# Habitat characteristics between different clusters of wolf (Canis lupus) activity before and after brown bear (Ursus arctos) emergence in Central Sweden.


By

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ABSTRACT

We describe the habitat used by wolves (C*anis lupus*) at different clusters of activity, namely at kill sites,  bed sites and other sites, before and after brown bears (U*rsus arctos*) emergence from dens in central Sweden. Field protocols were gathered in previous predation studies from 2010 to 2014 of both species in Scandinavia. Wolves of three different packs and brown bears which overlapped their territories were GPS collared. Field protocols resulted in 182 clusters of activity and were further divided into different cluster types: kill sites (n=47), bed sites (n=65) and other sites (tracks and nothing, n=11, n=59, respectively). We established two main thresholds in order to select wolf kill sites and other clusters, *(i)* first, a cutoff directly related to seasonal variation of brown bears – winter season, when bears are in their winter dens and – spring season, when bears come out of den, *(ii)* second, a cutoff related to the life cycle of their main prey, moose (A*lces alces*) in Scandinavia. We used multinomial logistic regression and Akaike´s information criterion (AIC) to select the best models. We picked those models within $\Delta$AIC < 2. The results revealed that kill sites and bed sites were common in mature forest (the availability of land use is not considered in the comparison). However, the frequency of other sites tend to be similar in both mature forest and other (clear-cuts and water related areas). Human population density was high in bed sites and other sites compared to kill sites during winter. In contrast, kill sites occurred in places with moderate human density in both seasons and near roads within young forest compared to mature forests (221 m ± 188 and 283 ± 207, respectively). Clusters type differed mainly due to the vegetation type, followed by human population density, whereas was lower in kill sites than other clusters type. Finally, human population density was the only variable which had effect, showing that kill sites within mature forest were located in areas with higher human density, while those in open areas (clear-cuts and water related) were located in areas with low human density. In conclusion, the wolf habitat use was influenced by vegetation type and human population density, but not by the presence of brown bear.

**Keywords:** vegetation type, wolf clusters, kill sites, wolves, brown bears, protocols

## INTRODUCTION

Wolves are considered habitat generalists, occupying a wide variety of land-use and vegetation types (Mladenoff *et al*. 1995; Mech and Boitani, 2003). Nevertheless, they show clear preferences for specific kill sites and travel routes (Kunkel and Pletscher 2001; Husseman *et al*. 2003). A good understanding of how wildlife use available space is important for their management and conservation, as it provides insight into the ecological requirements of the species. For example, Rostro-Garcia et al. (2014) found that, for cheetahs, there is a trade-off between prey abundance and predator avoidance in terms of habitat selection within their home range. Ecological requirements such as landscape attributes (Balme *et al*. 2007), resource availability (Yurewicz *et al.* 2004) and inter- and intraspecific interactions (Palomares *et al.* 1999) should be considered in order to obtain an integrated understanding of space use.

Scandinavia's boreal forest is among the most intensively exploited forest in the world, with very small amount of prime forest left (Linnell et al. 2000). The fragmentation of the boreal forests results in a set of clear-cuts, transitional woodlands and mature forest (Guraire *et al.* 2011), on a 70-80 years cycle with the use of heavely mechanised system (Linnell et al. 2000). Such forest modifications have important effects on biodiversity (Essen et al. 1992). A clear example of such modifications are the direct impacts on predator–prey relationships (Wittmer et al. 2007), where habitat loss and fragmentation (Chubbs et a. 1993; Smith et al. 2000), limiting resource availabiliy whereas animals seeking riskier environments increasing predation (Wittmer et al. 2007). Human presence is likely also an important factor for wildlife in modified boreal forests. A large number of gravel roads is built and used for commercial logging and forest management practices (Sand *et al*. 2008). These roads are used for travelling by wolves

(Zimmermann *et al.* 2014) and may enhance the chances of encounter with their prey (Kauffman *et al.* 2007, Courbin *et al.* 2013). Forest roads and habitat fragmentation increases the number of transitional habitats and successional growth of deciduous plants used by ungulates browsers (Edenius *et al.* 2002). Human population density is low within the distribution area of the Scandinavian wolf population, but, can affect wolf space use (Zimmermann et al. 2014). The main ungulate prey species in the area are moose *Alces alces* and roe deer *Capreolus capreolus* (Sand *et al.* 2005, 2008; Zimmermann *et al.* 2014). Moose is an abundant browser which have preference from young forest, indirectly benefitting from forestry practices (Edenius *et al.* 2002).

Ballard et al. (2003) argued that interactions between competing species of predators are an important driver of space use. There are two main types of interactions: *(i)* indirect, through resource competition when both species use the same food resource (Ballard *et al.* 2003; Mattison *et al.* 2011) and *(ii)* direct, such as interespecific killing (Palomares & Caro, 1999; Ballard *et al*. 2003). Wolves and bears use commom resources in a similar way (Ballard *et al*. 2003). In Katmai National Park (Alaska), Smith *et al.* (2003) showed that wolves can harass, and displace brown bears from carcasses and even steal fish from Grizzly bears. There are, on the other hand, many cases documented in which american bears [Grizzly] usurpate carcasses from wolves (Gunther et al. 2004). In Scandinavia, the majority of interactions between brown bears and wolves are indirect (Milleret C, 2011) with only a few direct interactions being recorded to date (Steyaert *et al*. 2010). Understanding the ecological interactions between wolves and brown bears in boreal forests can provide insights into their ecological roles as top predators, including the relationship with their prey which may be important to the conservation and management of these carnivores.

