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Habitat selection in moose and roe deer – A third order comparison

*Habitatval hos älg och rådjur – En jämförelse av tredje
ordningen*

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Habitat selection in moose and roe deer – A third order comparison

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Abstract

Ungulates are important animals in Swedish culture and economy, yet they are considered to cause considerable damage on forests to the disadvantage for the forest industry. At the same time, the forest industry is one of the reasons for the increased carrying capacity of moose and roe deer. Different factors affect the behaviours that cause the animals to inflict damage on the forest, but a main reason is access to browsing. The selection of habitat occurs on different spatial scales and this work looked closer on the selection at the 3rd order, selection of habitat within the home range. The data that was used came from GPS collars from 7 female moose and 17 female roe deer that were tagged within the area of Nordmaling in northern Sweden as well as from camera traps within this area. The GPS data was analysed using Brownian bridge kernel method to receive the utility distribution and home range of the animals. Thereafter the data was connected to the ground cover map allowing a comparison of the usage of different types of habitat using a logistic regression. The GPS data was analysed for the full year, but also sectioned into the periods when the animals were expected to fawn, the rutting period, winter and the full year but excluding fawning, rutting and winter. The results showed for high usage of deciduous trees for the full year in both moose and roe deer, while both groups seemed to avoid water. Moose also selected for clear-cuts throughout the year with an increase during winter. Urban areas showed for a higher usage than were expected for by roe deer. Rutting season increased the usage of arable land in moose while fawning season increased the usage of clear-cut areas by roe deer. The camera trapping data was also connected to the ground cover map and thereafter analysed with a Poisson regression. These results confirmed the high usage of deciduous forest but contained high standard errors, likely as a result of low amounts of data. They also covered less habitat types as an effect of the sampling method. To benefit the forest industry, further studies would be needed on how the animals behave within the different habitats. However, the access to forage seemed to be a driving factor in the habitat selection with the exclusion of the rutting season in moose and the fawning season in roe deer.

Keywords: GPS, camera trapping, habitat selection, order of selection, *Alces alces*, *Capreolus capreolus*, Brownian bridge kernel method

Sammanfattning

Klövdjur är viktiga inom såväl svensk kultur som ekonomiskt, trots det anses de orsaka stor skada på skogen som i sin tur är till nackdel för skogsbruket. Samtidigt är en av orsakerna till de ökade populationerna av älg och rådjur skogsindustrin. Olika faktorer påverkar de beteende hos djuren som anses skada skogen, men en viktig faktor är tillgången till foder. Habitatval sker på olika spatiala skalor och det här arbetet har sett närmare på habitatval av den tredje ordningen, habitatval inom ett djurs hemområde. Data som insamlades kom från GPS-halsband från 7 älgkor och 17 rågetter som var märkta i området av Nordmaling som är beläget i norra Sverige samt från kamerafällor inom samma område. Data från GPSerna analyserades med Brownian bridge kernel method för att få fram hemområden och nyttjandet av områden inom detta hemområde, därefter sammankopplades data med en karta över marktäckets för att få fram en jämförelse av nyttjandet av olika habitat med hjälp av logistisk regression. GPS-data analyserades för hela året, men också uppdelat i perioder för när djuren förväntades kalva, vara i brunst, för vintern och för hela året men med uteslutande av kalvning, brunst och vinter. Resultaten visade på ett högt nyttjande av lövskog över hela året för både älg och rådjur medan båda grupperna verkade undvika vatten. Älgkorna valde också kalhyggen under hela året men med en ökning under vintern. Bebyggda områden visade på ett större nyttjande än vad som förväntades hos rådjur. Brunsten ökade älgkornas nyttjande av jordbruksmark medan kalvningen ökade rådjurens nyttjande av kalhyggen. Data från kamerafällorna sammankopplades också med data över marktäckets och analyserades med en Poisson regression. Resultaten bekräftade det höga nyttjandet av lövskog men innehöll höga medelfel, sannolikt som effekt av den låga mängden data från kamerafällorna. De täckte också färre habitattyper som en effekt av metoden för datainsamling. För att gynna skogsindustrin behövs ytterligare studier som visar hur älg och rådjur betar sig inom olika habitat, men tillgången till foder tycks vara en drivande faktor då det kommer till habitatval med undantag för vid brunsten hos älgkorna och vid kalvningen hos rågetterna.

Nyckelord: GPS, kamerafällor, habitatval, val av ordning, *Alces alces*, *Capreolus capreolus*, Brownian bridge kernel method

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1 Introduction

Ungulates are important nature resources, ecologically, economically and culturally. Yet, today's populations of ungulates in Sweden are reckoned to cause considerable costs for the forest industry (Blenow & Sallnäs 2002; Ezebilo, Sandström & Ericsson 2012), even if different interest groups differ on the extent of the damage (Ezebilo, Sandström & Ericsson 2012). Moose (*Alces alces*) and roe deer (*Capreolus capreolus*) are important game species in Sweden and the acceptance for damage caused by these species is higher among hunters than among forest owners (Ezebilo, Sandström & Ericsson 2012), even so they are considered to be the biggest cause of damage on the forests, mainly because of dense populations (Bergquist 2017).

The carrying capacity for these animals has increased as an effect of modern forestry (Kaie, 2006). Forestry increases the number of shoots available to browse, but at the same times reduce bilberry that is important forage due to removal of older forest (Wam, Hjeljord & Solberg, 2010, Bergquist et al. 2009). This might cause difficulties in the decision-making process for management of moose and roe deer as well as in management decisions for forestry. In forestry, the decisions to plant less suitable tree species for the local habitat is a method used as an effort to avoid browsing damage caused by moose and roe deer (Kalén 2006), which is also considered a reason for the low interest in planting deciduous trees (Rytter, 2014). The degree of browsing damage is dependent on the size of the ungulate population as well as the available amount of forage (Blenow & Sallnäs 2002). Ezebilo, Sandström & Ericsson (2012) saw that the more energy that was spent on improving the moose habitat, the less severe the browsing damages were, and they concluded that a more holistic view in the management design would be beneficial for forestry. A holistic view would allow for creating forage in habitat that is lacking food supply, but otherwise is favorable (Bergqvist et al. 2018), as well as increased knowledge about selection of habitat would benefit for future decision making (Edenius et al. 2002).

Selection of habitat occurs at spatial (van Beest et al. 2010) as well as temporal scale (Street, Rodgers & Fryxell 2015; Neumann et al. 2018). Habitat selection at spatial scale can be divided into four orders according to Johnson (1980) and each scale is depending on the order above to be fulfilled. The first order concerns the geographical range/distribution of the species. The second order describes the

home range of an individual or a group and the third order of selection is the habitat selection within the home range. Finally, the fourth order of selection is the usage of microhabitats within the habitat of a given animal or group. The habitat can be interchangeable if the different habitats fulfill the same purpose for the animal (e.g. food and /or shelter such as woodland and hedgerows could be for roe deer (Morellet et al. 2011)). The selection of habitat is dependent on different factors, e.g., such as disturbance (Street et al. 2015), predation (Street et al. 2015; Decesare et al. 2014), and temperature (Street, Rodgers and Fryxell, 2015), but a main factor is access to forage (van Beest et al. 2010).

