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Estimating wolves (*Canis lupus*) and brown Bear (*Ursus arctos*) interactions in Central Sweden. Does the emergence of brown bears affect wolf predation patterns?

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Summary:

Little is know about wolves (*Canis lupus*) and brown bear (*Ursus arctos*) interactions. The recovery of wolves and brown bears population in Central Sweden offer a good opportunity to study these interactions. Because wolves and brown bears use the same resource, moose (*Alces alces*), in a similar way, competition between both predators might be intense. Knowledge about wolf kill rate on moose in area of high density of brown bears is necessary especially to adjust hunting harvest. This study is the first to present detailed empirical data on wolf and brown bear interactions using modern Global Positioning System (GPS collar techniques). Wolves predation pattern have been studied in two contrasted period without brown bears presence, when bears are in dens, and with brown bears presence, when brown bears are awake and active. A higher wolf-kill rate on moose was observed in spring compared to winter. This coincided with brown bear emergence but was probably more related to a high snow depth in winter in an area with low moose density limiting wolf and moose encounter rate. GPS positioning data showed that wolves did not get access to a food resource because of brown bear presence. By using cameras trapping, brown bears were found feeding on half of wolf-moose killed detected. The small dataset comprising only one wolf pack did not allow strong conclusion, but shape and methods used in this study showed encouraging results for further study.

Key words: gray *wolf (Canis lupus) - brown bear (Ursus arctos) - interactions- kill rate -Movement*

Résumé:

Les effets des interactions entre loups (*Canis lupus*) et ours bruns (*Ursus arctos*) ne sont pas très bien compris. Le rétablissement des populations de loups et d'ours bruns en Suède Centrale, offre une bonne opportunité pour étudier ces interactions. Parce que les loups et les ours utilisent une ressource de façon similaire, l'élan (*Alces alces*), la compétition entre ces deux prédateurs peut être intense. Des connaissances sur le taux de prédation des loups sur les élans dans un territoire ou la densité d'ours bruns est élevée est nécessaire en particulier pour ajuster les prélèvements de chasse. Cette étude est la première à présenter des données empiriques sur les interactions entre loups et ours par l'utilisation d'un système de positionnement global (techniques des colliers GPS). Les mouvements de prédation des loups ont été étudiés pendant deux périodes contrastées, sans la présence d'ours bruns, quand les ours sont en tanière, et avec la présence d'ours bruns, quand les ours sont réveillés et actifs. Un taux plus élevé de prédation des loups sur les élans a été observé au printemps comparé à la période hivernale. Cela coïncide avec l'émergence des ours bruns mais était probablement lié également à une forte haute hauteur de neige en hiver et une faible densité d'élan, limitant le taux de rencontre entre loups et élans. Les données de positionnement GPS ont montré que les loups n'ont pas obtenu l'accès à une source de nourriture à cause de la présence d'un ours brun. En utilisant des pièges photographiques, les ours bruns ont été trouvés se nourrissant sur la moitié des élans tués par les loups. La petite base de données comprenant seulement une meute de loups n'a pas permis la réalisation de conclusion significative, mais le contour et les méthodes de cette étude ont montré d'encourageants résultats pour de futures études.

Mot clés : l*oup gris (Canis lupus) – ours brun (Ursus arctos) - interactions- taux de prédation –- mouvements*

1. Introduction

The gray wolf (*Canis lupus*) is a flexible and opportunistic predator species (Peterson & Ciucci 2003), it inhabits all the vegetation types of the Northern Hemisphere, and it is one of the most adaptable mammals (Mech & Boitani, 2003). Despite the wolf being a charismatic species with a large support from the public, it is also highly controversial and often maintained in small fragmented populations (Boitani 2003, Liberg et al., 2005). Bounties were commonly accorded by local authorities or states for killing wolves (Boitani 2003, Wabakken et al., 2001). In the Scandinavian Peninsula, hundreds of wolves were killed every year in the nineteenth century (Vila et al., 2003) and the wolf population was considered as functionally extinct in the late 1960's (Wabakken et al., 2001). The wolf became legally protected in Sweden and in Norway in 1966 and 1973 respectively. In 1983, wolves successfully reproduced in south-central Sweden for the first time in more than 80 years in this region (Wabakken et al., 2001). Between 1983 and 1991, the wolf population was founded by only two individuals and comprised only a single pack (Vila et al., 2003, Liberg et al., 2005). After 1991 and the arrival of a new emigrant from the neighbouring wolf population in Finland, the wolves have regularly reproduced, starting to grow exponentially (mean annual growth rate of 29%) and to increase their range (Wabakken et al. 2001, Vila et al., 2003, Wikenros et al. 2010). Based on long distances of ground tracking on snow, radio-telemetry and DNA-analysis, a total of 252-291 wolves were estimated in the Scandinavian Peninsula during the 2009-2010 winter, 186-215 of which were located in Sweden (Wabakken et al. 2010). After a 45 years wolf-hunting moratorium, wolf hunting was reopened with 27 and 19 wolves killed in 2010 and 2011 respectively.

The brown bear (*Ursus arctos*) is an omnivorous carnivore species (Persson et al. 2001) and originally occurred throughout Europe (Zedrosser et al., 2001). Its distribution and numbers decreased considerably during the 19th century, particularly in Europe, mainly through overhunting and habitat loss due to human population growth (Swenson et al., 1995, Zedrosser et al., 2001). The extermination of the brown bear was even encouraged to decrease depredation on livestock, with bounties offered for brown bears killed (Zedrosser et al., 2001). The brown bear population in the Scandinavian Peninsula in the mid 1800s was about 4700 bears, of which 45% occurred in Sweden. This population declined in the second half of the 1800's with an annual rate of about 4.8% (Swenson et al., 1995). Hence, the population was exterminated in the south of Sweden by the end of the 1800's (Swenson et al., 1994) and was restricted to the northwest mountains of Sweden in the beginning of the 1900's (Swenson et al., 1995). The brown bear population declined in Sweden until 1927 when stricter protective measures were introduced (Swenson et al., 1994, 1995). Considering 1930 as the low point of brown bear presence in Sweden, the population bottleneck was founded by only 130 brown bears (Swenson et al., 1995). Even if brown bears have been hunted in Sweden since 1943 through a strict quota system, the population in Sweden has grown since 1930, to about 300 animals in 1942, and 1000 bears in 1990 (Swenson et al., 1995). In 2008, the brown bear population size in Sweden was estimated through DNA analysis to about 3200 (2,950-3,500) individuals, with an estimated growth rate of 4.5% between 1998 and 2007 (Kindberg et al. 2009).

The geographic overlapping between wolves and bears was relatively common in the past however the overhunting and habitat losses often separated those carnivores, and restricted them to small and isolated populations (Wabakken et al., 2001, Swensson et al., 1994, 1995). Hence both wolves and bears were gone from central Scandinavia by the mid-to-late 1800s. The recent protection of those species allowed their expansion and recovery but is also inducing new questions about the management and coexistence of these two predators. In Yellowstone National Park (North America), where wolves were recently reintroduced, Ballard et al., (2003) reported a significant difference in the proportion of types of interactions between brown bears and wolves to that reported outside the Yellowstone National Park. Competition between similar species of predators is one the most common types of interactions (Ballard et al., 2003). Both direct interactions (interference interactions) for example interspecific killing (Palomares & Caro, 1999, Ballard et al., 2003) and indirect interactions (exploitation competition) may occur because both species utilize the same food resources or through cleptoparasitism by the dominant species (Ballard et al., 2003, Kortello et al., 2007, Mattison et al., 2011). Both of these interactions may influence population size and structure, and cause the exclusion or modification of behaviour of competing individuals (Palomares & Caro, 1999, Ballard et al., 2003). Most of the direct interactions involving brown bears and wolves reported are bears and wolves chasing or fighting each other, mostly near their kill sites (Ballard et al., 2003).

