Bear in mind! A study about the effect of bear predation on the choice of calving site and site fidelity by female moose in Sweden

Master thesis

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Independent project • 30 credits
Swedish University of Agricultural Sciences, SLU
Wildlife, fish and environmental studies
Animal Sciences (Wageningen University)
Examensarbete / Master's thesis, 2022:15
Umeå, 2022

Bear in mind! A study about the effect of bear predation on the choice of calving site and site fidelity by female moose in Sweden.

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Credits:	30 credits
Level:	Second cycle, A2E
Course title:	Master thesis in Biology
Course code:	EX0971
Programme/education:	Animal Sciences at Wageningen University
Course coordinating dept:	Department of Wildlife, Fish and Environmental studies
Place of publication:	Umeå
Year of publication:	2022
Cover picture:	Lisa Dijkgraaf
Copyright:	All featured images are used with permission from the copyright owner.
Title of series:	Examensarbete / Master´s Thesis
Part number:	2022:15
Keywords:	Moose (*Alces alces*), brown bear (*Ursus arctos*), predation, calving site, site fidelity

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Abstract

Selecting a suitable calving site is important for ungulates, especially when predators are present. Brown bears (*Ursus arctos*) predate on moose calves (*Alces alces*) and therefore influence the reproductive success of the moose. Female moose learn to reduce the chances of predation on their calves, but it remains unclear which strategies female moose apply. Therefore, the aim was to study the effect of bear predation on the choice of calving site features and site fidelity of female moose. To study the effect of bear density on calving site choice, I compared calving site features (e.g. habitat structure like distance to the nearest road, vegetation cover and terrain ruggedness) with characteristics of random sites within seven areas with different bear densities in Sweden. To study the effect of bear density on site fidelity, I compared distances between successive calving sites between areas with varying bear densities and between females that lost their calves in the previous year compared to females with surviving calves. The effects were studied using movement data of female moose, survival data of their calves and maps of the site characteristics. Female moose in areas with bears selected for higher shrub cover, higher tree cover and slightly lower distance to the nearest road compared to females in the predator-free area. Shrub cover and tree cover both increase the chance of hiding the calf from predators. The selection for higher distance to roads was strongest in the predator-free area, which indicates that the presence of bears resulted in a selection closer to roads. The distance between calving sites during subsequent years was greater in areas with higher bear density compared to the area without bears, regardless of whether the female has experienced a calf loss or not in the previous year. There was no evidence that female experience with calf predation in the previous year had an influence on the selection in most weeks or on the distance between successive calving sites, which could be caused by the relatively low sample size. In conclusion, female moose are influenced in their site selection and site fidelity by bear presence but the effect of female experience with calf predation should be studied further.

Keywords: Moose (*Alces alces*), brown bear (*Ursus arctos*), predation, calving site, site fidelity

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1. Introduction

Herbivores are influenced by predators in their foraging behaviour, habitat choice, survival and reproductive success. Predators influence prey both by consumption effects (i.e. eating them) and by non-consumption effects (i.e. predation risk). Predation risk has an influence on prey behaviour like reducing feeding rate, reducing activity and the selection of sheltered versus open habitats (Preisser & Bolnick, 2008). Neonates are especially vulnerable to predation, which makes the selection of birth sites important for herbivores' reproductive success. Brown bears (*Ursus arctos*) influence moose (*Alces alces*) calf survival in Sweden. The study of Swenson et al. (2007) showed that the average moose calf mortality in Sweden is around 36%, with 26% estimated to be caused by bear predation and 10% by other causes. The average kill rate per individual brown bear is estimated to be approximately seven moose calves per calving season (Swenson *et al.,* 2007; Rauset *et al.,* 2012). Predation on adult moose is uncommon (Dahle *et al.,* 2013). Most bear predation occurs on calves younger than one month (Swenson *et al.,* 2007), indicating the importance of reducing the risk of predation in the first period after calving.

Responses to predation risk can be either innate or learned behaviour. Prey species that evolved in an area with a high risk of predation may react strongly to the return of a predator due to innate responses that stayed present during the time of predator absence (Chamaillé-Jammes *et al.,* 2013). Black-tailed deer showed an innate avoidance response to the smell of wolf urine, even though the wolves were absent in that area for ca. 100 years (Chamaillé-Jammes *et al.,* 2013). Moose have been shown to adjust their behaviour to reduce predation risk within a generation, like increased sensitivity to predator cues (Berger *et al.,* 2001), indicating a learning response to predation. Yet, so far we still lack details on the strategies female moose apply to enhance calf survival chances.

Some of these strategies were already partly studied, like reproductive compensation, unpredictable movements, calving site selection and changes in site fidelity (Swenson *et al.,* 2007; Bowyer *et al.,* 1999; Poole *et al.,* 2007; Testa *et al.,* 2000). One strategy is that moose show reproductive compensation by having more calves in a year after they lost a calf (Swenson *et al.,* 2007). However, reproduction in moose is closely connected to body condition (Sand, 1996). Females with a higher rump fat thickness give birth to more twins compared to females with less rump fat (Keech *et al.,* 2000). Another strategy is that moose tend to show more extensive movements just before giving birth which is, according to Bowyer et al. (1999), to be unpredictable for predators. However, after the birth of the calves, the moose stay around the same location for at least nine days as the limited mobility of the calf restricts larger movement (Testa *et al.,* 2000). A further strategy is that moose females can select certain calving site features. Poole et al. (2007) made a distinction between climbing and non-climbing selection strategies for calving site selection in mountainous areas. Moose using the climbing strategy move to areas with higher elevation with reduced forage quantity and reduced predation risk, while the non-climbers have a higher forage quality with a likely higher predation risk (Poole *et al.,* 2007). An additional strategy is that female moose reduce their calving site fidelity after losing a calf to predation of wolves (*Canis lupus*), black bears (*Ursus americanus*) or brown bears (Testa *et al.,* 2000). Because of time constraints, my study only focused on the effect of brown bears on the calving site selection and site fidelity.