Nowadays, as a result of studies on the ecology and conservation of large carnivores many people see an both an inherent intrinsic value in carnivores and perceives their role as important in ecosystem functioning (Miller *et al*. 2001). At large scale, large carnivores are threatened with both population size and their distribution ranges declining around the world (Ripple *et al.*

2014). At the continental scale, large carnivores may be stable or increasing their abundance in many countries of Europe (Chapron *et al.* 2014) but possibly losing their functional value at ecosystem level (Gilroy *et al*. 2015).

At local scale and focusing in the Scandinavian Peninsula (Norway and Sweden), the population of large carnivores declined strongly throughout the 19th and 20th centuries. The erradication was directly caused by persecution, including bounties, and indirectly by elimination of prey (Schwartz *et al*. 2003). Nowdays there is a small but growing wolf population of 450 wolves (winter 2014-2015, Anon. 2013) and a stable brown bear population of 3200 bears in Sweden (for 2008, Kindberg *et al*. 2011). The main prey, the moose, is present all across Sweden (except in the Island of Gotland) being the largest herbivore in the country (Jensen 2004). The Swedish population is estimated to be 200.000–300.000 individuals at the end of the hunting season (Singh *et al*. 2014).

Currently, the techniques to track animals are developing very fast (Urbano *et al.* 2010). GPS (Global positioning system) technology make it possible to track individuals everywhere providing greater knowledge of animal behaviour (Frair *et al*. 2010). In Scandinavia, every year wolves and bears are captured and collared with GPS radio collars within the frame of a long term research programs. The spatial locations can be used to identify clusters of local activity, potentially allowing the identification of kill sites (Anderson and Lindszey, 2003; Sand *et al*. 2005; Franke *et al.* 2006) and other areas more intensively used by wolves such as resting sites or other types of behaviour.

In this project, my aim was to investigate the habitat characteristics of different types of wolf activity sites (kill sites, bed sites and other sites; tracks and nothing) in *(i)* two different seasons, when bears are still in their winter dens (winter season), and after bears come out of their winter dens (spring season); *(ii)* and the habitat characteristics between wolf kill sites in both these seasons.

MATERIAL AND METHODS

**Study area**

The study was conducted in Jämtland, Gävleborg and Dalarna counties in central Sweden ($61^{o}$N, $15^{o}$E), covering an area of 2.848 km$^{2}$ (Figure 1). The mean daily temperature in winter and summer is -$7^{o}$C and $15^{o}$C, respectively. Mean precipitation during the period of vegetation growth is 350–450 mm (Swenson *et al*. 1999). Snow is present from November to early May (Steyaert and Frank, 2010).

The landscape is hilly, with elevations between 200 to 750 m a.s.l. Lakes and bogs are widespread in the area (Fiebre *et al*. 2001). Coniferous forest of Scots pine (P*inus sylvestris*), Norway spruce (P*icea abies*) and lodgepole pine (P*inus concorta*) dominates the landscape. Deciduous trees are also common, including birch (B*etula pubescens*), silver birch (*Betula pendula*), aspen (P*opulus tremula*) and grey alder (A*lnus incana*) (Friebe *et al.* 2001, Solberg *et al*. 2006, Nellemann *et al*. 2007). The ground layer is dominated by several species of berries (V*accinium myrtillus*, V*accinium vitis-idaea*, E*mpetrum nigrum and* R*ubus chamaemorus*), grasses, lichen and mosses (Nellemann *et al.* 2007). A large network of gravel roads has been developed due to extensive commercial logging and forest management practices (Sand *et al*. 2008). Nevertheless, human density within the distribution of the Scandinavian wolf population is low, having large areas with less than a 1 person per km2 (Wabakken *et al*. 2001; Mattison *et al*. 2013). Moose are the most important prey of wolves in Scandinavia (Zimmermann *et al*. 2014), representing up to 95% of the food consumed of Scandinavian wolf packs (Sand *et al*. 2008). Other ungulate prey are roe deer, red deer, mountain and European hares (*Lepus timidus* L., *Lepus europeus* Pallas), capercaillie (T*etrao urogallus* L.) and black grouse (L*yrurus tetrix* L.; Sand *et al,* 2008). Other carnivores are also present in the area, including wolverine (*Gulo gulo*), boreal lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), Eurasian badger (*Meles meles*) and Marten (*Martes martes*).

**Wolf and brown bear data**

Research on wolves is carried out by Skandinavian Wolf Research Project and that of brown bears by Skandinavian Brown Bear Research Project. The SKANDULV research project started in Sweden and Norway in the year of 2000 (based at Grimsö Wildlife Research Station, Sweden), while SBBRP works mostly in Sweden and Norway since 1984 (based at the Norwegian University of Life Science)

The three wolf packs included in this study overlap the area with the higgest brown bear density in Sweden. According to Kindberg *et al*. (2011), the overall estimated population of brown bears present in 2008 in the three counties was 608 individuals which. The three wolf territories were known as Tandjon, Tenskog and Kukumaki. We used information on the spatial location of GPS-collared brown bears and wolves whose home ranges overlapped and obtained in the course of previous studies on predation.

Wolves were captured using snow-tracking during winter to locate the pack. Then they were immobilized from a helicopter following standard procedures (Sand *et al*. 2006; Eriksen *et al.* 2011; Kreeger and Arnemo, 2012) and equipped with a GPS neck collar (GPS-Simplex, Web-Direct, or Tellus by Followit, Sweden, or GPS-Plus by Vectronic Aerospace, Germany). Brown bears are usually captured in early spring, after they come out of dens. Brown bears were darted from a helicopter using a remote drug delivery system. They are fitted with GPS collars and VHF abdominal implants (Arnemo, 2006; Evans *et al*. 2012).

