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Calving and post-calving habitat use of female moose in two contrasting landscapes

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Moose *Alces alces* is abundant throughout the boreal zone. However, in the landscapes occupied by moose the density of predators and human influence often vary considerably, as do the arrival of spring and phenology of vegetation – all crucial factors for moose, especially during their calving period.

During calving, female moose are faced with a dilemma between choosing a habitat offering high quality forage or one offering protection for the vulnerable calf. This study examined the timing of calving and habitat structure of female moose during and after calving in two areas of Finland with different predator and human densities. Data from 14 GPS-collared moose were integrated with data on landscape composition and forest structure from airborne Lidar.

In both study areas, calves were born in May and mostly in drained forests (with ditches) on peatland soils. After giving birth, females in the more human-influenced landscape moved to more fertile forests on mineral soils, whereas the females in the landscape with little human influence stayed mostly on the drained and pine-dominated peatland forests, which also had less shrub vegetation. Moose were also seen giving birth near human settlements (farms) and staying close to them (<500 m) throughout summer. Thus, females in both study areas illustrated a high degree of adaptability by selecting the highly modified drained landscapes or areas near humans for calving sites over other available landscapes.

Keywords: airborne laser scanning, calving, forest structure, GPS, habitat selection, lidar, moose, predation, remote sensing

It is common for ungulates to have tradeoffs in their habitat selection (Houston et al. 1993, Hebblewhite and Merrill 2009). These involve selecting between habitats that can offer safety against predation and ones that offer the best forage, for instance. These types of tradeoffs are especially true for females with a calf at heel. In general, calving period is one of the most critical life phases for a wild ungulate, and the forced tradeoffs exacerbate the situation: because of the threat of predation, the need for food and the yet poor movement abilities of the new-born calf, the females need to select calving sites that can offer both safety against predation and food for the lactating female and the growing calf (Robbins and Robbins 1979, Oftedal 1985, Bowyer et al. 1998a, b, 1999, Poole et al. 2007, Gurarie et al. 2011, Severud et al. 2019).

Bjørneraas et al. (2011a, b) showed that moose habitat selection is affected by forestry and agriculture: cultivated lands and forest stands with varying structure were used during different times of the day and phases of the summer, and this was further affected by sex and the presence of the calf. In their study, females with calves selected areas with cover more than males or females without calves and even avoided open areas (which are rich in food) during the first months after the calf's birth. In areas with substantial agriculture, studies have shown that moose can use or avoid the open agricultural areas during summer (Olsson et al. 2011, Bjørneraas et al. 2011b), and the avoidance of such areas can be especially strong for females with calves (Bjørneraas et al. 2011b). Such behaviour was also documented in mountain goats *Oreamnos americanus* by Hamel and Coté (2007), who saw females (and females with a calf at heel particularly) to forage closer to their preferred escape routes than males. In addition, the lactating females of the same species were also noted to spend more time foraging than the other groups (Hamel and Coté 2008). Similarly, Bowyer et al. (1998a, b) showed that neonatal black-tailed deer were favouring areas that offered herbaceous vegetation, indicating a behaviour driven by need for most digestible food over predator avoidance. Contrary to this, White and Berger (2001) found that Alaskan moose with a calf at heel did tradeoffs between forage availability and predator avoidance, the latter being a stronger driver of their behaviour. In Fennoscandia, coniferous forests and areas

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of peatland forests have been suggested as important areas for moose due to the presence of both cover and food (Markegren 1974, Bergström and Hjeljord 1987). Therefore, the existence of tradeoffs in calving moose seems more a rule than an exception.

Human presence, via settlements, agriculture and forestry, can have a considerable effect on how moose use the landscape (Bjørneraas et al. 2011a, b, Nikula et al. 2019). Therefore, in sparsely populated and forest-dominated areas, the composition of a moose summer home range has been shown not to differ significantly from that of the overall landscape (Nikula et al. 2004). However, the calving site selection of female moose is a process occurring at a finer scale than that of a landscape, and it has been proven to be affected by factors such as forest structure, topography (slope and elevation), presence of bogs, waterbodies and even islands (Bailey and Bangs 1980, Addison et al. 1990, Langley and Pletscher 1994, Bowyer et al. 1998a, b, Chekchak et al. 1998, Poole et al. 2007, Melin et al. 2016).

In addition to the varying habitat preferences during calving, the timing of the birth event also varies: previous studies have documented females giving birth at the end of April as well as in mid-June, but most typically, moose cows seem to give birth in May (Bertram and Vivion 2002, Bogomolova and Kurochkin 2002, Haydn 2012). The exact timing is highly dependent on factors such as the condition of the mother, the timing of the last autumn rut and conception and the progress of spring (availability of food), which in turn is also dependent on latitude and elevation (Sæther et al. 1990, Bowyer et al. 1998a, b, Keech et al. 2000, Melin et al 2016). In addition to field checks, the birth event has been inferred from the movements of radiotracked females during the calving period: patterns of increased movements were followed by periods of stagnation and, in some cases, a prolonged stay in a relatively small area (Poole et al. 2007, Melin et al. 2016, Severud et al. 2019). The facts that calving females seem to actively search for the spot to give birth in and that they use different forests than other moose at the time (Miquelle et al. 1992, Bowyer et al. 1999, McCullough 1999, Dussault et al. 2005, Bjorneraas et al. 2011a, Melin et al. 2016, McLaren et al. 2017) pose the question of how abundant or scarce suitable calving sites are in the landscape and whether they differ from where the female is found during other times.