Calving site selection in moose is influenced by a trade-off between minimizing predation risk and having sufficient nutrients available to handle the high energy costs of lactation (Poole *et al.,* 2007; Severud *et al.,* 2019; Haydn, 2012). Calving generally occurs shortly before plants leaf out to match the energy-demanding time with peaks in forage quantity and quality (Neumann *et al.,* 2020). However, this makes deciduous shrubs and saplings (i.e. better forage) less suitable for calf concealment compared to small conifers (Severud *et al.,* 2019), which shows the trade-off between predation risk and nutrient availability. Other factors influencing calving site selection of moose in Sweden are elevation, type of land cover and distance to roads, water and buildings (Haydn, 2012). These factors are all associated with either food or safety. Female moose tend to select elevated areas which give a better view on approaching predators (Wilton & Garner, 1991; Bowyer et al., 1999). Additionally, it is easier for females with newborn calves to escape from predators downhill compared to uphill which may also be a reason for selecting higher elevations (Wilton & Garner, 1991). Furthermore, bears tend to avoid humans by avoiding cities and roads (Nellemann *et al.,* 2007). Moose in Yellowstone use this by shifting their birth site locations towards locations closer to roads, away from the traffic-avoiding bears (Berger, 2007).

Moose show some level of site fidelity, which seems to be influenced by calf survival. Testa et al. (2000) found that calving site locations in successive years of moose in Alaska were closer together if at least one calf survived when predators are present in the area. Successive calving sites of the same female moose were closer together than the calving sites between two different females (Tremblay *et al.,* 2007). It is important to note that the study of Tremblay et al. (2007) looked at the site fidelity in the absence of predators, which makes it interesting for my research to study the site fidelity across a gradient of predator presence (e.g. bear density).

Understanding more about the strategies moose females apply to reduce predation risk is important for moose and habitat management. Sweden is a country with large amounts of forests for wood production (Fridholm, n.d.), so it is necessary to make sure that suitable calving sites stay present for the moose even in this human-controlled landscape to maintain healthy moose populations. Additionally, having more knowledge about the moose may help in forming strategies to reduce moose damage to production forests. Due to a lack of studies including both the predation risk (innate responses) and the experience with predation (learned responses), I tested the effects of bear predation on the site selection and site fidelity of female moose in seven study areas with different bear densities in Sweden.

To clarify my study, I formulated the following research question: "How does bear predation affect calving site selection and site fidelity in female moose in Sweden?", with the sub-questions:

1. How does the selection for site characteristics during the calving season differ between females with or without calf loss in the previous year in areas with different bear densities?

Hypothesis: Moose select calving sites more on safety features (higher shrub cover, more coniferous forest, higher terrain ruggedness, closer to roads) in areas with higher bear density and more on forage quality (deciduous forests) when bear density is lower or bears are even absent in the area. When fewer or no predators are present, the female does not have to focus on reducing predation risk and can therefore select areas with better quality forage. I expected that the females that lost their calves due to bear predation in the previous year will show the selection for safety features stronger compared to females of calves that survived.

2. What are the differences in calving site fidelity between female moose with and without loss of calves due to bear predation?

Hypothesis: Females that lost a calf in the previous year will select a calving site farther away from their previous calving site compared to females that did not lose their calf. Females that lose their calves may perceive this location as unsafe and therefore move to a different location in the next year.

These questions were studied using GPS data of female moose combined with survival data of their calves and maps with information about habitat characteristics (vegetation cover, vegetation type, terrain ruggedness and distance to nearest road).

2. Materials and methods

2.1 Study species and study locations

To investigate female moose behaviour during the calving season under different bear predation risks, I analysed moose movement data from seven different study sites with varying average bear densities ranging from no bears to 1.19 bears/km^2 (Bischof *et al.,* 2020). In Sweden, moose females give birth to either one or two calves in May or June, depending on latitude (Neumann *et al.,* 2020). Female moose give birth later at higher latitudes (Neumann *et al.,* 2020). During their first week of life, moose calves are relatively immobile, but their mobility quickly increases so they can easily follow when they are around three weeks (De Bord, 2009). For calves, the risk of predation by bears is highest during their first four weeks of life (Swenson *et al.,* 2007)

Data was collected within multiple moose monitoring projects over the years (Figure 1). The monitored female moose were from seven study areas located in the Swedish provinces of Norrbotten, Västerbotten, Gävleborg and Kronoberg (Figure 1).

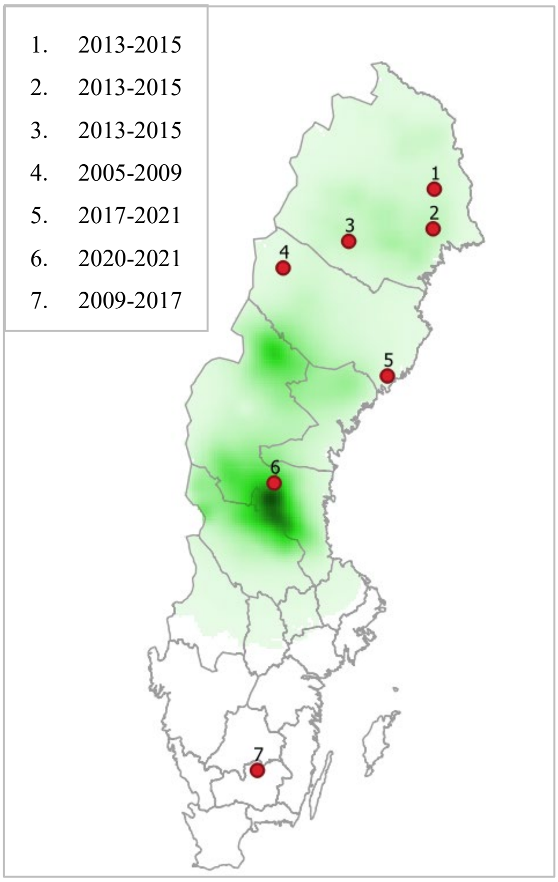

Figure 1. Study sites with their bear density and years of available data. Darker green indicates a higher bear density. The bear density data for making this figure is from Bischof et al., 2020. 1 = Ängesån (0.12 bears/km^2), 2 = Niemisel (0.19 bears/km^2), 3 = Arvidsjaur (0.17 bears/km^2), 4 = Hemavan (0.05 bears/km^2), 5 = Nordmaling (0.04 bears/km^2), 6 = Ljusdal (1.19 bears/km^2), 7 = Växjö (no bears). The dataset included 120 moose females in total, with 8 females in Niemisel, 6 in Ängesån, 7 in Arvidsjaur, 30 in Hemavan, 20 in Nordmaling, 11 in Ljusdal, and 38 in Växjö.

I pooled the study areas regarding their bear density as given by Bischof et al. (2020): low bear density (0.05 bears/km^2) = area 4-5, high bear density (0.41 bears/km^2) = area 1-3 and 6, and the control (no bears) = area 7. There were 120 moose females in the dataset with between two and nine years of data, which resulted in 357 year-moose combinations.