Wolves and brown bears are members of groups of species (guilds) using common resources in a similar way (Ballard et al., 2003). Moose (*Alces alces*) are the main prey of wolves in Scandinavia (Sand et al. 2005, 2008) and during the spring, moose may also be an important prey for the brown bear, making up 85% of the brown bear's estimated dietary energy (Persson et al. 2001, Svensson et al., 2007). The brown bear is also known to usurp kills made by wolves, and when wolves lose kills to bears, wolf kill rates may be higher than in a system without bears (Ballard et al., 2003). Accordingly, in an area of low moose density, exploitative competition between wolves and brown bears could be intense. One expected response may be that scavenging interactions between wolves and brown bears at kill sites will occur frequently and may result in change of the predation pattern of wolves. Furthermore, the body mass of an adult brown bear (80-220kg) is 2-4 times greater than the body mass of an adult wolf (35-50kg), and competition between carnivores has shown that larger species usually are dominant towards smaller species (Palomares & Caro, 1999, Ballard et al., 2003, Sand et al., 2006b).

The understanding and the effect of wolf and brown bear coexistence have strong implications and involve new challenges in management, especially ungulates management. Large predators are known to largely cause additive mortality on prey populations (Jedrzejewski et al., 2002; Sand et al, 2005; Swensson et al., 2007) but there is controversy regarding the magnitude of the impact of predator control on the moose population (Schwartz et al., 2003). Additionally, the impact of wolf predation is relatively well known (Schwartz et al., 2003; Sand et al., 2005, 2008) compared to the impact of predation by brown bears on moose populations (Swensson et al., 2007).

The moose population in Scandinavia has grown significantly during the last century, and is exposed to an intensive hunting management that has replaced most of the natural mortality. Moose hunting is a popular sport in Sweden and is considered to be of great economic value. Approximately 250 000 of the 300 000 Swedish hunters participate in moose hunting every year and approximately 100 000 individuals (or 30% of the total moose population) are harvested by hunters every year (Swedish Association for Hunting and Wildlife Management 2011).

Large predators may be considered as competitors to hunters, and so a component of adjusting hunting harvest on moose in areas with large predators is needed in order not to reduce total moose population size. One way of doing this is to estimate wolf kill rates in an area where wolf and brown bear territories are overlapping. (Schwartz et al., 2003 Sand et al, 2005, Swensson et al., 2007)

The Scandinavian Wolf Project (Skandulv) and the Scandinavian Brown Bear Research Project (SBBRP) were created in 2000 and 1984 respectively. Their objectives are a better understanding of the ecology of the Scandinavian brown bear and wolf and to provide a scientific basis for conservation and management of both species. The Skandulv and the SBBRP made the first step to enhance the understanding of their coexistence with a pilot study during spring 2010 (Steyaert & Frank 2010). Because direct observations of kills using global positioning system (GPS) is the best and most accurate method to estimate kill rates (Sand et al., 2005), it is also a powerful tool to study the behaviour and interactions between species (Mattisson et al., 2011, Wikenros et al., 2010). In 2010 both brown bears and a resident wolf pack were captured and equipped with GPS collars in the same area.

To my knowledge, this is the first interaction study between wolves and brown bears using GPS-collars on both species. The main objective of this study was to observe if brown bears emergence affect wolf predation-patterns. Three main research topics were identified:

i) Wolf-moose predation patterns before and after brown bears emergence
ii) Direct interspecific interactions in space and time at wolf kill site.
iii) Indirect interspecific interactions at wolf kill site.

Results were used to conclude the implications for wolves, brown bears, and moose management. Accuracy and bias of methods used were also discussed to improve further studies.

2. Material and Methods

2.1. Study area, prey and predator populations

The study area was located in the Dalarna and Gävleborg counties in Central Sweden (61°N, 15°E) surrounding the Scandinavian Brown Bear Research Station and encompassing about 1364 km² (the wolves' territory) (*Fig. 1*). The elevation ranges 200-464 m above sea level. Lakes and bogs covered large areas, but most of the area was covered by coniferous forest, dominated by Scots pine *(Pinus sylvestris*), Norway spruce (*Picea abies*), lodgepole pine (*Pinus concorta*). Various deciduous trees, such as common birch (*Betula pubescens*), silver birch (*Betula pendula*), aspen (*Populus tremula*) and grey alder (*Alnus incana*), are common in early successional stages of the forest (Friebe et al. 2001, Solberg et al., 2006 Nellemann et al. 2007). A variety of species of mosses, lichens, grasses, heathers and berries (such as *Vaccinium myrtillus, Vaccinium vitis-idaea and Empetrum hermaphroditum)* composed the ground vegetation (Nellemann et al. 2007). Characteristic bogs and lakes covered 20% of the remaining area (Friebe et al. 2001, Steyaert & Frank, 2010). This taiga forest is intensively managed with a turnover rate of 90-100 years and more than 60% of the forest is older than 35 years. The logging system has resulted in a patchy forest landscape (Steyaert & Frank, 2010) with a relatively extensive road system (0.3km/km²) (Nellemann et al. 2007). Snow covers this area from late October to early May, and average daily temperature ranges from -7°C in January to a maximum temperature of 15°C in July (Steyaert & Frank, 2010).

Figure 1 : Map of Scandinavia, study area located in Sweden (black square) and wolves territory (gray polygon).

One resident wolf pack (Tenskog territory), one male and one female, probably established during the summer of 2009, are monitored through GPS tracking (See below). Solberg et al. (2006) reported a population density of brown bear to be around 30 individuals/1000km². Other potential predators, lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) were also present in the area but in low densities.

Moose (*Alces alces*) was the most abundant prey species in the territory, with an average population density estimated from pellet counts during winter as 0.87 (± 0.25) moose/km² (Sand et al., 2010). But moose density differs between winter and summer, because in winter one part of the moose population migrates 40-50km south from Tenskog territory following the Voxna river (Ahlqvist Per, Brunberg Sven, personal communication). Other prey species available included roe deer (in very low density), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), hazel grouse *(Bonasa bonasia*), beaver (*Castor fiber*) and mountain hare (*Lepus timidus*) (Sand et al., 2005, 2008, 2010).

2.2. **Capture of wolves and brown bears**

The two resident wolves in Tenskog territory, the male (M 10-02 with collar number 9063) (3.5 years old) and the female (M 10-01 with collar number 9064) (5.5 years old) were re-captured and GPS collared the 25/01/2011. Wolves' presence was confirmed by intensive field work with skis, car, and snowmobile to find wolves tracks in the snow (snow-tracking). When wolves positions were approximately knew, a capture crew was called to track and locate the animals. Then the wolves were immobilized from the air (helicopter) using a CO2-powered dart gun and a drug dose (Arnemo et al., 2004; Sand et al., 2006a). Chasing time must not exceed 10 min and wolves were on average chased for 1-3min. (Sand et al., 2006a). This procedure with relatively short chasing times minimizes stress of wolves during immobilization, and severe stress with physiological side-effects (hyperthermia) was not observed (Sand et al., 2006a). All captured wolves were measured, weighted, blood and tissue were sampled according to procedures for free-ranging wolves (Arnemo et al., 2004).

