The secret life of moose - Patterns of foraging and behaviour based on video collars

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The secret life of moose - Patterns of foraging and behaviour based on video collars

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Abstract

To understand how moose forage in the wild, we have to study them without disturbing them then. Video cameras placed on moose are a novel method to study wild individuals without being intrusive. I analyzed video footage from four moose collars, filmed up to nine times a day and filmed from 4 to 11 months, for maximum of 4,5 minutes a day. The moose were located in Norway: Sør-Trøndelag and in Finnmark. I tested three hypotheses: 1) weather affects video quality, 2) that diet composition of moose varies across the annual seasons and 3) diet composition varies between individuals and study sites. I found that during the vegetation period the most common video limiter of the video quality was water. The video footage showed that the moose were clearly browsers during the whole year, but they increased their foraging on *Betula* sp. and *Salix* sp. during the vegetation period. I conclude that animal-borne video cameras, are able to provide moose researchers with observations of expected changes in forage patterns during a year and provide detailed data even when they record only short periods of the day. This methodology also has the potential to reveal rare and previously undescribed behaviors. My findings will help to further refine the methodology for more large-scale investigations of the secret lives of moose.

Keywords: Moose, *Alces alces*, Foraging, Video footage, herbivory, browsing

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1. Introduction

1.1 Wildlife collars with video cameras (‘collar cams’)

Habitat loss and biodiversity loss are driven by human disturbances such as forestry and agriculture and have effects on animals and their habitat selection (Dominoni et al. 2020). Good knowledge about such effects is important for the sustainable management of wildlife, particularly of long-lived species. Gathering reliable information from species that migrate or live in remote areas, however, is difficult. The most reliable used way to gather information about behavior of animals in the field is field observation (going out to observe) (Vuillaume, Richard and Côté 2020).

Since the 1960s when the first experiment of following sea turtles with helium-filled balloons started to monitor their movement, camera systems have been developed to work on land animals bigger than 200g (Egan 2019). The number of observed animals is determined by the time spent by the observer in the field, which may lead to an observer bias (i.e., when the observer has expectations about the data and this then influences the observer) (Lavelle et al. 2012). Automatic cameras have been developed and employed to minimize the observability bias (Lavelle et al. 2012).

Radiotracking is good for knowing where animals are or have been, and which habitat is preferred over their lifespan. However, one drawback with radiotracking is that the behaviour of the animal (e.g., feeding, interaction with other animals, breeding) is not recorded. Cameras can be used to capture local behaviors and the local environment that are used by individuals, which can be important for understanding wildlife populations (Vuillaume, Richard and Côté 2021). A major drawback with stationary cameras (i.e., camera traps with automatic triggers) is that they extract limited data from a fixed place. More recently, several developed alternative camera systems include: transmission-based, data-collecting video-camera systems and animal-borne video and environmental data-collection systems (bio-loggers) (Lavelle et al. 2012). With animal-borne collar cams, behaviour, interactions, and ecology can be measured (Egan 2019). Camera collars (hereafter referred to as ‘collar cams’) document not only the animal’s behavior but also the environment in its close proximity, while limiting the risk of observer bias during data collection (Vuillaume, Richard and Côté 2021). These newer collar cams can provide a comprehensive view of contact rates (number of contacts from 100 opportunities (with calf, or other individuals)) and different behaviours (foraging, ruminating, walking etc.) of all individuals in the field of view and not just the outfitted individual (Lavelle et al. 2012). Any animal-borne device (including bio-loggers and collar cams) has to be attached carefully to the animal. If improperly placed, it can cause changes in behaviour or be damaged if it gets stuck in vegetation or fences (Beringer et al. 2004).

1.2 Moose behaviour

In northern Scandinavia, the moose (*Alces alces*), which is in the Cervidae family, is the biggest land animal with a weight up to 550 kg in males and females weighing approximately 20% less than the males (Jägarförbundet 2021). Due to their large size, wide distribution, high density and high consumption of woody plants, moose can drive vegetation changes in the boreal forest (Persson et al. 2012). The moose migration in spring and autumn can be driven by the predation risk and the nutrition availability in food, they then migrate to places with less snow and easier accessible food places during winter months (White et al. 2014).

Moose are a sexually dimorphic species, i.e., distinct morphological differences allow for reliably distinguishing between the sexes on video camera footage. Male moose have bigger necks and bigger neckbeards than the female moose and also carry antlers, which are used to show status to other males and to the females. The antlers are shed in midwinter and start to grow back after a few months. Thus, the most distinguishing feature that can be used to identify a male moose is the antlers while the females have a white stripe inside of their back legs. Most of the female moose reach sexual maturity when they are two years old, and the moose rut takes place in autumn (Jägarförbundet 2021). Moose are solitary animals but can also be found in smaller groups (female-calves, young males or when migrating) especially in winter (Olsson 2021).

1.3 Moose foraging

The knowledge about food choices of ungulates is important for the knowledge on the impact on the ecosystem and human resources (Spitzer et al. 2020). Prey animals must always balance the acquisition risk (increased risk of predation, plant toxins, and possible antagonism from conspecifics) with the gains in nutrition when foraging (Felton 2020, Arias-del Raso et al. 2010). Moose are classified as being browsers, as opposed to, for example, red deer (*Cervus elaphus*) or fallow deer (*Dama dama*), which are mixed feeders that can switch from browsing to grazing when it is possible even if moose can graze a little bit (Hofmann 1989).

In winter, Scots pine (*Pinus sylvestris*) is known to be heavily browsed by moose and less commonly browsed in summer (Bergqvist, Bergström and Wallgren 2013). Pine is an extremely economically important species in Scandinavia and browsing on pine is a challenge for forestry companies (Ball and Dahlgren 2002). The identification of plants in moose faeces have shown that important summer and winter foods of moose include birches (*Betula* sp.), rowan (*Sorbus aucuparia*), lingonberry (*Vaccinium vitis-idaea*) and bilberry (*Vaccinium myrtillus)* (Wam and Hjeljord 2010, and Felton et al. 2020). *V. myrtillus* is known to be an important food for moose in spring and in autumn, when the leaves first come out and after leaf wilting because of their high nitrogen content (Persson et al. 2012).

In the Cervidae family, the diet has been shown to influence physiology and reproductive fitness; on an individual level, fitness changes through changes in body mass (Felton 2020). Moose need to get sufficient ratios of nutrients in the quantities demanded by their physiology, despite the variation in plants and over different seasons the moose must satisfy the complex nutrient needs in the body (Felton 2021).

1.4 Hypotheses

In this thesis, I used collar cam video material sampled from 4 moose individuals, for a maximum of 12 months and a minimum of six months to test several hypotheses and predictions relating to environmental effects and diet data (Table S1). The aim for this was to test how well camera collars work for moose and to see if the data gathered from the videos shows how moose are known to behave and forage. Based on this aim, I formulated three hypotheses to test and see if they show the expected result for a well-studied model organism like moose, and then see if the method works for investigating behaviors for moose.

Hypothesis 1: Weather affects the quality of videos produced by the collar cams, and these limiting factors are different depending on the season (Street et al. 2015, Ditmer et al. 2018). I predicted that the video quality will be adversely affected by snow or ice on the camera lens in winter (prediction 1a). I also predicted that the video quality will mostly be impaired by water on the camera lens and sun glare in the vegetation period (prediction 1b).

Hypothesis 2: Diet composition of moose varies across the annual seasons. I predicted that the diversity of plants eaten is higher in the vegetation period than in winter (prediction 2a) (Spitzer et al. 2020, Felton et al. 2021). Another prediction is that in winter, pine is more commonly eaten by moose than in the vegetation period (prediction 2b). However, I also predicted that some aspects of diet choice are stable across the year, such as the moose' focus on browsing and avoidance of graminoids, and their opportunistic intake of favoured broadleaf trees at any time of year (Clauss et al. 2010, Wam and Hjeljord 2009), simplified to that moose are browsers across the year (prediction 2c). I predicted that *V. myrtillus* is the most commonly browsed deciduous shrub in the vegetation period (prediction 2d) (Wam and Hjeljord 2009). I also predicted that *Betula* sp. and *Salix* sp. are favoured forage species (Wam and Hjeljord 2010) (prediction 2e).

Hypothesis 3: Diet composition varies between individuals and study sites. For moose, good foraging and protection is a trade-off, and priorities are assumed to be different in this regard between the two sexes (Bjorneraas et al. 2011). I predicted that diets are more similar between female individuals than between females and males (prediction 3a), and that dietary overlap is higher between individuals within a study site than between study sites (prediction 3b) (Speath et al. 2004).

2. Method

2.1 Study area

The study area encompassed two study sites in Norway, one in Sør-Trøndelag (64.9°N 11.5°) and one in Finnmark (70°N, 29°E) (Ueno et al. 2014 and Vindstad et al. 2014) (Fig. 1). The precipitation in Sør-Trøndelag is close to 1440mm a year and in Finnmark 400-500mm. Both locations had a close location to the tree border and bogs in the lowland. In Sør- Trøndelag the area is dominated by Scots pine, Norway spruce and birch (Ueno et al. 2014). Finnmark is heavily dominated by birch forest but there are other species in the location like Scots pine and aspen (*Populus tremula*) (Vindstad et al. 2014). Finnmark has a mixed landscape with agricultural land, bogs, lakes, forest, and open alpine landscape, but Sør-Trøndelag did not have the agricultural land.