Moose and roe deer are both browsers that utilize a range of different habitats. Difference in response to abiotic and biotic factors might differ between and within the species and factors such as sex and age contribute to these differences (Dussault et al. 2005; William et al. 2018). Kjellander et al. (2004) suggest that many of the differences seen in the home range selection in roe deer is an effect of the social and territorial systems that occur within the roe deer population. The selection at different orders (Johnson 1980) can vary. In moose, at the 2nd order, the selection of home range, animals selected quality over abundance, while at the 3rd order, when selecting habitat within the home range, they selected abundance over quality (van Beest et al. 2010).

Increased knowledge in the selection of habitat can be achieved with the help of modern technology and deeper understanding for the selection patterns for e.g., of moose and roe deer.

Various methods have been used to estimate the whereabouts of animals (Månsson, Andrén & Sand 2011) and they all build on the assumption that the collected data is representative for the area that is researched. These methods allow us to collect information about the animals' selection of habitat. Global positioning systems (GPS) allows collection of a high amount of data and can give knowledge of the animals' whereabouts with high precision (Månsson, Andrén & Sand 2011) this has opened for new ways to study them. However, the animals that are collared are often within a limited area, which makes the collected data representative only for a local population or build on the assumption that the subsample is representative for the whole population. GPS collars are also dependent on the functionality of the battery and this can affect the time and the interval that the data can be collected. Yet, the data that is collected with GPS can be used to connect animal behavioral to individual features. Another recently developed method is camera trapping.

During recent years, wildlife cameras have become a more easily available technique allowing higher quality on the data that is collected, which has led to an increase in the use of camera traps (Burton et al. 2015). As for the GPS technique, camera traps open for new methods of collecting information about animals. It is a noninvasive method that is cheap when it comes to collecting data and good to use in challenging settings such as dense forests where it is hard to directly observe an animal. Species data collected from camera traps, however can differ in their detectability (Sollmann et al. 2012). In summary, Hofmeester et al. (2018) identified 40 factors that could be affecting the detectability when using camera traps. For an animal to be detected, it needs to select the habitat where the camera is in the 1st

to 4th order. In addition, the animal needs to be detected by the camera and possible to identify from that photograph (Hofmeester et al. 2018).

With my study, I intend to find out how habitat selection occur within the home range for moose and roe deer in north of Sweden over the year at the 3rd order in relation to different land types (such as arable land, clear-cuts and coniferous forest). The usage of GPS collars allows me to collect data in high detail for a few animals to a high expense, while camera trapping data are less invasive to a lower cost, but do not give the same quality of information on a specific animal. Therefore, I compare these methods to see if it would be reasonable to use the cheaper camera trapping data when studying 3rd order habitat selection.

2 Method

I used GPS collar data from 7 moose and 17 roe deer collected between February 2017 and May 2018 and March 2017 to May 2018, respectively within the Beyond moose project (Neumann et al. 2018), in the area of Nordmaling municipality in northern Sweden (Figure 1). The GPS data were gathered at a high interval the first three months collecting datapoints once every hour, and thereafter at a rate of every third hour for the rest of the period that the animal wore the GPS. I selected datapoints that were taken within 5 minutes from the full hour and from those selected out the datapoints that were taken every third hour, beginning at midnight, 03, 06, 09, 12, 15, 18, 21 for all the time that the animals were GPS tagged to make it easier to compare the data over the full year. This way I only had datapoints that were taken within 5 minutes from midnight, 03 and so on. Spatial points were generated from the spatial data in the original file into a form of x and y coordinates.

For the analysis, I then used the Brownian Bridge kernel method. The burst of the animal movements was calculated with the function `as.ltraj` within the `kernelbb` package. I used the `liker` function to calculate `sig1` as the speed of the animals and set `sig2` to 20 as an estimate of the imprecision of the relocations. (Calenge, 2006)

I thus used the spatial points that were generated previously to create a grid where I could apply the Brownian Bridge kernel method. The Brownian Bridge kernel method accounts for the time that passed between the animal single movement steps, and thereby considers autocorrelation among positions as often present in GPS locations. This allows for an estimate of the likelihood of animal being at a given place and from that estimate it is possible to calculate utilization distribution. The grid size was set to the resolution of 500 cells. From the result of the Brownian

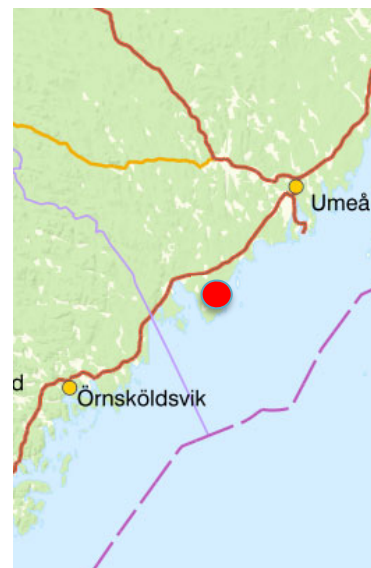


Figure 1. Nordmaling, the area where the camera data were collected and the animals were collared is pointed out with a red mark. Översiktskarta©Lantmäteriet

Bridge kernel method I could estimate 95%, 75% and 50 % home range and utility distribution were extracted.

I then tested if there was a correlation between the probability of use, as estimated from the utility distribution, and different habitat types. I used "Nationella marktäckedatan" (NMD), a map containing spatial information on the habitats in Sweden to extract habitat types. Due to the large number of classes, I reclassified biotopes that were available in NMD into 10 different habitat classes (*Table 1*). The logistic regression allows me to analyse correlation between a continuous (amount of usage) and a categorical (habitat type) variable (Samuels et al. 2016). To enable easy comparison, I used coniferous forest as the intercept in the logistic regression model since I expected both moose and roe deer to spend time in this vegetation type. In addition, I also used a post-hoc Tukey test to test for differences between the habitat classes, e.g. coniferous forest was not used as intercept instead all classes were compared to one another.