Wolves were equipped with a GPS neck collar (Vectronic Aerospace, GmbH, , Berlin, Germany).The weight of the collar GPS neck was below the maximum weight authorised by the Swedish agency of Animal Welfare, equalled to an average of 1.3% and 1.1% of the adult body weight of female and male respectively (Sand et al., 2006a).

A large number of brown bear in the study area have been captured and GPS-marked following the same process than wolves capture (Arnemo et al., 2004). During the study period, I used the GPS data from few brown bears (about 8) which home ranges overlapping with wolves territory.

2.3. **Monitoring of wolves and brown bears**

During the study period, the GPS collar (number of GPS collar was used as ID of animal) of the male wolf (9063) was programmed to obtain a location at hourly intervals (i.e., 24 locations per day), and the female (9064) at 6 locations per day. Because wolves of the same pack generally hunt together (Mech et al., 2003), and to save the life of the collar battery, the receiving of data by one GPS collar in the pack was assumed to be accurate enough to estimate the wolves' predation behaviour. The positioning schedule of the brown bears varied during the season, the year, and the individual but was ranged between 1 position per minute and 1 position per day.

The data was stored on GPS internal memory and sent with Global System for Mobile communications (GSM) network when 7 locations were saved. Positioning data were automatically received as e-mail messages (Short Message Service) through the software GPS PLUS Manager V3.0.0 (Vectronic aerospace).

Each location included coordinate system (RT 90), date, time, elevation, temperature, battery voltage, 2 quality estimates of each position taken (dilution of position [DOP]) and the number of satellites used for positioning (2-dimensional or 3-dimensional).

2.4. **Clustering process and wolves-prey-killed detection**

The GPS positions downloaded were plotted with Arc View 3.2 (ESRI, Redlands Calif.) in a metric grid system. On each position a buffer with a fixed radius of 100m was created and overlapping buffers were unified and defined as clusters with a unique cluster number (Sand et al., 2005, Knopff et al. 2009**,** Palacios & Mech, 2010). Sand et al. (2005) reported more that 85% of moose carcasses can be detected with a buffer radius of 100 m and a positioning interval of 1 hour (i.e., 24 positions per day).

All new positions included in a cluster were intensively searched in the field with a hand-held GPS (Garmin GPSMap 60CSx) on skis (when the snow condition allowed) or on foot. Some single positions (fixes not within cluster) were also visited in the field. For each cluster and position visited, all signs of wolves' presence were registered, carcass prey, resting place (bed site), tracks (wolves travelling straight), negative (no wolves signs), unknown (tracks, scats) (Zimmerman et al., 2007, Palacios & Mech, 2010).

When a carcass was found, I examined and saved the coordinates in a hand-GPS (Garmin GPSMap 60CSx). For all carcasses, I defined the species from the fur and the skeletal remains. I also estimated age of the prey: juvenile (<1 year old) or adult (≥ 1 year old) by collecting the mandibles; whereas sex determination was made by visual inspection of the sexual organ or by presence of antlers or anlter pedicles at the skull (Sand et al. 2005, Hayes et al., 2000 ; Sand et al., 2008). Moreover, the proportion of biomass of the ungulate consumed was assessed to the nearest 5 % excluding rumen, guts, bones and hide (Sand et al. 2005, 2008). Proportion of the edible biomass consumed, state of decomposition of the carcass in relation to the site (sunny or shaded) and previous weather conditions were used to estimate the date of the death in the field, and was later compared with the exact locations of GPS-collared wolves (Sand et al., 2008)

Carcasses found were classified in four different categories related to the cause of death (Sand et al., 2008):

1) *Wolf killed prey*, with excessive blood in connection to the carcass, and when a "pipe-bleeding" (pipe through the snow made by the warm blood that has pumped out via an artery or a vein of the prey animal) or clear tracks in the snow of wolves chasing the prey were present (Messier et Crête 1985, Hayes et al., 2000, Sand et al., 2005, 2008)

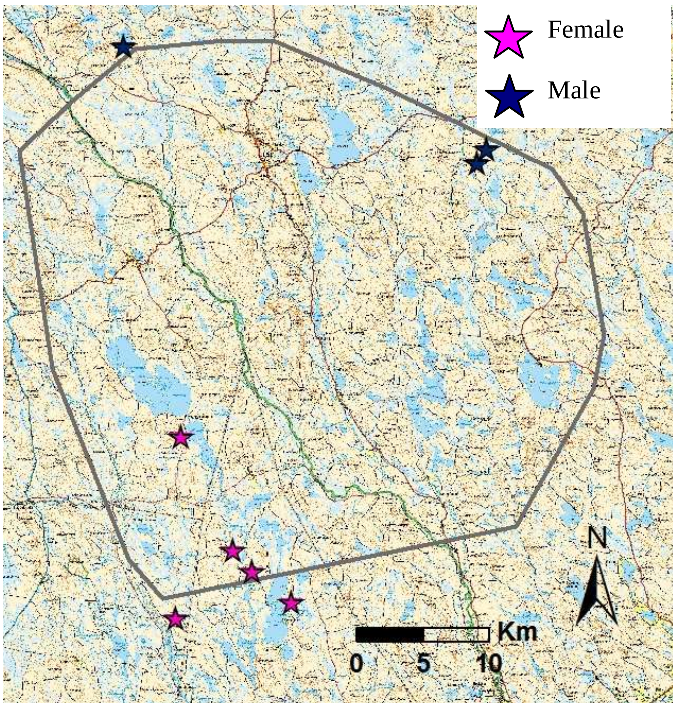
2) *Probably wolf killed*, with estimated time of death of the prey (degree of consumption and decomposition of tissue in relation to last weather conditions) coincided with time of the GPS-positions.

3) *Not wolf killed prey*, carcass which is not killed by wolf (e.g traffic accident or hunting)

4) *Unknown*, can not be classified into the previous categories.

2.5. Brown bear emergence

In the study area, male brown bears emerge from the den on average between 6 March and 25 April with the mean 4 April, whereas the females emerge on average 17 days later than the males (Friebe et al., 2001; Manchi & Swenson 2005). During the 2011 study period the mean of the emergence of the 8 brown bears GPS marked within Tenskog territory was 13 April 2011, the first emerged 27/03/2011 and the last one the 24/04/2011 (Source: Scandinavian Brown Bear Research Project). Because large intra sexual differences and intra-individual in the date of emergence have been observed among brown bears, I considered the period without brown bears (before emergence) from 14 March 2011 00:00h until 14 April 2011 00:00h and the period with bears (after emergence) from 14 April 2011 00:00h until 15 May 2011 00:00h. Both periods contained the same number of days (31 days).



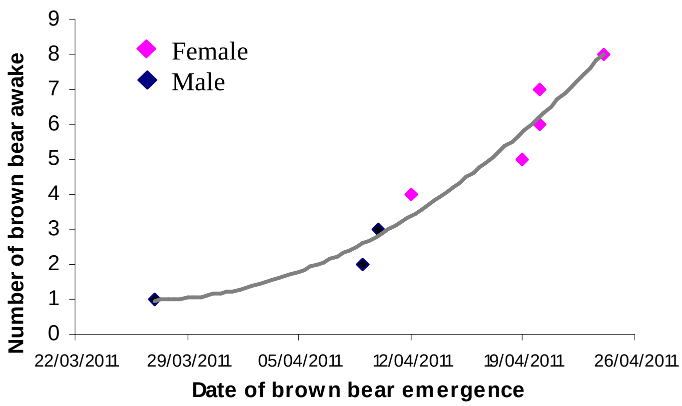


Figure 2. Emergence date of 8 brown bears GPS marked within or close to the Tenskog wolf-territory in 2011 (Source: Scandinavian Brown bear project).