The scheduling of the spatial locations of marked individuals is described by Milleret 2011. Briefly, a wolf male was located at hourly intervals (24 locations per day) and a female wolf every four hours (6 locations per day). In the case of brown bears the schedule varied along the season of the year. For the purpose of this study the schedule was one position per hour (24 positions per day). When 7 locations were saved in the internal memory of the GPS collar, they were sent by SMS (Short Message Service) using GSM (Global System for Mobile communications network) through GPS PLUS Manager V3.0.0 software (Vectronic aerospace).

The coordinate system used is RT 90 for Sweden. I used data from 2010 to 2014 for kill sites: Tandsjon 2012 and 2014; Kukumaki 2013 and 2014 and Tenskog 2010 and 2011. Data for bed sites and other sites (tracks and nothing) was obtained in during field work in 2014 for the packs in Tandsjon and Kukumaki.

**Data processing, clusters and identification of type of activity**

The analysis was based on hourly GPS positions of wolves showing spatial aggregation in clusters. In order to create a cluster, 100 and 60 meters buffers were created around all positions of wolves and bears, respectively. The overlapping area between buffers was defined as a cluster with a unique cluster identification number (Sand *et al*., 2005, 2008; Zimmermann *et al*., 2007). We used clusters of locations to identify potential kill-, bed- and other-sites. Clusters were visually identified including both consecutive positions and other positions as they represent revisits to the same site, potentially representing the re-use of a carcass. Identified cluster sites were visited in the field to identify the type of cluster. Every third day wolf clusters were visited. In each wolf cluster any sign wolf of activity was registered. We classified the clusters in four categories*: (i)* carcass sites *(ii)* bed sites, *(iii)* tracks and *(iv)* other. For the study we merged tracks and other into a single category other sites (Table 2). GPS coordinates were recorded in every cluster visited, defined as the exact location of carcass sites, bed sites in the case of resting places (always wolf hair present), and sites with only wolf tracks. In clusters with no sign of activity, the position was defined as the center of the defined cluster. We placed camera traps at carcass sites to record predator activity (*shot mode* – Reconyx HC600 or Scout Guard), far enough to take wide angle shots of the site.

To estimated date of death of killed prey carcass sites were classified using the first date and time of the GPS collar. For this study, we classified the clusters as belonging to different seasons considering two time thresholds. First, a cutoff directly related with seasonal variation of brown bear winter season, i.e. when bears are in their winter dens (before the first of April) and spring season, when bears come out of their den (after the first of April). The date of emergence of brown bears is different between males and females with male emergence on average between 6 March and 25 April, with a mean in the 4th of April, whereas females emerge on average of 17 days later (Friebe *et al*. 2001; Manchi and Swenson 2005).

Second, we used a cutoff related with the life cycle of moose in Scandinavia. Females give birth to one or two calves over a two week period in late spring (Solberg *et al*. 2007; Haydn, 2012); usually between the late May and early June (Jensen, 2004). Previous predation studies show that predation on moose calves by brown bears usually starts during the third week of May. Therefore, we decided to use the 15th of May as cutoff with the purpose identifying the two periods representing predation on adult and yearling moose (before 15th May) and juvenile moose (after 15th May), respectively. The identified clusters were nearly equally distributed between the two seasons.

**Habitat and other environmental data**

The clusters visited in the field were described following pertinent procedures, obtaining information on the type of carcass (if present), the habitat and other predator signs (Appendix 1). Carcasses were classified according to the: number of carcasses, species, estimated age (days) since death, earliest/latest date, cause of death, animal age, sex, and also including a sample (usually jawbone) from the killed animal. We described the habitat of the clusters using predefined vegetation categories and for the analyses we used the vegetation type assigned in the field (Table 1). Additionally, we used a GIS vegetation layer (SLU Forest Map with 25m x 25m pixel resolution, projection RT90 2.5 gon V of the year 2010) to classify the sites into different vegetation types. The layer is based on a combination of data from the Swedish National Forest inventory and satellite data (www.slu.se). We used the layers of roads network of Scandinavia and human density. The minimum distance to the roads was calculated by using Analysis tools, proximity, Near in Arc Toolbox. To extract information from human density layer we used Overlay, Arc Toolbox.

**Analyses**

We analyzed the information obtained in the field regarding kill sites (only those classified as wolf killed and probably wolf killed), bed sites and other sites (tracks and nothing) to test if there were differences in the habitat use (type of vegetation) for different activities before/after brown bears came out of winter dens. The potential predictors for the type of vegetation used were: old forest, young forest, and other (Table 1), season (factor) was either 0 when bears are in winter dens and 1 when bears are active, distance to nearest road (m), and human population density (persons/km$^2$). In the first analysis we looked for differences between the three types of cluster: kill sites, bed sites and other sites as response variable and using vegetation type, season (factor), distance to nearest road (m) and human density within county (persons/km$^2$) as potential predictors. In a second analysis, we explored, for kill sites only, if the vegetation types (response variable) differed between seasons (factor), distance to nearest road (m) and human density within county (persons/km$^2$). For both analyses we used multinomial logistic regression models (nnet package in R), using Akaike´s information criterion (AIC) for model selection (AICcmodavg package, Mazerolle 2015) and Multimodel Inference Based on (Q)AICc (Akaike 1974, Shibata 1981). Parameter estimates and standard errors in the set of best top models were examined to assess the reliability of each variable as a predictor of comparison of different clusters and between kill sites before and after bear emergence of winter dens. All statistical analysis was carried out in R studio (https://www.rstudio.com/).

## RESULTS

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In total we visited 182 clusters, and identified the activity performed by wolves in 68% of them (Table 3). The majority of the clusters where a certain activity was identified were classified as *other sites*. This is probably so because the centre of the cluster is located in slitghly different positions and the locations lie at the edge between two types of vegetation (Table 3), or due to vegetation growth since 2010 (See Material and methods). In general, kill and bed sites tended to be more frequent in oldforest (note that land use availability is not considered in this comparison). In contrast, the frequency of other sites tended to be proportionally distributed between old forest and other vegetation types. Human population density was higher in both bed sites and other sites compared to kill sites during winter (Table 4). Kill sites tended to be closer to roads when located in young forest in comparison with those in old forests (221 m ± 188 and 283 ± 207, respectively).