Table 1. *The classes from NMD and what they were reclassified to.*

Grid code	Class	Reclassified to
111	Pine forest not on wetland	Coniferous forest
112	Spruce forest not on wetland	Coniferous forest
113	Mixed coniferous forest not on wetland	Coniferous forest
114	Mixed forest not on wetland	Mixed forest
115	Deciduous forest not on wetland	Deciduous forest
116	Deciduous hardwood forest not on wetland	Deciduous forest
117	Deciduous forest with deciduous hardwood forest not on wetland	Deciduous forest
118	Temporarily non-forest not on wetland	Clearcuts
121	Pine forest on wetland	Coniferous forest
122	Spruce forest on wetland	Coniferous forest
123	Mixed coniferous on wetland	Coniferous forest
124	Mixed forest on wetland	Mixed forest
125	Deciduous forest on wetland	Deciduous forest
126	Deciduous hardwood forest on wetland	Deciduous forest
127	Deciduous forest with deciduous hardwood forest on wetland	Deciduous forest
128	Temporarily non-forest on wetland	Clearcuts
2	Open wetland	Natural open areas
3	Arable land	Arable land
41	Non-vegetated other open land	Other
42	Vegetated other open land	Natural open areas
51	Artificial surfaces, building	Urban
52	Artificial surfaces, not building or road/railway	Urban
53	Artificial surfaces, road/railway	Urban
61	Inland water	Water
62	Marine water	Water
0	Outside mapping area	Other

After running the analysis for the full period, I divided the data into different seasons to test if there were any differences in habitat selection as an effect of different natural events. The winter season were set according to weather data from

SMHI (www.smhi.se). For rutting and fawning the periods described by Bjärvall & Ullström (2010) were used for moose (Table 2) and roe deer (Table 3)

Table 2. *The periods that were used for moose and the amount of moose that I was able to use in each period.*

Season	Period	Moose
Full year	2017-02-01 -- 2018-05-31	7
Fawning	2017-05-15 -- 2017-07-14 2018-05-15 -- 2018-05-31	7
Ruting	2017-10-01 -- 2017-10-31	7
Winter	2017-02-01 -- 2017-03-31 2017-12-01 -- 2018-03-31	7

Table 3. *The periods that were used for roe deer and the amount of roe deer that I was able to use in each period.*

Season	Period	Roe deer
Full year	2017-03-01 -- 2018-05-31	17
Fawning	2017-05-01 -- 2017-06-30 2018-05-01 -- 2018-05-31	16
Ruting	2017-07-15 -- 2017-08-14	4
Winter	2017-03-01 -- 2017-03-31 2017-12-01 -- 2018-03-31	17

The camera trapping data that I was able to use for this study were collected at Järnåshalvön, a peninsula in the Baltic Sea in northern Sweden (63° 32' N, 19° 41' E) that is in Nordmaling municipality (Figure 1). The peninsula is a c. 200-km² and was divided into 11, 4 km long, transects that were evenly distributed over the area. For each transect, cameras were deployed at 18 pre-selected locations with 100 m between the locations. This resulted in 198 camera sites but 5 of those were excluded of from varying causes resulting in data from 193 cameras. The cameras were set up at the tree closest to a randomized GPS point within the transect and attached facing north to avoid direct sunlight into the camera lens. The cameras were also set at a level 60 cm above and parallel to the ground/snow cover. When triggered the cameras took a series of 10 pictures. The cameras were then moved within the transect after 6-10 weeks to next randomized point. This study resulted in a sampling effort of 10,491 camera-trap days that were distributed over 382 days. From this the data in the pictures were aggregated to passages, if the pictures were taken within 5 minutes from each other they were considered the same animal or group of animals. From these passages the amount of moose and roe deer were counted as well how many days the camera been active. This data could then be used as the base of a Poisson regression that modelled the numbers of animals as a function of the vegetation class and only used full numbers. In the

Poisson regression I used the offset function so that the analyse took into consideration that the cameras where used different amount of days.

All data was analysed in R version 3.5.3 mainly using package" adehabitatHR", "sp", "maptools", "rgdal", "raster" as well as "multcomp".

3 Result

3.1 Moose

3.1.1 Camera data

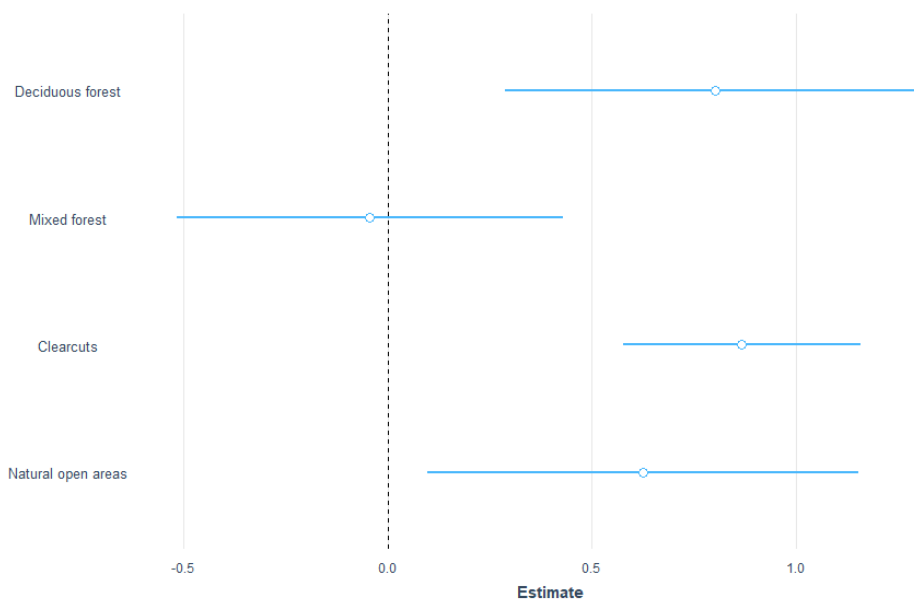


Figure 2 Estimates for moose over the full year with data from the camera traps where the different classes is compared to coniferous forest (0.0). The blue lines represent the standard error.

I used data from 193 camera locations with 263 moose observations to test for a correlation between moose passage rates and different habitat types. Moose passage rates on the cameras were higher in deciduous forest (est 0.8, z-value 3.1, p-value 0.002) and clearcuts (est 0.9, z-value 5.8, p-value 0.0001). Natural open areas also had a higher passage rate (est.0.6, z-value 2.3, p-value 0.02) and were more likely to be used by moose compared to coniferous forest (Figure 2). The post-hoc test for camera data showed a higher passage rate in clearcuts compared

to coniferous forest (est 0.9, z-value 5.8, p-value <0,001) and in clearcuts compared to mixed forest (est 0.9, z-value 3.9, p-value 0.001). Deciduous forests had higher passage rates (est 0.8) compared to clearcuts (z-value 3.1 p-value 0.02). Passage rates were higher in deciduous compared to mixed forest, but with a lot of variation (est -0.84, z-value -2.6, p-value 0.07975).

3.1.2 GPS data

Overall, I had selected 22964 observations that fulfilled the requirements stated in the method, divided over 7 individuals of moose, resulting in an average of 3280.6 positions \pm 785.5 per individual, in the analysis of moose habitat selection. Annually, moose preferred deciduous forest, clearcuts and mixed forests above coniferous forest. The deciduous forest was 1.7 times more likely to be used (z-value 15.7, $p < 0.0001$), clearcuts 1.68 (z-value 21.2, $p < 0.0001$) and mixed forest 1,37(z-value 9, $p < 0.0001$). The natural open areas were just slightly more used (1.1 times more used than coniferous forest) and had a lower significance (z-value =2.3, p-value 0.02). Arable land, urban areas and water where all less used by moose in comparison with the coniferous forest (Figure 3).