Figure 3. Den localisation (Star) of 8 brown bear GPS marked within or close the Tenskog wolf territory (Gray line) in 2011.
(Source: Scandinavian Brown bear project).

2.6. Estimating kills rates and prey's consumption

The correct estimation of kill rates is an important component to understanding the wolves' impact on the prey population's dynamics (Sand et al., 2005, Webb et al. 2008). I used data from the Tenskog predation study realised in 2011 (14-03-2011 to 15-05-2011) and also the predation study data in the same pack composed of the same wolves from winter 2010 (09-02-2010 to 07-04-2010) (Sand et al., 2010).

I defined the kill rate as the number of moose killed by each wolf, by wolf pack and per day (Hayes et al., 2000, Sand et al., 2008). Only the carcasses defined as wolf-killed and probably wolf killed within the study period were used for calculations. The date and the time of the kill were defined by the first positions of the wolves within 200m from the carcass (Sand et al. 2008, Webb et al. 2008). I calculated kill rate as the time interval in days between kills by dividing the number of study days by the number of moose and ungulates killed. The estimated winter predation was calculated by multiplying the daily kills rates by the number of days in the winter (Hayes et al., 2000). Number of days during winter period was assumed to be 242 days (start 1 October and end last day of May) (Sand et al., 2008)

I also determined the total biomass consumed by wolves by incorporating the proportion of biomass consumed at the day of the detection of the carcass. Food consumption was based on the species, the number and size (age) of prey killed by wolves during the study period. Calf body weight was estimated to be 160kg, because calves' body mass gained 6.9% from November to April-May in normal winter (Cederlund and Sand 1991) with a calf body mass in October of about 150kg (Sand et al.,2008). I assumed moose yearling body mass to be around 240kg (Sand et al., 2008). Adult moose body mass varies with age, sex and population characteristics, I considered the weight of each adult moose killed to be 350kg (Sand et al., 1995). Following Sand et al., 2008, for other prey species I assumed an average body weight of 25kg and 10kg for adult and juvenile roe deer respectively, and 2kg for birds spp. For yearling moose the amount of edible biomass was estimated to be 65% of the total body weight whereas for moose calves and roe deer 75 % of the total body mass was used, (Jedrzejewski et al., 2002; Sand et al., 2008). The proportion of the edible biomass consumed at the time of prey detection was visually estimated in the field to the nearest 5% of the edible parts of the carcass. For prey smaller than moose calves, all edible biomass was assumed to be wolf consumed, (Jedrzejewski et al., 2002, Sand et al., 2008). In the cases of wolves scavenging (moose killed by brown bears or traffic accident), I estimated a daily consumption of about 4.5kg/wolf (Jedrzejewski et al., 2002). The daily wolf consumption was compared to the minimum daily food requirements (3.25kg/wolf/day, i.e. 5x basal metabolic rate) estimated for wild wolves (Peterson and Cuicci 2003, Sand et al., 2008). Due to the small sample of prey detected, I did not run any statistics test. I used the mean and range of the data to evaluate the trends of kill rates and prey consumption across the studies and the different periods.

2.7. **Wolves predation patterns**

To compare the predation patterns of the wolves before and after the emergence of brown bears, I used cluster characteristics of GPS-positions, because they are used to detect wolf-killed prey (Sand et al. 2005, 2008; Palacios & Mech, 2010) and modelled the predation patterns of the wolves (Zimmerman et al. 2007). I only used cluster characteristics from the study in 2011 because only this study coincided with the period of brown bears emergence. I only used a 50 meter buffer radius, because a 100 meter buffer radius induced overlapping between cluster types (i.e. carcass clusters versus bed site clusters) and reduced the reliability of the results. Because of the small sample of feeding events, I did not make any distinction between predation and scavenging, considering only one class for feeding behaviour on moose and roe deer (carcass cluster) (Palacios & Mech, 2010).

Each cluster was described by: 1) the type of cluster (carcass, bed site, track, other, negative), 2) number of GPS positions, 3) time of the first and last position in cluster (day divided in four hours intervals : [00:00-04:00] ; [04:00-08:00] ; [08:00-12:00] ; [12:00-16:00] ; [16:00-20:00] ; [20:00-24:00]), 4) frequencies of positions at cluster in the six intervals, 5) number of visits, 6) ratio of positions per visit, 7) linearity of movement on entering a cluster (Dist [AC] /(Dist[AB]+Dist[BC]) 8) distance from the last prey killed (moose or roe deer), 8) distance from previous cluster, 9) distance from next cluster (Zimmerman et al. 2007, Palacios & Mech, 2010)

I analysed the variance by two-way factorial (ANOVA) to compare clusters characteristics among clusters types, periods (with and without bears), and interactions between clusters type and periods. To test simultaneously the independent variables, frequencies of positions at cluster in time interval, and the time of the first and last position in cluster, I used a multivariate analysis of variance (MANCOVA).

Home ranges using 100% and 95% minimum convex polygon (MCP) were calculated with all available locations from the male for both periods (before and after the emergence of brown bears) and before the start of the study (i.e.: 3 days after the wolf captures [28-01-2011], to minimize the possible effects of capture (Palacios & Mech, 2010), to the start of the study [14-03-2011].)

For statistical analyses I used R software (CRAN, http://CRAN.R-project.org). Statistical significance in all analyses was assumed at $P \leq 0.05$.

2.8. **Direct and indirect interactions**

I used data from few GPS marked brown bears with home ranges overlapping Tenskog wolf pack territory to detect direct and indirect interaction via a geographic information system (GIS) (ArcGIS 9.3 ESRI). Only interactions on feeding sites (i.e. remains of wolf-killed moose) were studied. Because not all brown bears in the study area were GPS marked, I also placed one camera trap (Scout guard SC550 or Stealth cam 5.0) on each wolf-killed moose detected. The camera traps were placed on all wolf-killed moose from 18-04-2011 to 30-05-2011 and were oriented on the biggest part of prey remains left. The photographic data from the camera trap was used to both quantify how many interactions could be missing using only the brown bear GPS data, and to characterize the behaviour of the brown bears towards the remains (i.e. eating or just smelling the carcasses).

3. **Results:**

Data from the GPS-collars of the wolves resulted in 1509 hourly locations for the male and 197 variable interval locations for the female. 0.2% (4 positions) of the overall male locations was missing.

In 2011, 100% of all the 101 clusters and in 2010 all of the 97 clusters were checked in the field. Resulting in 230km of field work in 2011 (estimated from the GPS tracks log, data non available in 2010).