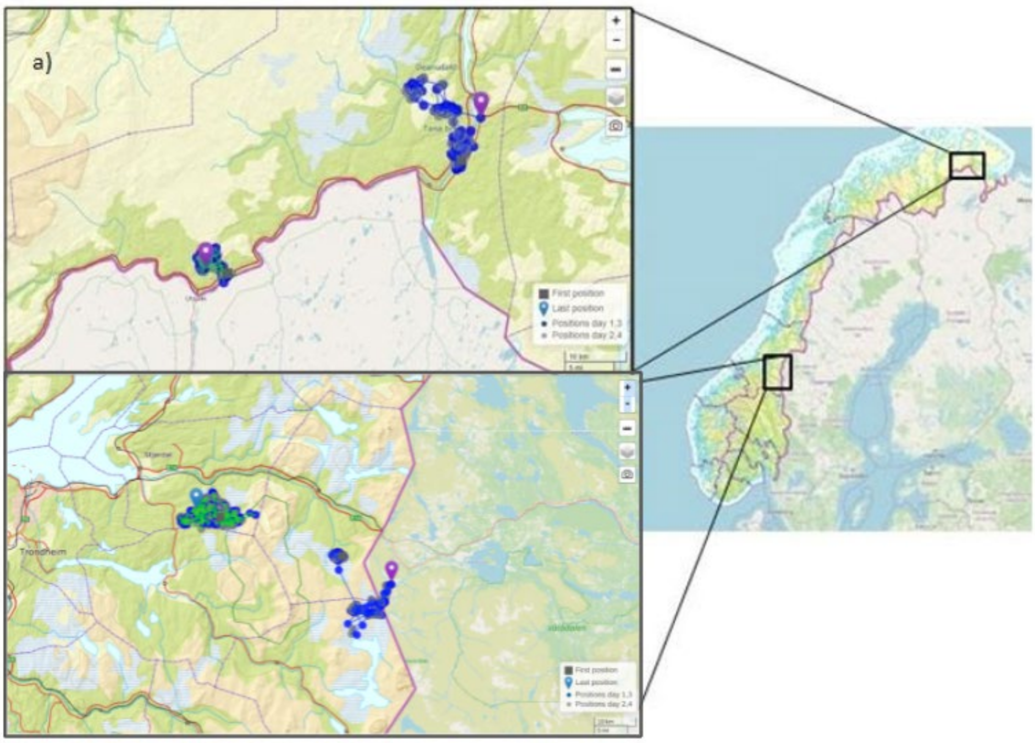

Figure 1: Placement and movement of the four collared moose in Norway. a) Top, Location for female moose in Finnmark (moose ID 1922, purple line with blue dots; moose ID 1933, green line with blue dots). Bottom, Location for female and male moose in Sør-Trøndelag (female ID 2209 blue line with blue dots, male ID 2213, green line with blue dots).

2.2 Collaring with video cameras

Two female moose in Finnmark were outfitted with a camera collar in 2017 (Fig. 1). The two female moose in Finnmark also had GPS locations taken and the video sequences were 20 seconds each. The collar cams on the female moose recorded for four to five months in Finnmark during 2017, starting in May and stopped in August-September, and always recorded 8 sequences per day.

One male and one female moose were outfitted with a camera collar in Sør-Trøndelag in 2018. In Sør-Trøndelag, the female was accompanied by a yearling, and did not get a new calf. The longest collected video material was from the male moose, which started 1st March 2018 and continued to 20th February 2019. For the female moose in Sør-Trøndelag, recording started in March 2018 and continued for nine months. GPS location was collected at the start of all video sequences and sequence length was 30 seconds. The recording schedule varied across the months ranging from 3 video sequences per day in February to 8 sequences per day in June (see Table S1 for details).

2.3 Data analysis

For my analyses, I divided the year into a vegetation period and winter depending on when the snow started to melt and when the leaves started to fall. The use of these 'phenological seasons' facilitated direct comparisons between the two study sites since conditions varied strongly based on calendar season due to the much more northerly latitude of Finnmark. The vegetation period in Finnmark was in June-September, the winter period for the Finnmark moose was in May (i.e., May was the only month outside the vegetation season for which collar footage was available). In Sør-Trøndelag the vegetation period corresponded to May-October and the winter period to November-April.

Prior to analyses, I first built a database by systematically classifying the collar cam video footage in a Google Spreadsheet. This approach allowed for efficient input and verification of ambiguous observations by the collaborators. The details of the data classification are provided in Table S2-S3. Briefly, I watched every video at least two times except for videos that were classified as unusable (too dark or in snow/vegetation). The first time, I assessed the video quality, the weather, and the habitat characteristics, whereas the second time, I focused on observing the behaviour of the individual (walking, ruminating, resting, foraging etc.), and on what plant was eaten. For the foraging data, I classified all sequences where the moose ate dicots including forbs (e.g., *Epilobium* sp.) as "grazing" even if forbs are counted as “browse” in most literature. I defined “browsing” as the consumption of woody vegetation, i.e., leaves, twigs (or both) of trees and shrubs, and also included feeding on lichens. Feeding bouts on different plant species within one video clip were recorded as different observations. Feeding on the same plant species within one video clip were recorded as one observation, even if another plant was consumed in between. Although feeding bouts on different plant species within the same video clip often differed in length, I chose the number of observations rather than the length of observations as the basis of quantification. I considered this to be less biased than time since videos frequently either began or ended with foraging observations of unknown length. Videos with more than the focal individual (the one carrying the collar), were played multiple more times to determine the behaviour of all individuals. When foraged plants were hard to determine, I saved the corresponding video clips separately for evaluation by two plant experts. If both identified the plant to the same species, this was used as the ‘consensus species’, otherwise the plant species was classified as ‘unidentified’. Once completed, the Google Spreadsheet was converted to an Excel file for further processing in R.

2.4 Hypothesis testing

All analyses were performed in R v4.1.1 (R core team 2021) at a significance level of alpha = 0.05 for statistical tests. For the initial video quality summary statistics, the full data set was used; for subsequent analyses, videos classified as ‘unusable’ were removed. All diet analyses were based on the subset of data that contained observations of foraging. Unless otherwise specified, diet analyses were carried out on a genus level taxonomic resolution since foraged plants could frequently only be identified to genus level. Depending on the question, I used either a monthly or seasonal (vegetation period and winter) temporal resolution. Diet compositions were calculated as proportions of observations. For example, the proportion of pine in the diet of moose ID SM M2213 in February, was calculated as the number of observations of pine foraging divided by the number of all foraging observations during February for this individual.

2.4.1 Hypothesis 1: Environmental conditions affect video quality

To test predictions 1a (in winter, video quality would be adversely affected by snow and ice) and 1b (during the vegetation season, sun glare and raindrops would be the most frequent quality limiters), I plotted video quality and the corresponding quality limiters by season as stacked bar plots for comparison.

2.4.2 Hypothesis 2: Diet composition of moose varies between the annual seasons

In order to test prediction 2a (that diet diversity is lowest in winter and highest in the vegetation period), I calculated the Shannon-Index as a measure for diet diversity for each moose and month using the function *diversity()* from R-package 'vegan' (Oksanen et al. 2017). I then fitted a locally weighted smoothing line (option 'loess' in R package ggplot2) to the monthly data points.
To test prediction 2b (that pine is mainly browsed in winter), I plotted the proportions of observed pine browsing across the available months for each moose.
To test prediction 2c (that moose are browsers across the year), I summarized the proportions of all woody forage items (see Table S3) into a variable called 'Woody forage' and plotted those proportions across all available months for each individual moose. For visualisation of temporal trends, I then fitted a locally weighted smoothing line (option 'loess' in R package ggplot2) to the monthly data points.
To test prediction 2d (that *Vaccinium myrtillus* is the most commonly browsed deciduous shrub in the vegetation period), I first calculated diet compositions at plant species taxonomic resolution for each moose and season. I then selected all deciduous shrub species (see Table S4) and plotted their proportions as bar graphs for comparison.

For testing prediction 2e (that *Betula* sp. and *Sorbus* sp. are the most common food for moose at each study site), I compared the monthly diet compositions of each moose using stacked bar graphs with the forage plants at genus level taxonomic resolution.

I did not have food availability measurements per se but used the 'dominant vegetation type' classifications of the observed habitats as a proxy of forage availability. Those included birch but not rowan. My assumption was then that in heavily birch-dominated habitats, birch should correspond to a major food item.

2.4.3 Hypothesis 3: Diet composition varies between individuals and study sites

To test if diets are more similar between female individuals than between females and males (prediction 3a), and to assess whether dietary overlap was higher between individuals within a study site than between study sites (prediction 3b), I used two approaches: First, I calculated pairwise Bray-Curtis dissimilarities between individual diet compositions (i.e., between the four moose) and ordinated the results using non-metric multidimensional scaling (NMDS) for visualization (Kartzinel et al., 2015). I then tested for differences in the diet composition using permutational analysis of variance (perManova) in the R-package 'vegan' (Oksanen et al., 2017; Pansu et al., 2019). These analyses could only be performed for the vegetation period, because a sufficient number of winter months were only available for one individual for the test (i.e., the male moose, ID SM M2213, SM M=Sør-Trøndelag moose male). Second, I calculated Pianka's index as a measure of dietary niche overlap between all individuals for both the vegetation period and winter using the R-package 'spaa' (Zhang 2016). Pianka's index ranges from 0 to 1 with zero indicating no overlap and 1 indicating complete overlap (i.e., identical diets). This enabled me to compare the dietary overlap between individuals within and between study sites for both seasons.

