



Is moose (*Alces alces*) habitat selection affected by wolf (*Canis lupus*) re-establishment in south-central Sweden?



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Abstract:

To avoid predation, prey take behavioural decisions to decrease the probability of being killed by a predator. Indeed, prey may use different habitat types in order to avoid predator detection or to escape an attacking predator. After being absent for more than 100 years in Scandinavia, wolves (*Canis lupus*) naturally re-established in the early 1980's and offer a unique opportunity to study the effect of wolves on their main prey, moose (*Alces alces*). I used Global Positioning System (GPS) locations from moose and wolves to study the impact of wolf exposure on moose habitat selection within their home ranges. By creating a landscape of risk based on wolf locations, and by comparing individual moose habitat selection before and after wolf re-establishment, I showed that moose habitat selection was not affected by wolf presence. Sex and reproductive status did not influence moose habitat selection patterns. However seasonal differences in food availability and climatic conditions governed moose habitat selection. Moose selected strongly young forest during winter, whereas during summer they selected forest offering cover during the day and open areas during the night. The lack of moose response to wolf predation risk confirms previous findings in Scandinavia and may be explained by an insufficient time for moose to adapt their behaviour to wolf presence. Alternatively, the high rate of hunter harvest of moose during the last century may have shaped their behaviour and prevented moose to respond to wolf presence.

Key words: moose (*Alces alces*) - wolf (*Canis lupus*) - habitat selection - GPS - landscape of risk

Résumé:

Afin éviter la prédation, les proies prennent des décisions comportementales dans le but de diminuer la probabilité de se faire tuer par un prédateur. En effet, les proies peuvent utiliser différents types d'habitat pour éviter se faire détecter par un prédateur ou pour échapper à leur attaque. Après avoir été absent pendant plus de 100 ans en Scandinavie, les loups (*Canis lupus*) se sont naturellement rétablis dans le début des années 1980 offrant une opportunité unique pour étudier l'effet de leur recolonisation sur leur proie principale, l'élan (*Alces alces*). J'ai utilisé les localisations GPS (Global Positioning System) d'élans et de loups pour étudier l'impact de l'exposition des loups sur la sélection des habitats des élans à l'intérieur de leurs domaines vitaux. En créant un paysage du risque basé sur les localisations des loups et en comparant la sélection des habitats des élans avant et après la recolonisation des loups, je n'ai pas pu mettre en évidence le fait que la présence de loups influençait la sélection des habitats des élans. Il n'y avait pas de différence de sélection de l'habitat suivant le sexe ou le statut reproducteur. Cependant des différences saisonnières en terme de disponibilité alimentaire et de conditions climatiques régissaient la sélection des habitats des élans. Les élans sélectionnaient fortement les jeunes forêts pendant l'hiver, alors que pendant l'été ils sélectionnaient le couvert forestier al journée et les zones ouvertes pendant la nuit. Le manque de réponse des élans au risque de prédation des loups confirme les résultats précédemment trouvés en Scandinavie et peut s'expliquer par un temps insuffisant pour que les élans adaptent leurs comportements à la présence du loup. De plus le taux élevé d'élan prélevé par la chasse pendant le dernier siècle pourrait avoir façonné leurs comportements et empêché les élans de répondre à la présence des loups.

Mots clés: élan (*Alces alces*) - loup (*Canis lupus*) – sélection de l'habitat - GPS – paysage du risque.

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1. Introduction

In predator-prey systems, prey may conduct behavioural decisions to decrease the probability of lethal encounters with predators (Lima and Dill 1990). Behavioural anti-predator strategies adopted by prey may include keeping vigilant to detect predators (Laundré et al. 2001), increasing group size (Caro 2005), increasing distance to predators (Edwards 1983) and using special habitat structure to hide from predators or escape from the predators once encountered (Hebblewhite et al. 2005). Anti-predator behaviour might have individual cost in terms of fitness, and may also have consequences on population dynamics levels (Creel and Christianson 2008). When prey alter their behaviour in response to presence of predators and the responses carry costs, it results in so-called risk effects. (Creel and Christianson 2008). For instance, if the best feeding habitat patch is also the most risky patch, prey may trade-off between energy gain and the risk of being killed. For elk (*Cervus elaphus*) an extended search for cover when wolves (*Canis lupus*) were present led to a lesser energy food intake (Creel et al. 2005, Christianson and Creel 2008) and caused a lower calf survival (Creel et al. 2007, Garrott et al. 2009).

Anti-predator behaviour may differ according to prey characteristics (Lima and Dill 1990). For instance, sex and reproductive status of prey might affect their response intensity (Edwards 1983, Dussault et al. 2005, Bjørneraas et al. 2011b). Indeed individuals that are more subject to predation are expected to express a higher response to predation risk (Creel and Christianson 2008). According to the predation sensitive hypothesis, both food and predation affect prey population dynamics as animals tend to take higher risk when food availability is limited (Sinclair and Arcese 1995). Then if the better habitat patch is also the more risky, prey would have to trade-off between energy gain and the risk of being killed.

After being absent for more than 100 years in central Sweden, wolves successfully re-established in the early 1980's (Wabakken et al. 2001) and reached a population size of 235-266 individuals in the winter 2010/2011 (Wabakken et al. 2011). In Scandinavia, wolves mainly prey on moose making up 95% of the biomass ingested in winter (Sand et al. 2005). Calves are strongly selected by wolves in both winter (70%: Sand et al. 2005) and summer (90%: Sand et al. 2008). Predation events have also been shown to occur mainly during night-time (Sand et al. 2005)

Moose (*Alces alces*) is a typical browser (Cederlund et al. 1980). Moose habitat selection is well documented and may be dependent on the seasonal forage availability (Cederlund and Okarma 1988, Olsson et al. 2011, Van Beest et al. 2010, Bjorneraas et al. 2011b), daylight (Bjorneraas et al. 2011b) and sex (Bjorneraas et al. 2011a) and dependent on the reproductive status of the cow (Bjorneraas et al. 2011a, 2011b). Bjorneraas et al. (2011a) found that moose select mainly high productivity coniferous forest which provides good forage and cover. Among habitat types moose generally select early successional forests over mature coniferous forest and avoid mires and agricultural areas (Cederlund and Okarma 1988, Olsson et al. 2011). As field layer is less accessible when covered by snow, moose tend to increase selection of pine forest during winter (Bjorneraas et al. 2011b). Avoidance of areas with high human activity has also been shown (Lykkja et al. 2009) and Bjorneraas et al. 2011b found that variation in short-term utilisation of habitat types providing cover and forage was likely a behavioural response to predation risk by humans. However all of these studies have been conducted in areas where moose were free from their main natural predator (e.g. wolves).

Natural wolf re-establishment in Scandinavia offers a unique opportunity to quantify the impact of a predator on moose behaviour. In this study, I used data from GPS-collared moose and wolves to examine how wolf risk exposure affects moose habitat selection. I predicted that (1) moose will modify their habitat selection in order to avoid wolf detection and encounter, (2) a sex-specific response to wolf-exposure with strongest response to predation risk for females with a calf at heel, (3) a seasonal-specific response with intense response to predation risk in summer compared to winter, and (4) a stronger response of moose to predation risk during the night compared to the day.

2. Methods

2.1. Study area

The study area (730 km²) encompassed the Grimsö wildlife research area located in south-central Sweden (59-60°N and 15-16°E; *Appendix 1*), within the southern boreal zone. Elevation ranges from 100 to 150m (digital elevation model, Geographical Data Sweden, GSD, National Land Survey of Sweden).

The annual mean air temperature is 5°C, in winter temperatures are usually down to -20°C and up to 25°C in summer (Vedin 1995). Mean daily temperature is 16°C and -4°C in July and January, respectively (Vedin 1995). Total annual mean precipitation is 600-700 mm, of which 30% (180-210 mm) falls as snow, normally covering the ground from December to late March, and the mean snow depth is 20-30cm (Alexandersson and Andersson 1995). The period of vegetative growth (i.e. total number of days with a mean temperature above 5°C) is 160 days (Alexandersson and Andersson 1995). The area consists of 78% forest, 8% bogs and swamps, 6% lakes and river, 8% meadow and farmland (see Table 2 and Appendix 1 for details). Mature forest stands are dominated by Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*) and birch (*Betula pubescens* and *B. pendula*) (Rönnegård et al. 2008). The forest has been intensively logged for several centuries for timber and pulp. Forest management is intensive with clear cut of 0.01-0.3 km² patches and old forest replaced by planting or natural regeneration (Swedish forestry agency <http://www.skogsstyrelsen.se>). Field layers consist mainly of dwarf shrubs, especially blueberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*) on the forested land, with dwarf birch (*Betula nana*) and heather (*Calluna vulgaris*) in the bogs (Månsson et al. 2007).

Aerial counts of moose were performed in 2002 and 2006 and the estimated densities were 1.2 and 0.8 moose/km² respectively (Rönnegård et al. 2008). The moose population is harvested annually, and hunting is the main mortality factor (Rönnegård et al. 2008). Other ungulates within the study area included roe deer (*Capreolus capreolus*), whose population densities ranged between approximately 1-5 roe deer/km² (Rönnegård et al. 2008).

In 2003, wolves naturally re-established in the study area (Wabakken et al. 2001, Wabakken et al. 2004). From 2003 to 2011 wolves' presence were continuously registered, by snow tracking until 2005 and by using both snow tracking and GPS data after 2005 (*Table 1*). First the Uttersberg pack established in the area in 2003 (Wabakken et al. 2004), and had a stable and small home

range (Table 1) compared to the average size of wolf home range in Scandinavia (900 km²) (Sand et al. 2007). However in 2009, the Uttersberg pack was replaced by the Hedbyn pack which had a larger home range than the previous Uttersberg pack (Table 1 and Appendix 1). Two other large predators that occur within the area are brown bears (*Ursus arctos*) (can also prey on moose, especially on new born calves; Swensson et al. 2007) and lynx (*Lynx lynx*) (main prey is roe deer; Liberg et al. 2010). However few individual brown bears were present in the study area (Swensson et al. 2010). Lynx naturally re-colonized the study area in 1995-1996 after having been absent from the area for >30 years (Liberg and Andrén 2006).

Table 1. Wolves presence from wolf snow tracking and GPS data within the Grimsö research area.

Winter	Number of wolves in the pack	Reproduction ^c	Alpha wolf collared ^d	Territory	Home range size (average km ²)
2003-2004 ^a	2	Yes		Uttersberg	
2004-2005	4-6	Yes	M	Uttersberg	
2005-2006	9	Yes	M-F	Uttersberg	≈500
2006-2007	4-6	No	F-M	Uttersberg	
2007-2008	2	Yes	F-M	Uttersberg	
2008-2009	4-5	No	M	Uttersberg	
2009-2010 ^b	2	No	F-M	Hedbyn	≈1000
2010-2011	2	Yes	F	Hedbyn	

^aWolf pair was first detected during the winter 2003-2004 and probably established during the summer 2003

^bThe Uttersberg pack was replaced by a new pair (Hedbyn) and extended the previous Uttersberg pack home range.

