption of woody vegetation, i.e., leaves, twigs (or both) of trees and shrubs; also includes feeding on lichens.
	Grazing	Consumption of non woody vegetation, i.e., graminoids and forbs. Includes roots.
	Supplemental_feeding	Feeding that cannot be categorized as browsing or grazing; refers to intake of human-supplied food sources specifically for wildlife such as hay, silage or root vegetables.
Plant_growth_form	Coniferous_tree	Coniferous tree, approximately

		dbh > 5cm
	Deciduous_tree	Deciduous tree, approximately dbh > 5cm
	Coniferous_shrub	Coniferous shrubs are typically woody vegetation that normally grow more than one stem and/or do not reach a height > 5 meters.
	Deciduous_shrub	Deciduous shrubs are typically woody vegetation that normally grow more than one stem and/or do not reach a height > 5 meters.
	Graminoid	Grasses like Poaceae, Cyperaceae and Juncaceae
	Forb	Herbaceous plant that is not a graminoid, flowering plants.
	FLH	Ferns, lycopods and horsetail
	Fungi	Fungi
	Lichen	Lichen

	Silage	A type of supplementary feed: Grass or other green plants compacted in an airtight condition.
	Hay	A type of supplementary feed: Dried green plants.
	Root_vegetables	Roots from plants (e.g., sugar beets); a type of supplementary feed
	Pellets	A type of supplementary feed provided by humans. Often in feeding stations.

Appendix 2

Table A2: Habitat types on Vega utilized by the three focal moose. Coding and description of habitat types are from the official system by NIJOS (Norsk institutt for jord- og skogkartlegging) and is translated by the author of this thesis.

Code	**Habitat type**	**Description**	**Typical species**
4c	Meadow birch forest	Highly productive forest that shows clear signs of long-time use (grazing). Due to this the ground vegetation is usually dominated by grass.	*Deschampsia cespitosa, Anthoxanthum odoratum L., Agrostis capillaris, Festuca rubra*
4g	Pastureland forest	Open forest with low abundance of brush due to long-time use (grazing).	*Geranium sylvaticum, Ranunculus sylvestris, Alchemilla spp.*
7b	Bilberry-rich spruce forest	Spruce plantation on former bilberry-rich birch forest.	*Vaccinium myrtillus*
7c	Meadow spruce forest	Spruce plantation on former meadow birch forest.	
8a	Moist-land Forest	Transition between wet and dry forested land. The soil is commonly low in nutrition and rich of humus. In areas dominated by deciduous trees the most common species is birch. Otherwise, it's usually pine.	*Molinia caerulea, Trichophorum cespitosum, Eriophorum vaginatum, Narthecium ossifragum*

8b	Mire forest	Wetlands that have developed a low tree layer of birch or pine. Can also be in the transition between wetland and dryer land.	*Calluna vulgaris, Empetrum nigrum, Rubus chamaemorus*
9b	Rush mire	Flat areas withstanding or very slowly flowing water.	*Trichophorum cespitosum*
9c	Grass mire	Divided into sub-types such as rich mire and lime mire and the species richness varies due to this. Often dominated by grass species.	Rich: *Carex rostrata, Carex lasiocarpa*, *Carex echinate, Molinia caerulea* Lime: *Carex lepidocarpa, Saxifraga aizoides, Carex pulicaris, Carex capillaris*
11a	Cultivated land	Land that can be cultivated by agriculture machines. Or that can come back into use without major interventions.	
12e	Scattered settlement	25-50% of the area consists of buildings, roads etc.	

Appendix 3

Table A3: The criteria for video quality, quality limiters and light condition. Modified from the work of Åström (2022).

Factor	**Factor levels**	**Remarks**
Video_quality	Good	Nothing is disturbing the visibility of the camera.
	Medium	Quality is slightly to moderately disturbed, but it is possible to see what is happening in the video.
	Poor	Quality is so bad that it is extremely hard to see what is happening in the video, or if approximately more than 3/4 of field of view is covered.
	Unusable	There is no time in the video with visible data. The video is either too dark, the camera is covered in snow/ too dirty, or it is too rainy or foggy.
Quality_limiter	In_snow	The field of view is partly or wholly covered with snow.
	Snow_on_lens	Ice or snow covering part of lens.

	Vegetation	Vegetation covers the field of view.
	Water_droplets	Water drops on lens, can come from fog, rain or swimming.
	Lens_misted	Video is blurry because of a misted lens.
	Too_dark	When it is too dark to see or determine what is shown in the video. Or if a body part (beard, leg etc.) is covering the field of view.
Light_condition	Dawn	The sun is rising.
	Day	The sun is up.
	Dusk	The sun is setting.
	Night	There is no light.

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