2.2 Data collection

Available datasets

For this research, a calf survival dataset was combined with GPS monitoring datasets of the moose females collected within multiple moose monitoring projects over the years. The datasets were linked with the use of female id. The data included the number of calves per female, the survival of the calves, birth date of calves and movement data of the female moose. The age of the females was recorded during the marking event, using tooth wear as an indicator (Ericsson & Wallin, 2001).

Researchers used field observations to determine the number and survival of calves. When movement data indicated that the moose had a calf (May-June), field observations were done for confirmation and for determining the number of calves (Neumann *et al.,* 2020). Another calf survival control was performed from August to September, before the annual moose hunt starts in Sweden. Additional calf survival checks were performed when the movement patterns of the female indicated possible calf loss (i.e. sudden larger movements with returned movements to the location of disturbance). Calf predation was confirmed by either finding calf remains with traces of predation using a dog or by seeing a clear movement pattern indicating predation linked with observing the female without a calf in the next control.

The GPS data was collected using GPS collars (VECTRONIC Aerospace (Vectronic Aerospace, 2022)), which calculated a location for every half hour during the calving season. I analysed movement data of the female moose starting from the calving date until four weeks after the calving date. Only female moose with at least two years of data were included in the final dataset to allow estimation of site fidelity and to access how female experience in the previous calving season affects her habitat selection. Only females with known age were included, to test if site fidelity was influenced by female age. The movement data was in the RT90 2.5w projection (EPSG:2400).

Maps of habitat features

A set of maps was used to determine habitat features at moose locations and thus to study moose habitat selection following calving. I used seven different maps including: cover of low vegetation (as a proxy of shrub coverage, in %), cover of high vegetation (as a proxy of tree coverage, in %), height of low vegetation (m), height of high vegetation (m), national land cover data, terrain ruggedness index and the distance to the nearest road (m) (Table 1).

Vegetation was considered as low vegetation when the vegetation height was between 0.5 – 5 m and high vegetation when between 5 – 45 m (Naturvårdsverket, 2020a). The national land cover data consisted of 26 different landcover types, which I regrouped into the following habitat classes that are relevant for moose: ‘conifer forest’, ‘deciduous forest’, ‘temporarily non-forest’ and ‘no forest’ (Naturvårdsverket, 2020b; Appendix 1). The terrain ruggedness index is a measure of topographic heterogeneity (Riley *et al.,* 1999) and thereby can indicate higher sites in relation to the surrounding environment. The index gives the amount of elevation compared to the adjacent cells on the map. The higher the value, the higher the ruggedness of the terrain (Riley *et al.,* 1999). The distance toward roads was available as Euclidean distances in meters based on the Swedish road map (Trafikverket, 2014).

Table 1. The studied habitat features with the year of collection, projection, resolution and source.

Variable	Year	Projection	Resolution	Source
Low vegetation cover (%)	2018	SWEREF99 TM (EPSG:3006)	10x10m	Swedish environmental protection agency[1]
High vegetation cover (%)	2018	SWEREF99 TM (EPSG:3006)	10x10m	Swedish environmental protection agency[1]
Height of low vegetation (m)	2018	SWEREF99 TM (EPSG:3006)	10x10m	Swedish environmental protection agency[1]
Height of high vegetation (m)	2018	SWEREF99 TM (EPSG:3006)	10x10m	Swedish environmental protection agency[1]
National land cover	2018	SWEREF99 TM (EPSG:3006)	10x10m	Swedish environmental protection agency[2]
Terrain ruggedness index	2009	RT90 2.5w (EPSG:2400)	50x50m	Swedish digital elevation model[3]
Distance to roads (m)	2014	SWEREF99 TM (EPSG:3006)	50x50m	Swedish transport administration[4]

[1](Naturvårdsverket, 2020a), [2](Naturvårdsverket, 2020b), [3](lantmateriet, 2009), [4](trafikverket, 2014)

2.3 Statistical analysis

All spatial and statistical analyses were performed in R - version 4.1.2 (R Core Team, 2021). I applied a significance level of $p < 0.05$ for all analyses.

2.3.1 Habitat selection following calving

For each study area, moose GPS data was available for every half hour. The GPS data was resampled to four times a day, at the times 0.00h, 6.00h, 12.00h and 18.00h. Moose are mostly active during dusk and dawn and less active in between (Neumann *et al.,* 2012), which made four samples a day sufficient for addressing my research questions.

For each female, the GPS data was linked to her reproductive success in a given year (i.e. calf survival data). Summer survival of the calves during a given calving season was grouped into: ‘alive’, ‘predation’ or ‘other/unknown cause of death’. The groups were used as a proxy for female experience and to test how the experience during the previous year affects females’ habitat selection. Other causes of calf mortality in the dataset were for example natural mortality (Swenson *et al.,* 2007). Stillborn calves were removed from the dataset. To study the effect of the experience with calf loss, a ‘calf survival in previous year’ variable was made using the *lag* function in R linked by female id. This *lag* function produced a lagged effect on the calf survival variable so that the calf survival was added to the data of the same moose female in the next year. Only female-year combinations with data for the 'calf survival in the previous year' were taken into account in the models, resulting in a total of 103 females and 217 female-year combinations in the final dataset (Table 2).

Table 2. Number of females in each bear density area and their experiences with calf loss

Bear density area	Calf survival in previous year	Number of females	Number of year-moose combinations
Low (0.05 bears/km^2)	Alive	34	65
	Predation	2	2
	Other/unknown	7	7
High (0.41 bears/km^2)	Alive	14	15
	Predation	9	9
	Other/unknown	11	11
Control (no bears)	Alive	37	89
	Predation	-	-
	Other/unknown	13	19
Total		127[1]	217

[1]Female moose (N = 103) can be in different calf survival groups in different years.

[2] Average of the bear densities of the study areas in each bear density group. Bear densities were given by the raster of Bischof *et al.,* 2020.

To analyse females' habitat selection over time, step selection functions were performed (R package 'amt', Signer *et al.,* 2019). With step selection functions, landscape variables of observed steps were compared to five random steps chosen from the same starting location (Thurfjell *et al.,* 2014; van Beest *et al.,* 2012). I spatially linked the ending location of each observed and random step to the underlying maps of habitat structure. With step-selection functions, the starting location of the step is associated with movement and the ending location with habitat selection (Signer et al., 2019), which is why I used the ending location of the step. When the movement data and the habitat map had different GPS projections, I transformed the projection of the movement data to be able to extract the habitat features using the *spTransform* function in R.