The types of clusters differed in their habitat characteristics mostly due to the type of vegetation (Table 5). The main effect was due to other sites, which were much more frequently located in open areas such as bogs and clear-cuts (other vegetation type, Table 6, Figure 2). Human population density was the second most important variable explaining differences between sites, and being lower in kill sites than in other cluster types of activity (Table 6). Season was the third variable included, with a very weak effect (Table 5).

We further explored the role of habitat characteristics on kill sites using vegetation type as dependent variable (Table 7). Human density was the only habitat variable having an effect, showing that kill sites in old forest were located in areas with relatively higher human density, while those in open areas (bogs and clearcuts) were located in areas with lower human density (Table 8, Figure 2). The effect was strong with statistical support (Table 7). Brown bear season had no apparent effect (Table 7).

## DISCUSSION

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It is known that wolf is a flexibe and opportunistic predator (Peterson and Ciucci, 2003) and one of the most adaptable mammals (Mech and Boitani, 2003). Therefore biological and ecological factors, such as moose abundance, may explain where wolf clusters of activity are located in a modified boreal landscape. The distribution of this ungulate depends on a suitable interspersion of food and protective cover (Dussault et al. 2006), with the seasonal changes in foraging patches affecting space use (Heikkilä and Härkönen, 1993). A previous study at Isle Royale showed that moose will use dense coniferous forest to decrease the probability of detection from wolves and to reduce the chance of wolf attacks (Peterson 1977). In a similar study, Creel et al. (2005) showed how elk are likely to use foraging sites in open terrain with no presence of wolves, but change into forest areas in the presence of them, most likely to benefit from increased forest cover protection. Moreover, Kunkel and Pletscher (2001) suggested that wolves prefer areas with significant forest cover, which enhances their chances to remain undetected by prey. The high number of kill sites detected in old forest could be correlated with moose density distribution.

The number of kill sites we found within young forest is lower than old forest (Figure 2), but still quite high compared to other (clear-cuts and water related) Previous studies suggest the use of young forest stands as foraging sites by moose (Parker and Morton, 1978). Some findings in boreal regions showed that there is a positive correlation between moose occurrence and young forests, clear cuts and young pine plantations (Cederlund and Okarma 1988; Cederlund 1989), showing that under some conditions moose have preference for young stands (Edenius, 2002; Bergqvist et al., 2003).

In terms of forest management, Gauthier et al. (2009) explains that many ecological, economic and biodiversity indicators are related to different combinations of forest units and age classes. Moose prefer to browse in regenerating clear cuts and in open, homogenous stands (Edenius et al., 2002; Potvin et al. 2005a). In contrast, a high proportion of recent clear-cuts (not regenerating ones) decrease moose browse availability (Courtois et al. 1998), potentially reducing the number of wolf prey within remaining forest patches (Potvin et al. 1999). Previous studies suggest that the response by wildlife to clear-cuts varies between species (Potvin et al., 1999; Smith et al., 1999; Simon et al., 2002). Therefore, species can get both benefits and disadvantages in response to clear-cuts. Caribou (*Rangifer tarandus*), for example, may increase foraging but also increase predation risk (Leclerc et al. 2014). In the case of wolves, Ciucci et al. (2003) suggest that travel routes have higher probability of being closer to a forest edge increasing chances of encountering prey in which wolves use forest as hiding place and prey could be more abundant. On Isle Royale, yearling moose were likely to be killed close to shoreline habitats, where they forage for browse (Montgomery et al., 2014).

Previous studies in Scandinavia found that wolves modified their behaviour in spring coinciding with brown bears emergence from winter dens (Manchi and Swensson, 2005 in Milleret C. 2011). Dahle et al. (2013) documented the succesful hunt from a male brown bear towards a radio-collared female adult moose in spring in Scandinavia. Steyaert and Frank (2010) reported two direct interactions between wolves and bears but due to GPS-collar problems was impossible to reveal the outcome of the encounter. Milleret (2011) showed only one direct interaction in which brown bear gained access by being dominant of the carcass. The same author, conclude that most of the interactions of the study were indirect. In Yellowstone National Park, Gunther and Smith (2004), recorded some interactions at wolf-killed carcasses between wolves and female grizzly bears with cubs. A study carried  in Slovenia (Krofel and Kos, 2010) showed the high effect of kleptoparasitism by bears on lynx predations. Previous studies showed that habitat selection by wolves is well known to vary between seasons (Mladenoff et al. 1995, Ciucci et al. 2003) and depends on seasonal variation in the habitat selection and body condition of wolves’ prey (Mao et al. 2005, Metz et al. 2012). The presence of old forest is an important component in winter habitat for moose (Hamilton et al., 1980; Welsh et al., 1980), when there is excessive snow cover (Thompson and Vukelich, 1981). In spite of all this previous evidence, we found no change in the type of habitat in which wolves located their activities before and after bear emergence.

We found that the number of kill sites in old forest in winter was almost double as compared to spring (Table 3). This is most likely due to snow depth, prey physical condition and the increase of wolf pack cohesion near prey wintering areas (Peterson et al. 1984; Fuller 1989). It is well known that wolves increase their hunting success with deeper snow conditions (Kolenosky, 1972; Peterson and Allen, 1974), and prey are more vulnerable to predators during late winter (Ciucci et al. 2003).