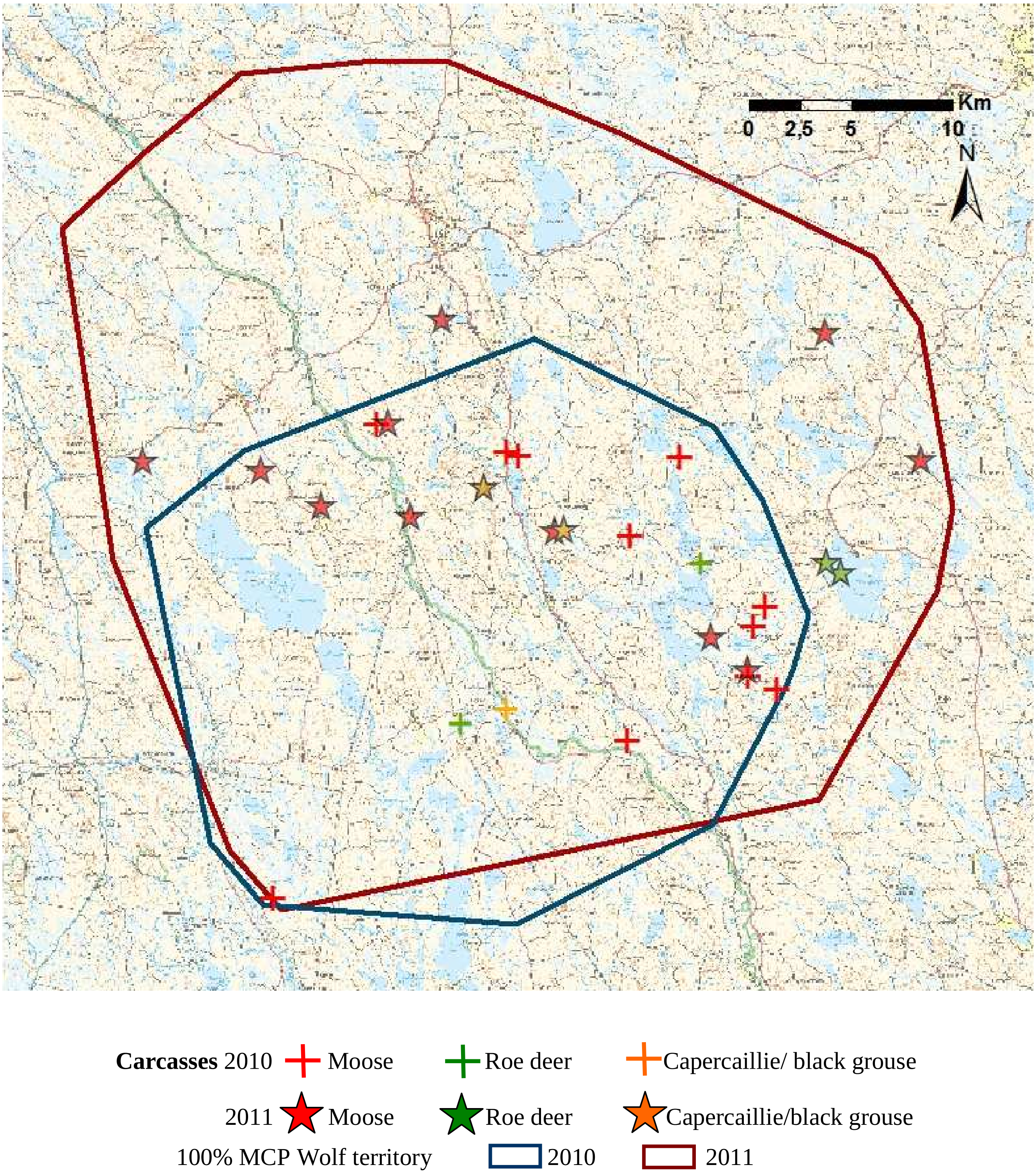


Figure 4: Distribution of the all carcasses found in the Tenskog territory in 2010 [10/02/2010 to 11/04/2010] and 2011 [14-03-2011 to 15-05-2011]

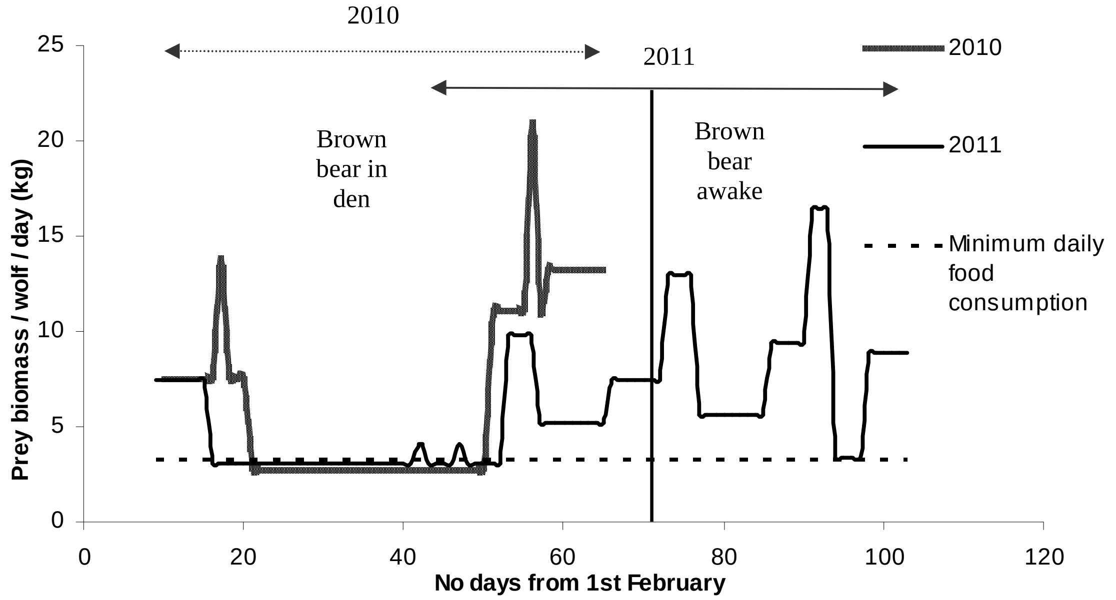


Figure 5: Moose biomass (kg) obtained/capita/day for Tenskog wolf pack (two wolves) in winter 2010 and 2011 from 9 February to 14 May. *Double arrows* indicate duration of predation studies. Estimation of the kilogram biomass obtained accounted for the variable interval between moose kills, biomass of small prey was added on the day of the date of death. Estimation of minimum prey consumption before the 2011 study was done with the two wolves' positions per day. *Dotted line* indicates the estimated minimum daily food requirements for wild wolves (Peterson and Ciucci 2003, Sand et al., 2008).

Signs of wolf presence were found in 63 clusters. 63% (172) of the overall locations (274) outside the clustering definition were also visited. In total 90% (1346) of the wolves' positions were checked.

The GPS positions were checked on average 3.4 days (range 1-11days) after the wolves left the area.

The locations indicated then twice per day (13:00 and 01:00) that the female was on average 1502m (range 1-23414 meters) from the male at the same time. But two periods were significantly different, certainly due to a modification of wolf behaviour because of a reproducing time: from 14-03-2011 01:00 to 20-04-2011 01:00 and from 20-04-2011 to 15-05-2011, the average distance between male and female was 105 meters (range 1-2575) and 3613 meters (range 2-23414) respectively, (Wilcoxon test; W=676.5 P<0.001).

3.1. Kill rates and prey consumption

During the winter 2010, 13 feeding events on carcasses were found. Six moose and two roe deer were killed by wolves (*Appendix 1*). Three events of wolves scavenging were detected, one a moose killed by a traffic accident, one a dumping place after the hunting season and one on an old moose probably dead by natural causes. One mountain hare and one black grouse were also found in relation to the wolves' positions and were likely killed by the wolves (F*ig. 4*).