Today, such questions can be more easily answered due to advanced techniques in animal tracking and remote sensing, and moose were one of the first species for which the use of tracking collars was tested (Rodgers et al. 1996, Edenius 1997). Since then, the setting has been coupled with satellite remote sensing to analyse their habitat use (Dettki et al. 2003, van Beest et al. 2012, Michaud et al. 2014). Recently, linking GPS radiotracking data with 3D remote sensing, lidar (light detection and ranging), has enabled the description of moose habitat use to an unforeseen degree of accuracy (Melin et al. 2013, 2014, Lone et al. 2014, Oyster et al. 2018). Lidar systems provide three-dimensional point cloud data on the structure of the target area's terrain and vegetation with sub-meter accuracy. For studying moose habitats, the suitability of lidar for the task lies in the fact that the depicted 3D structure of forest and vegetation accurately represents the availability and abundance of real-life attributes such as cover and food availability (Melin et al. 2013, 2014, Lone et al. 2014).

This study combines data from GPS-collared moose with lidar data and other spatial data on landscape configuration to study the structure of the sites where female moose were located during the calving period. The aims are to examine 1) the timing of calving, 2) the forest and landscape structure around the calving sites and 3) how the females' habitat use changes in time onwards from the birth of the calf. To assess the generality of the patterns revealed and their dependence on environmental conditions, the analysis is conducted in two geographic areas. The first area is the coast of Ostrobothnia in western Finland, and the second is a more continental area in Kainuu, eastern Finland.

Material and methods

Study areas

The locations of the two study areas are presented in Fig. 1.

The topographical variation is extremely low in Study area I, where the overall elevational differences are mostly less than 10 m. The forests are dominated mostly by Scots pine *Pinus sylvestris*, but Norway spruce *Picea abies* as well as downy and silver birch, *Betula pubescens* and *B. pendula*, are also present. Peatland soils are common in the area, and the proportion of birch can be relatively high (Luke 2018). Of the total forest area, peatland forests account for ca 38% and forests on mineral soil for about 62%. The intensity of drainage in the peatlands varies between 70 and 75% (Metla 2010). Agriculture is heavily present, with fields scattered across the landscape. Small lakes, ponds and rivers are also common features. Moose density during the study (after the hunting season) was around 3.5 moose per 1000 hectares, which is a typical density in the area (Pusenius et al. 2017). Apart from human hunting, predation was minimal during the study period. At the time of the study, grey wolves were absent from the area, and brown bears were present only in very small numbers (Luke 2018).

Study area II is the opposite in many ways, as both grey wolf and brown bear densities were among the highest in Finland. In addition, the area also hosts wolverines *Gulo gulo* and lynx *Lynx lynx* (Luke 2018). The landscape itself is also highly different and characterised by a varying topography, where ridges, ravines and small hills are common features. The forests are coniferous dominated, the presence of agriculture is minimal and human population density is low. Lakes, rivers and small ponds are typical, as well as peatlands. The proportion of peatland forests of the total forest area is 43%, while forests on mineral soils account for 57% of the total forest area. Of the peatlands, ca 60–65% were drained (Metla 2010). The main tree species are Norway spruce, Scots pine and downy birch. Moose density after hunting was around 2.5–3 moose per 1000 hectares (Pusenius et al. 2017).

Data

Moose data

Moose location data were provided by the Natural Resources Institute Finland. The used GPS collars (Vectronic) stored positions on an hourly basis, together with the date, time,

Figure 1. Location of the two study areas in Finland. Rectangles show the areas covering all movements of the target moose.

temperature and other auxiliary information on the animals' position. Every fourth hour, the collars sent the collected information to a database (Swedish University of Agricultural Sciences 2011) via a GSM-network. The average fix rate of GPS-positioning was ca 99%. The times of no fix seemed to happen with no reference to season or time of day. However, problems with the GSM network caused periods of blackout, from 4 h up to even a few days during the late summer and early autumn of 2009 and especially in June. Because of these reasons, not all positions were usable (as noted in Melin et al. 2014, 2016). The moose were collared in the winter of 2009 by the Natural Resources Institute Finland, in co-operation with the Finnish Food Safety Authority, Evira. Collaring was made in accordance with all regulations regarding animal safety and handling. The moose were located from helicopter, from where they were tranquilised with a dart gun using a ketamine–medetomidine solution.

The data for this study consisted of GPS collar data from 14 females, seven in both areas, who gave birth between 2009 and 2011. Their movements were analysed between 1 May and 30 August, i.e. the period when parturition likely occurred and when females were still nursing the calves. Also, moose hunting begins in September, and this period was therefore excluded from the analysis as the movements during this time would be affected by the hunt (Neumann and Ericsson 2019). The status of the calving females and the fact that the calf was alive were checked for every moose during autumn. Altogether, the data consisted of 20 calving events that occurred during the springs of 2009, 2010 or 2011, 9 in Study area I and 11 in Study area II.

Data on forest and landscape structure

Forest structure was assessed with metrics calculated from lidar data and with raster maps from the Finnish multi-source National Forest Inventory. The lidar data were downloaded from the open access file service of the National Land Survey of Finland (NLS 2018) and used to gain 3D estimates on the density of the vegetation throughout the vertical profile of the forest in addition to canopy height. Details about the lidar data collection and processing are provided in Melin et al. (2016). The raster maps of the forest structure provided information about the volumes of pine, spruce and deciduous species, mainly birch with minor portions of grey alder *Alnus incana* and European aspen *Populus tremula*. These raster maps were downloaded from the file service provided by the Natural Resources Institute Finland (LUKE 2018) and are based on data from the Finnish National Forest Inventory and Landsat 5 TM satellite images. These datasets provided information about the tree species composition of the forests in the study areas.