In Bialowieza forest wolves did not select for a particular type of forest for resting places (Theuerkauf et al., 2003). Most of the bed sites we found were within old forest category , followed by young forest and other. The number of bed sites described in spring season is higher than in winter, most likely due to the difficulty to reach them due to snow depth, e.g. in Tenskog territory the snow reached 105cm in mid February 2011 (Weather station Hamra and Lillhamra, in Milleret 2011). During winter bed sites tend to be in places with higher human density, with predominant old-young forest cover and closer to roads. Most likely they used areas with dense cover either for snow protection or avoiding human encounters. Zimmermann et al. (2014) showed that wolves preferred to rest at intermediate distances to gravel roads.

In previous studies, Fuller et al. (1992) found that most wolf packs in Minnesota were located in areas where human density was ≤ 8 humans/km$^2$. Light and Fritts (1994) found dispersing wolves in the Dakotas to be in areas with a mean human density of 3.5 humans/km$^2$ and with 8.2 humans/km$^2$. Jedrzejewski et al. (2005) revealed that when anthropogenic impact is not too high, wolves can get used to human presence by spatiotemporal segregation from people. It is remarkable that human density within the distribution of the Scandinavian wolf population is low, having large areas with less than a 1 person per km$^2$ (Wabakken et al. 2001; Mattison et al. 2013. In contrast, wolves avoid areas where human disturbance is greater (Kaartinen et al., 2015; Guraire et al., 2011). We found that human density best explains the differences between kill sites located in areas with more or less vegetation cover (from old forest to open areas). Thus kill sites within vegetation type «other»  shows the lowest  human density value (Table 4) most likely to avoid human encounters in open areas. In contrast, wolves tend to kill in areas with high human density and dense forest protection.

In conclusion , our results show that vegetation type and human density can influence the choice made by wolves to locate different types of activities. The high occurrence of kill- and bed sites in old and young forest during winter and spring from 2010 to 2014, and also the heavely used other habitat category (clear-cuts and water related areas) for other activities (tracks and nothing) most likely relates with wolves movement behaviour (marking, hunting, controlling territory). It is possible to hypothesize that wolves generally used open areas as other sites (clear cuts and water related) most likely during night when human activity drecrease but tend to refuse these areas, at least in activities which involve stay longer such as kill sites or resting places, maybe to avoid human encounter. Nevertheless, in order to provide an adequate assessment of the drivers of space use in relation with the interaction with bears, further monitoring of wolf –bear interactions and the consideraton of other variables such as wolf pack size, prey density or bear sex and age, would improve our knowledge towards interespecific interaction between large carnivores in boreal landscapes.

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TABLES AND FIGURES

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**Table 1.** Main habitat types used in field protocols. Re-classification of habitat into three main vegetation types -other, young and old forest used in the study.

| **Habitat type** | **Description** |
|---|---|
| RZ - Riparian zone | A river > 3m wide within the 30-meter plot. |
| B - Bog | Peat ground with very low productivity. Nor flow or ground water |
| TRB – Tree rich bog | Similar to bog but rich in trees. |
| I - Impediment | Natural barriers, rift, holes and other related. |
| SW/SF - Swamp/Swamp forest | Waterlogged ground (not on peat) often with broadleaf grasses and herbs. There is outflow of water and high productivity. |
| W – Water | River or lake within 30 m radius of the plot |
| Rd – Road | Small gravel roads, roadsides and main roads |
| OT – Other | Any habitat not described previously |

| **Vegetation types** | |
|---|---|
| **Old forest** (mature forest) | (G1/S1) with interval of age from 25 – 30 years and > 30 years old |
| **Young forest** | (R1/R2) with interval of age in between 5 – 25 years old |
| **Other** (clear-cuts/water related) | (K1/K2) with interval of age 0 – 5 years old and water related. |

**Table 2**. Definition of clusters types used in the study.

| **Cluster type** | **Description** |
|---|---|
| **Kill sites**<br><br>**(prey remains)** | Clusters defined as kill site place with the presence of a carcass. Evidences of fight between wolf-prey. Often the rumens prey is spread out. Often strong smell. Pipe bleeding. Ground scratches.<br><br>**Wolf killed prey**: clear evidences of fight. Warm prey blood pumped out of arteries/veins make little tubes called pipes through the cold snow which is called "pipe-bleeding" (Sand *et al*., 2008). Blood clots upon tree trunks or branches. Often rumens prey is spread out. Occasionally, we could observe clear tracks, scratches and urine typical of chasing prey (Hayes *et al.,* 2000, Sand *et al.,* 2005, 2008).<br><br>**Probably wolf killed**: the estimation of the time of prey death coincided with time of the GPS-positions (Sand *et al*. 2008). The degree of consumption and decomposition depends on the time elapsed and the weather.<br><br>**Not wolf killed prey**: the prey was bounded by hunting or road killed.<br><br>Other potential killers: difficult to discern between wolf and other predators, but with some evidence of other predator. For example, evidence of bear behavior around at similar date/time of collar positions.<br><br>**Unknown**: not classified into the previous categories. |
| **Bed sites** | Clusters related with resting behavior. Beds always confirmed with the presence of wolf hair on it. |
| **Other sites** | Combination of tracks and nothing clusters. In both type of clusters wolves spent time for behavioral reason.<br><br>**Tracks**: Clusters with clear wolf tracks and evidences of being a way of passing back and forth through the same spot.<br><br>**Nothing**: Clusters with no clear evidences at human view but wolves used these places. |

**Table 3**. Vegetation types in wolf different types of clusters in Scandinavia, as described in field protocols that were filled in during wolf predation studies and from GIS layers.