Table 1. Minimum wolf kill rates and wolf prey consumption per pack (2 wolves) in winter 2010 and winter/spring 2011 (before brown bear emergence [14/03/2011 to 14/04/2011] and after brown bear emergence [14/04/2011 to 15/05/2011]

		Kill rates Days interval between kills		Prey consumption (kg) per day	
		Moose	**Ungulates ***	**Moose**	**Total****
2010	**All period [10/02 to 14/04]**	10	7.5	12.5	13.1
2011	**All period [14/03 to 15/05]**	8.1	6.1	12.7	13.4
	Before brown bear emergence	10.3	6.2	8.9	10.1
	After brown bear emergence	6	6	16.6	16.6

*Including moose and roe deer killed and probably killed by wolves.
**Including all wolf prey killed and probably killed by wolves.

During the winter 2011, I found carcasses at 13 (12.8%) of the 101 clusters including 11 moose and two roe deer (*Appendix 1 and 2*). One adult moose and one moose calf were estimated to have been killed before the start of the study. One scavenging event on a moose calf probably killed by a brown bear was detected. The eight other moose including seven calves and one yearling were killed by wolves. Two killed capercaillies (female) were also found on one single location and on wolf tracks between two single locations (*Fig. 4*).

Across the Tenskog territory in the winter 2010, wolves killed on average 0.1 ungulates /pack /day or 0.065/ungulates /wolf/day and 0.1 moose/pack/day or 0.05moose/wolf/day. This corresponded to an average of 13.1kg prey biomass/pack/day or 6.55kg prey biomass/wolf/day.

In winter 2011, the wolves killed on average 0.12 moose /pack/day or 0.06 moose/wolf/ day and 0.16 ungulates /pack/day or 0.08 ungulates/ wolf/day. (*Table 1*)

Table 2 : Summary of cluster processing during the study period (2011) using positions from the male wolf (9063)

	Before brown bear emergence, 14-03-2011 to 14-04-2011	**After brown bear emergence, 14-04-2011 to 15-05-2011**	**Total**
Missing positions	1 (0.13)	3 (0.4%)	4 (0.3%)
Number of positions	759	755	1514
Number of singles positions (100m radius interval)	173 (22.8%)	170 (22.5%)	273
Number of clusters (50m radius)	74	60	134

After brown bear emergence, wolves killed moose 1.7 times more often (0.17/moose/pack/day or 0.085 moose/wolf/day) as compared to before brown bear emergence (on average 0.1 moose/pack/day or 0.05/moose/wolf/day) (*Table 1*).

Between 22 February and 23 March 2010 and between 16 February and 24 March 2011 (estimating with 2 GPS wolf positions/day) only one moose was killed resulting in a daily consumption below the minimum daily food requirements for wild wolves (*Fig 5*).

Considering 242 days as the number of days in the winter period (Hayes et al., 2000), the Tenskog wolf pack kills a total of 24.2-29.27 moose per winter.

3.2. **Wolf movement patterns**

In 2011 I identified 57 beds site clusters, 15 carcass clusters (including revisit old carcass cluster during the period with brown bear presence), 6 tracks clusters, 23 unknown clusters and 29 negative clusters. Only one cluster was not checked because that cluster was classified as a denning cluster and could not be checked during the field study period (*Appendix 2*). The female became stationary from the 10th of May to the end of the study the 15th of May showing reproductive behaviour, so to avoid all possible disturbance, no GPS positions were checked in a 2 kilometers radius buffer around the position of the female.

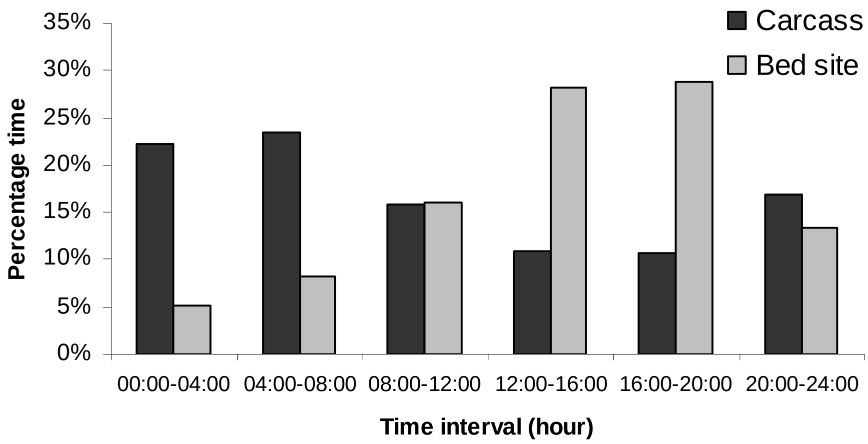


Figure 6: Percentage time spent by wolf (9063) within carcass and bed site cluster divided in 6 time interval. 1 hour spent in cluster was estimated by 1 GPS position within cluster.

The longest time spent at a cluster was 69 hours (bed site cluster) and the maximum number of visits was 12 (cluster contained wolf-killed moose). The average carcass cluster had 2.45 times more visits (F=16.75, df=5, P<0.001), 2.7 times more positions in cluster (F= 11.60 df=5 P<0,001), 2.4 more times positions in the time intervals [00:00-04:00] and [04:00-08:00] (F=2.75 df=5, P<0.001), and 2.2 times less positions in the time interval [12:00-16:00] and [16:00-20:00] (F=2.75 df=5, P<0.001) compared to the overall mean of non-carcass clusters (*Fig. 6*). I observed two different patterns of wolves' first arrival at a cluster and the last time spent there, depending on whether it was a carcass or a bed site cluster. The wolves first arrived at a bed cluster during the day mainly during the 2 periods during daylight ([08:00-16:00]) while they first arrived at a carcass cluster mainly during the 3 periods interval of the night ([20:00-08:00]) (F=2.75, df=5, P<0.001) (*Fig. 7*). The last position within the carcass cluster was mainly during the interval [00:00-08:00] while the last position within the bed site cluster was in the time interval [16:00-24:00] (F=8.48, df=5, P<0.001) (*Fig. 8*). Distance from the previous (F=1.93, df=1, P=0.16) and to the next cluster (F=2.144, df=1, P=0.14) were not related to the type of cluster.

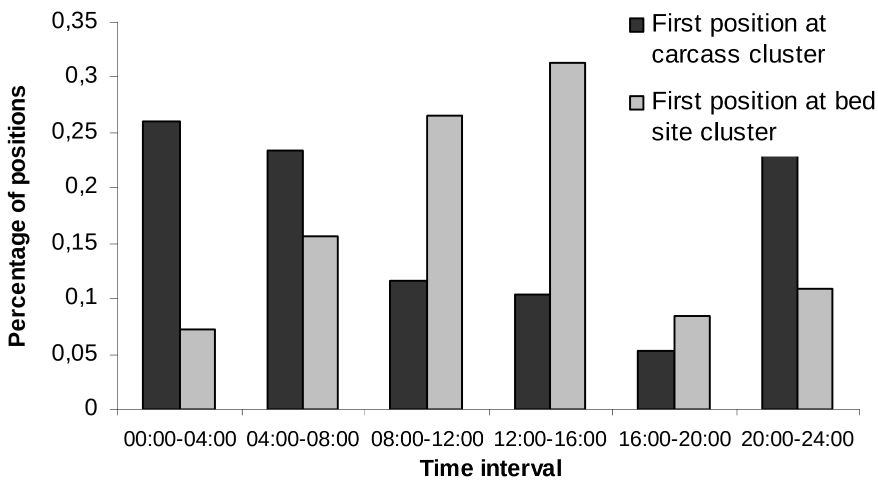


Figure 7: Percentage of first wolf (9063) GPS positions divided in 6 interval time within carcass and bed site cluster.