In the post-hoc test, I found that deciduous forest was the most used vegetation by moose, but the result was not significant when deciduous forest was compared to clearcuts (z-value 0.9, p-value 0.9). Over the full year the moose also selected clearcuts above mixed forest and mixed forest above arable land. Moose clearly avoided water

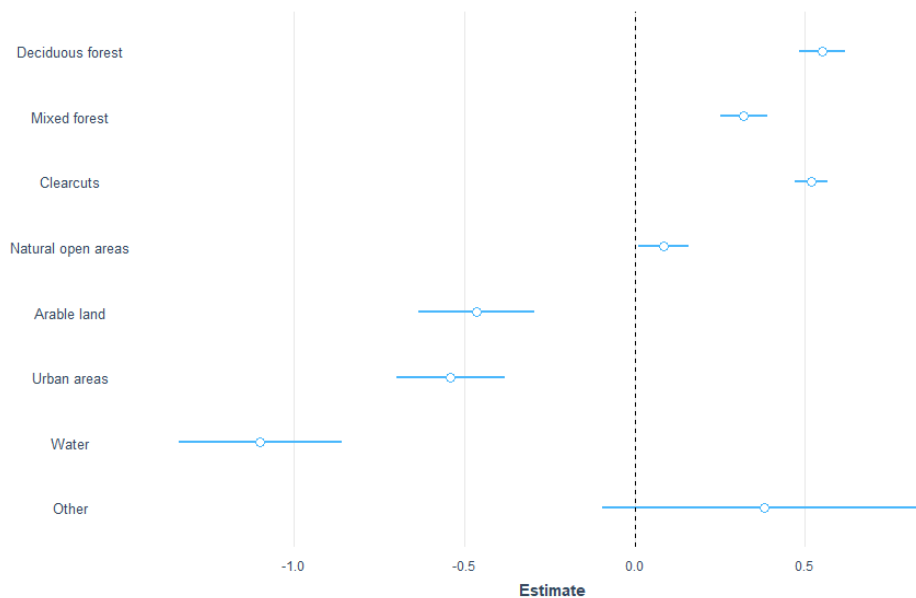


Figure 3 Estimates for moose over the full year where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

During winter (7697 GPS observations), moose showed a strong selection for clearcuts (z-value 21, p-value <0.0001) and was 2.3 times more likely to be found on those than in the coniferous forest. Mixed forest was selected 1.7 times more often than coniferous forest, deciduous forest 1.6 natural open areas 1.2. (Figure 4) Both water and the category other were less used than coniferous forest, especially water was negatively selected and the difference between these categories is confirmed in the post hoc test (z-value 12, p-value <0.001) where other is selected 3.7 times more often than water.

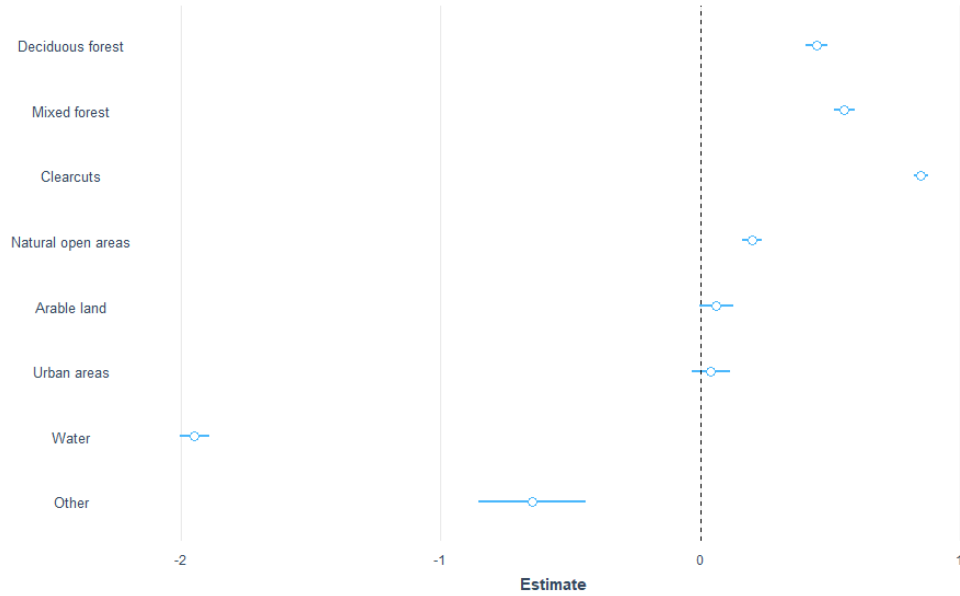


Figure 4. Estimates for moose during winter with data from the GPS where the different classes is compared to coniferous forest (0.0). The blue lines represent the standard error.

During rutting season, I analysed 1470 observations on moose. My results did not suggest any differences in utilization between neither deciduous or mixed forest compared to the coniferous forest. The class that I found were most used where arable land that moose selected 2.1 times more often than coniferous forest (z-value 21.9, p-value <0.0001). Clearcuts, natural open areas and urban areas are slightly less used during this period. Class other had a very low usage and a high uncertainty. (Figure 5)

The post hoc test confirm that arable land is selected in front of other vegetation types during the rut.

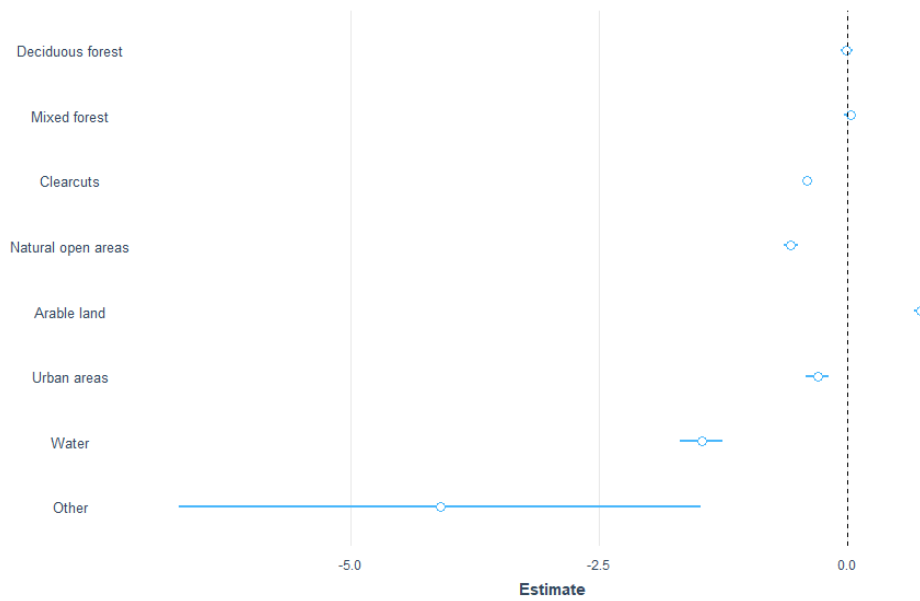


Figure 5. Estimates for moose during rut with data from the GPS where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