^cIf pack successfully reproduced

^dM: male and F: female

2.2. Moose and wolves data

Adult moose ($n_{\text{total}}=37$) were captured in March 2007 ($n_{\text{females}}=20$, $n_{\text{males}}=4$) and 2010 ($n_{\text{females}}=10$, $n_{\text{males}}=3$) and were fitted with Global Positioning System (GPS)/Global System for Mobile Communications (GSM) collars (GPS/GSM Plus 4D; Vectronic Aerospace GmbH, Berlin, Germany) to acquire two locations every second hour. Two of the moose (1 female and 1 male) have been re-captured and fitted with a new GPS collar at the second capture event. Moose were tranquilized by dart gun from helicopter (for more details about capture handling see Arnemo et al. 2003). Age at capture was on average 5.4 years old (ranged: 1-16 years old). During the study period (2007-2011), a total of 331 726 locations were recorded with a 99.2% locations rate. Each

moose provided between 886 and 22 648 locations ($\bar{x}=8\ 345$) (*Appendix 2*). With this high success rate, bias in habitat selection estimates owing to specific detection rate is expected to be low (Frair et al. 2010)

Wolves were immobilized in winter from the air according to standard procedures presented in Arnemo et al. (2004). Wolves were equipped with GPS neck collars (GPS/GSM Plus 1D; Vectronic Aeospace GmbH, Berlin, Germany). From the 13th March 2005 until 15th February 2011, 12 482 locations were gained almost continuously (e.g. GPS data were missing for four months necessary to capture the newly established pack; Hedbyn pack) from at least one of the alpha wolves (male and/or female) with a maximum interval of 12 hours between locations (ranged from 30 minutes to 12 hours). Locations success rates averaged 83% ranged between 73% and 94% among individuals. Within the study area, Hedbyn and Uttersberg were the only pack present, furthermore lone wolf presence was not revealed by intensive snow tracking data (Wabakken et al. 2011). Handling protocols were examined by the animal ethics committee for central Sweden and fulfilled the ethical requirements for research on wild animals (decision C315/6).

2.3. Seasonal definition

I divided data into two seasons, winter and summer. Data on snow depth was obtained from the Swedish Meteorological and Hydrological Institute (SMHI, <http://www.smhi.se>) using data from the Spannarboda weather station (located southwest from the study area). The numbers of days with snow cover more than 10 cm affected moose habitat selection (Månsson 2009). I therefore defined the period with more than 10 cm snow depth as the winter season (28th November \pm 18days -24th March \pm 10 days). Mean calving date for females was the 20th May (n=31; range : 11th May- 1st June). I defined summer season from the 1st May to the 31st August, the end of the vegetation growing season and the start of the rutting season (Olsson et al. 2011). Because gestating females may modify their movement and habitat selection one month before parturition (Ciutti et al. 2006), I considered the GPS locations of gestating females before their parturition (i.e. from 1st May to parturition) as females with a calf.

2.4. Moose data

Data were screened for positioning errors (i.e. locations errors of successfully acquired locations (Frair et al. 2010) following the non-movement method and the script developed by Bjørneraas et al. (2010). To remove all locations farthest from the surrounding points, I set $\Delta=100\text{km}$, and $\mu=10\text{km}$, and to remove locations forming a spike (three successive locations forming a back and forth with high speed limit) I set $\alpha=1.5\text{km/h}$ and $\theta= -0.97$. Error locations ($n=125$, ranged between 0 and 10 per individual) were identified and removed from the analysis (see details in Bjørneraas et al. 2010). I removed GPS locations from the seven days after the moose capture to avoid the effect of immobilization on moose behaviour (Neumann et al. 2011). Also, because 15 individual moose have been subject to 27 experimental dog chasing disturbances, I also excluded all locations seven days after every disturbance event. Because of irregular interval positioning for five moose due to malfunction of the GPS collar, I removed another 1758 locations (range from 6 to 1378 per individual) containing irregular interval. Moose with less than 300 GPS locations (<25 days) in each season were excluded from the analysis (Girard et al. 2002).

To monitor reproductive status of the cow, experienced field personnel observed females with working GPS collar using the VHF (Very High Frequency) device of the collars. The reproductive status were surveyed on three occasions per year, namely in May (calving success), September (summer survival), and April (winter survival). Observations of the individual females were conducted until reproduction status was verified by good observation conditions. I categorised each moose female-season into two groups: females with calf at heel (ranged between 1 and 3) and females without calf. When a female lost her calf between two survey occasions (i.e. unknown date of death) or when field check was impossible because of non working VHF-device, moose reproductive status was considered as unsure during that particularly period and therefore excluded from the analysis (17 moose-seasons, 14% of total number of seasons). Moose GPS data were categorised into two daylight categories (day/night) according to monthly sunset and sunrise mean time.

2.5. Wolf predation risk

I constructed predator-specific landscapes of predation risk based on wolf locations (Valeix et al. 2009b, Thaker et al. 2011). To ensure that wolf predation risk was not overestimated because of high interval positioning or because two wolves were collared at the same time, I kept regular GPS data every 12 hours and used data from only one wolf per pack (Hebblewhite and Merrill 2007, Robinson et al. 2010). I estimated the relative wolf spatial density on a 25x25m grid using kernel density estimator (KDE, Worton 1989). For each pixel of the study area, an Utilisation Distribution (UD) was calculated. This value represents the probability that wolves were located within the given pixel relative to other pixels (Figure 1.). I calculated 99% moose kernel home ranges method using GPS position every second hour. To calculate the kernel utilisation distribution, I used the mean of the smoothing parameter h obtained for wolf ($\bar{x}=1452.47$; $SD=105.93$), and moose ($\bar{x}=287.23$; $SD=131.34$) by using the “href” method. I calculated wolf UD and moose kernel home ranges for each moose-season by using all moose and wolf GPS data available until the last day of the season, assessing for each moose-season if and how much they have been exposed to wolf predation risk.

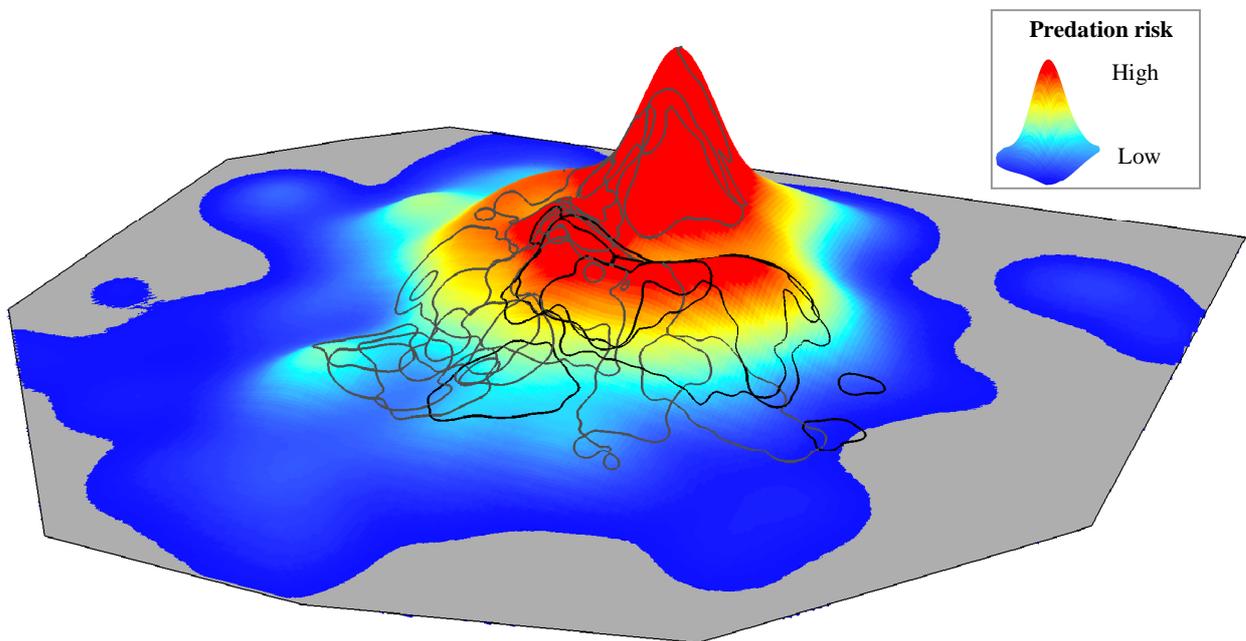


Figure 1. Three dimensional predation risk map constructed with the wolf Utilisation Distribution (UD) for the summer 2010 (n=2925 GPS locations). High predation risk is represented by peak (red) and low predation risk by flat area (blue). Grey area represents no predation risk, and the contour of the study area. Contour of 99% kernel moose home ranges are superimposed to the map. Black and grey polygons are males and females moose home ranges respectively. Home ranges of 13 females and 4 males are represented for readability convenience. Predation risk index was created by extracting and summing values of the map contained inside each moose home range.

I extracted and summed UD predation risk values inside each seasonal individual 99% kernel moose home range (*Figure 1*). To take into account the different size of moose home ranges, I divided the sum of the UD values by the number of pixels of the predation risk map contained in each moose home range. I then created an index of moose-wolf exposure by rescaling values obtained across the season between 0 and 1 by dividing each value obtained by the maximum value observed. Four exposures classes characterising the specific moose-season exposure to wolves were created from the wolf predation risk index: (1) moose outside wolf home ranges ([0-0.05] n=21), (2) low exposure ([0.05-0.25] n=43), (3) medium exposure ([0.25-0.50] n=67), (4) high exposure ([0.50-1] n=12) (*Appendix 3*). For moose identified *outside wolf home ranges*, percentage of overlapping area between moose and wolf 99% kernel home ranges were also calculated by using all GPS locations available for moose and wolves. Overlap of wolves' home ranges on moose home ranges never exceeded 15% (*Appendix 4*). This 15% overlapping threshold was considered as low enough to classify moose as outside wolf home ranges, especially because predation risk has been shown to be particularly low in the edge of wolf ranges ([Mech 1977](#)).

2.6. Habitat variables

Vegetation type was obtained from a 25m x 25m vegetation map classified by satellites imagery (Swedish CORINE Land Cover: SMD, National Land Survey of Sweden). The 38 classes represented within the study area were reclassified into 11 vegetation classes (*Table. 2; 3*).

Because logging activity is intense in the study area and the SMD was constructed from satellites images taken the 12-09-2002, I updated the SMD map with the new clear cuts done from 12-09-2002 to March 2007 (i.e. date of the first moose GPS locations available) obtained at the Swedish forestry agency (<http://www.skogsstyrelsen.se>). To take succession of the vegetation into account, the classes defined as *Clear Cuts* and *Young Forest* in 2002 were moved into classes *Young Forest* and *Middle age coniferous forest* respectively in the 2007 updated SMD map.

Elevation was obtained from a 50m x 50m digital elevation map (Geographical Data Sweden, GSD, National Land Survey of Sweden). A Terrain Ruggedness Index (TRI) was calculated from the elevation map using the tool “Vector Ruggedness Measure” (VRM; Sappington et al. 2007) in ArcGIS 9.3.1TM (© 2009 ESRI Inc). The VRM neighbourhood size was set to three, resulting in a local scale ruggedness index based on eight neighbouring cells. The 50m x 50m cells raster obtained was then reduced into a 25m x 25m raster cells map to fit with other maps.

Table 2. Reclassifications of vegetation classes (Swedish Corine Land Cover, SMD, National Land Survey of Sweden) and the proportion of each class within the study area.

Original ID represented	Reclassification	Area (ha)	%
1.	Human settlements	380	0.52
2.	Pastures	6067	8.31
3.1.1.1 & 3.1.1.2	Deciduous forest	1577	2.16
3.1.2.1.1 & 3.1.2.2	Coniferous forest on lichen and mire	5018	6.87
3.1.2.1.2.1	Middle age coniferous forest	17440	23.89
3.1.2.1.2.2	Mature coniferous forest	16247	22.25
3.1.2.3 & 3.3.2	Coniferous forest on rocky area	1041	1.43
3.1.3.1 & 3.1.3.2	Mixed forest	3637	4.98
3.2.4.1 & 3.2.4.3	Young forest	9285	12.72
3.2.4.2	Clear cut	1698	2.33
4.	Bogs/Mires	6183	8.47
5.	Water Lake	4442	6.08

I calculated Normalized Difference Vegetation Index (NDVI) from the RED (band 2) and Near Infrared (NIR: band 3) of the IRS-P6_LISS-3 satellite imagery taken on 14-07-2010 (available at: www.saccess.lantmateriet.se). The index is based on contrasting reflectance by vegetation of red (absorbs by chlorophyll) and near infrared (scatters by the mesophyll leaf structure) wavebands (Gamon et al. 1995, Pettorelli et al. 2005). NDVI indicates net primary above ground production and is often used as a proxy for vegetation density (Gamon et al. 1995, Pettorelli et al. 2005, Steyaert et al. 2011)

I derived raster data (25m x 25m) on the Euclidean distance in meters from lakes, main roads, secondary roads (gravel roads) and human activity. In the study area, human activity was defined by distances from human settlements and from houses. GPS locations falling inside Human settlements (n=112) and lakes (n=471) (<0.5%) were removed from the analyses (Bjorneraas et al. 2011b).