Correlations between variables were checked before they were put into the model using Spearman rank correlation with a cut-off value of $\rho = 0.7$. Vegetation height had a strong correlation with the vegetation cover (low vegetation: $\rho = 0.72$, high vegetation: $\rho = 0.83$), therefore only the vegetation covers were included in the final model.

To analyse how bears affect the site selection of moose, I applied a conditional logistic regression using a generalized linear mixed model (R package 'glmmTMB', Brooks *et al.,* 2017) with observed versus random steps as dependent variable (1 = observed, 0 = random). I chose the Poisson distribution as suggested by Muff *et al.,* 2020. The included independent variables (i.e. fixed effects) were cover of low vegetation (shrub cover), the cover of high vegetation (tree cover), terrain ruggedness and distance to roads. The factor ‘calf survival in the previous year’ (alive, predation, lost due to other/unknown reason) was included as an interaction term with the other independent variables, with ‘alive’ being the baseline category. Both step id (one observed with five random steps) and animal id were included as random effects (Table 3).

The variables were all standardized before putting into the models using the *scale* function in R, to account for differences between areas and to simplify a comparison among study areas (e.g. road network is denser in southern and coastal areas compared to northern and interior areas). The land cover type could eventually not be added because the models did not converge. Therefore, I decided to focus on habitat structure only (cover of high/low vegetation, terrain ruggedness and distance to nearest roads). To avoid making too complex models, I made separate models for the different bear density areas (control, low and high).

Calf vulnerability to bear predation decreases with time, while the calf mobility increases. Therefore, I decided to split the data into different time periods: birth (calving date), first week (1-7 days after birth), second week (8-15 days after birth), later in calving season (third/fourth week; 16-28 days after birth). I assumed that the bear predation was the highest during the first two weeks and less in the last part of the study period. Also, the mobility of the calf does not change much between the third and fourth week anymore, therefore I decided to group these weeks. Each bear density model was run separately for the birth date, the first week, the second week, and for later in the calving season (Table 2). The relative risk (exp(coef)) is in habitat selection modelling interpreted as relative selection strength (Avgar *et al.,* 2017), which I used to determine the selection for habitat features.

2.3.2 Site fidelity

I used the same dataset for both the calving site selection and calving site fidelity analysis. To check the site fidelity, the random steps were excluded from the analysis to only look at observed locations.

Four GPS locations per day were available in this dataset, which were averaged to get one location per day. The recording dates were numbered starting from the birth date (e.g. 0 = birth date and 1 = day after birth). Female positions (i.e. the coordinates) with the same assigned number were linked to the positions of the same female in the previous year. I calculated the distance between the positions using the Euclidean distance (in km).

Distances among calving sites between years were studied using a linear mixed model with distance as the dependent variable and as independent variables (i.e.

fixed effects) ‘calf survival in the previous year’ (alive, predation, lost due to other/unknown reason), bear density (low, high, control) and female age. Female id was included as a random variable to account for individual heterogeneity and repeated measures (Table 3). To ensure a normally distributed response variable, I transformed the dependant variable distance using the cube root transformation (Distance^(1/3)).

ANOVA was used to analyse the effects of different factors in the model. Pairwise comparisons using the *emmeans* function with Tukey were used to analyse differences between factor levels. I applied the model for the calving dates and for the first week after calving, thereby estimating site fidelity for the calving site itself as well as for the area utilized during the calf’s first week of life when they are most vulnerable.

Table 3. (Generalized) linear mixed models to test the habitat selection of moose during the first four weeks after calving using a step selection function (1) or to test for site fidelity (2).

Research question	**Fixed effects**	**Data**
Site selection (features)	Case[a] ~ (low vegetation[b] + high vegetation[c] + terrain ruggedness[d] + road[e]) * calf survival in previous year[f] + (1|step id) + (1|female id)	Twelve different subsets with combinations of a bear density area[g] and a specific time after birth (birth date, week 1, week 2, week 3+4)
Site fidelity	Distance ~ age[h] + bear density area[g] + calf survival in previous year[f] + (1|female id)	All moose females, separately for the birth date and the first week after birth.

[a] Observed or random step, binary

[b] Cover of low (0.5–5 m) vegetation (%), continuous

[c] Cover of high (5-45 m) vegetation (%), continuous

[d] Terrain ruggedness index, continuous

[e] Euclidean distance to the nearest road (m), continuous

[f] Alive, lost due to bear predation or lost due to other/unknown reason

[g] Control, low bear density, high bear density

3. Results

3.1 Habitat selection following calving

Bear density influences female moose in their selection for shrub cover and distance to roads during the first weeks of the calving season. Females in areas with higher bear density selected stronger for shrub cover compared to the other areas (Table 4; Figure 2a, 3a, 4a). Females in the predator-free area selected for a higher distance to the nearest road compared to the areas with bears. I also found that female experience (calf survival in the previous year) influenced the selection in specific areas in some weeks.

Table 4. Overview of the results of the habitat feature selection of female moose in the first month after calving in areas with different bear densities. Low = female moose selected for lower values compared to random locations. High = female moose selected for higher values compared to random locations. Both = opposite results in different weeks after calving. - = no significant results found. Separate models were made for the calving date, the first week after calving, the second week after calving and a combination of the third and fourth week. The results in this table can be from either one or multiple weeks.

Variable	Predator-free area	Low bear density	High bear density
Main effects			
Shrub cover	-	High	High
Tree cover	Low	High	High
Terrain ruggedness	Low	Both[1]	-
Road distance	High	High	High
Female moose that experienced calf predation compared to females with surviving calves			
Shrub cover	-	-	-
Tree cover	-	Low	Low
Terrain ruggedness	-	Low	-
Road distance	-	-	High

[1] ’Low’ at the calving date and ’High’ during the second week after calving

3.1.1 Area without bears (control)

In the predator-free area (Figure 1 - area 7), tree coverage and road distance were the most important habitat features influencing habitat selection by moose during the calving season. Female moose selected for a low tree cover and greater distances to the nearest road (Table 4; Figure 2a). Over the weeks, females increased their selection for lower tree cover, while their selection for greater distances toward roads decreased (like the first week (*Figure 2a- road - purple dot*) compared to later in the calving season (*Figure 2a – road - grey dot*)). Additionally, moose selected for low terrain ruggedness later in the calving season.

At the calving date, females that lost their calf (n = 89) in the previous year selected for calving sites with higher tree cover compared to females with surviving (n = 19) calves (Figure 2b). During the first week after birth, females that experience calf loss selected less rugged terrain.