During the time when moose were expected to give birth, I analysed 4041 observations. Deciduous forests and clearcuts are strongly selected for above coniferous as well as slight preference for mixed forests while the arable land, natural open areas, urban areas, water and other areas is significantly less selected for than clearcuts in the logistic regression analysis. (Figure 6)

The post hoc test confirmed that clearcuts is significantly selected for compared to all types of vegetation except for deciduous forest that was equally selected for (estimate 0.01, z-value 0.7, p-value 0.99). Class other were 1.7 times more used than water (z-value 13.9, p-value <0.0001) but less than urban areas (0.3 times the usage of urban areas, z-value -31.2, p-value <0.0001).

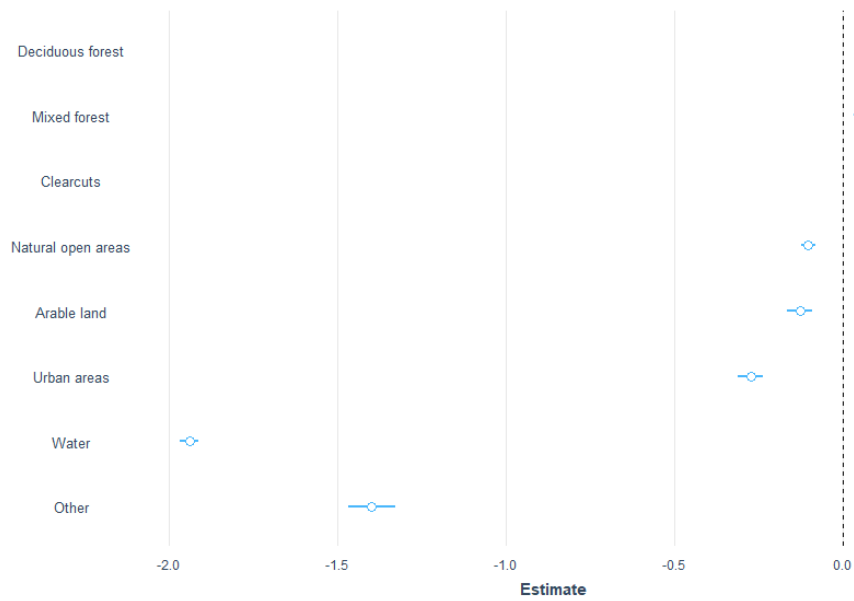


Figure 6. Estimates for moose during fawning with data from the GPS where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

I also looked at periods over the year when the moose wasn't expected to be directly impacted by calving, the rut or winter conditions. Excluding observations from those periods, I had 9756 observations left for analysing. I found that between the calving, rutting, and winter season, moose showed higher usage of deciduous forest, mixed forest and clearcuts than for coniferous forest while all other classes were less used. (Figure 7)

The post hoc test shows that clearcuts was selected for prior to other classes but the result where not significant between clearcuts and deciduous forest (p-value 0.88984). Deciduous forest where preferred to coniferous forest, mixed forests as well as other classes except clearcuts, and thereafter mixed forest was selected for, all with a p-value of <0.001. Water was negatively selected for.

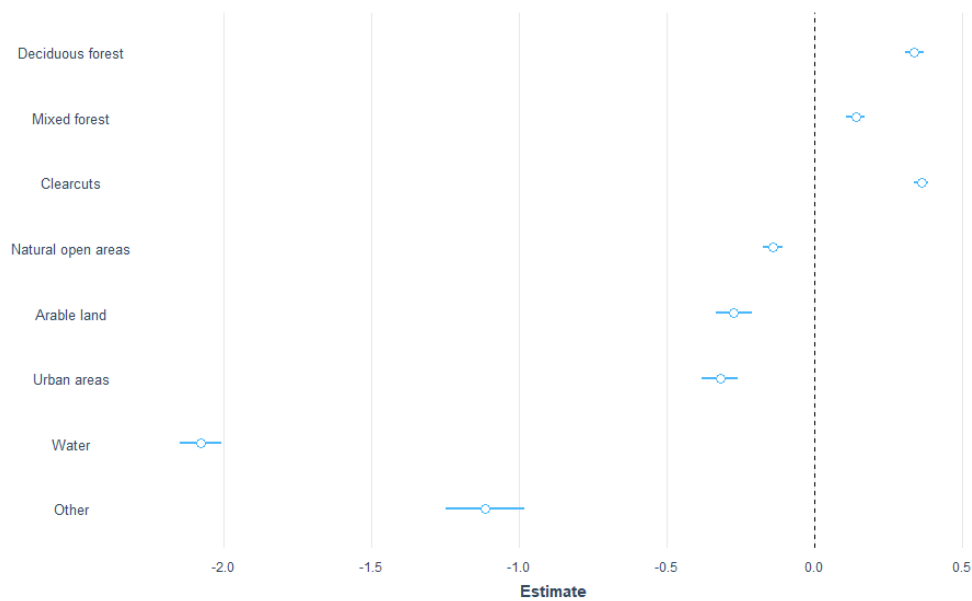


Figure 7. Estimates for moose over the full year but with fawning, rut and winter season excluded, data from the GPS where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

3.2 Roe deer

3.2.1 Camera data

The camera trapping data for the roe deer were based on data from 193 camera locations with 658 observations of the GPS tagged roe deer. Here I saw that deciduous forests were selected with an estimate of 0.6 more often than coniferous forests (z-value 4.2, p-value < 0.0001). Clearcuts were used more often than coniferous forests but were not significantly different (est 0.2, z-value 1.7, p-value 0.09). Since no cameras were placed in arable land or urban areas, values for those can't be presented in this result. (Figure 8)

The post hoc test confirmed the Poisson regression.