Table 3. Description of habitat variables used to study moose habitat selection.

Category	Variable	Remarks	Scale
Terrain ruggedness index	TRI	Calculated with the 8 neighbouring cells of the focal cell	Continuous variable (0-0.11)
Habitat Types	Bog	<i>Bogs and mires</i>	Nominal habitat types, one map for each habitat type were created, coding 0 for absence of the habitat, and 1 for presence.
	Clear_cut	<i>Clear cut</i> ≤5 years old	
	Con_lich	<i>Coniferous forest on lichen and mire.</i> Forest ground cover >30% with >75% conifer trees, H>5, on lichen and mires	
	Con_rocky	<i>Coniferous forest on rocky area.</i> Forest ground cover >30% with >75% conifer trees, H>5, on rocky area	
	Deciduous	<i>Broad leaved forest not on mires.</i> Forest ground cover >30% with >75% deciduous trees, H>5.	
	Mature	<i>Coniferous forest >15m.</i> Forest ground cover >30% with >75% conifer H >15	
	Middle	<i>Coniferous forest 5-15m.</i> Forest ground cover >30% with >75% conifer, 5<H <15	
	Mixed	<i>Mixed forest.</i> Forest ground cover >30%, neither conifer nor deciduous trees >75%, H>5	
	Pastures	<i>Cultivating land, grassland</i>	
	Young	<i>Young forest.</i> Clear cut >5 years old and H<5m	
Distances to:	Human	Euclidean distances from human activity (houses and human settlements)	Continuous variable (0-3240m)
	Road_1	Euclidean distances from main roads	Continuous variable (0-4600m)
	Road_2	Euclidean distances from secondary roads (Gravel roads)	Continuous variable (0-1400m)
	D_lakes	Euclidean distances from lakes and open water	Continuous variable (0-3245m)
Vegetation density	NDVI	Normalized difference vegetation index Negative values indicate vegetation absence	Continuous variable (-0.5-0.78)

H :dominant height of the forest stand

2.7. Habitat selection within home ranges

To explore moose habitat selection, I used K-select analysis (Calenge et al. 2005), which is designed for hindcasting studies of habitat selection using radio-tracking data. Hindcasting studies should precede predicting forecasting studies (e.g. Resource Selection Function, Manly et al. 2002) to identify and reduce the number of explanatory variables that should enter in further predictive analyses (Calenge et al. 2005). K-select studies are not limited by the number of habitat variables (i.e. strong correlation among habitat variables has no negative effect on the results) or by the number of animals. K-select analysis corresponds to the third order of habitat selection (i.e. within home ranges habitat selection: Johnson 1980) in which each individual study unit remains identifiable (i.e. Manly's design type III: Manly et al. 2002). This analysis is used to define one or several groups of animals that select the same habitat characteristics. For each individual animal, differences between used and available habitats in a multidimensional ecological space define the marginality vector. Its length reflects selection strength and its direction indicates which habitat variables are selected. K-select is similar to a PCA (Principal Component Analysis) on the marginality vectors and returns a linear combination of the environmental variables that maximizes the mean marginality, thus extracting the relevant part of the habitat selection. If all animals have the same habitat preferences, their marginality vectors will be in the same direction, and the first axis of the analysis will explain a large part of the total inertia. For more details on K-select procedures, see *Figure 2.* and Calenge et al. (2005). Individual moose resources availability was defined by using 95% Minimum Convex Polygon (MCP).

Different K-select analyses have been done to identify factors affecting habitat selection. Firstly, K-select analyses were performed on all moose individuals (n=35) that were characterised by a specific level of predation risk exposure (hereafter referred to as the variable predation risk design). Secondly, K-select analyses were carried out on a reduced data set including moose (n=3) that were originally outside wolf home ranges and then became inside the Hedbyn home ranges (here-after referred to as the before-after design). To simplify the interpretation of the results, seasonal K-select (winter and summer) and including the distinction of the time of day (day/night) were carried out separately. Individuals were characterised by their sex, reproductive status, level of predation risk and the time of day and were considered as the main factors

affecting moose habitat selection. Because seasonal variation and individual specific characteristics were considered to affect moose habitat selection more strongly than the annual variability did, years were not considered in the analysis (Richard 2010). All analyses were conducted in the statistical programming language environment R 2.14.1 (R Development Core Team 2011) with the *adehabitatHR* (for home ranges analysis) and with the *adehabitatHS* package for the K-select analysis (Calenge 2006).

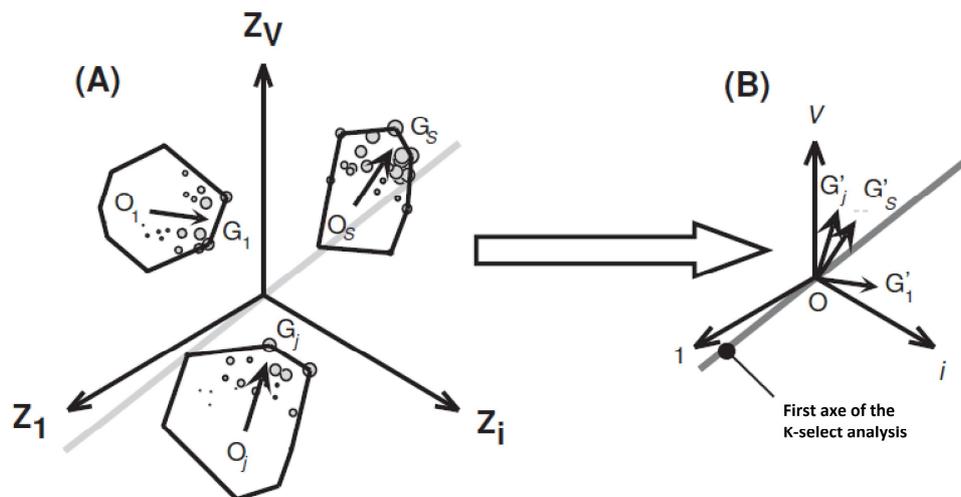


Figure 2. Principle of the K-select. (A) Each O individual has his own available space in the ecological space defined by the variables Z , and each available point (non represented here for readability convenience) is associated to a utilisation weight. For each animal (j ; 1; s), the average available habitat conditions define a point O and the average used conditions define a point G (barycentre of used point G). The vector O_jG_j is the marginality vector for animal j . The axis that explains the largest marginality (in light grey) is centered. (B) The K-select analysis proceeds in two steps: first, a translation is applied to each vector O_jG_j , so that they all have a common origin O (the origin of the space); second, an eigenanalysis is performed on the table of coordinates of the translated vectors OG_j on habitat variables, so that the mean marginality projected on the first axis of the K-select is maximized (adapted from Calenge et al. 2005, Richard 2010).

3. Results

Data from all moose ($n=35$) resulting in 125 moose-seasons, of which 47 ($n=58\ 352$ locations and $n=22$ individuals) were in winter and 78 ($n=112\ 546$ locations and $n=35$) in summer were used to characterise habitat selection of moose in the variable risk exposure design. GPS locations of three females initially outside wolf home ranges and later inside wolf home ranges resulting in 14 moose-seasons in summer ($n=19\ 361$ locations) and 11 moose-seasons in winter ($n=14\ 665$ locations) were also used to characterise habitat selection in the before-after design.

3.1. Winter moose habitat selection

The two first axes of the K-select analyses were retained in the analysis because they accounted for most of the marginality of individuals (71.5% for the 22 moose in the variable risk exposure design: *Figure 4.A*), 81.5% for the 3 female moose in the before-after design (*Figure 4.C*).

3.1.1. Habitat selection patterns

In both designs, the first axes accounted for most of the marginality of individuals meaning that all animals expressed similar habitat preferences (*Figure 3.A and C*). A common habitat selection pattern emerged from the analysis with all individuals strongly selecting young forest (*Figure 4.A and C; Appendix 5.B and 6.B*). Areas with high NDVI and TRI values were also selected but to a lesser extent. All individuals avoided bogs, pastures, mixed forest, coniferous forest on lichen area and deciduous forest (*Figure 4.A and C; Appendix 5.B*). Characterising day and night-time in the K-select analysis did not explain differences in moose habitat selection. Both designs show same habitat selection pattern.

3.1.2. Effect of wolf exposure

In the variable predation risk design, females without calves and males tended to select young forest more strongly when they were exposed to low predation risk (*Figure 4.A*). In the before-after design, females without calves tended to select more intensively young forest after wolf re-establishment (*Figure 4.C*). However in both designs, only trends were found for differences in habitat selection differences and no strong habitat selection pattern emerged when individuals were classified according to their predation risk exposure.

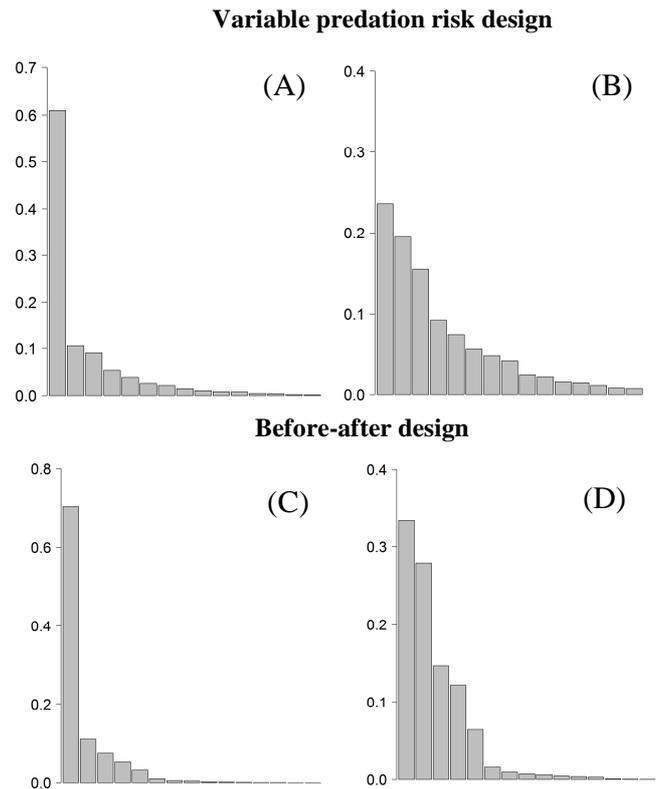
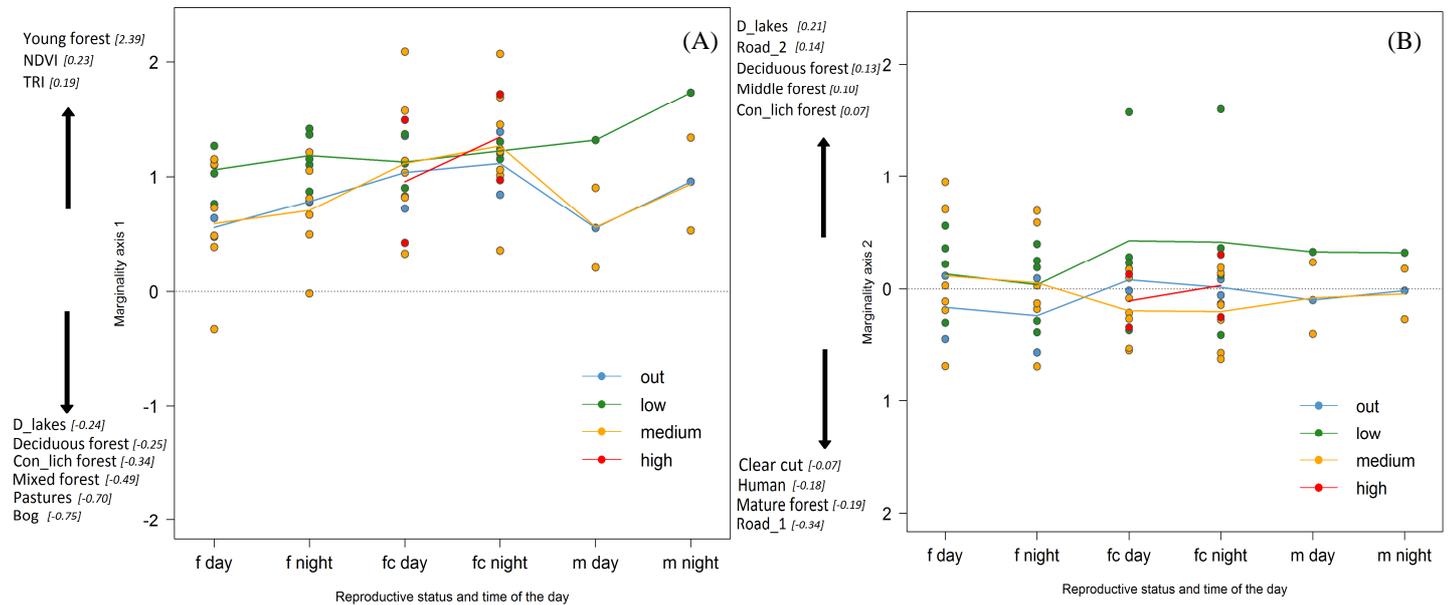