Data about the landscape structure were also obtained from the National Land Survey. These data contained information about the location of waterbodies, rivers, roads, agricultural fields and peatland areas and were used to assess the characteristics of the landscape beyond the forest structure.

Methods

Identifying calving times and sites

The time of calving was assessed based on the females' movements. The method is based on the assumption that movement patterns during calving can be distinguished from the movements outside this period: the female herself, at the moment of giving birth, cannot move as she did before, whereas the newborn calf has also restricted moving abilities during the first days after calving, which would show in the females' behaviour as a prolonged stay around the same location (Poole et al. 2007, Severud et al. 2015, McLaren et al. 2017). This was attainable from GPS data by looking at the displacement between consecutive locations as well as the total amount of movements in a 24-h period, for instance. Field validations were also done in both study areas to check when the females had given birth (based on the sighting of a calf). These field checks were done for four of the moose in total, and the results were used as auxiliary information to guide the temporal assessment of the occurrence of calving events from the GPS data. That the calf had survived and was at heel during the whole summer was confirmed for every moose during autumn (after the hunting season).

Linking the forest and landscape structure to moose movements

To analyse the landscape in which the moose moved during summer, a grid of 100 × 100-m cells was created over the females' full summer home ranges, after which all the grid cells that intersected with any GPS locations were chosen for further analysis to calculate cell-specific metrics about the structure of the forest and the landscape. These included Euclidean distances from the cell centroid to the nearest waterbody (lake or pond), agricultural field, peatland area, ditch and roads. The roads were classified into two classes based on their width and the number of lanes: class I (5–8-m wide, two lanes) and class II (3–5-m wide, one lane). Highways with four or more lanes did not occur in the study areas. In addition, metrics about the volume of different tree species in each cell were calculated for the tree species groups pine, spruce and deciduous (birch, aspen, alder) trees. The deciduous tree species were merged into one group as the volumes of aspen and alder are comparably low. The 100-m cell was chosen as the study unit to account for the potential deviations in GPS positioning. These deviations, up to 20–30 m, were assessed from cases where a collar had dropped and was positioning itself whilst lying motionless on the ground. In addition, it was thought that the 100 × 100-m environment is a valid area to assess a metric such as average canopy height or the volume of a tree species, which was already assessed in a unit of $m^3 ha^{-1}$.

For analysing the more detailed structure of the forest at the locations where the moose were assumed to have given birth, the area of the assumed calving site was delineated with minimum concave polygons based on the GPS-locations (Fig. 2), and the same metrics as described above were calculated for the delineated calving sites. In addition to the metrics of landscape structure, lidar point cloud metrics of forest structure were also calculated for each of the calving sites. All the created metrics used in the analysis are listed in Table 1.

Statistical analysis

To analyse the female positions in relation to the forest and landscape structure, the GPS-location data from consecutive days were combined into a new variable, *CalvingPeriod*. The variable split the whole study period at three-day intervals. Individually for each moose, the cells they used during the first three days of assumed calf birth were *CalvingPeriod* value 1, the cells used during the following three days were given the value 2, the ones used during the next three days were given the value 3 and so on.

In the next phase, the *CalvingPeriod* variable was used as a factorial predictor against the metrics describing the