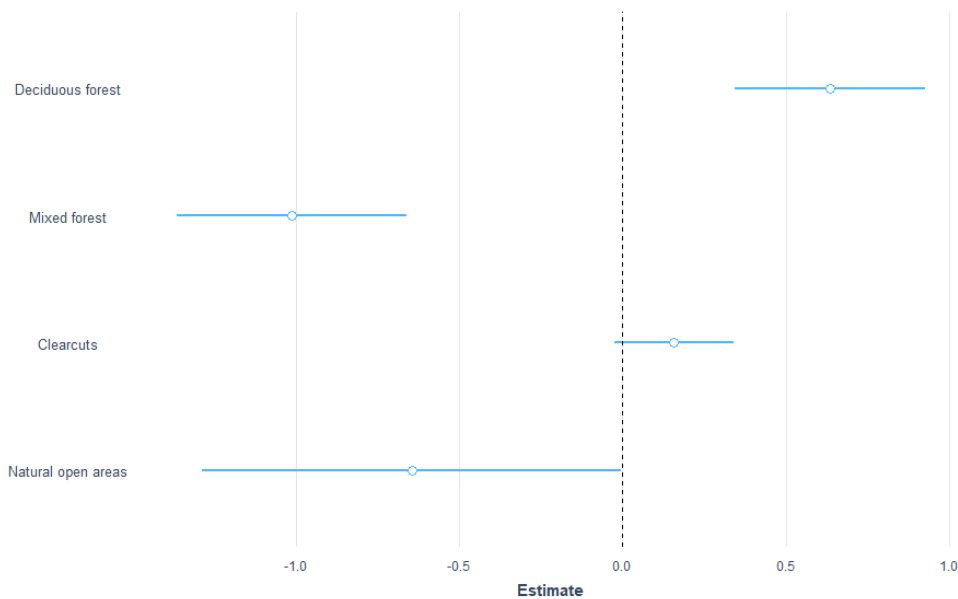


Figure 8. Estimates for roe deer over the full year with data from the camera traps where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

3.2.2 GPS data

For roe deer, I analysed 23339 observations with an average of 1372.9 ± 767.3 (n=17 individuals) and found that roe deer annually showed a strong preference for deciduous forest (1.7 times more often than coniferous forest z-value 27.2, p-value <0.0001). Animals also had a strong selection for the class other that was equally selected to deciduous forest (1.7 times more often than coniferous forest z-value 2.2, p-value 0.03) Mixed forests, natural open areas where all used more than coniferous forest while usage of clearcuts arable land and water were lower. (Figure 9)

The post hoc test showed that urban areas were selected above clearcuts, coniferous forests, water, arable land (p-values <0.001) while deciduous forests were selected before urban areas (p-value <0.001). The post hoc also confirmed that the selection for class other were not significantly different from deciduous forest (z-value 0.022, p-value 1).

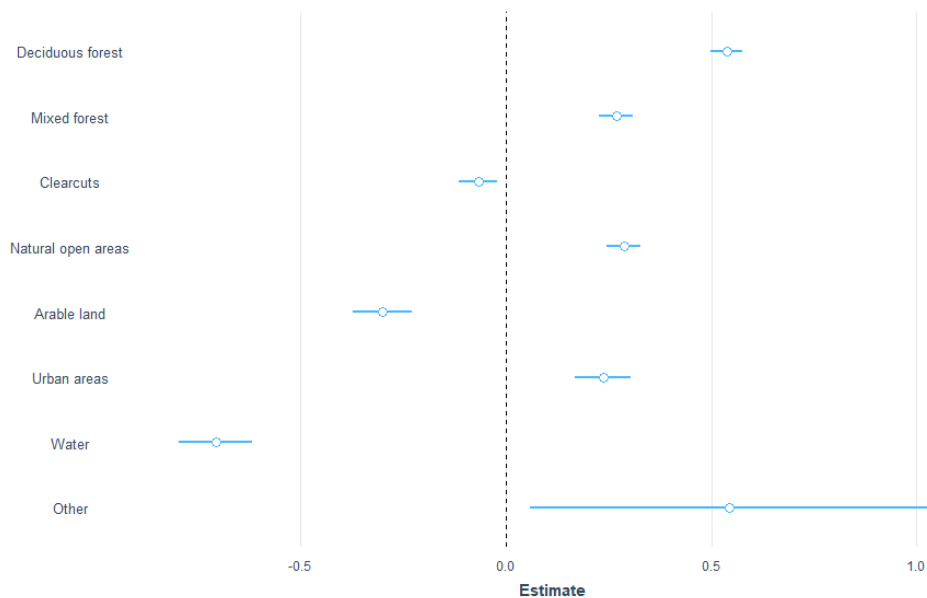


Figure 9. Estimates for roe deer GPS data over the full year where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

During the winter (10070 observations), roe deer used arable land most (2.1 times more often than coniferous forests, z-value 33.4, p-value < 0.0001) and thereafter mixed forests and deciduous forests. The only classes that were less used than coniferous forests were water and other. Closest to coniferous forests in usage were natural open areas (1.03 times more used, z value 2.3, p-value 0.0236) and clearcuts (1.1 times more used, z-value 7.8, p-value < 0.0001). (Figure 10)
 The post hoc test shows for a high usage of arable land confirming the logistic regression.

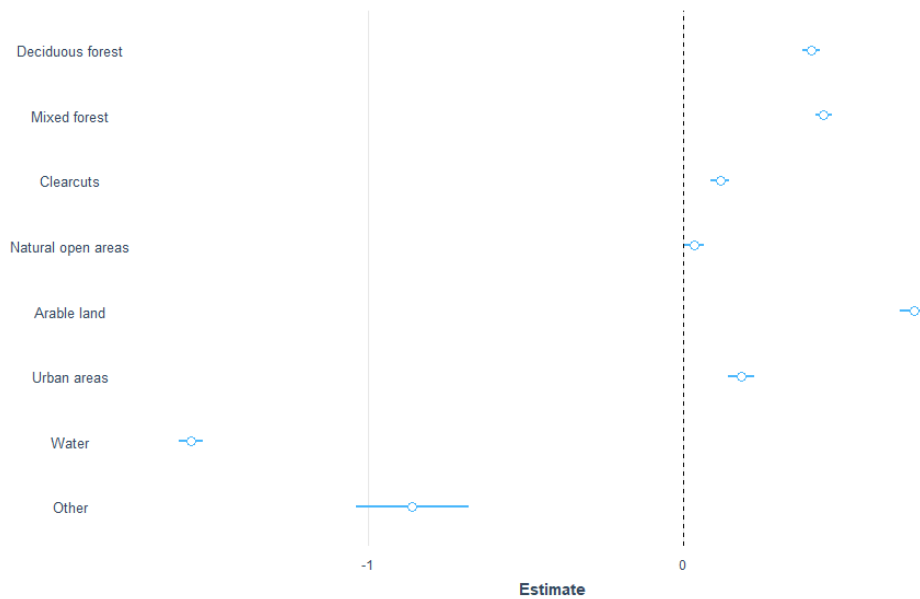


Figure 10. Estimates for roe deer during winter with data from the GPS where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

During rutting period (953 observations from 4 individuals), roe deer preferred deciduous forest (2.7 times more used than coniferous forest, z-value 30.1, p-value <0.0001), clearcuts (1.6 times more used than coniferous forest, z-value 18.5, p-value <0.0001), and natural open areas (1.3 times more used than coniferous forest, z-value 10.3, p-value <0.0001), that are all selected above coniferous forest while mixed forest and urban areas is slightly less selected than coniferous forest. Other, arable land and water are all significantly less used (p-value <0.0001). The post hoc test showed no significant difference between coniferous forest and mixed forests or urban areas in this period and suggests that there is no significant difference between mixed forests and urban areas.