Figure.3 Bar charts of the K-select eigenvalues, measuring the mean marginality explained by each factorial axis (%). The winter K-select are shown in A and C, and the summer K-select in B and D.

Variable predation risk design



Before-after design

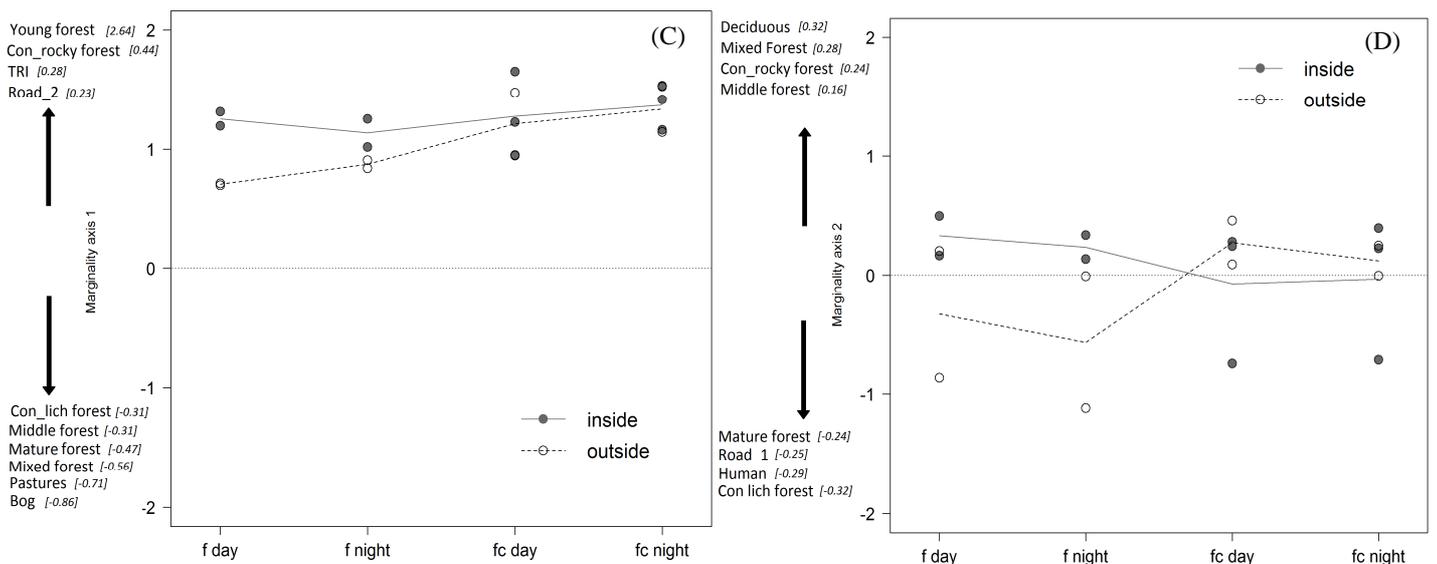


Figure 4. K-select analysis for habitat selection within home ranges (third order selection) in winter. Results of the K-select analyses for moose ($n=22$) in the variable predation risk design (A) and (B) and for females ($n=3$) in the before-after design (C) and (D). In (A; C) and (B; D) are shown the individuals marginality on the first axis and second axis respectively. One dot represents the marginality score of a specific individual characterized by sex and reproductive status (*fc*: female with calf, *f*: female without calf, *m*: male), risk exposure (*outside*: outside wolf territory, *inside*: inside wolf territory or *out*: outside wolf territory, *low*: low predation risk, *medium*: medium predation risk, *high*: high predation risk) and time of the day (day/night). Lines represent average marginality for individual exposed to low, medium and high predation risk (A; B) and outside and inside wolf home range (C; D). On the left side of each graphics are represented habitat variables having the highest (negative and positive) scores (number within bracket) on the factorial axes. More details on K-select are showed graphically in *Appendix 5 and 6*

3.1.3. Effect of individual characteristics

In both designs, sex and reproductive status were not important to explain individual differences in moose habitat selection (*Figure 4*). However inter-individual variability in moose habitat selection was pointed out by the K-select analyses. For instance, in the variable predation risk design some moose selected intensively young forest, whereas other moose showed less strong selection for this type of habitat (*Figure 4.A*).

Although the second axes of the K-selects explained low variation in the marginality of individuals ($\approx 10\%$; *Figure 3.A and C*), inter-individual variability between moose was more pronounced on the second axis in both designs (*Figure 4.B and D*). For instance, in the variable predation risk design, some moose tended to avoid areas close to lakes, secondary roads, selected deciduous forest, middle age forest, whereas others moose showed the opposite pattern and avoided main roads, human activity, and selected mature forest and clear cuts (*Figure 4.B*).

3.2. Summer moose habitat selection

The four first axes of the K-selects accounted for most of the marginality of individuals (67.8% for the 35 moose in the variable risk exposure design (*Figure 3.A*) and 88.3% in the before-after design (*Figure 3.C*) and were retained in the analysis. Because the components of the marginality were explained by several axes, habitat selection differed substantially more between animals in summer than in winter.

3.2.1. Habitat selection patterns

On the first axis of the K-select for the variable risk exposure design, most of the moose showed a pattern of habitat selection towards deciduous forest, young forest and for areas with high NDVI values (*Figure 5.A*). On the second axis of the K-select, two contrasting patterns of habitat selection were pointed out according to the time of the day. During the night, all moose selected clear cut, pastures and young forest whereas during the day moose selected mixed, middle age, deciduous and coniferous forest and selected less intensively pastures, clear cut and young forest (*Figure 5.B and F*). The same habitat selection pattern was found for the before-after design (*Figure 6*).

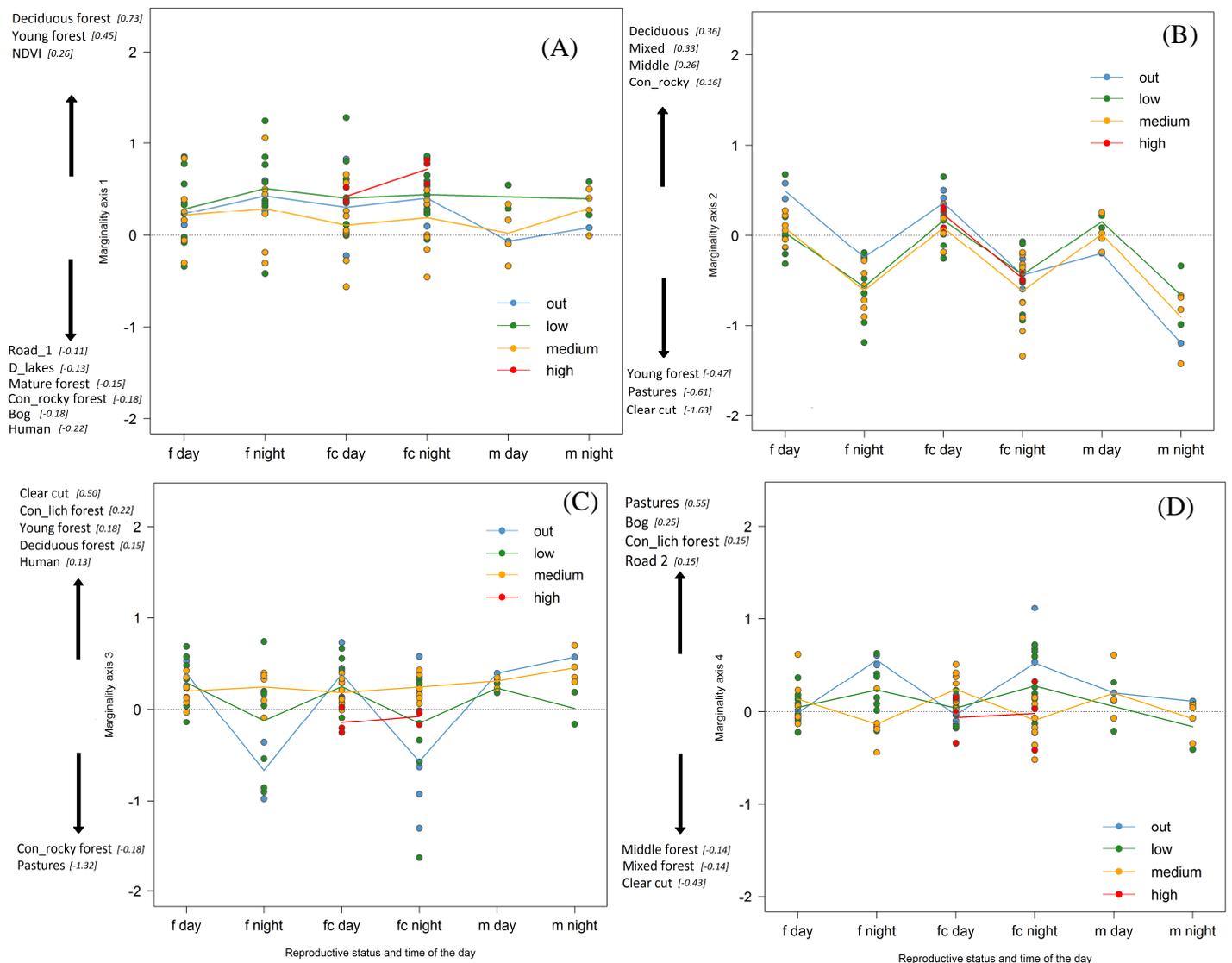


Figure 5. Results of the K-select analysis for habitat selection within home ranges (third order selection) in summer for 35 moose individual in the variable predation risk design (A-D). In A; and B are shown individuals marginality scores on the first axis and second axis respectively. In C and D are the marginality score on the third and fourth axes of the K-select respectively. One dot represents the marginality score of a specific individual characterized by sex and reproductive status (*f*: female with calf, *fc*: female without calf, *m*: male), time of the day (day/night) and risk exposure (*out*: outside wolf territory, *low*: low predation risk, *medium*: medium predation risk, *high*: high predation risk). Lines represent average marginality for individual outside wolf home range, exposed to low, medium and high predation risk. On the left side of each graphics are represented habitat variables having the highest (negative and positive) scores (number within bracket) on the factorial axes. More details on K-select are showed graphically in *Appendix 7*