| | **Field sampling** | | | | | | **GIS data** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Cluster type** | **Kill sites** (n=47) | | **Bed sites** (n=65) | | **Other sites** (n=70) | | **kill sites** (n=47) | | **Bed sites** (n=65) | | **Other sites** (n=70) | |
| **Period** | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| **Vegetation type** | | | | | | | | | | | | |
| Old forest | 16 | 9 | 14 | 19 | 12 | 15 | 17 | 15 | 14 | 27 | 15 | 14 |
| Young forest | 6 | 9 | 12 | 13 | 7 | 8 | 8 | 0 | 9 | 4 | 3 | 19 |
| Other | 3 | 4 | 3 | 4 | 5 | 23 | 1 | 6 | 4 | 7 | 6 | 13 |
| TOTAL | 25 | 22 | 29 | 36 | 24 | 46 | 26 | 21 | 27 | 38 | 26 | 44 |

Period: 0 (winter season), 1 (spring season)

**Table 4.** The table represents the values (mean ± S.E) of independent variables used in the study in relationship with different cluster types (n=182). Results of human density values (mean ± S.E) in kill sites (n=47) in relationship with vegetation type.

| | Distance to roads (m) | | Human density (person/km2) | | | | |
|---|---|---|---|---|---|---|---|
| **Period** | **0** | **1** | **0** | **1** | **Old forest** | **Young forest** | **Other** |
| **Cluster type** | | | | | | | |
| Kill sites | 247 ± 168 | 302 ± 232 | 3.44 ± 2.01 | 3.36 ± 2.18 | 3.98 ± 1.92 | 3.61 ± 1.97 | 0.87 ± 0 |
| Bed sites | 243 ± 152 | 261 ± 250 | 4.34 ± 2.01 | 3.64 ± 2.28 | - | - | - |
| Other sites | 219 ± 179 | 286 ± 368 | 4.05 ± 1.92 | 3.84 ± 2.32 | - | - | - |

Period: 0 (winter season), 1 (spring season)

**Table 5.** Model selection of different cluster types (kill sites, bed sites and other sites) before and after bear den emergence in Scandinavia based on AICc, ΔAIC and wAIC.

**Kill sites, bed sites and other sites**

| | **K** | **cAIC** | **ΔAIC** | **wAIC** |
|---|---|---|---|---|
| Vegetation type | 6 | 388.30 | 0.00 | 0.33 |
| Vegetation type + Human density | 8 | 388.52 | 0.23 | 0.30 |
| Vegetation type + Human density + Season | 10 | 390.07 | 1.78 | 0.14 |
| Vegetation type + Season | 8 | 390.37 | 2.08 | 0.12 |
| Vegetation type + Distance roads | 8 | 392.44 | 4.14 | 0.04 |
| Vegetation type + Distance roads + Human density | 10 | 392.95 | 4.66 | 0.03 |
| Vegetation type + Distance roads + Season | 10 | 394.48 | 6.18 | 0.02 |
| Vegetation type + Distance roads + Human density + Season | 12 | 394.56 | 6.26 | 0.01 |
| Vegetation type x Season | 12 | 395.43 | 7.14 | 0.01 |
| Season | 4 | 398.86 | 10.56 | 0.00 |
| Intercept only | 2 | 398.95 | 10.65 | 0.00 |
| Human density + Season | 6 | 399.46 | 11.16 | 0.00 |
| Human density | 4 | 400.26 | 11.96 | 0.00 |
| Distance roads + Season | 6 | 402.83 | 14.54 | 0.00 |
| Distance roads | 4 | 402.93 | 14.64 | 0.00 |
| Distance roads + Human density + Season | 8 | 403.70 | 15.71 | 0.00 |
| Distance roads + Human density | 6 | 404.43 | 16.13 | 0.00 |
| Distance roads x Human | 8 | 408.13 | 19.83 | 0.00 |

**Table 6.** Results of multinomial logistic regression with a set of top models ($\Delta$AIC $<2$) to compare wolf kill sites, bed sites and other sites (nothing and tracks), before and after bear emergence in Scandinavia.

| | | Predictors | | | | | |
|---|---|---|---|---|---|---|---|
| | | **Vegetation type** | | | **Human density** | **Season** | |
| | Intercept | other | young | old | | winter | spring |
| **Model 1: Vegetation type** | | | | | | | |
| Kill site | - 0.277 (0.265) | 0.277 (0.596) | -0.233 (0.420) | 0 | - | - | - |
| Other site | -0.200 (0.259) | 1.586 (0.495) *** | -0.310 (0.417) | 0 | - | - | - |
| Bed site | 0 | 0 | 0 | 0 | - | - | - |
| **Model 2: Vegetation type + Human density** | | | | | | | |
| Kill site | 0.168 (0.437) | 0.172 (0.604) | -0.264 (0.423) | 0 | -0.114 (0.089) | - | - |
| Other site | -0.499 (0.458) | 1.642 (0.503)*** | -0.290 (0.418) | 0 | 0.069 (0.087) | - | - |
| Bed site | 0 | 0 | 0 | 0 | 0 | - | - |
| **Model 3: Vegetation type + Human density + Season** | | | | | | | |
| Kill site | -0.023 (0.473) | 0.267 (0.610) | -0.251 (0.425) | 0 | -0.124 (0.090) | 0.430 (0.394) | 0 |
| Other site | -0.409 (0.478) | 1.596 (0.507)*** | -0.301 (0.419) | 0 | 0.076 (0.088) | -0.259 (0.375) | 0 |
| Bed site | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Estimates (S.E). ($P \leq .001$) ***

**Table 7.** Model selection of wolf kill sites before and after bear den emergence in Scandinavia based on AICc, ΔAIC and wAIC.