3. Results

Of the total number of videos (N = 6452), there were 20.3% videos with good quality, medium quality videos were 63.9%, there were 10.8% poor videos and 5% unusable videos. The shortest filmed video time was in December with close to 1.5 minutes filmed per day, because of the short periods were the light were up in the winter period. The most video material filmed were in June with 4.5 minutes filmed per day in Sør-Trøndelag, and in Finnmark 2.4 minutes were filmed every day.

3.1 Hypothesis 1: Environmental conditions affect video quality

During the vegetation period, the medium quality dominated, with mostly water droplets disturbing the view (Fig. S1) (1b, during the vegetation season, sun glare and raindrops would be the most frequent quality limiters). Video quality percentage of good and medium videos was higher in winter, and the main quality limiter was [lens] 'in snow' (1a in winter, video quality would be adversely affected by snow and ice). I found that the Finnmark study area showed higher proportions of overcast weather than Sør- Trøndelag (Fig. S2). Sør-Trøndelag had a rainier vegetation period but also more clear weather than Finnmark. In winter, Sør-Trøndelag had more clear weather and less overcast than Finnmark.

3.2 Hypothesis 2: Diet composition of moose varies between the annual seasons

Overall, the moose predominantly spent their time resting, foraging or ruminating (Fig. 2). All individuals had an increase in foraging time in the vegetation period, while the female moose in Finnmark was increasing their time ruminating while laying down in winter.

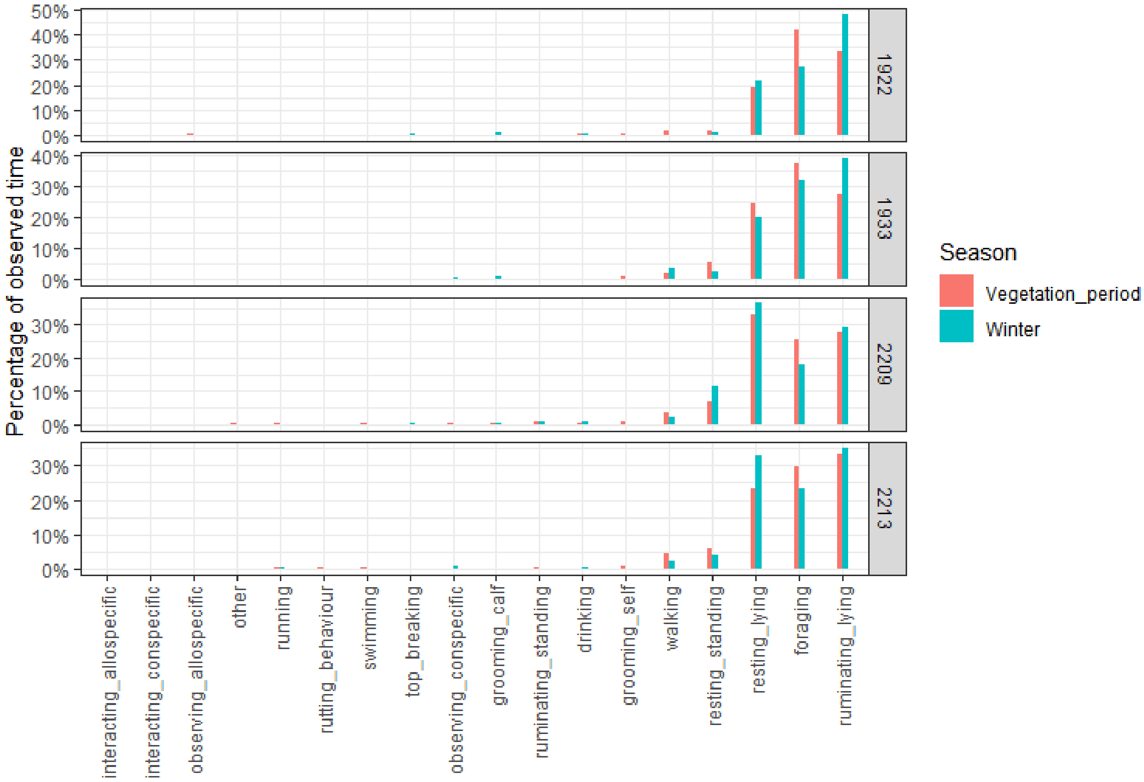

Figure 2: Summary of observed behaviour for the moose in the vegetation period (orange) and winter (blue). Moose ID FM F1922 (FM F= Finnmark moose female), Moose ID FM F1933 (FM F= Finnmark moose female), Moose ID SM F2209 (SM F= Sør-Trøndelag moose female), Moose ID SM M2213 (SM M= Sør-Trøndelag moose male).

All moose from Finnmark and the male moose from Sør-Trøndelag showed an increase in diet diversity in the vegetation period (2a). The Shannon index for moose FM F1922 in Finnmark increased for eaten plants the later the vegetation period got (Fig. 3). The second moose in Finnmark (FM F1933) had a peak (diet diversity) in the vegetation period, with lower variation close to winter. In Sør-Trøndelag, moose SM F2209 had the highest foraging diversity in April and then declined towards August, to start to increase again towards the winter period. The second individual in Sør- Trøndelag (SM M2213) had the peak in the middle of the vegetation period, and then showed decreasing foraging diversity with October marking the lowest point, and afterwards started to increase again in the winter period.

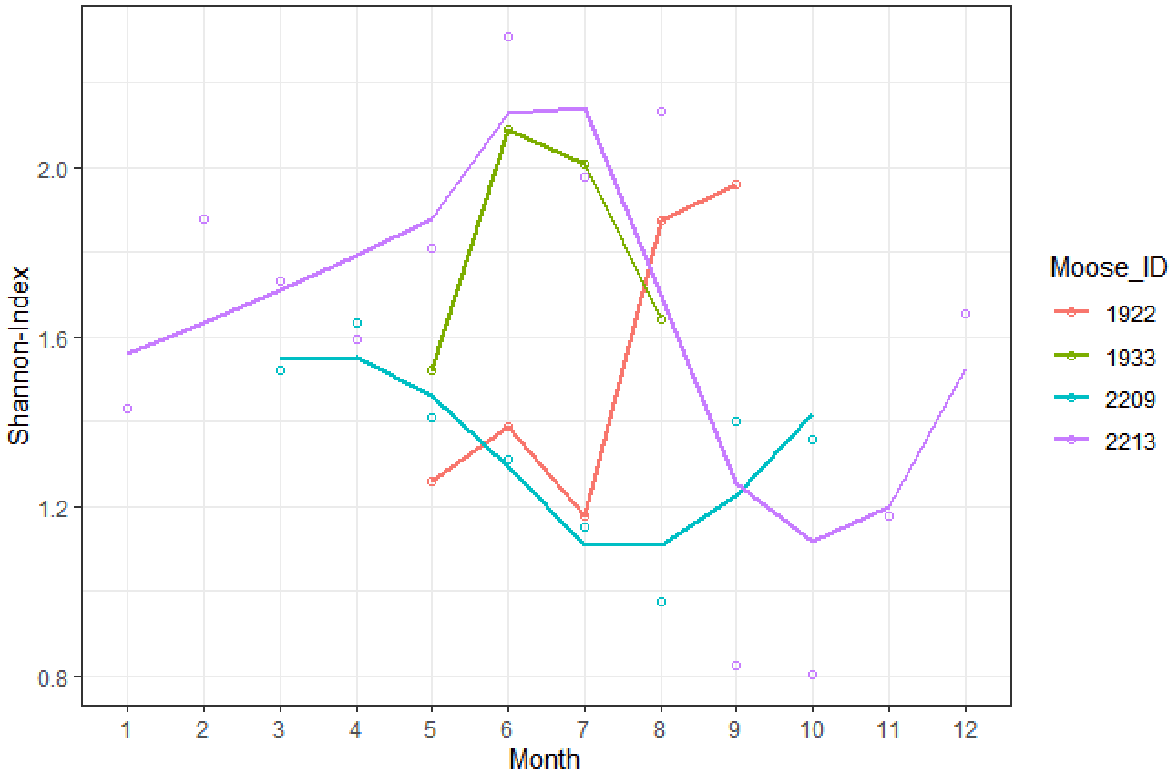

Figure 3: Moose diet diversity (Shannon-index) changes for each month and moose. Moose ID FM F1922 (Finnmark female moose, orange), Moose ID FM F1933 (Finnmark female moose, green), Moose ID SM F2209 (Sør-Trøndelag female moose, blue), Moose ID SM M2213 (Sør-Trøndelag male moose, purple).

Both moose in Sør- Trøndelag ate *P. sylvestris* in the winter period (Fig. S3) (2b). Moose SM M2213 showed an increase in pine foraging during winter months up to 35% of the diet, and in the vegetation period this moose stopped eating pine. Individuals in Finnmark were not observed eating pine at all in the recorded months.