During fawning period (includes 5315 observations), roe deer had a high usage of clearcuts, deciduous forests, arable land and natural open areas selected 1.8, 1.8, 1.6 and 1.4 times more often than coniferous forests in the logistic regression. Urban areas are almost equally selected for (1.1 times more often than coniferous forest, z-value 2.9, p-value 0.004) while mixed forests, other and water were less selected for. The post hoc test gives results that confirm the logistic regression in exception of a non-significant result when comparing urban areas and coniferous forest (z-value 2.9, p-value 0.07). (Figure 11)

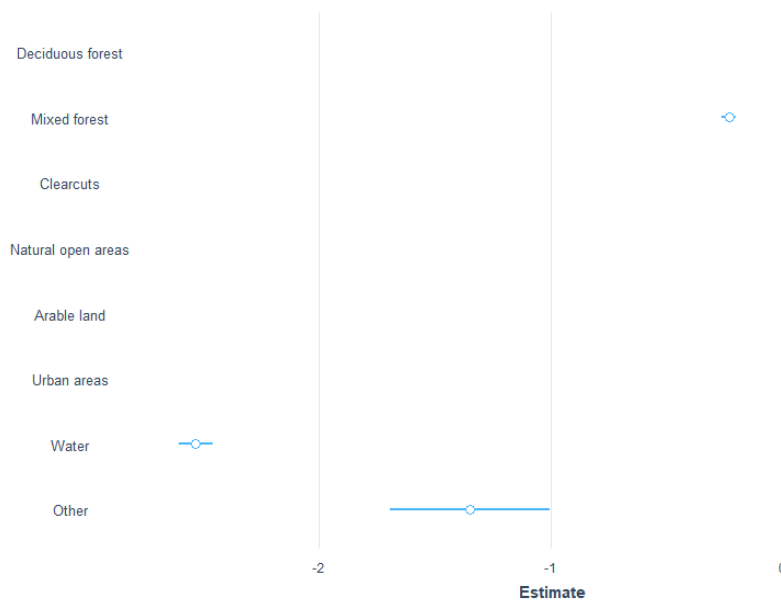


Figure 11. Estimates for roe deer during fawning with data from the GPS where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

When excluding fawning, rutting season and winter there were 7455 observations left. Here I found that roe deer had a higher usage of arable land (2.8 times more often than coniferous forest, z-value 51.2, p-value <0.0001), deciduous forest, (2.5 times more often than coniferous forest, z-value 67.9, p-value <0.0001) urban areas (1.6 times more often than coniferous forest, z-value 22.5, p-value <0.0001) and other (1.6 times more often than coniferous forest, z-value 5.9, p-value 0.0001) in comparison to coniferous forest. Mixed forest clearcuts and water were all less used than coniferous forest while natural open areas showed no significant difference. The post hoc test confirms the result in the logistic regression. (Figure 12)

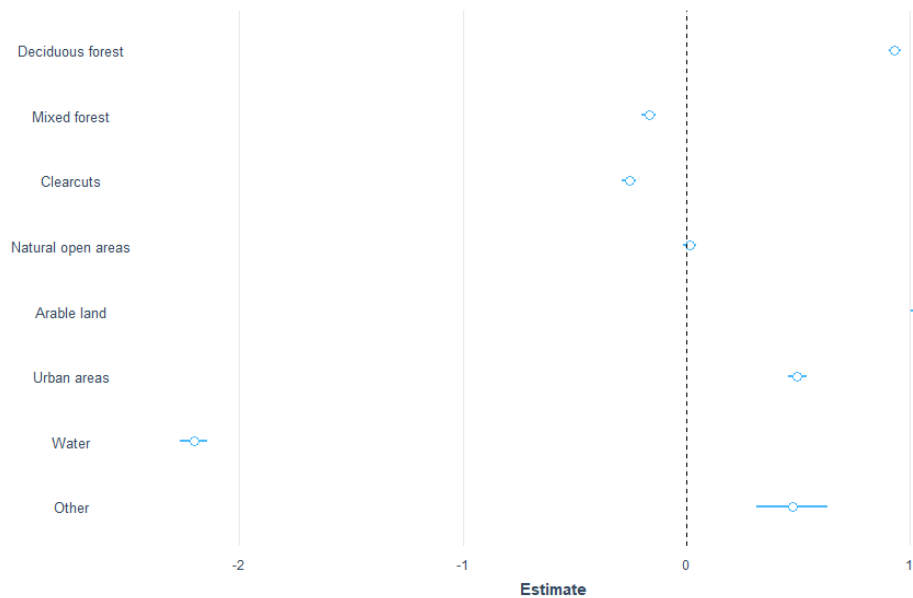


Figure 12. Estimates for roe deer over the full year but with fawning, rut and winter season excluded, data from the GPS where the different classes are compared to coniferous forest (0.0). The blue lines represent the standard error.

4 Discussion

As was expected, habitat selection varied over the year for both moose and roe deer and the causes for these variations are likely to be the effect of many interacting factors such as access to forage (Wam, Hjeljord & Solberg, 2010, van Beest et al. 2010, Samelius et al. 2013), temperatures (van Beest, Van Morter & Milner, 2012, Street, Rodgers & Fryxell, 2015, Månsson, Andrén & Sand, 2011), and human activities (Bonnot et al. 2013, Street et al., 2015,). The camera trapping data coincided with the data from the GPS collars when it came to what seemed like the strongest preferences among the animals, while looking at habitats that were less selected for there were more difference between the results.

4.1 Moose

Over the full study period moose, as could be expected as an effect of greater access to forage, at the 3rd order of selection preferred deciduous forest, clearcuts and mixed forest over coniferous forest. Over the full year mixed forest seems to be less used than both deciduous forests and clearcuts. The fact that natural open areas were used in a similar amount to the coniferous forest I see as likely to be an effect of the same amount of available food therein or the same usage of the habitat as a transit area. During the winter I saw an increase in the usage of areas that been clear-cut recently which coincides with previous knowledge about moose browsing preference (van Beest et al. 2010, Bergqvist et al. 2018). Moose preferably browse on rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and sallow (*Salix caprea*) in the north of Sweden during the summer months (Wam, Hjeljord & Solberg, 2010), but since those are not available during winter pine (*Pinus sylvestris*) becomes an important food source and those are easily accessible in young forests and recently clear-cut areas.