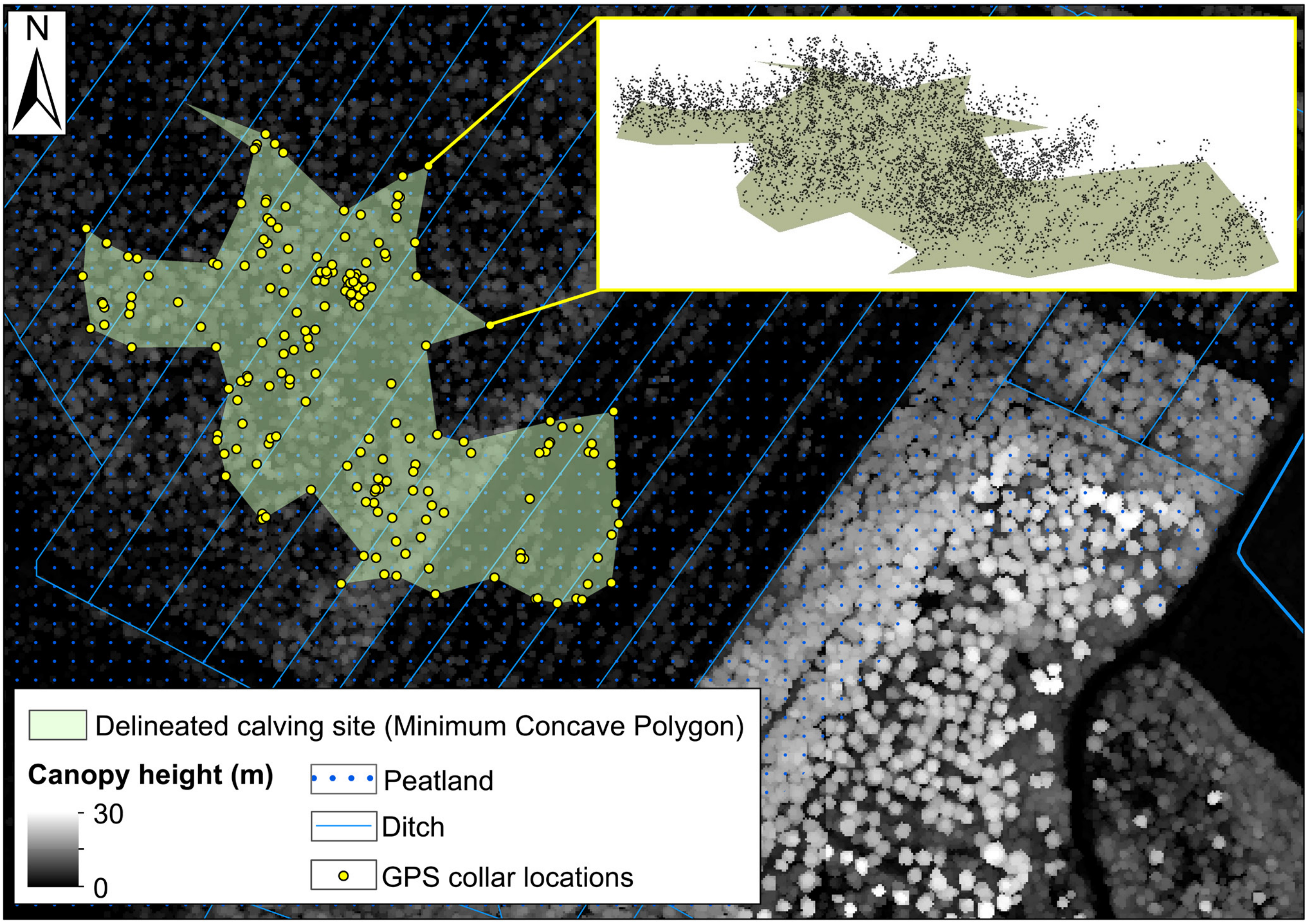

Figure 2. An example of using the minimum concave polygon method to delineate a calving site (Moose 4829 in 2010 – Study area I) and of extracting lidar point cloud data from this site.

structure of the forest and the landscape around the females (Table 1). Modelling was done with linear mixed-effects models (LME); they extend the basic linear regression and can therefore handle grouped data via random effects. Here, the individual 'moose id' was used as the random effect. Models were created separately for each of the variables described in Table 1 and separately for the two study areas. In each model, the metric of interest was designated as the response variable (continuous), with *CalvingPeriod* as the factorial predictor.

The models quantified the effect that time since the birth of the calf (as indicated by different values of *CalvingPeriod*)

Table 1. Metrics used to analyse the structure of areas used by females during the study period.

Metric	Explanation
Landscape level metrics	
d_water	Euclidean distance (in meters) to the nearest lake or pond
d_ditch	…to the nearest ditch
d_road	…to the nearest road (two classes)
d_field	…to the nearest agricultural field
d_peat	…to the nearest peatland soil
VolSpruce	Volume of spruce (m^3 ha^{-1})
VolPine	Volume of pine (m^3 ha^{-1})
VolDeciduous	Volume of deciduous trees (excl. birch) (m^3 ha^{-1})
Lidar point cloud metrics	
MaxHeight	Maximum lidar echo height within this cell/calving site
CanopyCover	Vertical canopy cover. Estimated from the proportion of echoes above 1 m. A *p1* value of 0.9 would mean that 90% of all the echoes within this cell/calving site came from vegetation above 1 m. The method of calculation gives values that are highly correlated with field-measured vertical canopy cover (Korhonen et al. 2011, Melin et al. 2017)
ShrubCover	Proportion of echoes between 0.5 and 5 m. A *p0_5* value of 0.3 would mean that 30% of all the echoes within this cell/calving site came from vegetation between 0.5 and 5 m in height. This metric describes the amount of the shrub layer vegetation in relation to the total amount of vegetation.

had on the metrics of the landscape and forest structure, i.e. the models gave information about how the habitat around the female moose changed at three-day intervals. The aim of the modelling was thus to assess the values of the metrics in Table 1 against time, and by doing so, to see how the structure of the habitats changed from the time when the female gave birth to the time when she, later in the summer, was moving with the calf at heel, and whether any observed changes were statistically significant. All modelling was done using the R software (<www.r-project.org>) and the function lme from the package 'nlme' (Pinheiro et al. 2018).

Results

Timing of calving

In general, the calving events were detectable from the females' movement patterns. They were shown as a period of decreased movements when compared to movements before and after birth. Figure 3 shows the assumed dates of calving for each moose and examples of the described pattern of decreasing movements during the birth event.

All assumed calving events took place in May and mostly around and before mid-May. The length of the estimated period varied, because in some cases, the females stayed in the same small area for up to two weeks, and therefore, the exact day of the birth event was impossible to infer based on movement data alone. After giving birth, the female and the assumed newborn calf, started to gradually widen their movements, and prolonged stays at any single spot were not detectable thereafter.

Structure of the calving sites

The structure of the exact calving sites largely differed between the two landscapes (Table 2). Yet, there were also interesting similarities. The calving sites in Study area I were, on average, located closer to agricultural features, as these are common in the area. Similarly, the road density in Study area I is, overall, higher, which may have resulted in the calving sites being closer to roads as well (although this difference was only minor – Table 2).

A common phenomenon in both areas was that the calving sites were most often located on peatland soils or very close to them. In both study areas, the females could have chosen forests on mineral soils as well, but nearly every moose gave birth on or very near to peatlands. These are typically mires dominated by Scots pines in both study areas, which can also be seen from the highest volumes of pines at the calving sites (Table 2). Most of the peatlands in both study areas were also drained, which did not seem to be negative for the females, as can be seen from simultaneously occurring small distances to ditches and peatlands (Table 2). The forests at the calving sites were comparably high, with the maximum heights being close to 20 m in both study areas and over 25 m in some cases. However, the density of the canopy varied greatly not just between the two study areas, but also within them. Some calving sites were found from peatland areas with low amounts of vegetation (moose 4840 in 2009 – Table 2), while some had nearly all of their lidar echoes coming from above 1 m, indicating a very dense canopy layer (moose 4483 in 2009 – Table 2).