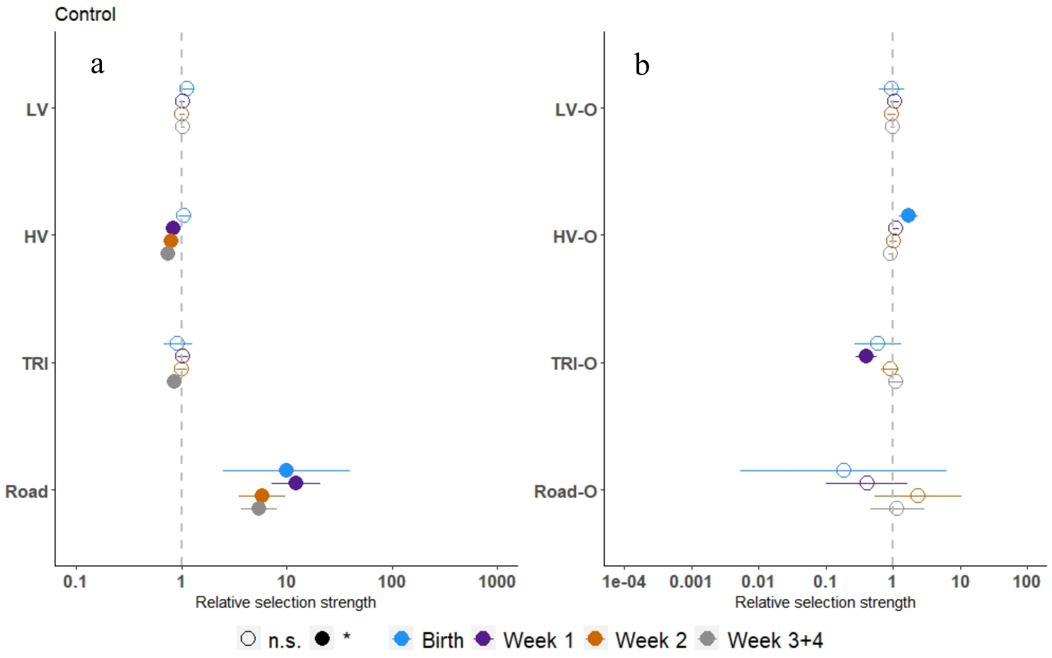

Figure 2. The relative selection strength of habitat features (LV = cover of low vegetation (shrubs), HV = cover of high vegetation (trees), TRI = terrain ruggedness, Road = Euclidean distance to roads) by female moose during the first four weeks after calving in an area without bears. Separate models were made for the birth date, the first week after birth, the second week after birth and the combination of the third and fourth week, which were shown together in the graphs. The graphs show the main effects of the models (a) and the interaction effects between the habitat features and the calf survival in the previous year (b). Selection is compared between females with surviving calves (intercept) with females that lost their calves (indicated by the O behind the variables) in the previous year (plot 2b). Data was collected in Sweden, from 2009-2017. Significance ($p < 0.05$; coloured dots) indicates a selection for or against a certain habitat variable. The dashed vertical line indicates no differences between selection in observed and random locations, with a selection for lower values on the left side of the line and selection for higher values on the right side. The horizontal lines show the confidence intervals.

3.1.2 Low bear density area

In the low bear density areas (Figure 1 – areas 4 and 5 pooled), female moose selected for high shrub cover during the first four weeks after calving (Table 4; Figure 3a). Selection of terrain ruggedness differed between the weeks with selection for less rugged terrain on the calving date (*Figure 3a- TRI – blue dot*) and selection for more rugged terrain in the second week (*Figure 3a- TRI – orange dot*). During the first week after calving, females selected for high tree cover and greater distances to roads.

Habitat selection of females that experienced calf predation in the previous year (n = 2) and females of surviving calves (n = 65) differed only from each other during the first week after birth where the females that lost their calf selected for lower tree cover and less rugged terrain (Figure 3b). Females with calves lost due to other/unknown reasons (n = 7) selected for higher shrub cover compared to the females with the surviving calves, yet only in the third/fourth week after calving.

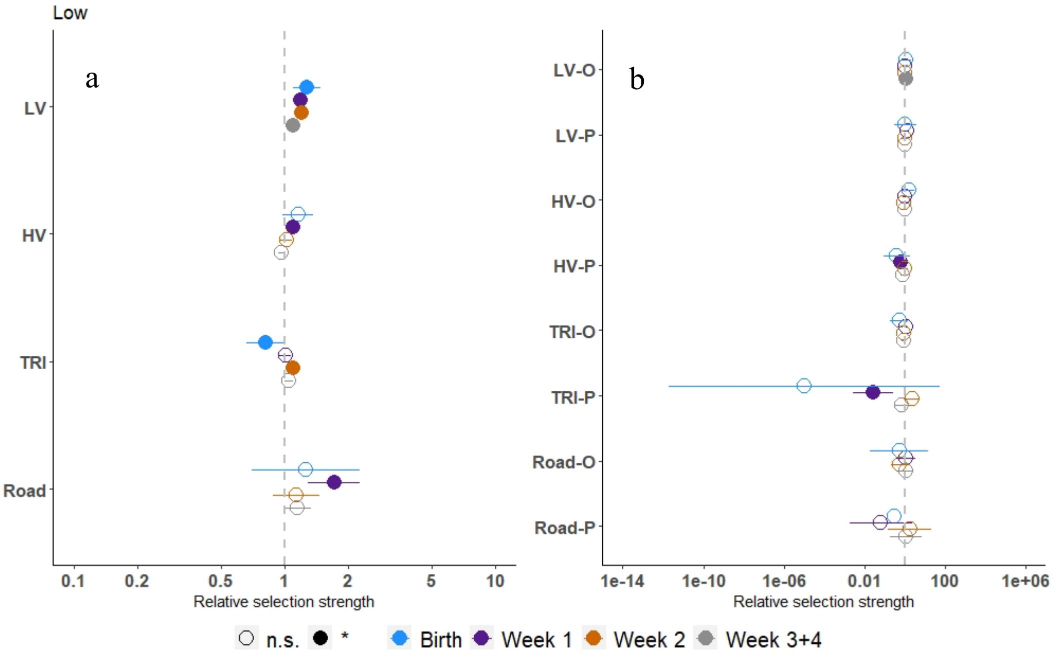

Figure 3. The relative selection strength of habitat features (LV = cover of low vegetation (shrubs), HV = cover of high vegetation (trees), TRI = terrain ruggedness, Road = Euclidean distance to roads) by female moose during the first four weeks after calving in areas with a low bear density. Separate models were made for the birth date, the first week after birth, the second week after birth and the combination of the third and fourth week, which were shown together in the graphs. The graphs show the main effects of the models (a) and the interaction effects between the habitat features and the calf survival in the previous year(b). Selection is compared between females with surviving calves (intercept) and females that lost their calves due to predation (indicated by the P behind the variables) or due to other/unknown reasons (indicated by the O behind the variables) in the previous year. Data was collected in Sweden, from 2005-2021. Significance ($p < 0.05$; coloured dots) indicates a selection for or against a certain habitat variable. The dashed line indicates no differences between selection in observed and random locations, with a selection for lower values

on the left side of the line and a selection for higher values on the right side. The horizontal lines show the confidence intervals.