The female moose (SM F2209) browsed on woody vegetation in > 80% of the observations for all available months (Fig. 4) (2c). Browse constituted nearly 100% of the forage for the male (SM M2213) during the winter and declined to a low of still 60% in June. The data for Finnmark was less clear; it showed a steep decline in woody forage from the one available winter month (May) towards the vegetation period. The lowest observed value, however, still constituted 43% in July (FM F1933).

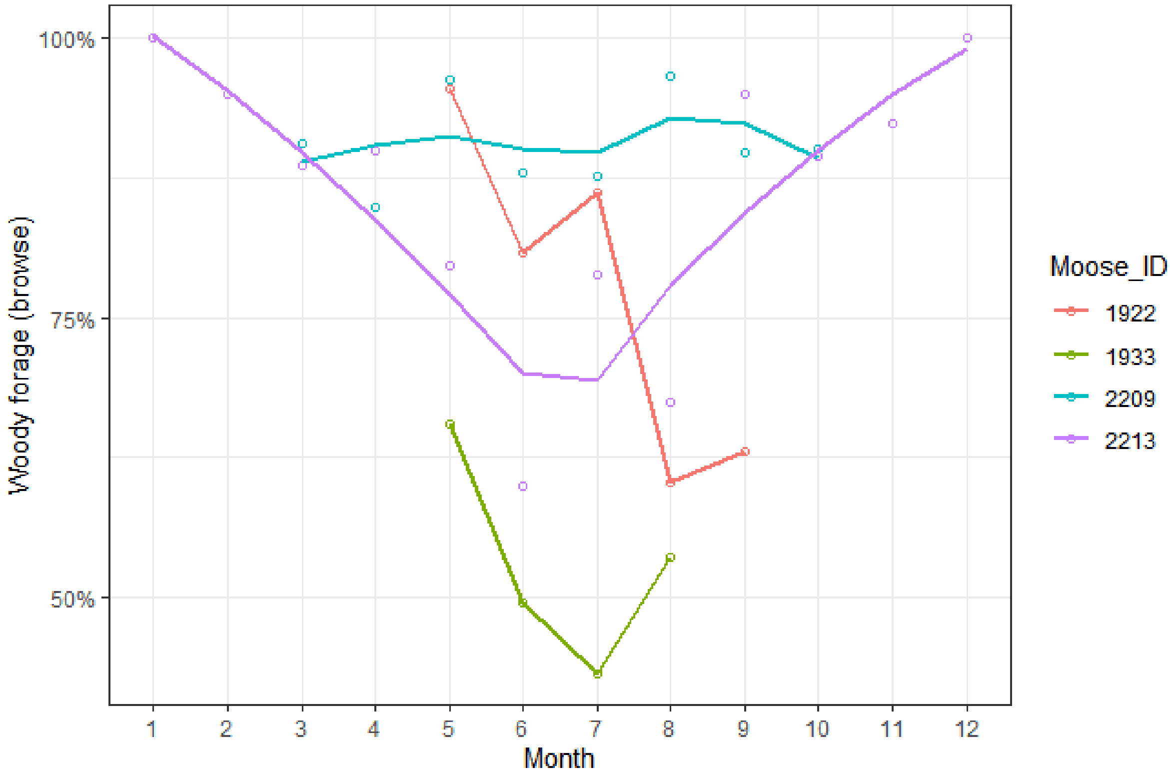

Figure 4: Woody forage changes for captured months for each moose. Moose ID FM F1922 (Finnmark female moose, orange), Moose ID FM F1933 (Finnmark female moose, green), Moose ID SM F2209 (Sør-Trøndelag female moose, blue), Moose ID SM M2213 (Sør-Trøndelag male moose, purple).

When I tested for prediction 2d, I found that deciduous shrubs represented a large share of the observed diet in summer for all moose (Fig. S4). *Salix lapponum* was the most common deciduous shrub observed in the moose diets from Finnmark and female moose from Sør-Trøndelag in the vegetation period.

When prediction 2e was tested, I found that the moose in Finnmark mostly utilized birch-dominated habitat, while the Sør-Trøndelag moose used a higher diversity of habitat types (Fig. 5). In Finnmark, willow and birch habitat dominated (90%) for the filmed period. For Sør-Trøndelag spruce and birch dominated (>50%) for most of the year for both the female and male.

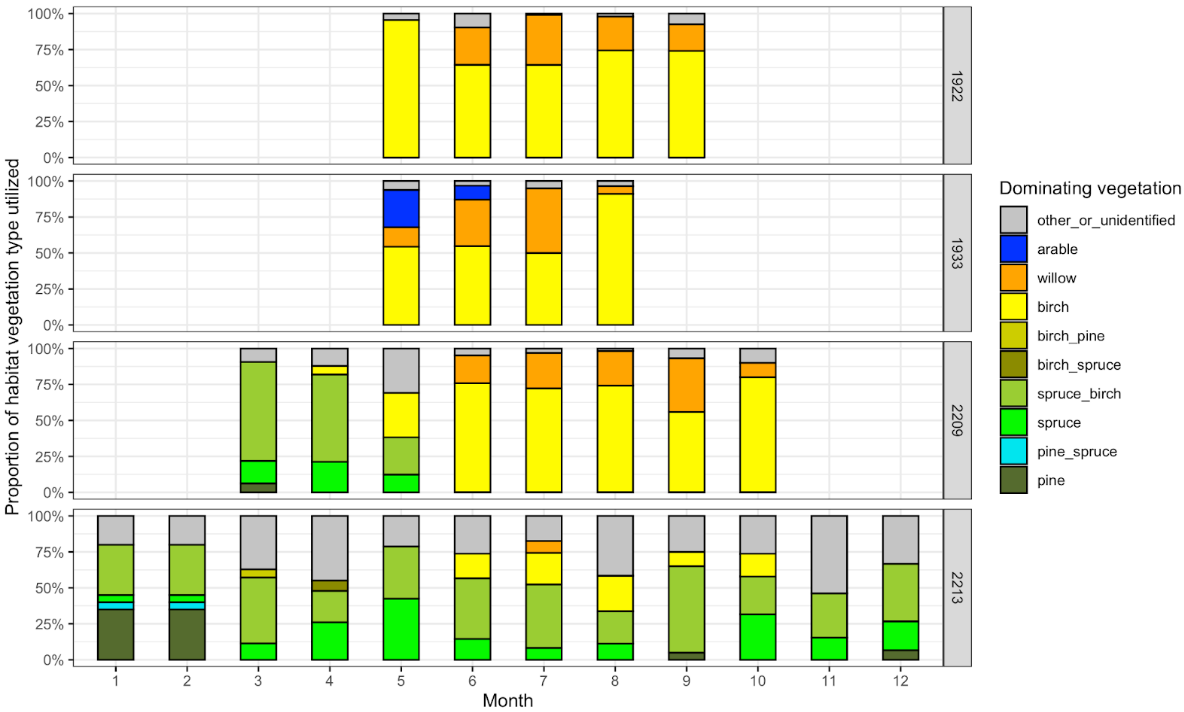

Figure 5: Summary overview of the dominating vegetation types within habitats used by four individual moose (ID 1922 - ID 2213) across the year. Within each month, vegetation types that comprised less than 5% of observations or could not be identified are summarized as 'Other or unidentified' (grey). Moose ID FM F1922 (FM F=Finnmark moose female), Moose ID FM F1933 (FM F= Finnmark moose female), Moose ID SM F2209 (SM F= Sør-Trøndelag moose female), Moose ID SM M2213 (SM M= Sør-Trøndelag moose male).

I found some support for prediction 2e, i.e., *Betula sp.* comprised substantial proportions in the diet of all moose (Fig. 6). Moose in Finnmark in particular, foraged mostly on *Betula sp*. and *S. lapponum* during the vegetation period. In Sør-Trøndelag *Salix sp., Betula sp*. and *Vaccinium sp*. were the dominant foraged food items in the vegetation period, whereas in winter *Juniperus sp., Pinus sp*. and *Betula sp*. were the dominantly foraged items. Although browsing on *Sorbus sp*. was frequently observed, it amounted to less than *Betula sp.* or *Salix sp.*