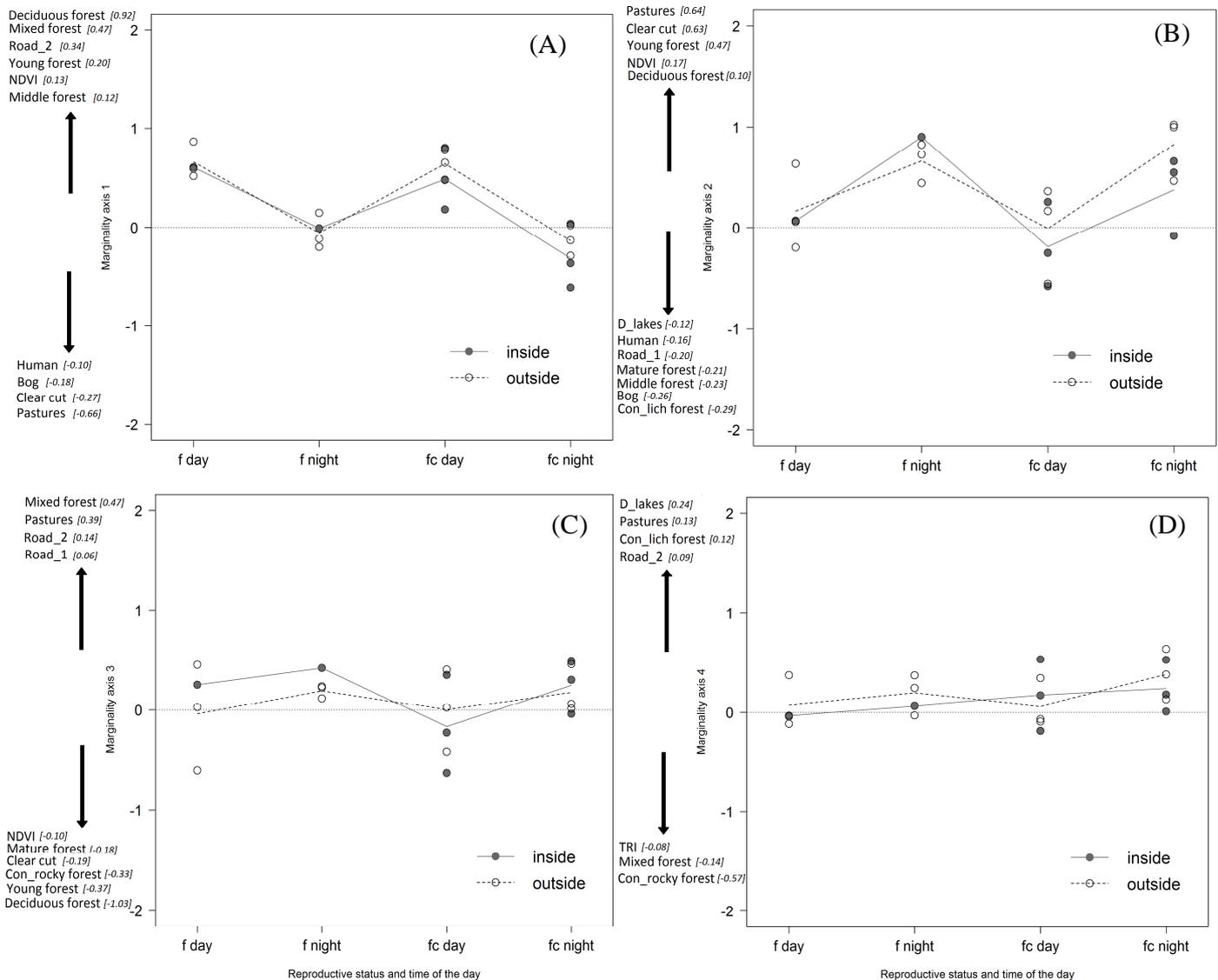


Figure 6. Results of the K-select analysis for habitat selection within home ranges (third order selection) in summer for 3 females in the before-after design (A-D). In A; and B are represented individuals marginality scores on the first axis and second axis respectively. In C and D are the marginality score on the third and fourth axes of the K-select respectively. One dot represents the marginality score of a specific individual characterized by sex and reproductive status (*f*: female with calf, *fc*: female without calf, *m*: male), risk exposure (*outside*: outside wolf territory, *inside*: inside wolf territory) and time of the day (day/night). Lines represent average marginality for individual outside and inside wolf home range. On the left side of each graphics are represented habitat variables having the highest (negative and positive) scores (number within bracket) on the factorial axes. More details on K-select are showed graphically in *Appendix 8*

3.2.2. Effect of wolf exposure

In the variable predation risk design, moose characterized by a high and medium predation risk tended to have a smaller niche than moose exposed to low predation risk and outside wolf home ranges (*Appendix 7.K*) but no strong habitat selection patterns emerged irrespective of predation risk (*Figure 5.A-D*). In the before-after design, K-select analysis did not reveal any change in habitat selection pattern after wolf re-establishment (*Figure 6.A-D*).

3.2.3. Effect of individual characteristics

In both designs, sex and reproductive status did not affect moose habitat selection. Indeed, even if average marginality scores on the axis of the K-select might differ between females and males or between females without calves, inter-individual variability was too large to allow firm conclusions. For the variable risk exposure design, the third axis (*Figure 5.G*) indicated that females had a larger inter-individual variability in their patterns of habitat selection during the night compared to the day with some females that strongly selected pastures compared to others females that tended to avoid it (*Figure 5.E*). In both designs, a large amount of marginality was explained by the first axes of the K-select analysis in winter compared to those in summer (*Figure 3*), showing that inter-individual variability in moose habitat selection stronger during the summer than during winter.

4. Discussion

The predation risk has been shown to affect ungulates habitat selection by forcing them to modify their habitat selection and to select poorer habitat types (Edwards et al. 1983, Creel et al. 2005, Mao et al. 2005, Christianson and Creel 2008). However my prediction that moose that became exposed to wolves will select different habitat in order to avoid wolf detection and encounter was not confirmed. Risk exposure between moose individuals was not an important factor affecting moose habitat selection. This was further supported by the fact that female moose that faced two contrasting periods, outside wolf home range and inside wolf home range after 2009 did not modify their habitat selection due to wolf re-establishment. Also contrary to my predictions, a higher wolf predation risk was not important for affecting habitat selection patterns of females with calves with regard to season (summer/winter) or time of day (day/night).

My results support previous findings and show that moose did not alter their behaviour (i.e. their habitat selection in this study) in response to wolf re-establishments (Sand et al. 2006b, Eriksen et al. 2011). Neither wolf hunting success on moose (Sand et al. 2006a; 2006b, Wikenros et al. 2009) nor moose activity patterns changes as a result of wolf re-establishment (Eriksen et al. 2011). Several studies dealing with prey behavioural adjustments reported behavioural changes within a single prey generation and were even faster when predation was directed to offspring (Berger et al. 2001, Laundré et al. 2001, Mao et al. 2005). Although wolves mainly prey on calves in Scandinavia (Sand et al. 2005; 2008), I found no evidence for an adaptation in their habitat selection behaviour. It is possible that moose adaptation takes longer time than the period covered by this study (with an up to eight years of wolf presence). Another study suggested that moose in Scandinavia were still “naïve” towards wolves, because even after being subject to wolf exposure for up to 21 years, wolf hunting success on moose was not affected (Sand et al. 2006a). One possible explanation to the lack of changes in moose behaviour might be the extent and mode of moose hunting and combined with the long absence of predators (more than 100 years) in the south-central parts of Scandinavia (Sand et al. 2006a, Eriksen et al. 2011).

When studying the effect of predation risk on ungulates, studies generally compare ungulates habitat selection among different individuals (Mao et al. 2005), among different ungulates populations (Hernández and Laundré 2005) or the effect of wolf proximity on ungulates

individual behaviour (Creel et al. 2005). To my knowledge this is the first study dealing with the effect of wolf re-establishment on ungulates individual behaviour. Indeed by studying the same individual moose that faced two contrasted conditions; outside and then inside wolf home range, the short term impact of wolf re-establishment (two years) on moose individual behaviour should have been possible to detect if present. Also, by comparing moose habitat selection exposed to different risk exposure within the same population, environmental variations that are normally included in between-population comparisons were eliminated. By using these data, the result obtained strongly suggests that moose habitat selection is not affected by wolf re-establishment at the scale studied.

Wolf predation risk is generally reported to be higher in open areas (Creel et al. 2005, Winnie and Creel 2007). Studies reporting that ungulates selected cover in response to wolves' presence generally occurred in heterogeneous landscapes with high elevation heterogeneity where both, open and forest areas are represented and selected by ungulates (Mao et al. 2005, Creel et al. 2005). However, Creel et al. (2005) suggested that there is a variation among species and ecosystems whereby habitat features affect the level of predation risk. In the present study area, the landscape is homogeneous without strong heterogeneity in elevation and mainly covered by forest which is largely selected by moose (Cederlund and Okarma 1988, Olsson et al. 2011, Van Beest et al. 2010, Bjorneraas et al. 2011a, 2011b). Among forest habitat types, cover and forage quality vary (Bjorneraas et al. 2011a, 2011b) but the use by moose was not found to be affected by wolf presence. Habitat selection occurs from the geographical range of a species to the selection of food item inside a habitat patch (Johnson 1980). By studying the third order of habitat selection (i.e. habitat selection within home ranges) it is possible that wolf predation risk shapes moose habitat selection at a finer scale than the habitat variables used in this study. However, Rettie and Messier (2000) argued that habitat selection is a hierarchical process and that the most limiting factors should be avoided at a coarser scale (Dussault et al. 2005). If wolf predation risk would have been an important limiting factor for moose fitness, I expect that moose response would have been obvious and detected at the scale at which I conducted the study.

Creel and Christianson (2008) argued that anti-predator behaviours produce many small actions which have small individual and complex effects on prey fitness. Then depending on the level at which the study is conducted, different responses might be observed (Gaillard et al. 2010). In this study, I assessed consequences of predation risk by attributing for each moose, the probability of having an encounter inside their home range. For instance, moose may change their selection of habitat when considering predation risk on a shorter timeframe than I measured (e.g. an encounter-by-encounter basis). Furthermore, the scale at which I conducted my study might not allow detecting fine-scale adaptation in habitat features selection. For instance, when selecting open areas during the night, females with calves might select it closer to forest edges in order to have good escape opportunities if a predator attack occurs (Hernández and Laundré 2005).

I constructed a predation risk map based on wolf intensity of use, which have previously been found to affect ungulates habitat selection (Kittle et al. 2008, Valeix et al. 2009b, Thaker et al. 2011). Prey behavioural responses to predator's presence can be assessed by characterising predation risk from long term predation risk (e.g. presence or absence of a predator in the area) to a short term predation risk (e.g. response of prey after a direct encounter). For instance, elk changed their habitat selection after wolf re-introduction (Mao et al. 2005) or when wolves were near on a daily basis (Creel et al. 2005). As revealed by Hebblewhite et al. (2005), the risk of being killed by a predator is not only relative to the probabilities of encounter but also to specific habitat characteristics. By using the probability of wolf presence to construct the predation risk map and not the probability of moose to being killed by wolf, I might have under- or overestimated the predation risk in specific habitat types possibly masking the detection of differences in moose habitat selection due to the presence of wolves.