The majority of the variables used to assess the structure of the calving sites did not show significant differences between the two study areas. Those that did (*dField*, *dWaterbody*, *Vol_Spruce*: $p < 0.05$) can also be linked to different landscapes than to differences in calving strategies. The amounts of fields and roads in Study area I, for instance, are higher by default when compared to Study area II.

Changes in female habitat use in relation to time

When assessing the entire study period, there were clear changes in relation to the forest and landscape type the females were found in, depending on the summer phase. In addition, there were major differences between the study areas. Figure 4 plots the predictions from the mixed-effects modelling. That is, the structure of the areas occupied by the females is plotted against time (*CalvingPeriod*); for instance, how the females' distance to peatlands varies during the summer at three-day intervals. The images only contain the metrics that showed variations during the calving period. There were no clear temporal patterns in relation to the distances to roads, rivers or waterbodies in either of the two study areas. In addition, distances to ditches are indicative of the distances to peatlands, mainly because the peatland used by the females in both study areas were commonly drained.

In Study area I, females stayed in forests with a height of ca 19–21 m (Fig. 4 – *h*Max, *red line*) and where the main structural component changing over time was the density of vegetation and understorey. Here, the densest forests were used immediately after giving birth, but as summer progressed, the females were generally found in forests with less understorey and vegetation (Fig. 4 – *CanopyCover*, *ShrubCover*, *red line*). A similar trend was observed in Study area II, where the densest forests were also used immediately after birth (Fig. 4 – *CanopyCover*, *ShrubCover*, *blue line*). Tree species composition, in either study area, did not show any major changes. The females were mostly found in mixed-forests where Scots pine (based on volume) was the dominant species (Fig. 4– *VolPine*, *VolSpruce*, *VolBirch*). In Study area I, the proportion of deciduous species was higher in mid-summer, as the proportion of the two coniferous species dropped simultaneously (Fig. 4, *VolPine*, *VolSpruce*, *red lines*). For Study area II, the analysis shows a clear rising trend in the volume of deciduous species at the female's locations later in summer (Fig. 4, *VolBirch*, blue line).

In Study area II, the clearest pattern was the preference towards peatlands during the entire analysis period. Calving occurred on peatlands, after which the female and the calf at heel mostly preferred forests on peatland soils, especially towards the end of summer, when the preferred peatlands had also more deciduous trees (Fig. 4 – *dPeat*, *VolDecid*, *blue line*). This was contrary to Study area I, where the females began to move further away from peatland forests towards the end of summer (Fig. 4 – *dPeat*, *red line*). Cultivated areas also seemed to have an effect: in Study area II, where agriculture is minimal, the females showed a very strong shift towards agricultural fields at the end of summer (Fig. 4 – *dField*, *blue line*). On contrary, in Study area I, which a