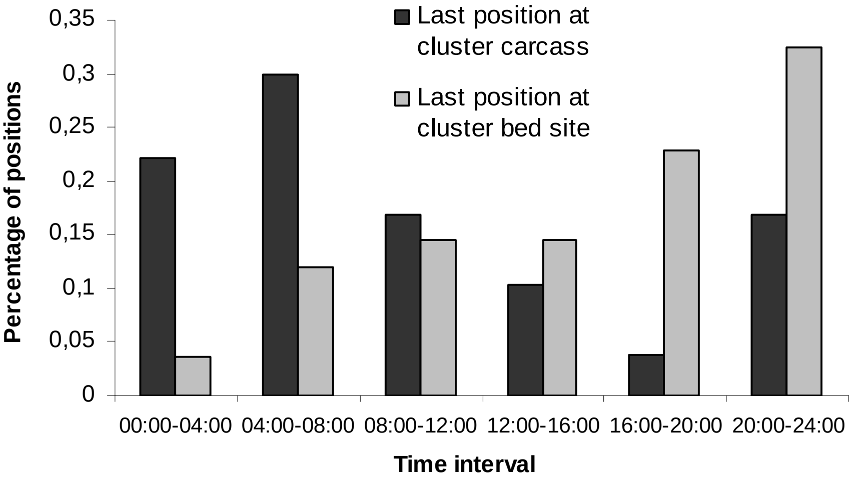


Figure 8 : Percentage of last wolf (9063) GPS positions divided in 6 time interval within carcass and bed site cluster.

Wolves visited bed site clusters usually only once (88% of all cases), and bed site clusters had the highest ratio of positions/visits. Track, negative, and unknown clusters had a low ratio of mostly 2 positions and 2 visits. The linearity of the movement among the cluster types indicated that wolves moved generally nearly straight (linearity $\bar{x}$=0.88) to the clusters with not significant differences among cluster type and period (F=0.63, df=1, P=0.43).

Before the brown bears emerged, 7 carcass clusters and 33 bed site clusters were found against 8 and 24 respectively after they emerged. Wolves spent on average twice as much time (31.4 hours) in a carcass cluster when brown bears were present compared to the period of brown bear absence (F=4.403, df=3, P=0.0056) (*Fig. 9*). With brown bear presence the average time per visit within a carcass cluster was 2.3 times greater (7.23 hour/visits) than in the period without brown bear presence (3.1 hour per visits) (F=3.65, df=3, P=0.01) while time spent per visit in bed site clusters was the same between the two periods (5.8 hours/visits) (F=0.0366, df=1, P=0.8488) (*Fig*.10). Bed site clusters were 2.2 times more distant from the last prey killed after the wake up of the brown bear (*Fig. 11*) (F=3.7163, df=3, P=0.012).

Figure 9: Time spent by wolf (9063) in cluster (hour) ± SD, among each cluster type before brown bear emergence and after brown bear emergence

The sizes of the wolves' home ranges were smaller during the winter than during the spring (*Fig.11*). Before the start of the study the wolves had a small territory (95% MCP), 182 km² and 75.17km² in 2010 and 2011 respectively but after the brown bears emerged, sizes of wolf home ranges were 4 and 13 times larger in 2010 (726.33km²) and 2011 (1043.94km²) respectively (*Fig. 11*).

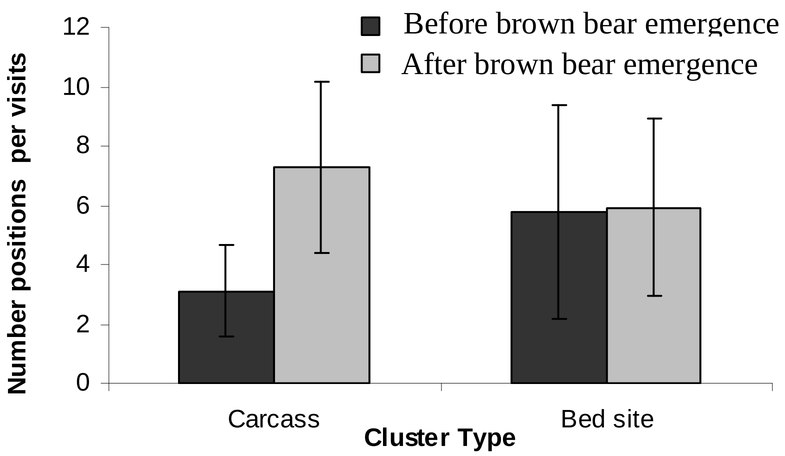


Figure 10: Number of wolf position (9063) ± SD, within carcass and bed site cluster before and after brown bear emergence.

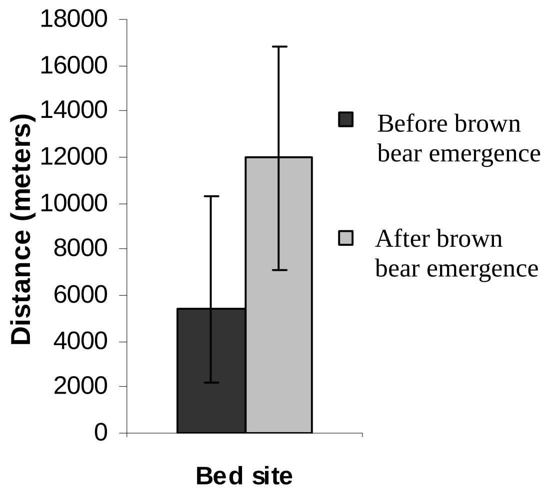


Figure 11: Wolf (9063) bed site cluster distance from last prey killed

The wolves daily travel (straight line distances between consecutive hourly GPS positions) was on average 9963.5 meters (ranged 2527-22058km) from 14/03/2011-23/03/2011, but on 24 and 25/03/2011 the average distances travelled were 25726 and 28496 meters respectively. This increase of daily movement coincided with a marked change of snow conditions (crusty snow on the upper layer) due to warmth during the day with on average +6. 3°C and cold during the night with -3°C during the 5 previous days (Weather data: Weather station Hamra and Lillhamra, 2011).

Table 3 : 95% and 100% minimum convex polygon using fixed mean in 2010 and 2011

	2010		2011	
MCP (%)	**100**	**95**	**100**	**95**
Before study [10-02-2010 to 13-03-2010] [28-01-2011 to 13-03-2011]	313.3	182.5	178.5	75.2
Before brown bear emergence [14-03-2010 to 14-04-2010] [14-03-2011 to 14-04-2011]	570.6	548.9	665.8	462.4
After brown bear emergence [14-04-2010 to 15-05-2010] [14-04-2011 to 15-05-2011]	752.8	726.3	1357.1	1043.9

The home range (100% MCP) of the wolves after brown bear emergence was 103% largest (1357 km²) than their home range before brown bear emergence (665km²) in 2011. The same pattern was also observed in 2010 (*Table 3, Fig. 12*).