3.1.3 High bear density area

In areas where bears occurred in higher densities (Figure 1 – area 1, 2, 3 and 6 pooled), female moose selected for higher shrub cover, higher tree cover at the calving site and during the first week after birth and for a larger distance to roads at the birth date (Table 4; Figure 4a).

Females that experienced calf loss due to bear predation (n = 9) in the previous year selected for lower tree cover at the birth date and a higher distance towards the nearest road later in the calving season compared to females with surviving (n = 15) calves (Figure 4b). There was no evidence that females that experienced calf loss due to other/unknown reasons (n = 11) selected differently compared to females with surviving calves.

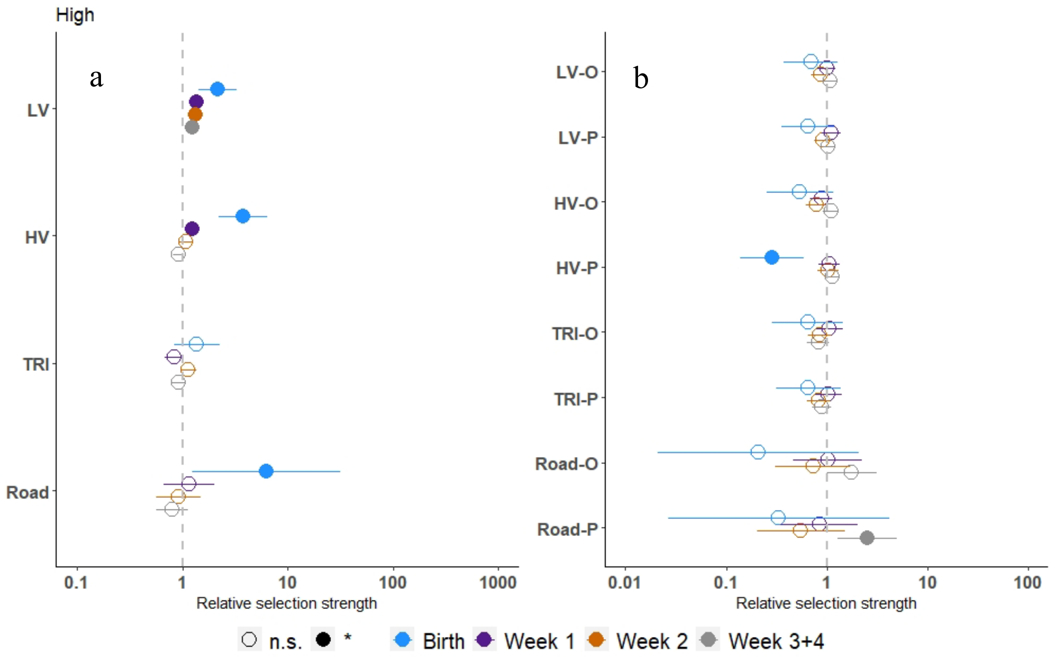

Figure 4. The relative selection strength of habitat features (LV = cover of low vegetation (shrubs), HV = cover of high vegetation (trees), TRI = terrain ruggedness, Road = Euclidean distance to roads) by female moose during the first four weeks after calving in areas with a high bear density. Separate models were made for the birth date, the first week after birth, the second week after birth and the combination of the third and fourth week, which were shown together in the graphs. The graphs show the main effects of the models (a) and the interaction effects between the habitat features and the calf survival in the previous year (b). Selection is compared between females with surviving calves (intercept) and females that lost their calves due to predation (indicated by the P behind the variables) or due to other/unknown reasons (indicated by the O behind the variables) in the previous year. Data was collected in Sweden, from 2013-2021. Significance ($p < 0.05$; coloured dots) indicates a selection for or against a certain habitat variable. The dashed line indicates no differences between selection in observed and random locations, with a selection for lower values on the left side of the line and a selection for higher values on the right side. The horizontal lines show the confidence intervals.

3.2 Site fidelity

3.2.1 Site fidelity - calving date

Site fidelity of female moose at the calving date was influenced by bear density (F(2,98) = 9.88, p < .001). There was no evidence for influences of female age and calf survival in the previous year on the distance between calving sites, suggesting that female experience during the previous year did not alter the choice for a calving site. In areas without bears, female moose calved the closest to their calving sites of the previous year compared to females in areas with bears (control: mean = 1.0 km; low: mean = 4.0 km, t(98) = -4.44, p < .001; high: mean = 2.3 km, t(98) = -2.11, p = .09).

3.2.1 Site fidelity – during the first week after calving

During the first week after calving, both calf survival during the previous year and bear density influenced the site fidelity of female moose during the first week after calving (survival: F(2,1385) = 3.13, p = .04; bear density: F(2,98) = 11.66, p < .001). There was no evidence for effects of the age of the female (F(1,1385) = 2.28, p = .13).

Female moose with surviving calves in the previous year had lower distances during the first week after birth in successive years (mean distance = 2.4 km) compared to females that lost their calves to other/unknown reasons (mean = 2.7 km, t(1385) = - 2.31, p = .05) but not to females with bear-predated calves (mean = 3.0 km, t(1385) = -1.252, p = 0.42). There were 169 moose-year combinations in the ‘alive’ group, 37 in ‘other/unknown’ and 11 in ‘predation’.

In predator-free areas, female moose were closer to their locations in the previous year compared to areas with bears (control: mean = 1.2 km; low: mean = 4.9 km, t(98) = -4.82, p < .001; high: mean = 2.7 km, t(98) = -2.41, p = 0.05).