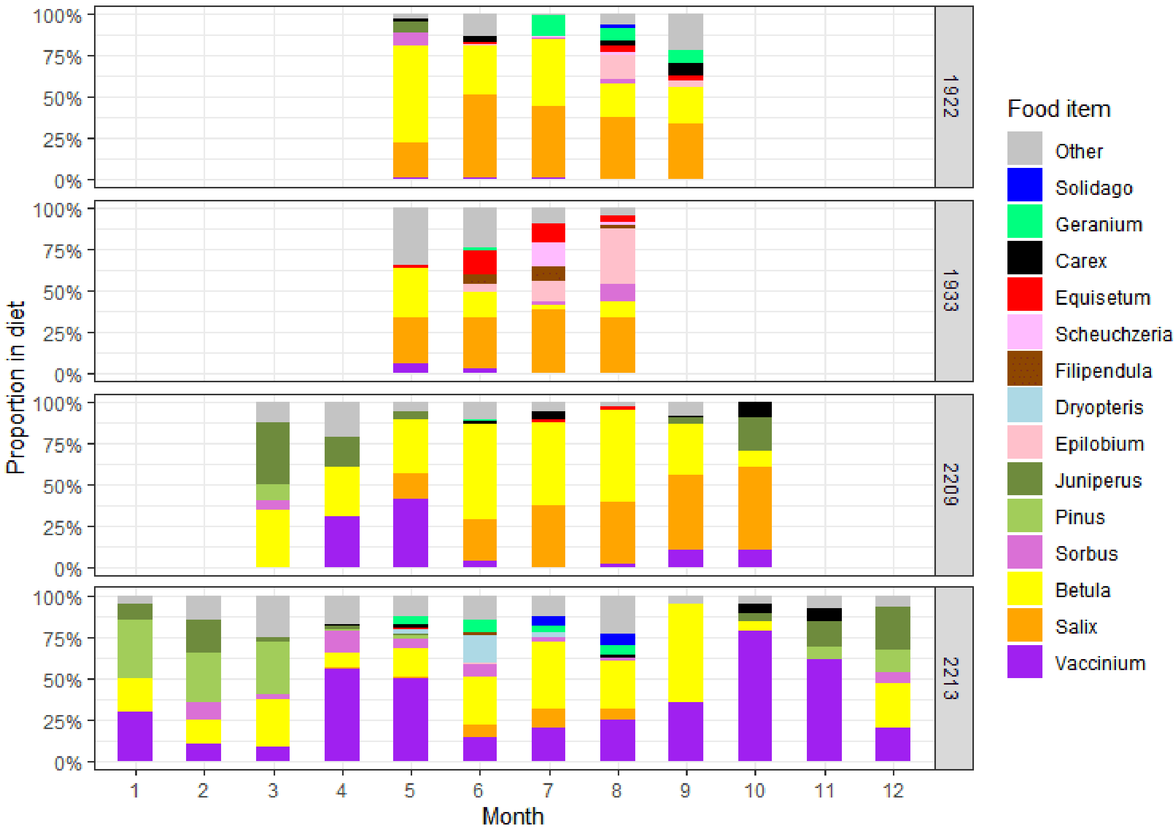

Figure 6: Proportions of foraged food items in the diet of four moose individuals (ID 1922-2213) for each month. Food items that comprised less than 5% of observations or could not be identified are summarized as 'Other' (grey). Moose ID FM F1922 (FM F=Finnmark moose female), Moose ID FM F1933 (FM F= Finnmark moose female), Moose ID SM F2209 (SM F= Sør-Trøndelag moose female), Moose ID SM M2213 (SM M= Sør-Trøndelag moose male).

3.3 Hypothesis 3: Diet composition varies between individuals and study sites

NMDS of diet composition data showed that female moose clustered more separately from the male (Fig. S5). For example, the polygons for moose FM F1922 and SM F2209 are close to one another, which indicates that these individuals had similar diets in the vegetation period. Moose FM F1933 was to the left of the other moose on axis NMDS, which is an indication that moose FM F1933 had a different diet from the other moose in the vegetation period. The polygon for individual SM M2213 did not overlap with any of the other moose, indicating a markedly different diet for this individual.

In the vegetation period, the diet of individual FM F1922 strongly overlapped with individuals FM F1933 and SM F2209 (i.e., Pianka's index was near 1), and in winter the dietary overlap was similar to FM F1933 (Tab. 1). The diet of moose 1933 overlapped strongly with SM F2209 in the vegetation period (Pianka's index = 0.706; Tab. 2), and in winter there was some similarity to SM F2209 and very low similarity to SM M2213. The diet of individual SM M2213 was quite similar to moose SM F2209 during the vegetation period but relatively different from individuals FM F1922 and FM F1933. In winter, moose SM M2213 showed a similar diet to SM F2209 but had low dietary overlap with FM F1922 and FM F1933.

Table 1: Dietary niche overlap (Pianka's Index) between the four different moose individuals during the vegetation period (upper right quadrant, orange color) and winter (lower left quadrant, in italics and blue color). Moose ID FM F1922 (FM F=Finnmark moose female), Moose ID FM F1933 (FM F= Finnmark moose female), Moose ID SM F2209 (SM F= Sør-Trøndelag moose female), Moose ID SM M2213 (SM M= Sør-Trøndelag moose male).

	1922	**1933**	**2209**	**2213**
1922	-	0.847	0.933	0.442
1933	*0.725*	-	0.706	0.260
2209	*0.735*	*0.531*	-	0.670
2213	*0.427*	*0.363*	*0.748*	-

4. Discussion

In my study, I found that collar cameras can help us get a glimpse into the secret life of moose. Some of the issues I found with collar cams were the weather effects on video quality, which revealed a limitation with this methodology. In this study, I found that without interfering with the animals' natural behaviour, we can answer interesting research questions. The habitat-use, foraging and behaviour in an area is important to study to understand how moose may behave in a habitat.

4.1 Hypothesis 1: Weather affects video quality

There was strong support for prediction 1a that snow affected the lens in winter. Prediction 1b had support that water was the main lens disturber, but sun glare was never a problem in the video footage. The biggest problem resulting in unusable data was "too dark" in the vegetation period. In winter there was a problem with "too dark" as well, but the bigger problem was the camera being submerged in or covered by snow (Appendix Fig. S1). To see when it was raining was hard when it wasn't stormy weather. In the alpine area the weather changes quickly, but even if it was hard to see if it was raining there was a difference in the recorded rainy days during the vegetation period (Appendix Fig. S2). Problems with water on or in the camera have been found to not be challenging problem to solve, but could be costly (Egan 2019); with moose it is important to make the camera waterproof so the lens does not get misted.

4.2 Hypothesis 2: Diet composition of moose varies across the annual seasons

Although the total amount of filmed material per day was very low (only 1.5 to 4.5 minutes per day), I was nevertheless able to discern clear differences in diet composition between individuals. This suggests that collar cams could be a suitable method to study foraging and other behaviors despite the current technical limitations in terms of available recording time.

In Sør-Trøndelag, ruminating while lying down was equally recorded during the vegetation period and winter (Fig. 2). The moose in Finnmark was ruminating more in winter, which could be because of the higher percentage of browsing in winter with a combination with the increased foraging and walking in summer (Wam and Hjeljord 2010).

I did find support for my prediction 2b that pine would be mostly browsed in winter and to a much lesser extent during the vegetation period as was shown in studies by Wam and Heljord, 2020 and Bergqvist, Bergström and Wallgren, 2013. However, except for individual SM M2213, pine was largely absent from winter diets, most notably in Finnmark. This was most likely due to availability of pine in the winter habitats. Although I could not measure food availability, observations of the dominant vegetation types suggest that pine was absent in the area. Contrary to Swedish studies where moose are foraging on pine to a great extent in winter (Danell et al. 1991), I found that only one moose in Sør-Trøndelag foraged up to 35% pine in winter. How much pine moose forage in different areas would be interesting to study with a bigger sample size and for different areas.

The female moose (FM F1933) from Finnmark and male from Sør-Trøndelag showed an increase in diet diversity during summer, the low sample size and limited amount of months for the Finnmark moose makes it hard to make generalizations. In Sør-Trøndelag, the female moose had a declining diversity when foraging, this could be because she did not get a new calf and thus did not require the extra energy to produce milk for a calf (Vuillaume, Richard and Côtè 2021). Prediction 2c (that moose are browsers across the year) was strongly supported by the data from the Sør-Trøndelag study site, and the methodology showed that for moose, the known and expected moose behaviour was supported with the small amount of video footage each day.

Both female moose in Finnmark moved to a birch and willow dominated habitat in the vegetation period, which may explain their increased *Salix sp.*, *Betula sp.,* and forb consumption. The increase of browsed *Betula sp.* in the mountain area in the vegetation period where dominated by *B. pubescens* most of the time and is the dominating habitat, but shown to not be favoured by moose (Shipley et al. 1998). In Sør-Trøndelag, both moose stayed in a spruce, birch and pine area with a diet dominated by pine and birch in winter and when they moved into a birch dominated habitat their diets got dominated by *Betula sp.* and *Salix sp.* in the vegetation period. All individuals consumed a similar amount of the present vegetation captured in the video footage. Moose SM M2213 continued to forage on *Vaccinium sp*. during the vegetation period when SM F2209 stopped over the summer. The male moose (SM M2213) stayed in a spruce and birch dominated forest for the summer, and this could be one explanation to the more diverse diet. It could also be because moose SM F2209 did not have a yearling calf and did not need as much energy to increase in weight compared to if she had had a young calf.

4.3 Hypothesis 3: Diet composition varies between individuals and study sites

Prediction 3a had strong support in the vegetation period. Finnmark female moose and individual SM F2209 (female from Sør-Trøndelag) foraged a lot on *Salix sp.* in the vegetation period. Sør-Trøndelag had a longer vegetation period and had more rainfall because it was located in the middle of Norway, which made it possible for the moose to forage on more nutritious plants earlier and for a longer period (Danell et al. 1991). Both the female and male from Sør-Trøndelag foraged on *V. myrtillus* which the Finnmark moose did not. There was weak support for prediction 3b in both the vegetation period and winter because the data were based on one male moose, and it has been shown that there is a foraging specialisation difference between the sexes (Spaeth et al. 2021). Moose in the same location seemed to have some similarities but the females seemed to have more similar diets. The low sample size did make it difficult to fully test my hypotheses. But even under such conditions a pilot study is very important for understanding the new methodology and what problems there could be and what new knowledge could be found. Moreover, the footage was not filmed at the same time of day for all individuals and the two different sites had a different amount of videos per day, which could have affected the results. That the sites were filmed at two different years could also affect the results, so it would be good to study this at the same year with video footage starting at the same time.