Individuals that are the most subject to direct predation should express a higher response to predation risk (Creel and Christianson 2008). Females and young are generally more often subject to direct predation (Sand et al. 2005; 2008, Winnie and Creel 2007) and have been shown to respond to it accordingly (Edwards 1983, Lima and Dill 1990, Laundré et al. 2001, Dussault et al. 2005, Bjørneraas et al. 2011a; 2011b). I did not detect any differences in habitat preferences between sexes or individual of different reproductive status which is similar to what has been

found for moose that were free from natural predators in south-western of Sweden (Olsson et al. 2011). However in Norway, in areas without wolves, females with calves at heel selected areas providing cover and avoided open areas during the first months after their calves were born (Bjorneraas et al. 2011a; 2011b).

Edwards (1983) reported evidences that moose with calf selected islands in order to protect themselves from predators. One of the female moose studied gave birth on an island and left it with her calf eight days after having given birth. This empirical data may give support that moose select special habitat types during calving. Then it is possible that during a restricted period, for instance at the calving time when calves are not as mobile as adults, females select habitat features in order to protect themselves from the predator. But when calves are as mobile as adults, female with or without a calf at heel might be subject to the same factor affecting their behaviour, as was reflected by the same habitat selection patterns found between females with and without calves in my analysis (Rettie and Messier 2000).

If the wolf re-establishment did not affect moose habitat selection, seasonal variation in food availabilities and environmental conditions appeared to strongly impact moose habitat selection. The results show that moose were selective in their choice of habitat types. In winter moose selected intensively young forest during day and night whereas in summer moose selected forest offering cover, with deciduous forest (cover areas) during the day, and clear cuts, pastures and young forest (open areas) during the night. The strong selectivity for young forest during winter was similar to previous findings on moose habitat selection (Cederlund and Okarma 1988, Bjorneraas et al. 2011a; 2011b, Månsson et al. 2011). Indeed, the field layer being generally covered by snow and the lack of deciduous leaves force moose to select young forest to increase their browsing on young trees and especially on pine (Cederlund et al. 1980, Månsson 2009, Van Beest et al. 2010).

Habitat selection has been reported to change with the time of the day for red deer (Godvik et al. 2009) and for moose (Bjorneraas et al. 2011b). During summer, I found that moose selected open habitat types during night-time and forest during day-time. The use of deciduous forest and mixed forest during the summer is generally reported because of good foraging opportunities

(Bjorneraas et al. 2011b). Using open areas is considered as a trade-off between having access to high quality forage and having a high exposure to predators, human and weather (Lykkja et al. 2009, Godvik et al. 2009, Herfindal et al. 2009). However wolf predation risk exposure and wolf re-establishment did not affect the selection of open areas during the night. In the study area temperature regularly exceeds 15°C and moose might be affected by heat stress at ambient temperature above 14°C in summer (Renecker and Hudson 1986). Mixed support concerning the avoidance of hot temperature during summer was found. Whereas Lowe et al. (2010) did not detect any relationships between moose habitat selection and thermoregulation thresholds, Dussault et al. (2004) found that moose selected shelter during the day, and increased their activity rhythm during the night as a response to heat stress. Because human activity and hunting often replaced mortality by predators, avoidance of human activity is considered as a response to perceived predation by humans (Frid and Dill 2002). In Scandinavia moose has been hunted for centuries and is among the most productive and heavily harvested moose population in Europe (Lavsund et al. 2003). Therefore the night-time utilisation of habitat types providing cover and forage is more likely a response to multiple factors such as, avoidance of heat stress and a behavioural response of perceived predation risk by humans (Lykkja et al. 2009, Bjorneraas et al. 2011b). Unlike results found by Lykkja et al. (2009), moose studied did not avoid human activity. Variables representing human activity (i.e. distances from main, secondary roads and human activity) were not an important factor to explain moose habitat selection. By using all houses as a proxy for human activity, human activity might have been overestimated because it was not possible to distinguish inhabited from uninhabited houses (e.g. summer houses) which are expected to induce few disturbances.

Inter-individual variability in habitat selection should not be ignored (Myysterud et al. 1998) and has been largely documented (Calenge et al. 2005, Hebblewhite and Merrill 2008, Martin et al. 2010, Richard 2010, Bjorneraas et al. 2011b). When availability differs among individuals, changes in the relative use of habitat types is expected (i.e. functional responses) (Myysterud and Ims 1998, Godvik et al. 2009). However in the present study area, availability of habitat types is homogenous and relatively similar among individuals. Most of the forests (i.e. privately owned forest) are managed by the same forest owner who conducts similar forest management over the area. Furthermore, the results did not reveal different patterns of habitat selection according to the

available niche inside moose home ranges (Appendix.5,6,7,8. D). Then modification in habitat selection pointed out by the K-select analysis is most likely due to modification in moose habitat selection rather than a moose functional response.

My results also revealed that inter-individual variability in habitat selection was more important in summer than in winter. In an elk-wolf system, Winnie et al. (2006) showed that a limiting factor (i.e. predation) forced elk to show less complexity in their winter habitat selection. During winter, the results support this hypothesis and indicate that when the presumed most limiting factor are climatic conditions and food availability, all moose are forced to use identical habitat types to meet their requirements. However during summer when more forage opportunities are available and conditions are cooler, inter-individual variability in habitat selection is possible.

5. Conclusion and perspectives

The recent wolf re-establishment in Scandinavia offers unique possibilities to study their impact on their main prey, the moose. I did not detect that moose habitat selection was affected by wolf re-establishment; however moose habitat selection was driven by seasonal variation in food availability and climatic conditions. In line with Sand et al. (2006b), I argue that the absence of wolves, the extent of hunting pressure during the last century and an insufficient period of wolf exposure explained why moose habitat selection was not affected by wolves in my study.

This study considers for the first time to my knowledge the impact of wolf re-establishment on individual moose habitat selection. By using such data, the results obtained confirms that moose did not adapt their habitat selection in response to wolf. Furthermore it highlights the need of acquiring data on a long term basis making this kind of study possible and may help to answer to the question of Sand et al. (2006b); “will naïve moose in Scandinavia ever lean?”

Anti-predator behavioural adjustments may have consequences on the prey population dynamics and might be as important as the direct numerical impact of predation (Preisser et al. 2005, Creel and Christianson 2008, Garrott et al. 2009). However, my results suggest that moose in Scandinavia might not be affected by risk effects but only by the impact of direct predation (Sand et al. 2008, Gervasi et al. 2011).

Because of the spatial and temporal scale at which I conducted my study, I might have not detected finest habitat selection adaptation of moose to wolf predation risk. I stress that this point deserves further consideration and need to be taken into consideration in further studies. My study only covers moose habitat selection but others anti-predator strategies might also be employed by moose in order to avoid predation. For instance, time spent in vigilance in order to detect predator and form larger groups to reduce the per capita predation risk are common behaviour reported by ungulates to avoid predation (Laundré et al. 2001, Caro 2005, Winnie and Creel 2007).

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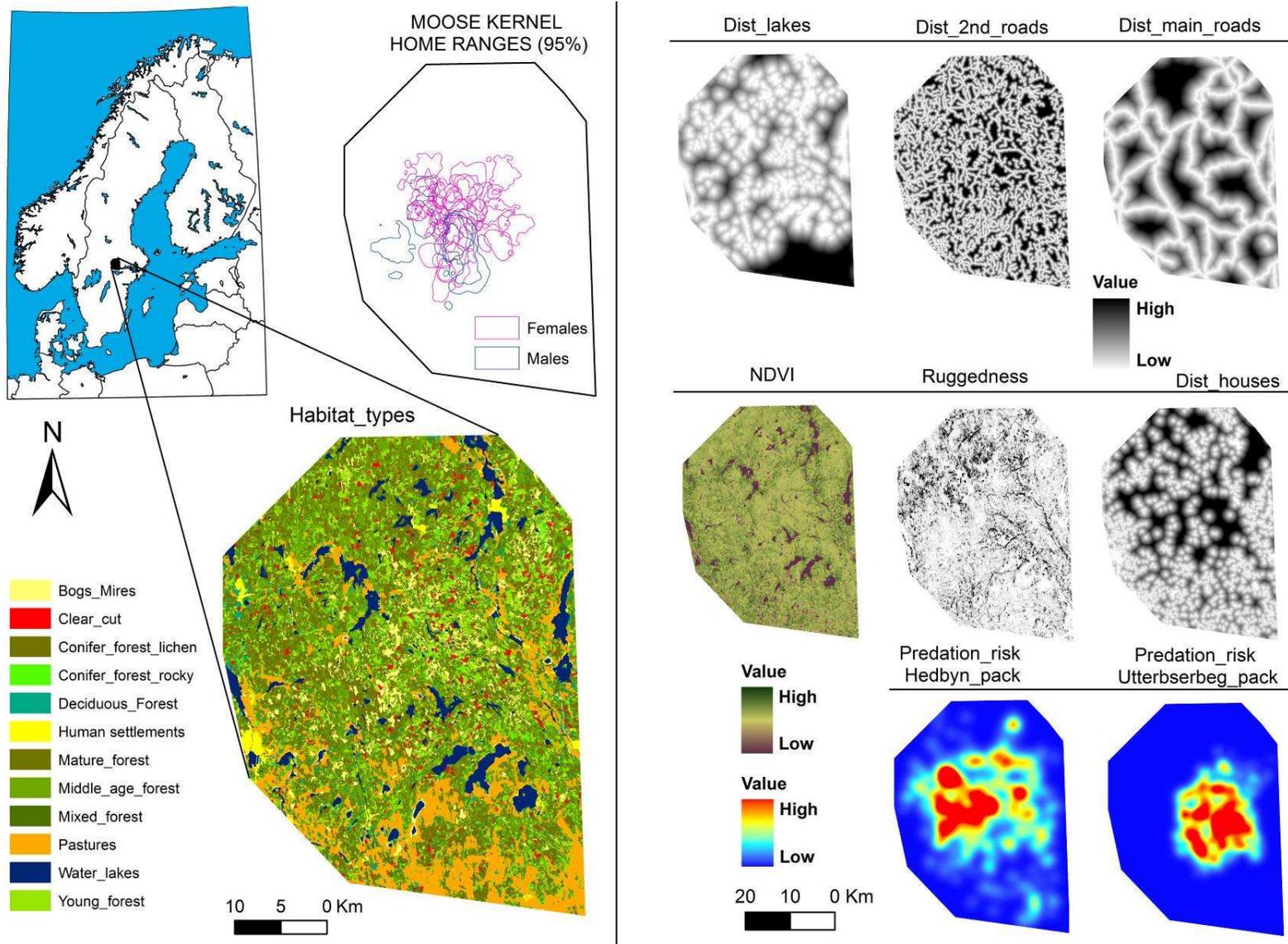
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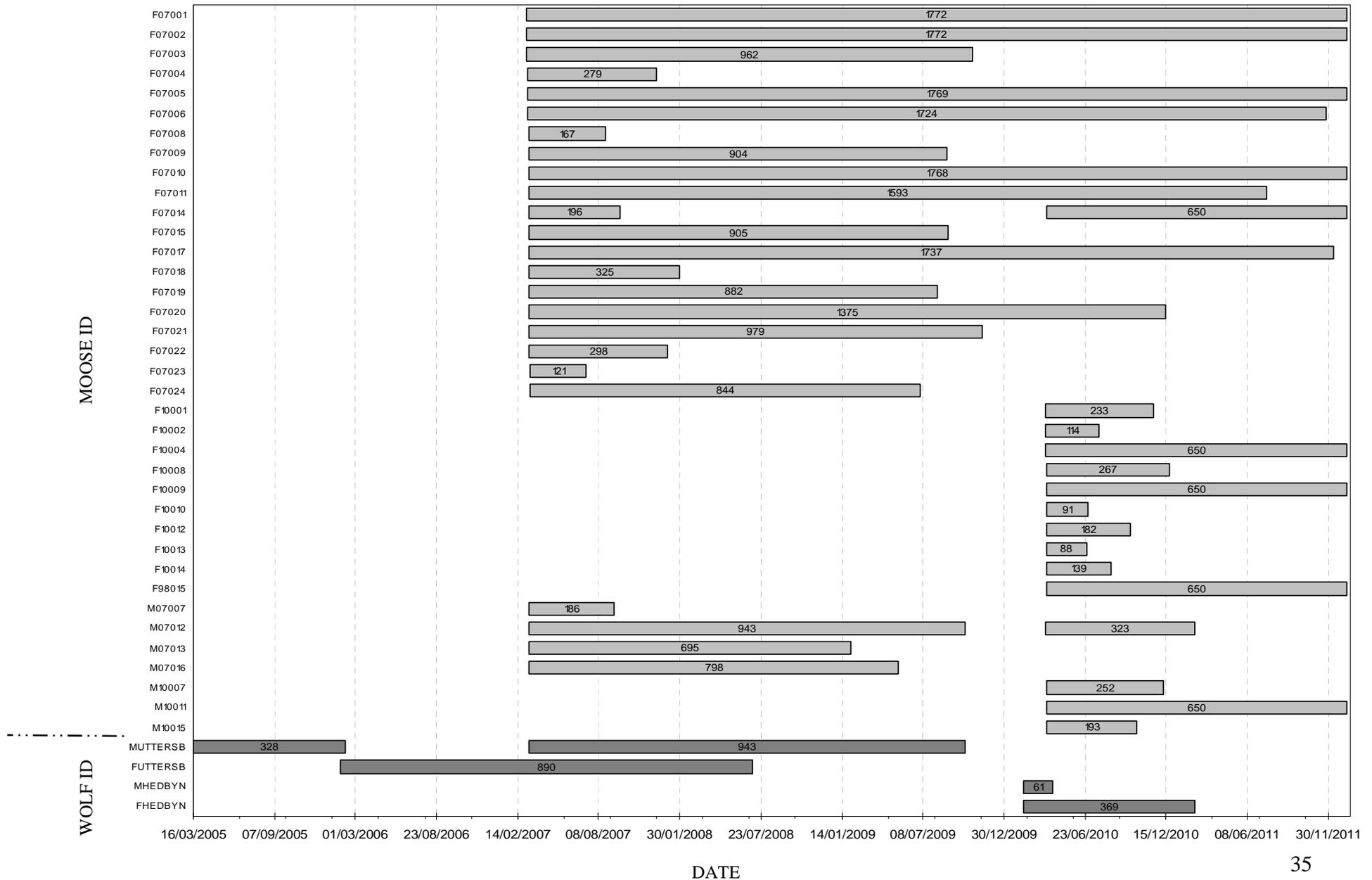
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Appendix 1: Maps describing the study area. On the left side are represented location of the study area, locations (home ranges) of the 37 individual moose and a map representing different habitat types defined within the study area. The maps Habitat-types, Dist_lakes, Dist_2nd_roads, Dist_main_roads, NDVI, Ruggedness and Dist_houses were used in the K-select analysis. The predation risk maps show the spatial distribution of wolves for the Hedbyn pack and the Uttersberg pack, and have been created using GPS locations and the kernel density estimators.