During the rut there was a clear change in the behavioural patterns of the moose in this study, and they clearly selected for arable land. This suits my second hypothesis that certain events such as the rut will override the search of forage, still, another reason for this could be that certain crops are still standing on the field offering high energy forage. Another reason could be that hunting season begins ap-

proximately a month before the rut (www.jagareforbundet.se) and this possibly altered the moose movement patterns, but this were shown in a study by Neumann, Ericsson and Dettki (2009) to not be the case for the moose population. However, they saw that individuals could be affected by hunting and since the study construct on so few individuals (7) it might be so that the presence of one or a few individuals in this dataset that show a response has a big impact on the result.

As for my third hypothesis moose never seemed to select for urban areas but the result didn't suggest that those areas were avoided either. On contrary I would say that avoidance was true for water. Still, both water and urban areas are comparatively rare within the study area and therefore these results would need to be tested over a bigger area with bigger amounts of animals to say something for certain.

Looking at the moose GPS data, in comparison with the camera trap data, that had a lot fewer observations, the higher usage of mixed forests was missing out and the result were not significantly different from coniferous forest. I could still see a strong preference for deciduous forest and clearcuts among moose. Contradicting the result from the GPS data, natural open areas were more used in the camera trap data, one cause for this difference could be the few observations in the camera trap data, another could be that the camera trap photograph an animal even if it is just passing and gives this information the same value as a longer stay while the GPS data is less likely to send out a signal in areas where the animal is only passing. Still I would argue that the likeliest cause would be the difference in detectability by the camera trap in different settings since it would be reasonable to assume that an animal is easier to detect by the camera's sensor in an open area than in a forest, this is described to be a relevant factor by Hofmeester et al. (2018). Comparing the result from the camera trap data with the result from the GPS data over the full year the strongest selected habitats, deciduous forest and clearcuts, were approximately equally selected for in both methods for moose.

4.2 Roe deer

Roe deer showed a greater variation in habitat selection over different seasons. Over the full year, I could see a preference for deciduous forest but also a high usage of the class other, although there was a high standard error for that class. The high usage of deciduous forest was confirmed by the Poisson regression of the camera trapping data. In winter there was a high usage of arable land, that habitat had also a high usage during fawning, but deciduous forest showed for almost the same amount of data points. The high variation in habitat selection might be the result of the roe deer's pursuit of high-quality forage throughout the year an coincides with Moser, Schültz & Hindenlang (2006) that suggest that roe deer alter their forage selection to find the highest quality food.

This pursuit of high-quality forage could also explain why I didn't see any clear changes in habitat selection during fawning except for an increase in the usage of clear cuts. According to Vospersnik & Reimoser (2008) roe deer preferable reside

in areas that quite recently been clear cut since it provides food as well as cover-age. This could explain why roe deer increased their usage of clear-cuts during the fawning. However Samelius et al. (2013) suggested that quality of the habitat (and the available forage within) had bigger effect on roe deer than did the presence of lynx (*Lynx lynx*) and this could suggest that the access to forage might be more important than shelter and this could explain why there wasn't that big change in usage for the other habitats. During rutting there was a strong selection for deciduous forest, but this result was constructed on datapoints from only four individuals and therefore contains a high uncertainty.

Unlike moose, roe deer often selected urban areas above coniferous forest contradicting Coulon et al. (2008) that suggested avoidance within 400 meters from buildings. Still the urban areas in the NMD might also cover areas above 400 meters from buildings and if so, there would be a positive effect above that distance and still possible to count as urban area.

The analyse of the GPS data for roe deer over the full year suggested that clearcuts were less used than coniferous forest while mixed forest was more used. This is contradicted by the result from the camera trap data that suggests that clearcuts is more used than both coniferous forest and mixed forest. This difference I result might be caused by random chance or by the setup of the camera. It is not possible to tell witch one has the "true" result for describing roe deer selection however, less dwelling in recently clear-cut areas is beneficial for regeneration of forest, therefore it would be relevant to ascertain if an increase of mixed forests is reducing dwelling in clear cut areas.

4.3 Comparing GPS and camera trapping data

Due to the type of data that are the result of the GPS trackers, with highly specific times for datapoint and no knowledge about what the animal is doing at a given time, it is possible that a low used forage is given the same value as a high used passing by area. The benefit of the camera trap data is that even at a low number of pictures, it is possible to say what the animal been doing at a given place and time. Even if the GPS gives a high knowledge about the whereabouts of one individual it gives limited information on the total use of a specific habitat. Camera traps on the contrary gives little or no information on animal movement (if it's not possible to identify individuals from pictures (Sollman et al.2013), which rarely is the case with ungulates in Sweden) but gives good information on what the animal is doing in a specific habitat. The GPS studies the individual animals' selection of habitat (Rempel et al. 1995), while the camera trap studies animals at a given habitat. Therefore, for the purpose of finding ways of a more sustainable forestry with less foraging damages the important question might be how a habitat is used, and thereby camera traps might be a good tool and a logical direction to continue in to

find the answer on how to improve methods of forestry to avoid foraging (Caravaggi et al. 2017).

However, there are places where it's not reasonable to set up camera traps such as water due to the low usage of the habitat and urban areas due to the high number of pictures that would be taken on humans and thereby intrude on their privacy. In such areas GPS might be the only way to go to find out more, but either way it's not likely to have a huge impact on forestry. Overall for the purpose of this study I would argue that the GPS data was best suited to answer the first three hypothesis.

In this study there was a lot fewer datapoint in the camera trap data, and it held a higher uncertainty, thereby confirming my last hypothesis and this is likely to be the result since camera traps are highly dependent on the amounts of passing animals and the number of cameras set up. Still, the overall result in both GPS data and camera trapping data showed for a high usage of deciduous forest and clearcuts by moose and deciduous forest by roe deer. This suggests that to reduce damage on coniferous forest an increase of deciduous forest could be established as a preventive measure. But more studies would be needed in that specific matter.

4.4 Conclusion

Both moose and roe deer seemed to be very dependent on access to forage and that risks affecting forest in a way that might be considered to damage forest industry. The habitat that seemed most favourable over the year for both species where deciduous forest while the most avoided habitat type where water, however a future study would likely benefit from observing usage of areas that is nearby water. Effects on habitat selection driven by biological factors such as rut and fawning were seen in both moose and roe deer, but not always and the usage of urban areas were higher than expected, especially in roe deer. This suggests that the factors that drives the habitat selection by these ungulates in the area of Nordmaling needs future research and that it might be more complex than what was hypothesised in the beginning of this work.

For the future it would be relevant to more thoroughly examine the camera data to find out what animals are doing at the 4th order of selection, thereby pictures only used for passing through could be excluded and pictures where the animal is using a behaviour considered to damage the forest can be analysed. It would also be relevant to see difference of usage of forest of different ages, since it is reasonable to believe that young forest is under a higher predation pressure than older forest while old trees might be more exposed to behaviours such as peeling of the bark and antler rubbing. For this work I looked closer at the full year, the rut, the fawning season and winter, this sectioning could be done differently and would likely highlight different aspects the animals ecology in response to other abiotic and biotic factors.

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