4. Discussion

This study focused on calving site selection and site fidelity of female moose in response to bear predation in Sweden. Females in areas with bears selected for higher shrub cover, higher tree cover and lower distances to roads compared to females in predator-free areas. The distances between calving sites in successive years were higher in areas with bears compared to areas without bears. Female experience with calf predation in the previous year resulted in selection for lower tree cover, lower terrain ruggedness and higher distances to roads in the bear density areas in specific weeks after calving.

Shrub cover (0.5 – 5 m) can be used for calf concealment as well as it provides forage for the female and her calf (Severud *et al.,* 2019). The use of protective cover limits the predators in their use of vision for locating prey which reduces predator-encounter rates and thereby the probability of attack (White & Berger, 2001). Female moose use forests with low amounts of vegetation below five meters during the calving date and move to forests with dense vegetation shortly after calving, which was explained by the growing demand for food of the female and her calf (Melin *et al.,* 2016; Severud *et al.,* 2019). In contrast, the study of Melin et al. (2019) showed that females went to areas with lower shrub density after calving. In agreement with Melin et al. (2019), I found the highest selection for shrub cover at the calving date with decreasing, but still positive, selection over the weeks. Unexpectedly, female moose did not show a stronger selection for shrub cover after experiencing calf predation in the previous year. My research set-up did not allow me to determine if the females selected the shrub cover for predator avoidance, food availability or both. However, the highest selection for shrub cover was in the high bear density area while no selection occurred in the predator-free area. This indicates the increasing importance of shrub cover with increasing bear density, which can be seen as a predation risk-reducing strategy for the female moose.

Tree cover (5 – 45 m) is an indicator for forests, with high values relating to more forested landscapes and lower values relating to more open areas. My results showed that females in the areas with bears selected for higher tree cover while the females in the predator-free area selected for lower tree cover. One of the main food sources of the moose are *Vaccinium* shrubs (Spitzer *et al.,* 2021) which grow best in shaded environments like forests (Persson *et al.,* 2012). Bears also eat the berries from the *Vaccinium* shrubs, but the berries are not ripe in the first part of the moose calving season, and therefore not an important food source for bears at that time (Stenset *et al.,* 2016). For this reason, there is not necessarily a higher chance of encountering bears in areas with higher *Vaccinium* availability in the first month of the moose calving season. The availability of *Vaccinium* can be the reason for the selection of forest cover. However, this does not explain why the females in the control area selected for lower tree cover than could be expected based on random locations. Another reason to select tree cover is for the selection of thermal shelter. When temperatures increase, moose tend to select coniferous forests and avoid open habitats (van Beest *et al.,* 2012). The temperature in the south of Sweden is on average higher than in the north (SMHI, 2017), which suggests a higher selection for tree cover as thermal shelter in the south of Sweden. In contrast, my results showed a selection for lower tree cover in the predator-free area (south) and a selection for higher tree cover in the low/high bear density areas (central and north), which makes the thermal shelter an unlikely explanation for differences in tree cover selection between the study areas. A more likely explanation is that variability in crown cover can help camouflage the calves as it creates sunny and shaded patches (Bowyer *et al.,* 1999), which matches with my results of the selection of higher tree cover in low and high bear density areas compared to the predator-free area. In the predator-free area, this protection from predators is not needed which makes it possible for the moose to select lower tree cover.

The terrain ruggedness index can be viewed as the possibility for the moose to place themselves on elevated spots compared to the surroundings. The moose can use the elevated spots to have a better overview for detecting bears (Wilton & Garner, 1991; Bowyer *et al.,* 1999). In contradiction with this expectation, the moose in the low bear density area selected on the calving date for low terrain ruggedness values and females with bear-predated calves in the previous year selected for even lower values. A possible explanation for this can be that moose females select areas that are less selected by bears. According to Nelleman et al. (2007) bears prefer rugged forested terrain as terrain ruggedness has an influence on (food) plants, availability of denning sites and lower disturbance by humans. In contrast with the selection of lower terrain ruggedness at the calving date, females in the low bear density area selected for higher terrain ruggedness in the second week. This may be related to the safety aspect of the elevated spots with having a better overview and the fact that the calf mobility increased over the weeks (Testa *et al.,* 2000). For females with calves, it is easier to escape from predators downhill compared to uphill which may also be a reason for selecting elevated sites (Wilton & Garner, 1991). As there are conflicting selections in different weeks and only selection in the low bear density area while not in the high bear density area, there is not a clear strategy shown concerning terrain ruggedness selection by female moose.

Distance to the nearest roads is regarded as a safety feature, as bears are road-avoidant (Nellemann *et al.,* 2007). For example, moose in Yellowstone selected birth sites closer to roads, away from road-avoiding bears (Berger, 2007). In contradiction, the moose in all my study areas selected for greater distances to the nearest road. A possible explanation for this can be that the moose perceive humans as a larger risk than the bears. Mehlhoop et al. (2022) found reduced browsing pressures by moose and increased tree recruitment around roads and houses, which can be seen as an indication of risk avoidance driven by fear of humans. In agreement with this, Bowyer et al. (1999) found that birth sites were located farther away from human areas compared to random sites. There is likely a difference in the distance towards larger and smaller roads, but this was beyond the scope of my research. The selection of higher distances to roads was visible in both the predator-free and the areas with bears, with selection for the largest distances in the predator-free area. This indicates that the presence of bears shifts the selection to slightly closer to the roads where the bear encounter risk is lower. However, bear sightings in Sweden showed that bears occur close to roads during the moose calving season which is something that should be explored further in the future.

Site fidelity was expected to be higher in females with surviving calves in the previous year compared to females that experience calf loss. Calving sites in successive years of moose (in Alaska) were closer together if at least one calf survives (Testa *et al.,* 2000). I found similar results for the site selection in the first week after calving for females that lost their calves (not because of predation). I was unable to find this association for the calving date itself, or for females that experience calf predation in the previous year. However, my results showed that the distances between sites were higher in both the low and high bear density areas compared to the predator-free area which can be seen as an indication that bear presence, and their predation, influence moose site fidelity.