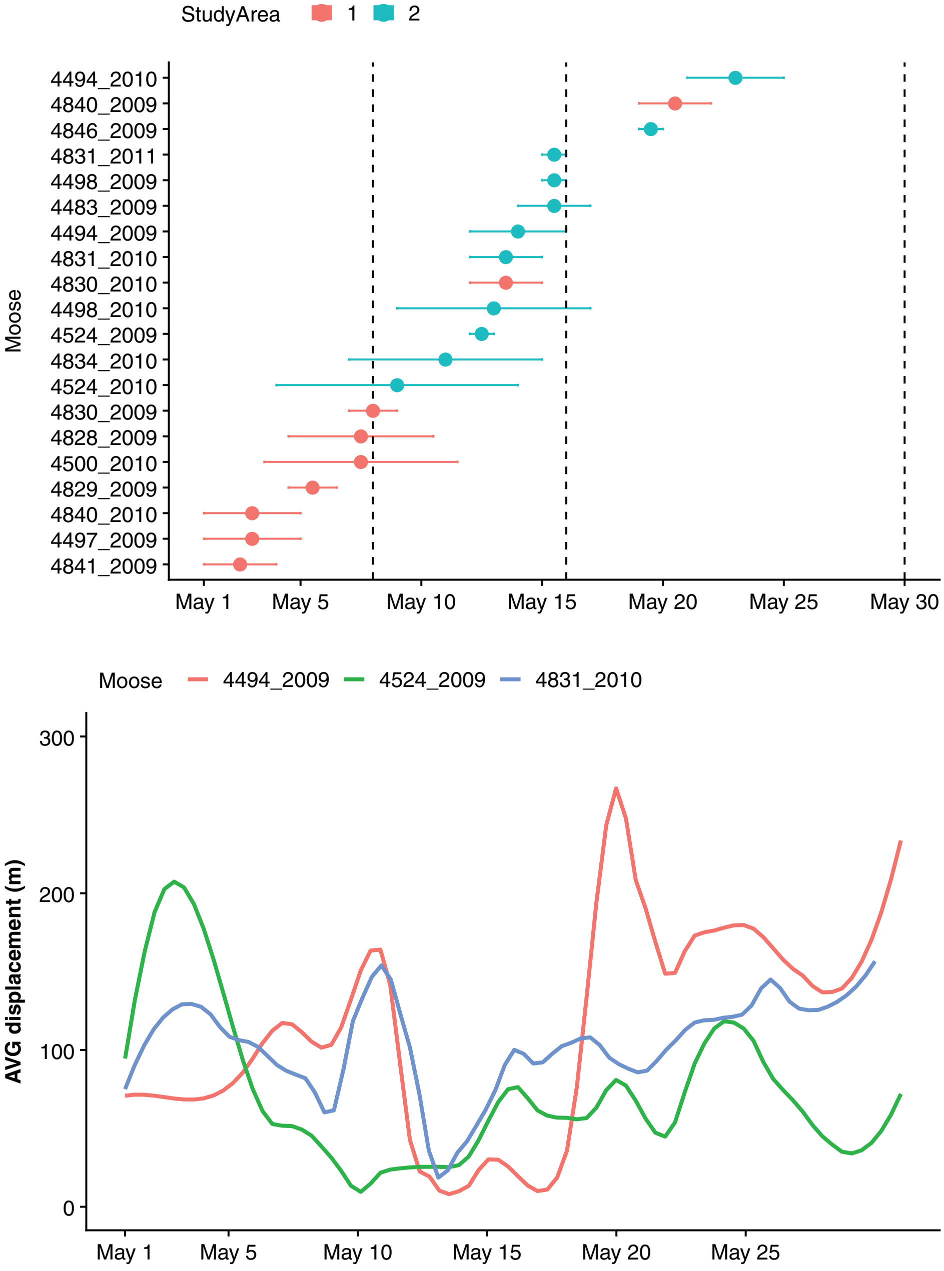

Figure 3. Top: assumed dates of calving of each moose (points) and the error in estimating this day due to a prolonged period of decreased movements (horizontal whiskers). The dashed vertical lines show days when female moose were field-confirmed to be mobile with calves. Bottom: examples of moose movements in May from three moose. Y-axis shows the average displacement between two consecutive GPS-locations during the given day. The lines are smoothed averages that were used to visualize the phenomenon.

higher proportion of cultivated fields, females were mostly within 500 m from agricultural fields.

Discussion

This paper combined GPS tracking with remote sensing and additional data about landscape structure to study female moose habitats during and after calving. The focus was on analysing the timing of births and the vegetation and landscape structure of the calving sites. Further, we studied whether females changed their habitat as summer progressed and the calf at heel grew. The used method of integrating GPS tracking with remote sensing, lidar in particular, has been proven useful in assessing where and in what kinds of forests moose are found (Lone et al. 2014, Melin et al. 2016, Oyster et al. 2018).

The study revealed that calving occurred solely in May, but with minor differences between the study areas. In Study area I, most birth events occurred in the first half of May, whereas in Study area II, they predominantly occurred around mid-May. These differences are likely to be related to phenological differences between the study areas. A study by Bogomolova and Kurochkin (2002) highlights the importance of phenology on the timing of calving; the authors found that 70% of the studied moose were born in the first

Table 2. Structure of the female calving sites based on landscape- and lidar metrics within the minimum concave polygons (Fig. 2).

			Average volume (m^3 ha^{-1}) of			Euclidean distance (m) to						Forest structure			
Study area	Moose	Year	Deciduous	Spruce*	Pine	Peatland	Ditch	Road I	Road II	Field*	Waterbody*	Max height	Canopy cover	Shrub cover	Area (ha) of calving site
1	4497	2009	20.2	21	102.3	0	0	3529	2030	901	1812	23.34	0.8	0.03	1.04
1	4500	2010	37.6	65.9	32.9	141	112	1350	391	100	3516	27.84	0.67	0.13	7.55
1	4828	2009	23.7	17.2	116.9	0	0	1055	1250	255	2695	21.35	0.62	0.07	2.31
1	4829	2009	11.2	27.4	119.7	158	150	364	1188	316	7233	21	0.78	0.05	1.82
1	4830	2010	19.5	44	61.3	50	206	3667	112	765	539	7.38	0.58	0.58	0.1
1	4830	2011	18.4	37.9	106.3	71	71	4159	224	492	255	17.11	0.69	0.22	1.02
1	4840	2009	6.1	7.4	5.9	316	255	3806	2396	502	2425	19.11	0.21	0.19	1.79
1	4840	2010	34	83.9	44.6	50	224	2804	1626	141	1200	24.01	0.83	0.12	1.45
1	4841	2009	60.7	15.2	34.2	50	711	1850	320	150	1301	20.68	0.56	0.1	0.23
Mean values			**26**	**36**	**69**	**93**	**192**	**2509**	**1060**	**402**	**2331**	**20.20**	**0.64**	**0.17**	**1.92**
2	4483	2009	10.9	25.3	98.7	50	206	1883	2067	1286	283	27.65	0.75	0.05	0.31
2	4494	2009	32.1	21.8	58.8	0	0	728	982	2482	495	18.9	0.56	0.1	1.93
2	4494	2010	14.1	10.6	54.6	0	0	158	472	1701	1365	18.51	0.51	0.09	6.87
2	4498	2009	13.3	19	47.8	100	71	2484	269	550	559	25.64	0.58	0.26	3.22
2	4498	2010	20.7	42.2	77	0	0	350	453	255	200	17.54	0.64	0.08	1.41
2	4524	2009	17.2	7.4	45.3	0	0	1790	2121	2051	381	15.07	0.45	0.17	1.09
2	4524	2010	17.9	20.5	73.1	0	0	292	320	532	602	16.22	0.74	0.19	3.99
2	4831	2010	4.2	2.2	32.2	0	50	2132	2930	1503	1909	20.46	0.27	0.07	1.35
2	4831	2011	7	1.2	31.4	0	0	2750	3233	1471	1209	16.45	0.29	0.16	4.2
2	4834	2009	28.3	15.5	56	224	0	9458	250	112	141	25.24	0.62	0.16	0.77
2	4846	2009	15.8	7	33.5	0	200	4561	3200	4226	532	22.05	0.46	0.09	3.75
Mean values			**17**	**16**	**55**	**34**	**48**	**2417**	**1482**	**1470**	**698**	**20.34**	**0.53**	**0.13**	**2.63**

* Indicates significant differences between Study area I and II as based on Welch's t-tests with $p < 0.05$.