**Kill sites**

| | K | cAIC | ΔAIC | wAIC |
|---|---|---|---|---|
| Human density | 4 | 83.44 | 0.00 | 0.65 |
| Human density + Season | 6 | 86.06 | 2.62 | 0.17 |
| Human density + Distance roads | 6 | 87.06 | 3.61 | 0.11 |
| Human density x Distance roads | 8 | 88.76 | 5.32 | 0.05 |
| Human density + Distance roads + Season | 8 | 89.90 | 6.46 | 0.03 |
| Intercept only | 2 | 96.76 | 13.32 | 0.00 |
| Season | 4 | 98.90 | 15.45 | 0.00 |
| Distance roads | 4 | 99.38 | 15.94 | 0.00 |
| Distance roads + Season | 6 | 101.72 | 18.28 | 0.00 |

**Table 8.** Results of multinomial logistic regression with the best top model (ΔAIC <2) to compare wolf kill sites before and after bear emergence in Scandinavia.

| **Model: Human density** | | **Predictor** |
|---|---|---|
| **Vegetation type** | **Intercept** | **Human density** |
| Old forest | 0 | 0 |
| Young forest | -0.116 (0.723) | -0.103 (0.171) |
| Other | 4.146 (23.93) | -4.370 (27.49) |

Estimates (S.E)

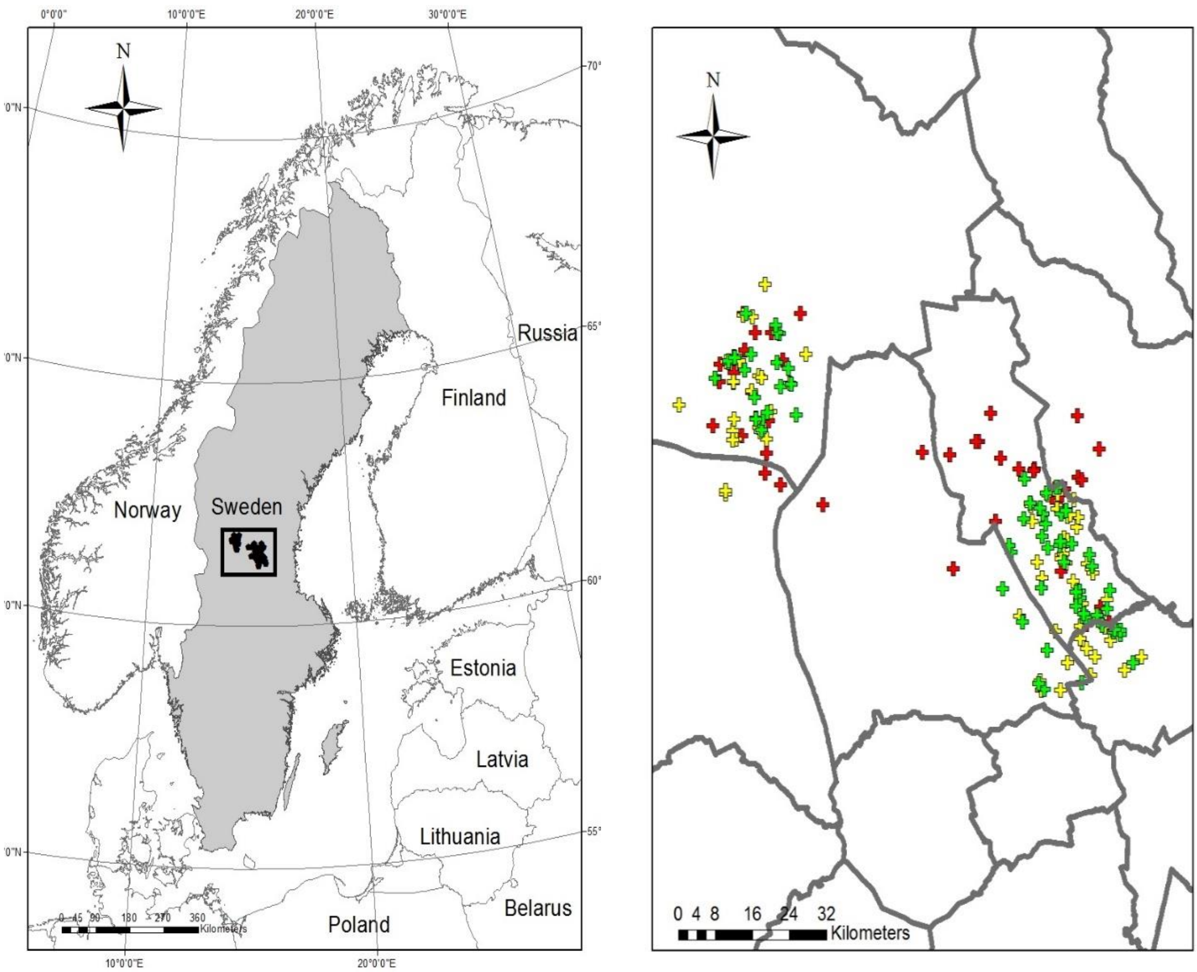


**Figure 1.** Map of the study area in Scandinavian Peninsula (grey area, black square) and wolf territories (black dots) within three counties – Jätmland, Gävleborg and Dalarna in central Sweden. Total of wolf kill sites (red crosses), bed sites (green crosses) and other sites (yellow crosses) in the study area.