4.4 Additional interesting information captures with the videos

Knowledge gained from video cameras, which otherwise would be hard to get, could be easier to capture in wild populations with cameras giving a similar view as the focal individual (Vuillaume, Richard and Côté 2021). Below, I have listed 6 behavioral observations that either have not yet been reported or contradict / confirm commonly held beliefs:

A new behaviour captured with the video footage was coprophagia (consumption of feces) by one individual (ID SM F2209) during May. To the best of my knowledge, coprophagia of conspecific dung has never been observed for cervids. I am only aware of one study that recorded coprophagia of deer at all, that of sika deer (*Cervus nippon*) feeding on feces of macaques (*Macaca fuscata yakui)* (Nishikawa and Mochida 2010). Coprophagia in large herbivores has, however, been observed in foals of racing horses, possibly as an adaptation to build their gut microbiome (Correa et al. 2020).

Although a single observation is anecdotal, this should be evaluated in the context of the short recording times (4.5 min per day, only 0.3% of a 24h period), which would make it likely to miss even moderately rare behaviors. How common coprophagia is among moose is potentially important to know as this could have implications for the spread of diseases like chronic wasting disease (CWD) (Lawelle et al. 2012).

2) Adult moose are known to be solitary individuals (Olsson 2021), but in the spring in Finnmark one female moose with an old calf was moving in a group with another cow with calves during the winter and spring. Large aggregations of male moose have been observed in Sweden (Olsson 2021). It would be interesting to know how common it is for females to be as social as the males are in winter.

3) A big part of the pine browsed in winter came from branches from piles in a recent clear-cut and would not have been reached by the moose otherwise.

4) Moose (ID FM F1933) were also observed eating poisonous plants such as *Ranunculus* sp. and *Caltha palustris*. Studying why moose eat potentially poisonous plants (e.g., do they need something in them, accident or something else) could be an interesting aspect to understanding the feeding in summer. Animals have been found to self-medicate to treat parasites and skin infections (Morrogh-bernard et al. 2017).

5) One moose in Finnmark (FM F1922) was observed swimming in a lake trying to eat water plants. Eating aquatic plants is known from moose in North America but not commonly observed in Scandinavia (Olhson and Stand 2001, Fraser, Chavez and Palohelmo 1984).

6) Scavengers were also captured in the video footage close to one female moose (FM F1922) during calving. One time the cow stood up when a fox walked toward the female and another time the female moose looked at a raven walking in front of her. Brown bears and wolves are known important predators on young calves (Brockman et al. 2017) but were not captured in any of the videos.

5. Conclusion

The diet diversity was increasing during the vegetation period for the female moose in Finnmark and the male moose in Sør-Trøndelag, and up to ⅓ of the male's diet consisted of pine in the winter. In the video footage, it is visible that all individuals were dominantly browsers during the filmed period. The foraged food items were influenced by the habitat type, which the moose were in. It is important to study the new behavior I found like coprophagia to understand how important this could be for the spread of diseases and if there could be more new behaviors to find for moose. Camera collars appear to be a suitable technique to find out how wild animals forage and their behaviour when they are not influenced by people. I found that water droplets, misted lenses and snow were the most common factor that negatively affected the video quality. This could help in the future to know what problems could arise.

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Appendix 1

Supplementary Tables Table S1 - S4

Table S1: information about video length for individual moose

Individual	Months filmed	Number of videos
2209	01/03/2018-17/10/2018	1546
2213	02/03/2018-20/02/2019	2017
1922	01/05//2017-09/09/2017	1057
1933	01/05//2017-22/08/2017	907

Table S2: Video coding protocol information gathered about video name, video limiter and weather, and habitat and species info.

Factors	Factor levels	Remarks
collar_id		Collar number of the moose
file_name		Name of the file handled
Area		Area moose was located (Sør- Trøndelag or Finnmark)
year		The year that the collar filmed
month		The month that the collar filmed
day		The day that the collar filmed
recording_time		The time on the day the collar filmed (24h format)
total_runtime_sec		Total time of the video in seconds

video_quality	good	Nothing 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 so 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 was no time in the video with visible data (covered in snow/ to dirty/ 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
	none	Nothing limiting the video quality
light_condition	day	The sun is up
	night	There is no light
	dawn	Sun is rising
	dusk	Sun is setting
weather	clear	The sun is brightly shining through the video at day, at night moon/stars
	cloudy	Clouds can be seen either in video or the shadows of the clouds, shadow that do not come from threes
	overcast	The full sky is full with cloud, obscuring the sun
	foggy	Condensed water vapor close to the ground and limiting visibility
	raining	Water propps is falling from the sky

	snowing	Snow flakes is falling from the sky
snow_cover	none	No snow visible in the video
	continuous	Snow visible everywhere in the video
	patchy	Snow visible in some areas of the video

Factors	**Factor levels**	**Remarks**
habitat*	Unidentified (0)	The habitat was not visible in the video
	Coniferous (1)	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of the crown cover consists of one coniferous species. Trees are higher than 5 meters
	Mixed coniferous (2)	Tree-covered areas with a total crown cover of >10% where >70% of consists of pine or spruce, but none of these species are >70%. Trees are higher than 5 meters.
	Mixed forest (3)	Tree-covered areas with a total crown cover of >10% where neither coniferous nor deciduous crown cover reaches >70%. Trees are higher than 5 meters.
	Deciduous forest (4)	Tree-covered areas with a total crown cover of >10% where >70% of the crown cover consists of deciduous trees (primarily birch, alder and/or aspen). Trees are higher than 5 meters.
	Temporarily non-forest (5)	Open and re-growing clear-felled, storm-felled or burnt areas. Trees are less than 5 meters.
	Forest on wetland (6)	Tree-covered areas on wetlands with a total crown cover of >10%. Trees are higher than 5 meters.
	Open wetland (7)	Open land where the water for a large part of the year is close by, in or just above the ground surface.
	Arable land (8)	Agricultural land used for plant cultivation or kept in such a condition that it can be used for plant cultivation. The land should be able to be used without any special preparatory action other than the use of conventional farming methods and agricultural machinery. The soil can be used for plant cultivation every year. Exceptions can be made for an

		individual year if special circumstances exist.
	Non-vegetated other open land (9)	Other open land that is not wetland, arable land or exploited vegetation free surfaces and has less than 10% vegetation coverage during the current vegetation period. The ground can be covered by moss and lichen.
	Vegetated other open land (10)	Other open land that is not wetland, arable land or exploited vegetation free surfaces and has more than 10% vegetation coverage during the current vegetation period.
	Artificial surfaces, building (11)	A durable construction consisting of roofs or roofs and walls and which is permanently placed on the ground or partly or wholly below ground or is permanently placed in a certain place in water and is intended to be designed so that people can stay in it.
	Artificial surfaces, not building or road/railway (12)	Artificial open and vegetation-free surfaces that are not building or road/railway.
	Artificial surfaces, road/railway (13)	Road or railway
	Inland water (14)	Lakes or water-courses.
	Marine (15)	Sea, ocean, beach, estuaries or coastal lagoons.
dominating_vegetation		Biggest % of the vegetation
individual	focal	The individual carrying the collar
	calf	The focal individual’s calf(s)
	conspecific	Another moose that is not the focal individuals calf recorded by the focal individual
	allospecific	Another animal species recorded by the focal individual
species		This refers to the species for which behaviors are recorded; in most instances those will be moose, but in case of ‘allospecific’ recordings by the focal individual, it can include any identifiable mammal or bird species.
Calf_observed	yes	If a calf can be found in the video
	no	If a calf can not be found in the video
sex	male	If the individual was identified as male (with antlers or other caraqtericters)

	female	If the individual was identified as female (with no antlers or other caraqtericters)
	unidentified	If it was impossible to determine the sex of the individ
behaviour_type	walking	Slowly moving in a direction, with small movements of camera.
	running	from the camera at speed greater than walking.
	resting_standing	Can not see that the camera is moving, and is far from the ground.
	resting_lying	Can not see that the camera is moving, and it is close to the ground.
	ruminating_standing	Chews previously consumed food further by regurgitating the food, standinding
	ruminating_lying	Chews previously consumed food further by regurgitating the food, lying
	grooming_self	Scratching, mud bath or licking self
	grooming_calf	Touching the calf in any way, including scratching or licking the calf
	swimming	The camera is in or bove water and movements can be seen
	top_breaking	Breaking tops to eat or let other (calf) eat
	rutting	Mating behavior of moose
	drinking	Drinking water or eating snow/ice
	foraging	Eating of plants can be browsing, grazing or supplementary feeding
	observing_conspecific	The focal individual is looking at other moose without going to the moose to interact, only observing from a distance.
	observing_allospecific	The focal individual is looking at other species without going to the species to interact, only observing from a distance.
	interacting_conspecific	Going to other mooses to interact or interacting with other moose.
	interacting_allospecific	Going to other species to interact or interacting with other species.
	other	Is behaviour that don't fit with the other categories

	foraging	Eating plants, lichens

Table S3: Video coding protocol (foraging and plant info)