Appendix 2 : Gantt diagram representing the number of days (number within each horizontal bars) that each moose individual collar was functioning and the GPS locations were available. In dark grey, functioning of wolves' collar is also represented. Moose ID are defined by a letter (F:female/ M:Male), the two first number on the left represent the year of capture (07:2007) and the 3 numbers on the right the order of the capture(001: moose captured first in the corresponding year). For instance the Moose F07001, was the first female captured in 2007. Wolves ID are represented by a letter (F:female/M:Male) and the name of the pack they belong (Hedbyn:Hedbyn/ Uttersb:Uttersberg)



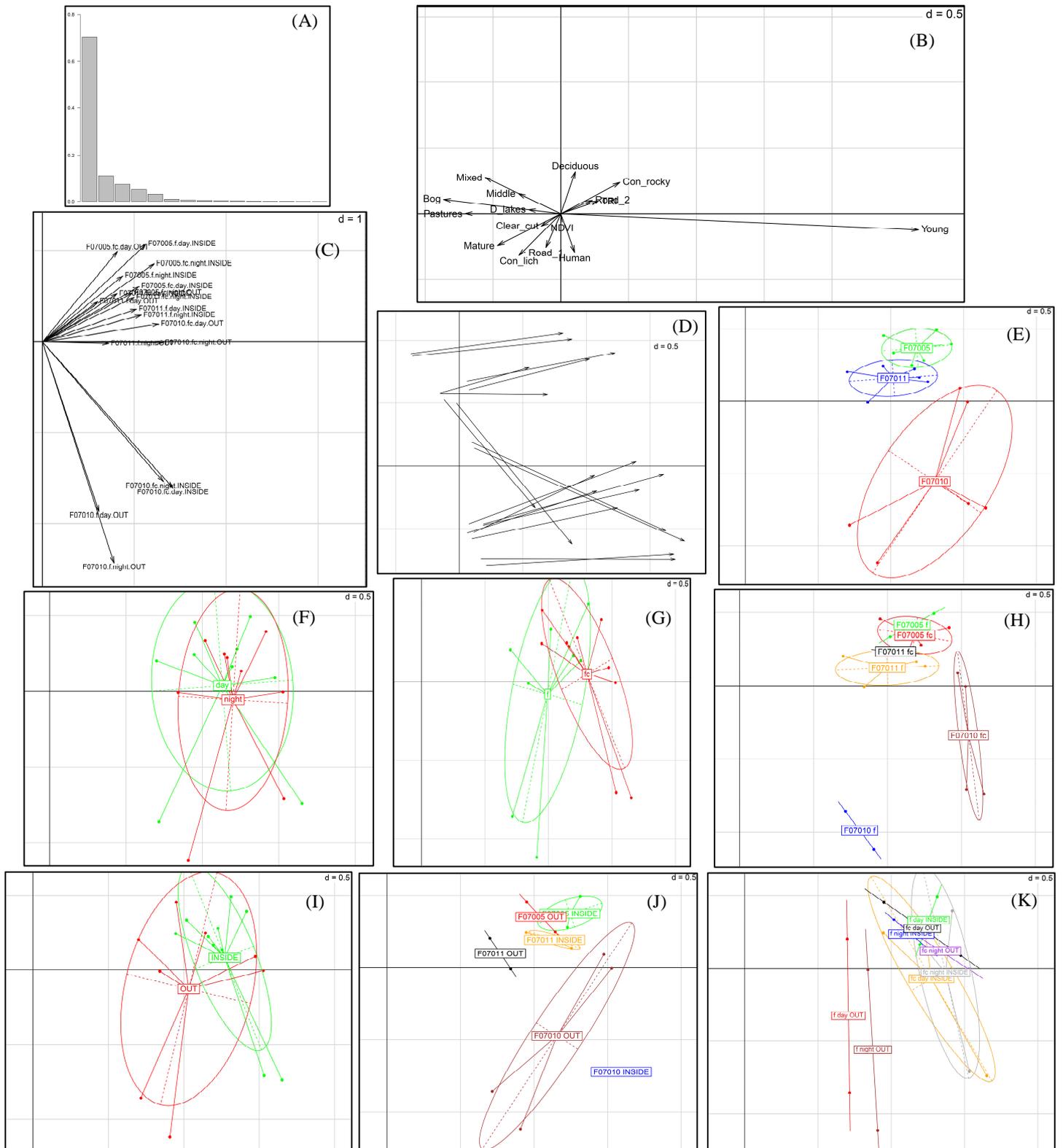
Appendix 3. Seasonal moose exposure to predation risk. Four classes are represented and were defined by the values obtained by the predation risk index: OUT [0-0.03], LOW [0.03-0.25], MEDIUM [0.25-0.50] HIGH [0.50-1]. WIN: winter; SUM=summer.

ID	SUM 07	WIN 07/08	SUM 08	WIN 08/09	SUM 09	WIN 09/10	SUM 10	WIN 10/11	SUM 11
F07001	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM
F07002	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM
F07003	OUT	OUT	OUT	OUT	LOW	-	-	-	-
F07004	LOW	-	-	-	-	-	-	-	-
F07005	OUT	OUT	OUT	OUT	OUT	LOW	LOW	LOW	LOW
F07006	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM
F07008	MEDIUM	-	-	-	-	-	-	-	-
F07009	LOW	LOW	LOW	LOW	LOW	-	-	-	-
F07010	OUT	OUT	OUT	OUT	LOW	LOW	LOW	LOW	LOW
F07011	OUT	OUT	OUT	OUT	OUT	LOW	LOW	LOW	LOW
F07014	LOW	-	-	-	-	-	LOW	MEDIUM	MEDIUM
F07015	HIGH	HIGH	HIGH	HIGH	HIGH	-	-	-	-
F07017	HIGH	HIGH	HIGH	HIGH	-	-	-	-	-
F07018	HIGH	HIGH	-	-	-	-	-	-	-
F07019	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	-	-	-	-
F07020	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	-
F07021	LOW	LOW	LOW	LOW	LOW	-	-	-	-
F07022	LOW	MEDIUM	-	-	-	-	-	-	-
F07023	MEDIUM	-	-	-	-	-	-	-	-
F07024	MEDIUM	MEDIUM	MEDIUM	HIGH	MEDIUM	-	-	-	-
M07007	MEDIUM	-	-	-	-	-	-	-	-
M07012	MEDIUM	MEDIUM	MEDIUM	MEDIUM	MEDIUM	-	MEDIUM	MEDIUM	-
M07013	OUT	OUT	OUT	-	-	-	-	-	-
M07016	MEDIUM	MEDIUM	MEDIUM	MEDIUM	-	-	-	-	-
F10001	-	-	-	-	-	-	MEDIUM	-	-
F10002	-	-	-	-	-	-	MEDIUM	-	-
F10004	-	-	-	-	-	-	LOW	MEDIUM	LOW
F10008	-	-	-	-	-	-	MEDIUM	-	-
F10009	-	-	-	-	-	-	LOW	LOW	LOW
F10010	-	-	-	-	-	-	LOW	-	-
F10012	-	-	-	-	-	-	LOW	-	-
F10013	-	-	-	-	-	-	LOW	-	-
F10014	-	-	-	-	-	-	LOW	-	-
F98015	-	-	-	-	-	-	MEDIUM	LOW	LOW
M10007	-	-	-	-	-	-	MEDIUM	-	-
M10011	-	-	-	-	-	-	LOW	LOW	LOW
M10015	-	-	-	-	-	-	LOW	-	-