In my study, I looked at the response to predator presence (innate response) or experience with bear predation (learned responses). However, it is debatable if the response to predator presence (i.e. predation risk) is an innate or learned behaviour in moose. Black-tailed deer showed an innate avoidance response to the smell of wolf urine, even though the wolves were absent in that area for ca. 100 years (Chamaillé-Jammes *et al.,* 2013). In moose, this innate response is not clearly shown. Naïve moose in America did not abandon sites with wolf urine (Berger *et al.,* 2001), indicating that moose do not have a strong innate response to predators. However, there are differences between moose in America and Sweden in their response to predators (Sand *et al.,* 2006). For example, moose in Scandinavia are more likely to flee instead of fight when attacked by wolves compared to moose in America (Ausilio *et al.,* 2021; Sand *et al.,* 2006). This is likely caused by the high human hunting pressure and the use of hunting dogs in Sweden, which makes fleeing a better approach to reduce the risk of being shot (Ausilio *et al.,* 2021). The behavioural change of moose in Scandinavia is not only shown in response to the human hunters but also to the wolves, indicating some sort of innate response to general predation risk. These papers were specifically about the response to wolf predation, but differences may be present between the response to bears or wolves which should be studied in future research.

There were some limitations to this study. Firstly, I only had habitat feature maps of one specific year available for each variable while the movement data was collected over multiple years. The results may be less reliable when there are more years between the movement data and the habitat feature collections. Secondly, I did not have data about vegetation type, which made it hard to differentiate between selection for forage or selection for safety. In future studies this can be solved by including shrub type and/or adding a calf visibility score. Thirdly, I made separate models for each bear density area. This means that I did not formally test for the differences between the areas. Future studies may develop the model further to incorporate the bear density into the model. Lastly, the calf survival in the previous year group ’predation’ had a small sample size, which may be the reason for the non-significant results for this group given the large variation among individual females as indicated by the larger confidence interval. This could be improved by collecting more data in bear dense areas, like including more moose or increasing the number of sampling years.

As my study completely focused on bear predation, future research may want to include wolves. It could be interesting to see if the responses of moose differ between wolf predation and bear predation. This could be done in a similar way as my research, but instead of the ’control’, ’low’, ’high’ bear density areas, I would suggest using ’wolf’, ’bear and wolf’, ’bear’ and ’no predator’ study sites. Another interesting aspect to take into account in future research is if losing twins results in different and/or stronger responses than losing one calf. Lastly, this study focussed on possible strategies female moose apply during the calving season, but it did not look at the success of these strategies. It is an interesting follow-up study to link site selection and site fidelity to the likelihood of increasing calf survival.

5. Conclusion

In conclusion, female moose in Sweden are influenced in their site selection and site fidelity by bears and by experiences with bear predation in the previous calving season. Female moose did not select for shrub cover in the predator-free area while selecting for high shrub cover in the areas with bears. This indicates that the shrub cover is used as a way to reduce the bear predation risk. Selection for higher tree cover in areas with bears is likely related to the safety aspect that trees create shaded patches that help camouflage the calf. The selection for higher distance to roads was strongest in the predator-free area, which indicates that the presence of bears shifted the selection towards closer to the roads, away from the road-avoidant bears. There does not seem to be a clear strategy for terrain ruggedness selection, as there were conflicting selections in different weeks and no selection in either direction in the high bear density areas. There was no evidence that female experience with calf predation in the previous year influenced selection in most weeks or for the distance between successive calving sites. It could be the case that female moose are not influenced in these aspects by the experiences or that this resulted because of the low sample size of predated calves in the dataset. Future research should test if the calf predation does indeed not influence the females in most weeks after calving. My research did not take into account the effectiveness of the applied strategies, which could be an interesting follow-up study. This study shows the importance of tree and shrub cover for the female moose during the first four weeks after calving. Moose habitat management should focus on having enough suitable cover available for the moose during the calving season.

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Acknowledgements

I want to start by thanking my main supervisor Wiebke Neumann for being wonderful in guiding me throughout the whole thesis process. I like to thank Fredrik Stenbacka for answering all my questions about the data and letting me join on some amazing fieldwork days in which I could see my data in real life from extremely close! The calf check fieldwork was an awesome experience which I will never forget. Thanks to my supervisor from Wageningen University Pim van Hooft for helping me get started and answering all my questions. Thanks to Lukas Graf, Johannes Signer and Hilda Edlund for answering all my statistical questions.

I am grateful for all the mental support and nice talks during the breaks with the other students, my friends and the staff of SLU. I had a lot of fun in Umeå!

Lastly, I want to thank my friends and family for proofreading parts of my thesis and for supporting me in my decision to go to Sweden and while working on my thesis.

For everyone that helped me during my thesis: Tack så mycket!

Appendix 1

Table 5: The grouping of the landcover type variable in 'coniferous forest', 'deciduous forest', 'Temporarily non-forest' and 'no forest' with the exact description of all the categories. Descriptions are derived from Naturvårdsverket, 2020b.

Coniferous forest	
111. Pine forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of the crown cover consists of pine. Trees are higher than 5 meters
112. Spruce forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of the crown cover consists of spruce. Trees are higher than 5 meters
113. Mixed coniferous not on wetland	Tree-covered areas outside of wetlands 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.
121. Pine forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where >70% of the crown cover consists of pine. Trees are higher than 5 meters
122. Spruce forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where >70% of the crown cover consists of spruce. Trees are higher than 5 meters
123. Mixed coniferous on wetland	Tree-covered areas on wetlands 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.
Deciduous forest	
114. Mixed forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where neither coniferous nor deciduous crown cover reaches >70%. Trees are higher than 5 meters.
115. Deciduous forest not on wetland	Tree-covered areas outside of wetlands 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.
116. Deciduous hardwood forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which >50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
117. Deciduous forest with deciduous hardwood forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which 20 - 50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
124. Mixed forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where neither coniferous nor deciduous crown cover reaches >70%. Trees are higher than 5 meters.

125. Deciduous forest on wetland	Tree-covered areas on wetlands 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.
126. Deciduous hardwood forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which >50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
127. Deciduous forest with deciduous hardwood forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which 20 - 50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
Temporarily non-forest	
118. Temporarily non-forest not on wetland	Open and re-growing clear-felled, storm-felled or burnt areas outside of wetlands. Trees are less than 5 meters.
128. Temporarily non-forest on wetland	Open and re-growing clear-felled, storm-felled or burnt areas on wetlands. Trees are less than 5 meters.
No forest	
2.Open wetland	Open land where the water for a large part of the year is close by, in or just above the ground surface.
3. Arable land	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.
41. Non-vegetated other open land	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.
42. Vegetated other open land	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.
51. Artificial surfaces, building	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.
52. Artificial surfaces, not building or road/railway	Artificial open and vegetation-free surfaces that are not building or road/railway.
53. Artificial surfaces, road/railway	Road or railway.
61. Inland water	Lakes or water-courses.
62. Marine water	Sea, ocean, estuaries or coastal lagoons.

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