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 can-not 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 horsetails
	Fungi	Fungi
	Lichen	Lichen

	Silage	Grass or other green plants compacted in an airtight condition; a type of supplementary feed
	Hay	Dried green plants from humans; a type of supplementary feed
	Root_vegetables	Roots from plants (e.g. sugar beets); a type of supplementary feed
	Pellets	Eating in a feeding station with pellets
Plant_part_available_deciduous	twigs	To capture phenology and to asses preference of leaves vs twigs, eating twigs
	leaves	To capture phenology and to asses preference of leaves vs twigs, eating leaves
Plant_part_eaten	Leaves_stripped	When the moose strippes the twig from leaves and do not disturb the woody twig
	Leaves_individually	Eats leaves one by one
	Twigs	Eats twig with no leaves
	Twigs_leaves	Eats twig and leaves
	Twigs_leaves_fruits	if fruits are consumed alongside twigs and leaves, e.g., browsing on fruit-bearing ericaceous shrubs where no clear differentiation can be made between the consumption of berries and leaves/twigs
	Fruits	if predominantly fruits are consumed, e.g. apples off a tree or clear selective feeding of berries on shrubs (e.g., selective “picking” of raspberries…)
	Bark	Eats bark from trees
	whole_plant	Eats the big part of the plant (can leave roots), applies to non-woody forage items

Plant_Genus	**“unidentified”** in case the genus cannot be determined	Which genus the plant belongs to
Plant_Species	***“spp.”*** in case a plant cannot be identified to species level **“unidentified”** in case the genus could not be determined	Which plant species it is or as close as possible
Nearest_plant_not_eaten		What plant species in reach of the moose one or two steps from it that can be determined as close to species as possible, only recorded in instances of observed foraging on another food source
	Nearest_plant_not_eaten_1	
	Nearest_plant_not_eaten_2	
	Nearest_plant_not_eaten_3	
	type_of_other_behaviour	

* The description was used from Naturvårdsverket.2020. National Land Cover Database (NMD) - Product Description.

Table S4: Plant species eaten by moose

Genus	**Species**	**Growth _form**	**Genus**	**Species**	**Growth _form**
Alchemilla	*sp.*	Forb			
Alchemilla	*vulgaris*	Forb	*Hypericum*	*sp.*	Forb
Alnus	*incana*	Deciduous tree	*Juniperus*	*communis*	Coniferous shrub
Alnus	*sp.*	Deciduous tree	*Luzula*	*pilosa*	Graminoid
Anemone	*nemorosa*	Forb			
Anemone	*sp.*	Forb	*Menyanthes*	*trifoliata*	Forb
Athyrium	*distentifolium*	FLH	*Myosotis*	*sp.*	Forb
Betula	*nana*	Deciduous tree	*Paris*	*quadrifolia*	Forb
Betula	*pubescens*	Deciduous tree	*Picea*	*abies*	Coniferous tree
Betula	*sp.*	Deciduous tree	*Pinus*	*sylvestris*	Coniferous tree
Calluna	*vulgaris*	Deciduous shrub	*Plasmatia*	*sp.*	Lichen
			Platismatia	*sp*	Lichen

Caltha	*palustris*	Forb	*Potentilla*	*sp.*	Forb
Carex	*rostrata*	Graminoid			
Carex	*sp.*	Graminoid	*Rubus*	*chamaemorus*	Forb
Cicerbita	*alpina*	Forb	*Rubus*	*idaeus*	Forb
Cornus	*suecica*	Forb	*Rubus*	*saxatilis*	Forb
Deschampsia	*flexuosa*	Graminoid	*Rumex*	*acetosa*	Forb
Deschampsia	*sp.*	Graminoid	*Rumex*	*sp.*	Forb
Deschampsia	*caespitosa*	Graminoid	*Rumex*	*longifolius*	Forb
Dryas	*sp.*	Forb	*Salix*	*lapponum*	Deciduous shrub
Dryopteris	*sp.*	FLH	*Salix*	*sp.*	Deciduous shrub
Empetrum	*nigrum*	Deciduous shrub	*Scheuchzeria*	*palustris*	Graminoid
Epilobium	*angustifolium*	Forb	*Solidago*	*virgaurea*	Forb
Equisetum	*fluviatile*	FLH	*Sorbus*	*aucuparia*	Deciduous tree
Equisetum	*sp.*	FLH	*Stellaria*	*nemorum*	FLH
Eriophorum	*sp.*	Graminoid	*Succisa*	*pratensis*	Forb
Eriophorum	*vaginatum*	Graminoid	*Trientalis*	*europaea*	Forb
Filipendula	*ulmaria*	Forb	*Usnea*	*sp.*	Lichen
Galium	*sp.*	Forb	*Vaccinium*	*myrtillus*	Deciduous shrub
Geranium	*sp.*	Graminoid	*Vaccinium*	*sp.*	Deciduous shrub
Geranium	*sylvaticum*	Graminoid	*Vaccinium*	*uliginosum*	Deciduous shrub
Geum	*rivale*	Forb	*Vaccinium*	*vitis_idaea*	Deciduous shrub
Gymnocarpium	*dryopteris*	FLH	*Valeriana*	*sambucifolia*	Forb
Gymnocarpium	*sp.*	FLH	*Viola*	*sp.*	Forb

Appendix 2

Supplementary Figures Figure S1 - S6

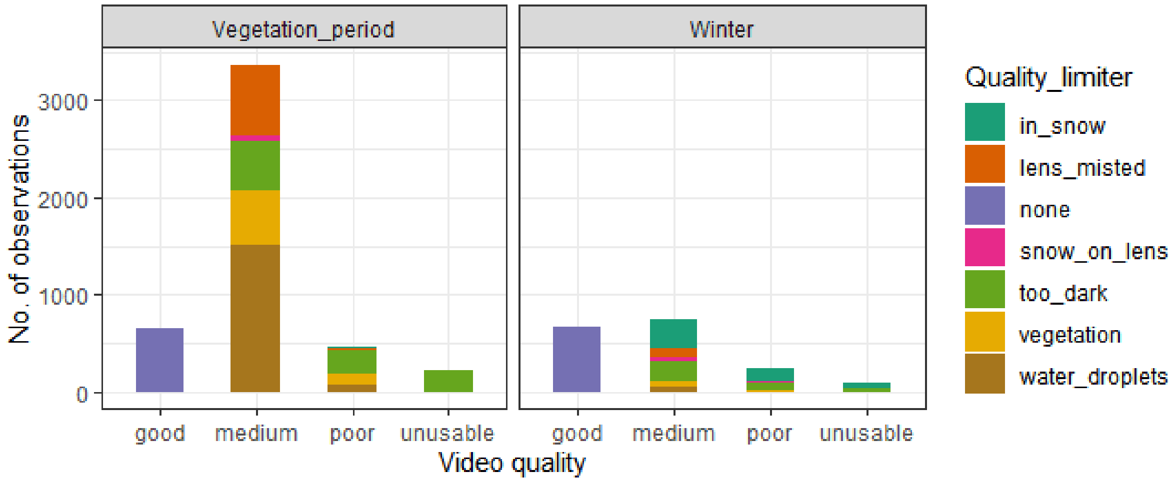
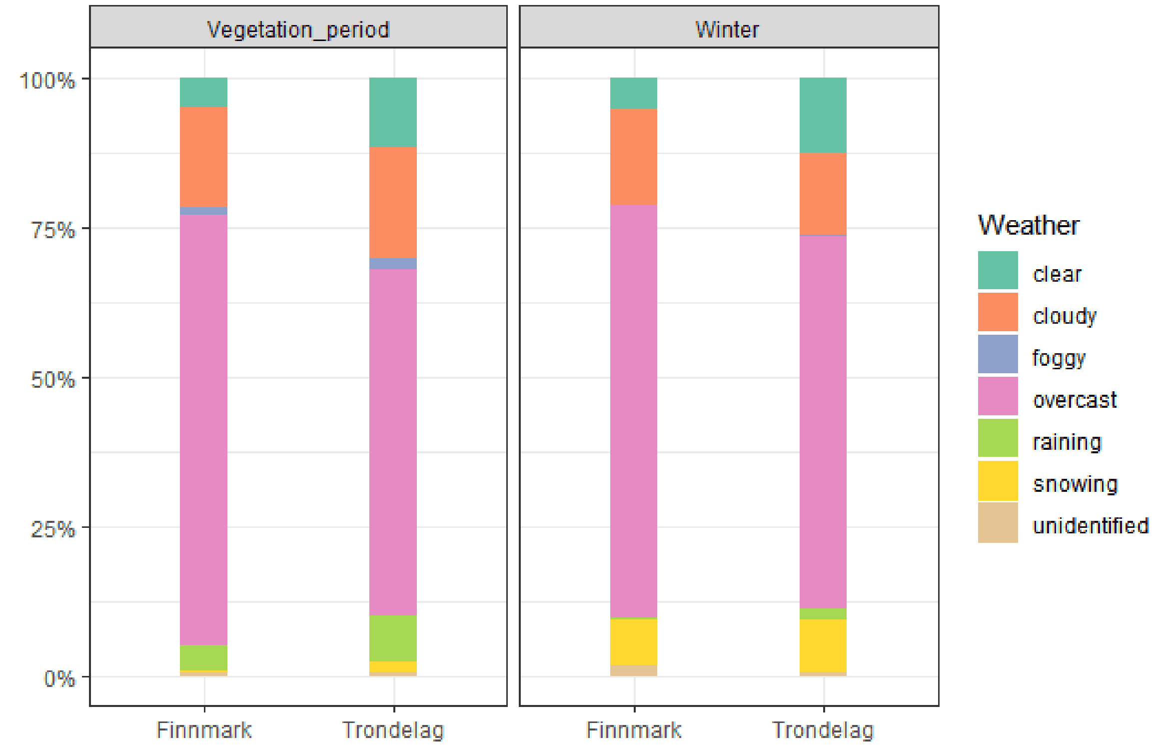


Figure S1: Summary of the video quality with the corresponding factors affecting the quality (‘quality limiters’) for the vegetation season and winter.