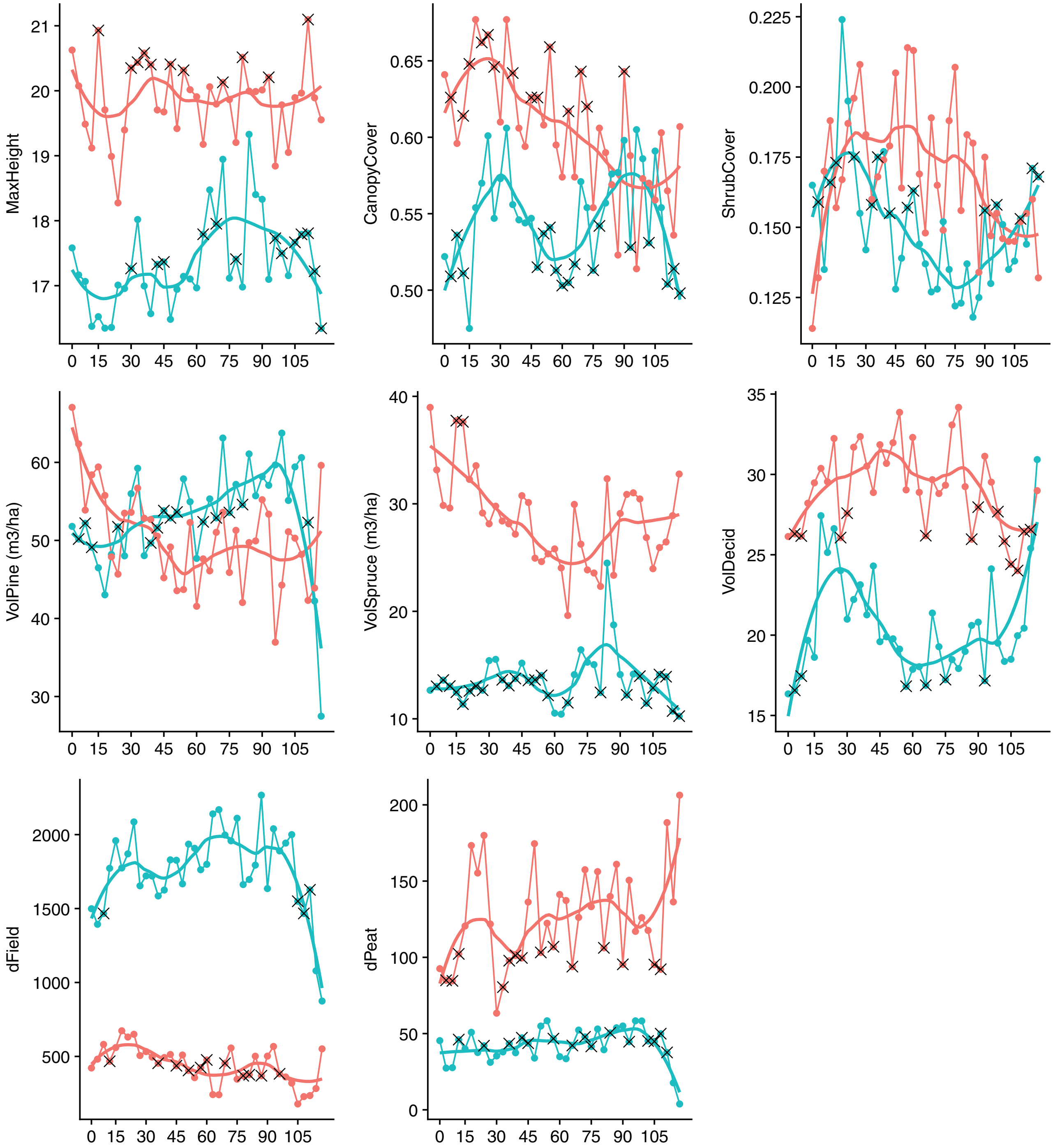

Figure 4. Changes in forest and landscape structure around females in relation to days since calving (x-axis). The distance between the points along the graph lines is three days (*CalvingPeriod*). The red lines indicate Study area I, the blue line indicates Study area II. The solid line overlaying the point-lines shows a smoothed average trend. A cross overlaying a point indicates that, in terms of the variable in question, the area where the females were during this day of *CalvingPeriod* did not differ significantly ($p < 0.05$) from the area she gave birth in.

half of May, which they attributed partly to the progress of spring and the abundance of green emerging vegetation, the main food for the mother and the calf at that time. Their study was conducted in the Kostroma region in Russia, which is further south-east from our study areas. In the Alaska/Yukon region, Bertram and Vivion (2002) found calves to be born between 14 May and 9 June, with the median date 24 May. In Sweden, Haydn (2012) documented mean calving dates between 12 May and 8 June, with the majority of the recorded events occurring in the second half of May. Our Study area I was located slightly further south and on the western coast of Finland, where temperatures are generally milder than in Study area II. Study area I has less harsh winters, less snow and thus an earlier arrival of spring, which could explain the noted differences in the assumed calving dates (Fig. 3).