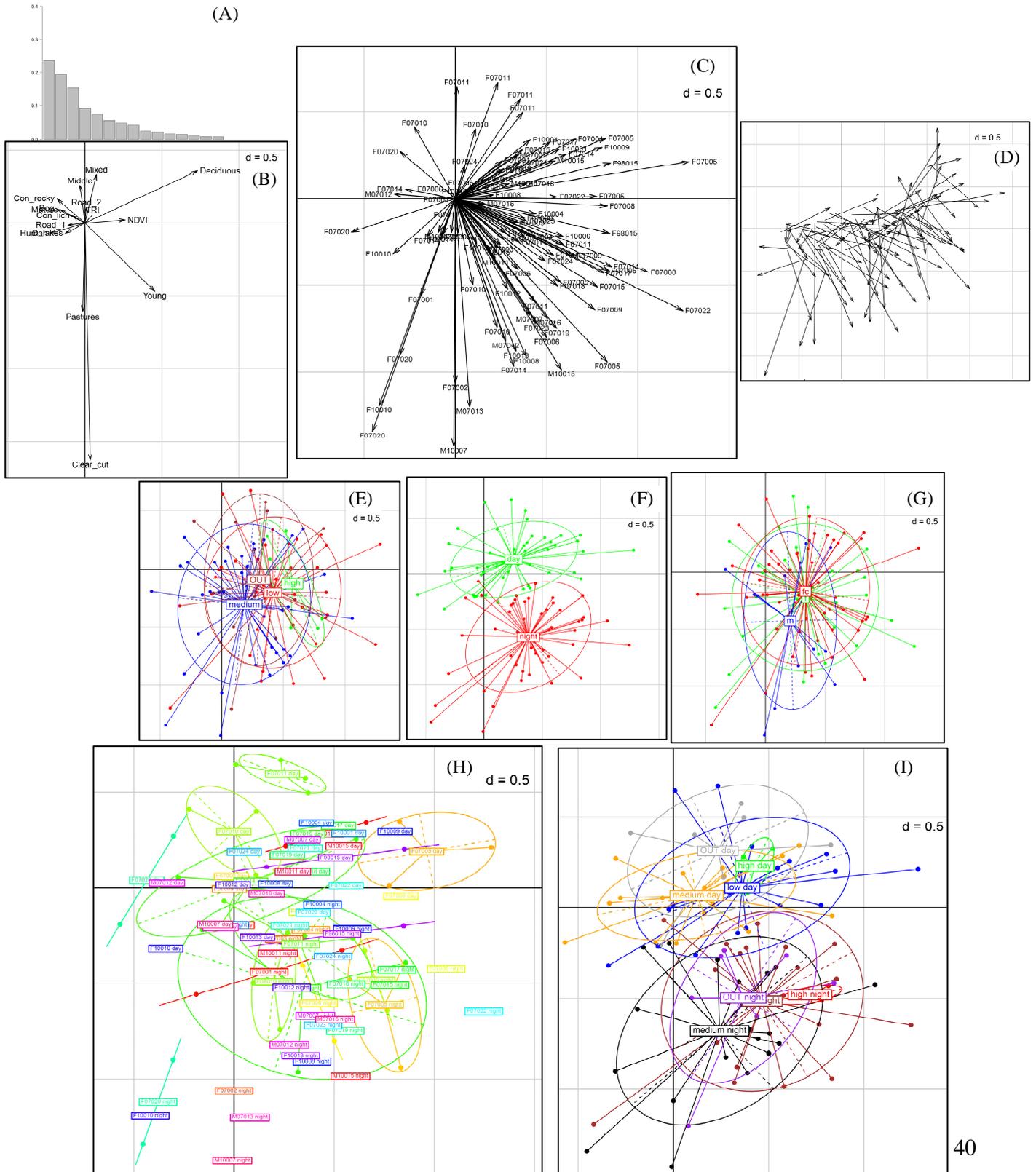
Appendix 4. Seasonal percentage of overlapping area between wolf and moose home ranges for each . 99% kernel home range was used. Gray cells represent moose considered as outside wolf home range.

ID	WOLF SUM 07	WOLF WIN 07/08	WOLF SUM 08	WOLF WIN 08/09	WOLF SUM 09	WOLF WIN 09/10	WOLF SUM 10	WOLF WIN 10/11	WOLF SUM 11
F07001	100	99,97	99,85	100	100	100	100	100	100
F07002	100	100	100	100	100	100	100	100	100
F07003	4,90	10,30	14,71	12,61	29,02	-	-	-	-
F07004	90,33	-	-	-	-	-	-	-	-
F07005	0,00	0,00	0,00	0,00	0,00	96,29	100	100	100
F07006	100	100	100	100	100	100	100	100	100
F07008	99,79	-	-	-	-	-	-	-	-
F07009	63,59	59,19	64,23	62,82	100	-	-	-	-
F07010	0,00	4,64	4,36	3,05	19,11	100	100	100	100
F07011	0,00	0,30	0,11	0,09	7,11	100	100	100	100
F07014	94,41	-	-	-	-	-	100	100	100
F07015	100	100	100	100	100	-	-	-	-
F07017	100	100	100	100	-	-	-	-	-
F07018	100	100	-	-	-	-	-	-	-
F07019	100	100	100	100	100	-	-	-	-
F07020	100	100	100	100	100	100	100	100	-
F07021	45,41	62,99	60,97	63,82	67,30	-	-	-	-
F07022	60,61	81,62	-	-	-	-	-	-	-
F07023	100	-	-	-	-	-	-	-	-
F07024	100	100	100	100	100	-	-	-	-
M07007	96,65	-	-	-	-	-	-	-	-
M07012	100	99,11	99,50	99,91	100	-	100	100	-
M07013	1,66	2,10	1,91	-	-	-	-	-	-
M07016	100	85,07	88,20	90,49	-	-	-	-	-
F10001	-	-	-	-	-	-	100	-	-
F10002	-	-	-	-	-	-	100	-	-
F10004	-	-	-	-	-	-	100	100	100
F10008	-	-	-	-	-	-	100	-	-
F10009	-	-	-	-	-	-	100	100	100
F10010	-	-	-	-	-	-	100	-	-
F10012	-	-	-	-	-	-	100	-	-
F10013	-	-	-	-	-	-	100	-	-
F10014	-	-	-	-	-	-	100	-	-
F98015	-	-	-	-	-	-	100	100	100
M10007	-	-	-	-	-	-	100	-	-
M10011	-	-	-	-	-	-	100	100	100
M10015	-	-	-	-	-	-	57,62	-	-

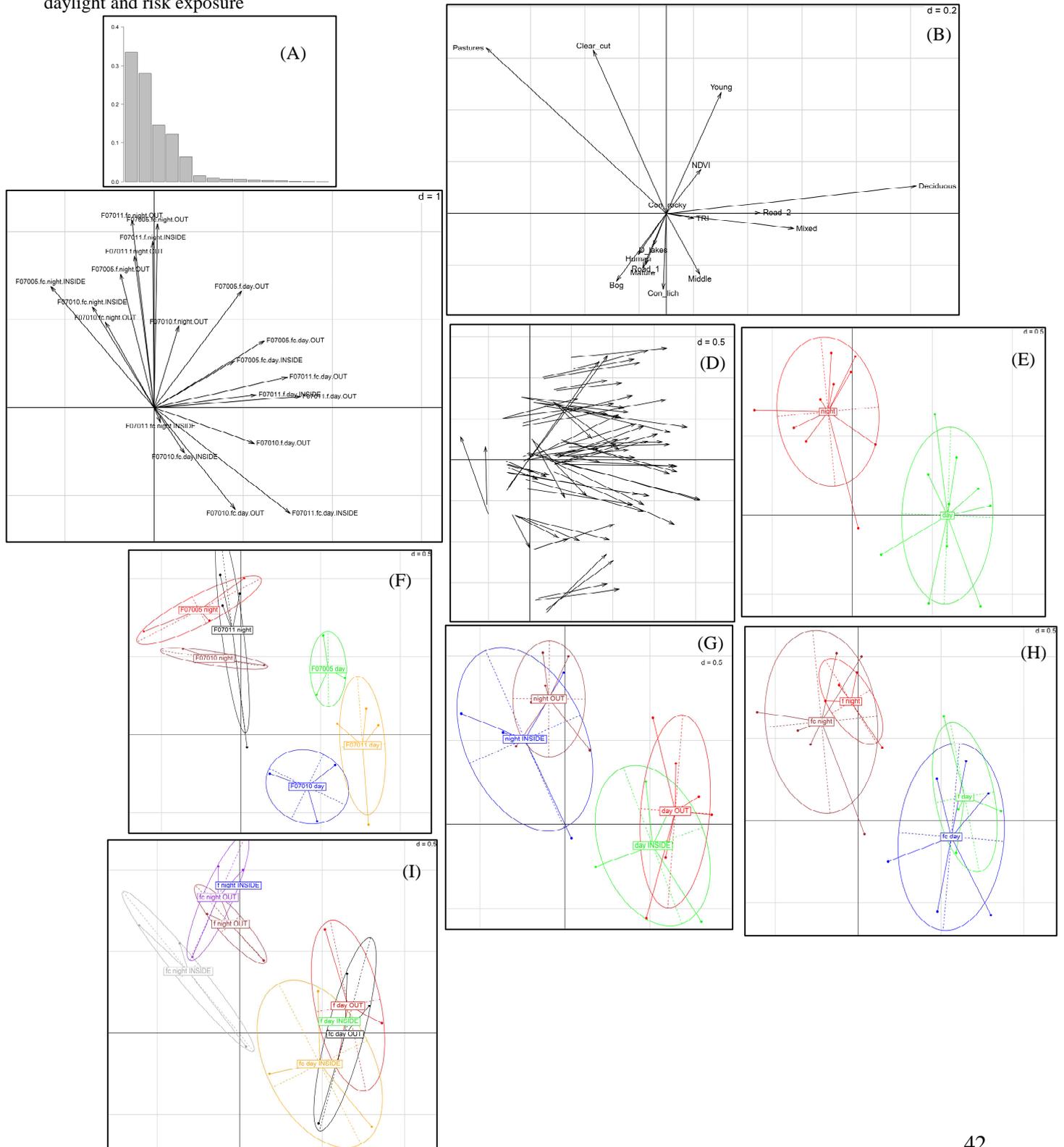
Appendix 6 Winter habitat selection of 3 female moose in the before-after design. (A) Bar chart of the K-select eigenvalues (in percent), measuring the mean marginality explained by each factorial axis. (B) Variables loadings on the two first factorial axes (axis 1: x axis; axis 2: y axis). (C) The marginality vectors of individuals after recentering on each individual home range composition (i.e. the origin of the vector). Individual are characterised by reproductive status (fc: female with calf, f: female without calf), time of day (night and day), risk exposure (OUT: outside wolf territory before wolf re-establishment, INSIDE: inside wolf territory after wolf re-establishment). (D) Plot of marginality vectors projected on the Kselect analysis. The start of the arrow corresponds to the average available inside individual home range and the arrowhead to what is selected by the individual. Marginality vectors differences merged by: (E) Individual, (F) time of the day, (G) reproductive status, (H) reproductive status and individual, (I) risk exposure, (J) individual and risk exposure, (K) reproductive status, individual and risk exposure.



Appendix 7. Summer habitat selection of moose in the variable predation risk design. (A) Bar chart of the K-select eigenvalues (in percent), measuring the mean marginality explained by each factorial axis. The four first axes were kept for the analysis. (B) Variables loadings on the two first factorial axes (axis 1: x axis; axis 2: y axis). (C) The marginality vectors of individuals after recentring on each individual home range composition (i.e. the origin of the vector). Individual are characterised by sex and reproductive status (fc: female with calf, f: female without calf, m: male), time of day (night and day), risk exposure (OUT, low, medium, high). (D) Plot of marginality vectors projected on the Kselect analysis. The start of the arrow corresponds to the average available inside individual home range and the arrowhead to what is selected by the individual. Marginality vectors differences merged by: (E) risk exposure, (F) time of the day, (G) sex and reproductive status, (H) individual and time of the day, (I) risk exposure and time of the day.



Appendix 8 Summer Habitat selection of 3 female moose in the before-after design. (A) Bar chart of the K-select eigenvalues (in percent), measuring the mean marginality explained by each factorial axis. (B) Variables loadings on the two first factorial axes (axis 1: x axis; axis 2: y axis). (C) The marginality vectors of individuals after recentering on each individual home range composition (i.e. the origin of the vector). Individual are characterised by reproductive status (fc: female with calf, f: female without calf), time of day (night and day), risk exposure (OUT: outside wolf territory before wolf re-establishment, INSIDE: inside wolf territory after wolf re-establishment). (D) Plot of marginality vectors projected on the Kselect analysis. The start of the arrow corresponds to the average available inside individual home range and the arrowhead to what is selected by the individual. Marginality vectors differences merged by: (E) time of the day, (F) time of the day and individual, (G) time of day and risk exposure, (H) reproductive status and time of the day, (I) by reproductive status, daylight and risk exposure



Appendix 8 continued Summer Habitat selection of 3 female moose in the before-after design on the 3 and 4 factorial axes (axis 3: x axis; axis 4: y axis). (J) Variables loadings on the two first factorial axes. (K) the marginality vectors of individuals after recentering on each individual home range composition (i.e. the origin of the vector). Marginality vectors differences merged by: (K) risk exposure, (L) individual and time of the day.