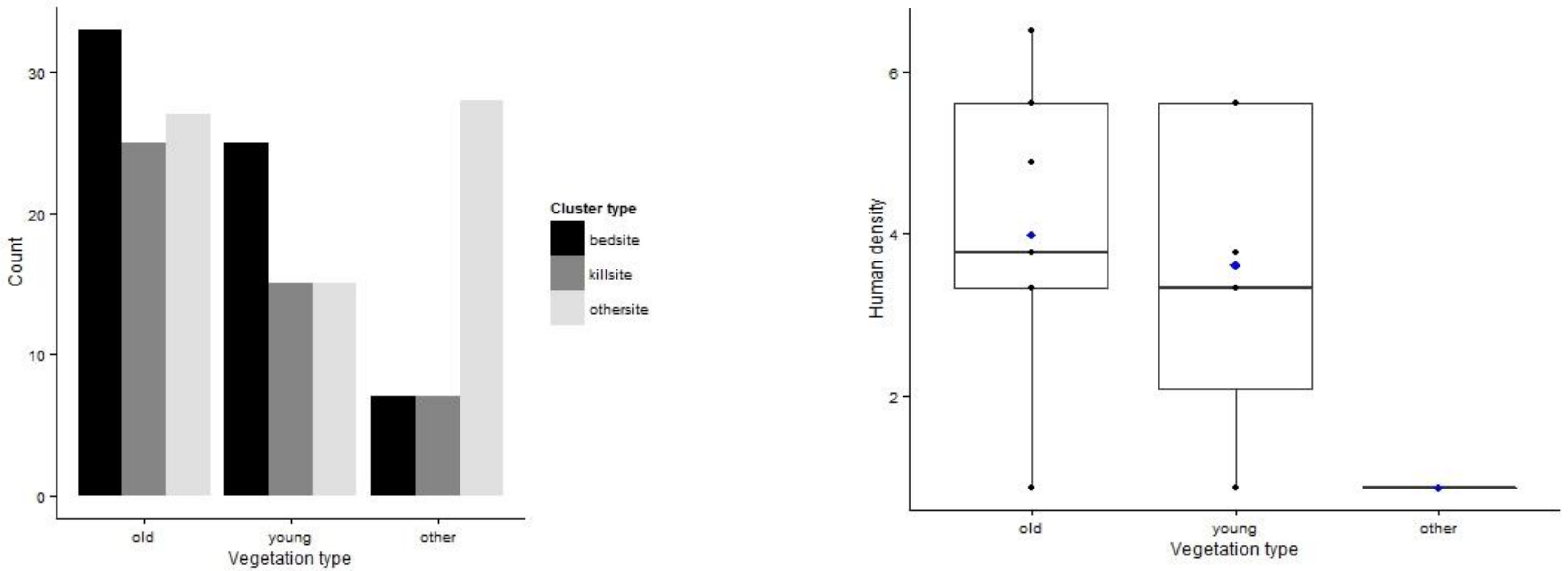


**Figure 2.** Bar plot representing cluster type counts resulted in field protocols (n=182) in relatioship with vegetation type. Box plot representing the values of human density on wolf kill sites (n=47) in relationship to vegetation type.

APPENDIX

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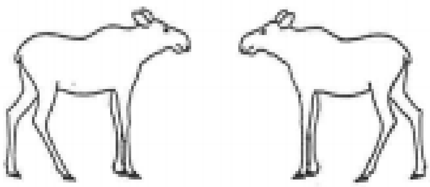
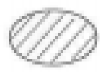
**Appendix 1**: Field protocol used for predation studies in Scandinavia.

## Wolf-Bear Pilot Study: Carcass Protocol 2011

(last updated on 2011-05-27 by ShFr, JoKi, GRRa, and KrAu)

| | | | | |
|---|---|---|---|---|
| **Protocol Information** | **Protocol_ID:** e.g. PR… | **Observer:** | **Year_____Month_____Day____** | **Start:** **Stop:** |
| | **Related to:** | | **Plot Selection:** ☐Wolf-bear cluster ☐ Bear cl ☐ Wolf cl Other:___ | |
| | **Cluster Coord. N: E:** | | | |
| | **Wolf Name(s)** | **ID:** | **Date:** | **Time:** |
| | **Bear Name(s)** | **ID:** | **Date:** | **Time:** |
| **Carcass** | **No. of Carcasses:** | | **Carcass Coord. N: E:** | |
| | **Species:** | | **Carcass Est. Age (days):** ____ | |
| | **Earliest / Latest Date:** ___-___-___ / ___-___-___ | | **Animal Age:** ☐ 0-1 ☐ >1 ☐ unknown | **Sex:** ☐M ☐F ☐Unkown |
| | **Cause of Death:** ☐Wolf ☐Bear ☐Other predators (sp.) __________ ☐Non predator __________ ☐ Unknown __________ | | | |
| | **Carcass # of Pieces (☐sampled):** Mandible: ___ (☐) Bone(s): ___ (☐) Skull: ___ (☐) Hair: ___ (☐) Other: ________ (☐) | | | |
| **Habitat** | **In Habitat:** **Ground/Field:** | **Moisture:** | **Ruggedness:** | **Picture Taken:** ☐Yes ☐No |



Ingested/Missing Parts: 

Consumed/Missing of Carcass: _____%

Fresh Bleeding on Snow/Ground: ☐Yes ☐No

Concentrated "pipebleeding": ☐Yes ☐No

| | Sign Type | Bear | Wolf | Otherspecies:______ |
|---|---|---|---|---|
| **Predator Signs** | **Tracks** (Picture ☐Y☐N) | ☐Y☐N☐Unsure | ☐Y☐N☐Unsure | ☐Y☐N☐Unsure |
| | **Scat** (Sampled ☐Y☐N) | ☐Y☐N☐Unsure | ☐Y☐N☐Unsure | ☐Y☐N☐Unsure |
| | **Hair/Fur** (Sampled ☐Y☐N) | ☐Y☐N☐Unsure | ☐Y☐N☐Unsure | ☐Y☐N☐Unsure |
| | **Bed** (confirmed with hair) | ☐Y☐N # ____ | ☐Y☐N # ____ | ☐Y☐N # ____ |
| | **Other sign:**________ | | | |

| **Other: (clarification, comments, sketch of area/hunt)** |
|---|
| |