Analysis on the structure of the exact calving sites showed that coniferous-dominated forests on peatland soils were most frequent calving sites in both study areas, but especially in Study area II (Table 2). In addition, drained peatlands were specifically acceptable as habitats in both study areas. McLaren et al. (2017) also found coniferous stands as most frequent calving sites, which they suggested was linked to predator avoidance. Also, in our study, in addition to being on peatlands, the calving sites were mostly pine-dominated, which is contrary to what Haydn (2012) found in Sweden. In their study, the calving sites were most often located in broadleaved forests, which are more abundant in their region than in either of our study areas. Bowyer et al. (1999) suggested calving site selection to be driven by three factors: forage, visibility and aspect. In our study cases, the use of peatland sites might be explained by forage: peatlands (and the ditches) grow plants such as willow *Salix* sp., bog whortleberry *Vaccinium uliginosum*, water horsetail *Equisetum fluviatile* and yellow water-lily *Nuphar lutea*, which are all plants favoured by Fennoscandian moose for food (Hjeljord et al. 1990). The different landscapes between the two study areas did cause some differences in relation where the calving sites were located: in Study area I, the density of agricultural features is the highest in Finland, while it is amongst the lowest in Study area II. As a result, the calving sites were closer to fields in Study area I (Table 2). However, there were four cases in Study area II where the females' calving site was located very close (<500 m) to fields and active farms. The size (area) of the exact calving sites was also estimated based on the females' movements, which gave results in line with past studies: Bowyer et al. (1999), for instance, saw most female moose staying within ca 100 m from the place where the calf was born, which agrees well with our estimates of 1.5–2 hectares as the average size of the calving site.

Similarities and differences were found between the study areas also concerning the sites where the females stayed with their calf at heel. The favouring of peatlands was evident especially in Study area II, where the females were found mostly in peatland forests during the whole survey period, whereas in Study area I, they began to move gradually away from peatlands as the summer progressed (Fig. 4 – *dPeat*). Bjorneraas et al. (2011b) found that females with calves selected forests over all other land cover types more frequently than males or non-calving females. In our study, the calving females also stayed in the forested landscape during the whole summer, but more often on peatland forests, even though forests on mineral soils would have been available as well. The role of agricultural features was basically non-existent in our Study area II due to their minimal amount. Due to this, the clear shift closer to agricultural fields by the female moose at the end of the summer suggests that this pattern is due to preference: the fields are scarce features in the landscape that the females would have had to search for. In Study area I, the females were considerably close (mostly less than <500 m) to fields throughout the whole summer, which does not imply that it was obligatory. Even though agriculture is heavily present in Study area I, the females, had they wanted to do so, could have easily moved further away from fields. We do not have data on what crops were grown in the fields, but earlier studies have confirmed that, when available, moose often use agricultural features as a source of food (Bjørneraas et al. 2011b). However, the extent to which this affected the females of our study cannot be verified. Still, the moose in Study area I were at least not avoiding the fields, since they were always at their near surroundings, and those in Study area II were clearly preferring areas closer to fields at the end of the summer.

The fact that calving females are generally affected by both the need for cover and food was supported by our analysis on the 3D structure of forests. This showed that the density of vegetation at the females' locations was at its maximum during the moment of giving birth (Fig. 4 – *pShrub*). This, combined with the fact that the drained peatlands would grow the food plants listed earlier, is in alignment with, for example, Dussault et al. (2005), who found females with calves to prefer habitats that offer both food and cover. Poole et al. (2007) also found support for this view: after calving, the female moose in their study area selected either higher elevations to significantly reduce the risk of predation or areas with higher forage values, but with a slightly reduced predation risk (close to water, increased visibility). Indeed, after the birth event, the females began to use areas where the overall vegetation density, also in the understorey layer, was less than where they gave birth (Fig. 4, *CanopyCover*, *ShrubCover*) – a pattern also observed by White and Berger (2001). Contrary to these findings, Severud et al. (2019) found that female's calving sites offered excess visibility at the expense of nutrient availability (as made evident by bark stripping). After giving birth, the habitat selection then turned to areas containing more forage, which was evident especially during the peak lactation period. Even though it is known that moose and their calves are favoured prey for Finland's grey wolf and brown bear population (Gade-Jorgensen and Stagegaard 2000, Lavsund et al. 2003, Gurarie et al. 2011), our research setting did not allow us to explicitly assess whether the calving females showed tradeoffs between predator avoidance and forage. A study of wolf habitat use that overlapped our study area and the study period showed that wolves preferred open woodland habitats over bogs, and that they avoided bogs while homing, but showed a weak preference to them while hunting (Gurarie et al. 2011). Therefore, we cannot state whether the preference of our calving females to bogs or to areas with more dense vegetation were due to better forage availability, predator avoidance or both. Furthermore, unlike in Alaska, where the moose populations have been subjected to a continuous high-level predation by bears and wolves (White and Berger 2001), the situation in Finland is different as these carnivores were extirpated from large parts of the country in the 19th and 20th centuries (Pulliainen 1993, Ermala 2003).

Overall, our results confirm the earlier studies that habitat selection during the calving period is a dynamic process where vegetation and landscapes with different kinds of structures are favoured during different phases of the calving period. However, our results also show that the female moose adapts to specificities of vegetation (e.g. drained peatland that have only occurred since the 1960s) if they serve its basic needs for forage or shelter. In the future, the topical question is to assess how a changing climate (Ruosteenoja et al. 2016) may impact vegetation and landscape structures and, consequently, how this may influence the behaviour of female moose during the calving period.

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