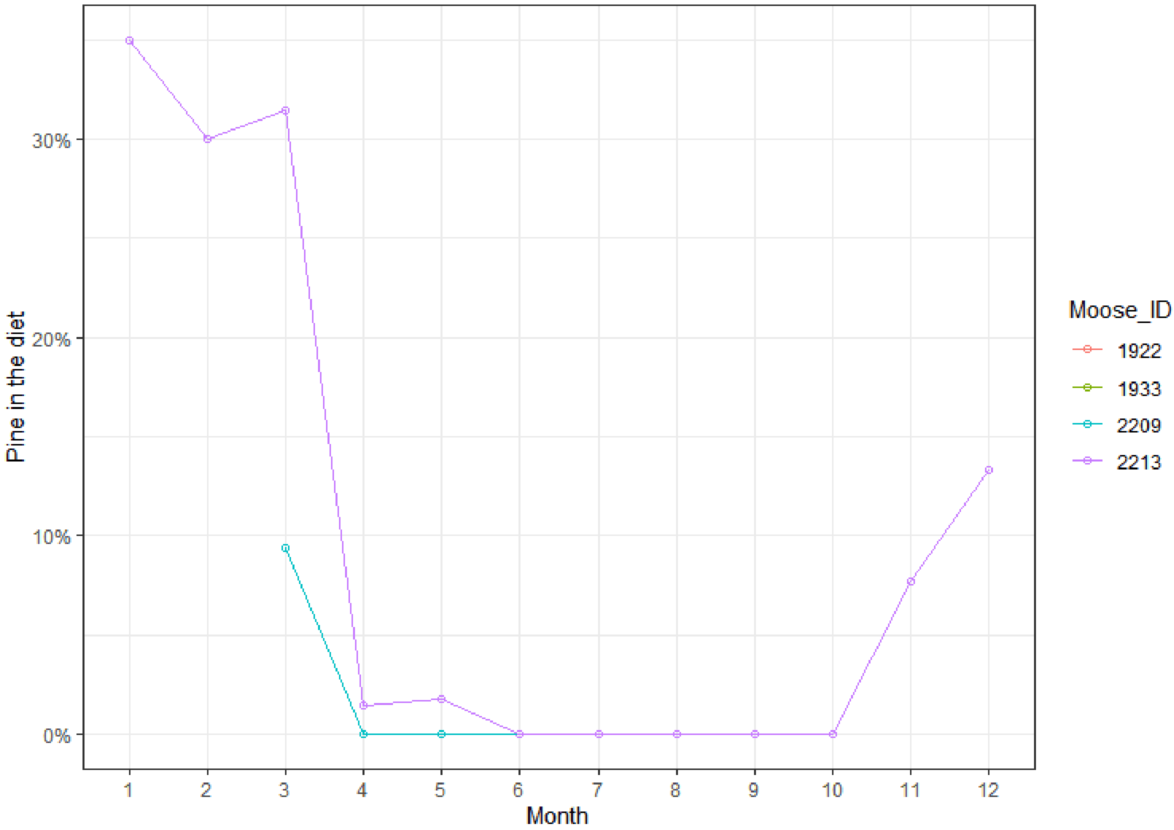


Figure S3: Forage average on pine in moose diet, with changes per month for individuals.

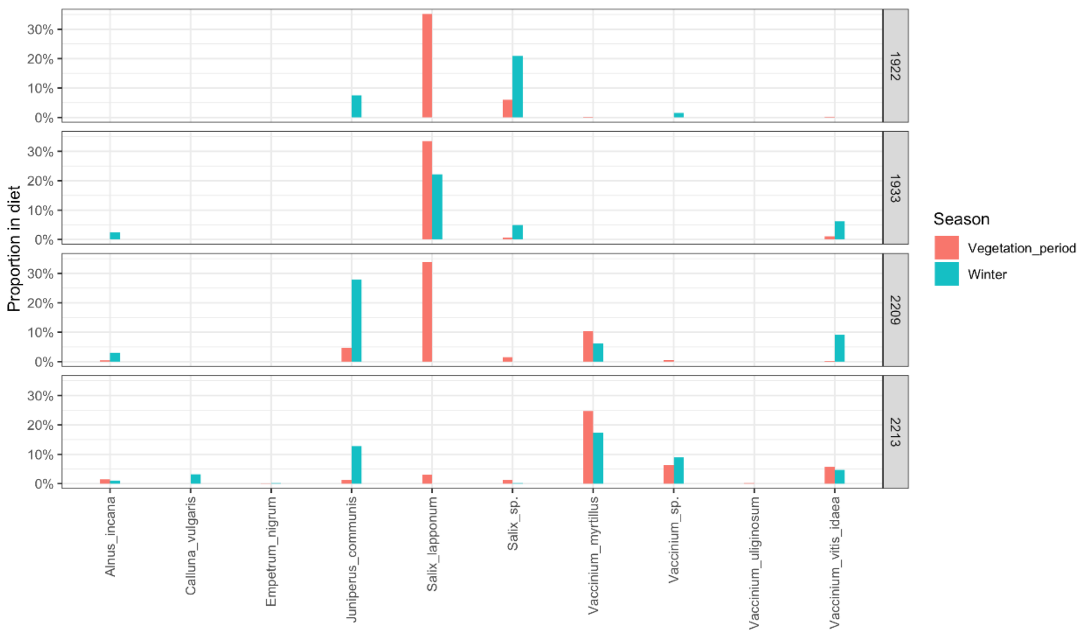


Figure S4: Proportion of shrubs in diet for the vegetation period and winter for each moose.

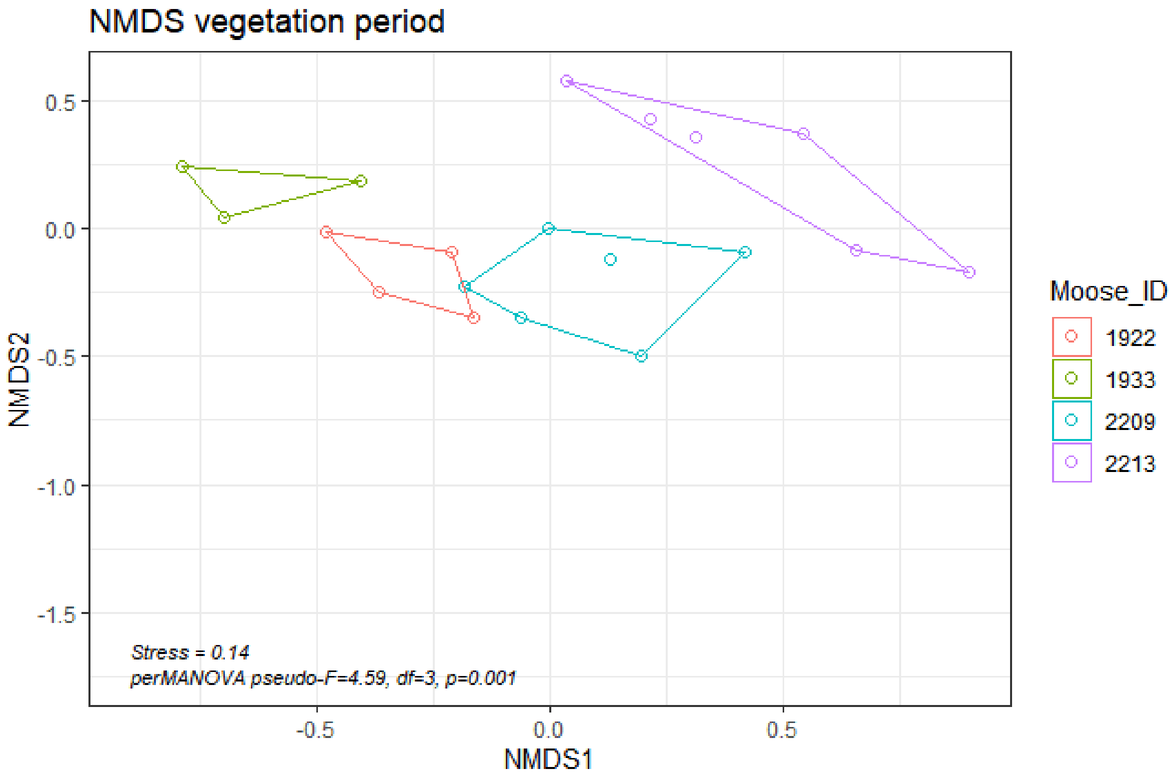


Figure S5: Indication of significant difference between individuals, not overlapping is an indication of significance between individuals.