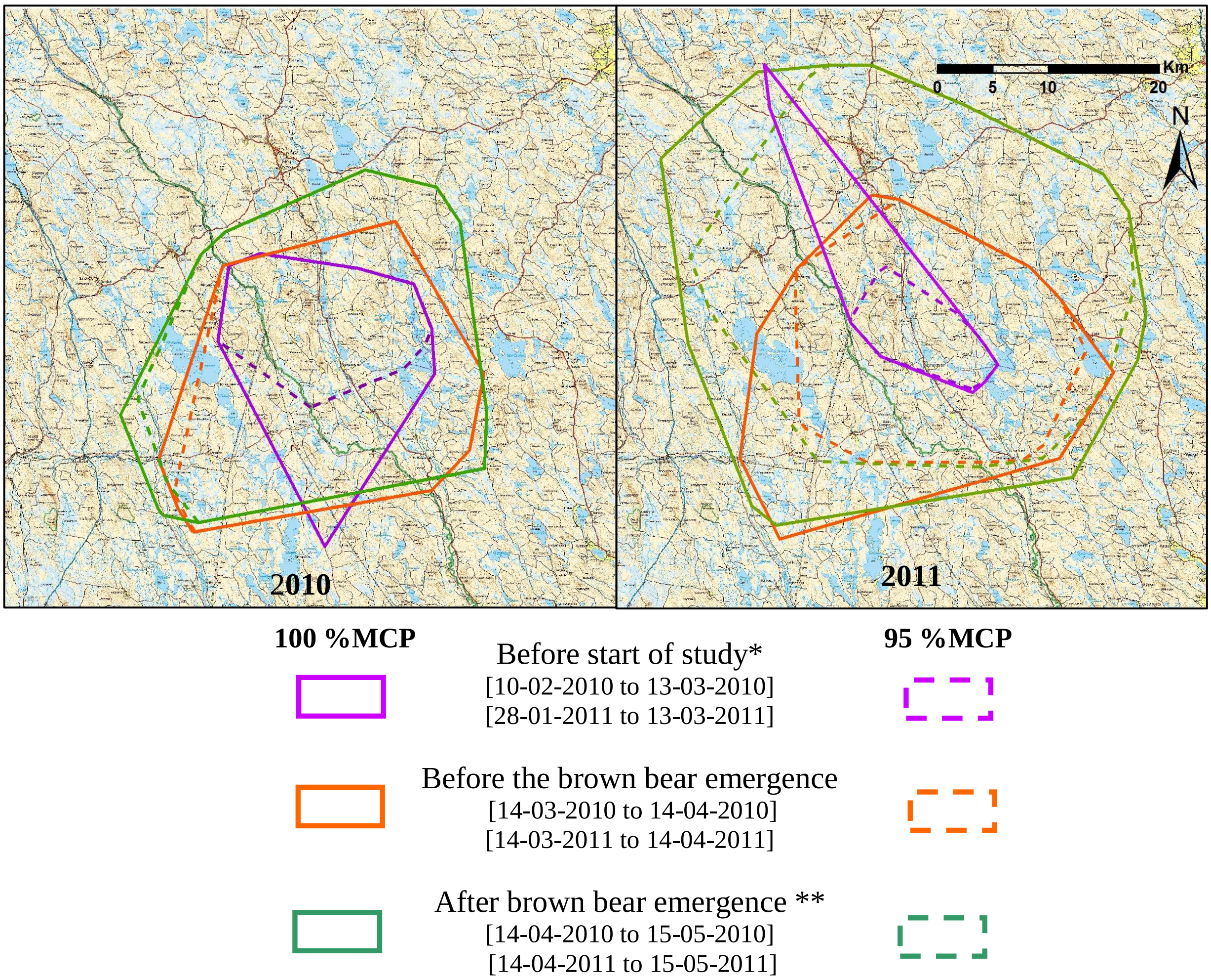


Figure 12: Wolves home ranges in 2010 and 2011 using all GPS positions available from male GPS collar (9063)

*using 2 positions per day in 2011 ** using 2 positions per day in 2010

The Tenskog pack reproduced on 10 May 2011, 5 days before the end of the study. During that time, the female was very stationary (0.036 km²) and the male had a small territory of about 84.5 km². The male went back and fourth (6 trips back and fourth recorded) between a killed moose and the den.

3.3. **Direct interactions**

Only one direct interaction was detected between a GPS marked brown bear (2967) and the male wolf (9063) (*Fig. 13*). I assumed that only the male wolf was present because the female wolf (09064) was 3.7 km away on her last available position at 13:00. The male wolf revisited his own moose killed the 23/04/2011 02:00 (25 days after the estimated date of the death). But it did not get to the carcass, because a male brown bear (9 years old, 120kg, source: Scandinavian Brown Bear Project) was feeding on the remains of the carcass. The wolf stayed 3 hours at about 50 meters from the remains, and then moved at 270m from the carcass to a resting place. He returned close to the carcass (50 meters) 10 hours later, but the bear was still on the remains of the carcass. The male wolf then moved 2.5km away from the carcass whereas the bear stayed on the carcass one more day. A likely conclusion is that the wolf tried to gain access to the moose remains but that this was made impossible because of brown bear presence.

3.4. **Indirect interactions**

Indirect interactions involved brown bears feeding on the remains of a moose carcass killed by wolves. In total, 5 events of indirect interactions were detected involving 4 moose carcasses. Only two indirect interactions were detected involving GPS-collared bears. In one case the bear (2967) stayed 2 days around the remains (*Fig. 13*), and in the other case, the bear (8795) stayed about 30 minutes near the carcass (*Fig.14*).

Camera traps placed in 9 different wolf-killed moose sites detected 4 different brown bears eating remains of 4 different wolf-killed moose carcasses. In only one case, the bear was GPS marked. Another bear was GPS-marked but its collar was not working, (and the 2 others were unmarked brown bears). The other 5 cameras did not detect any brown bear presence. The bears visited the wolf-killed moose on average 13.45 days (ranged 8-22.4 days) after the estimated date of death and stayed on average 2.4 days (ranged to 0.45-4.54 days) around the carcass. Using the criteria of one visit on the moose remains based on less than 1 hour between 2 pictures taken, the bears visited the remains 3.75 times (ranged 3-6). Red foxes (*Vulpes vulpes*), and ravens (*Corvus corax, C. cornix*) also used remains of wolf-killed moose.

Using GPS positioning (30min between GPS positions) of the brown bear (2967) resulted 10, 37 and 61 positions in a 25m, 50m and 100m radius buffer respectively, around the moose remains (*Fig.13*). Using the same criteria as for the pictures of ≤1 hour between two positions to determine one visit, the bear visited the carcasses 6 times using all GPS positions within the 25m radius buffer and with the pictures taken. However the time of the visits did not match (50% of all visits) between the camera and the GPS positioning showing possibly missing information with only coarse GPS data. A visual observation during field work was also done of an unmarked bear eating a moose carcass the7 April 2011.

GPS data indicated that wolves returned (after carcass being checked in the field and camera was set up) to 5 of their own killed-moose sites (wolf GPS position ≤200m of kill site) on average 26 days (range 12-65 days) after the killing event. Despite camera traps were set up on the main parts of remains left, wolves were captured in photographs in only one case.

On one occasion both wolves used and consumed a *probably* bear-killed moose, because the estimated date of moose death did not match with the date and time of the first position of the wolves on the carcass. Furthermore, signs of brown bear presence were found around the remains of the moose.
Photographs taken by cameras revealed that brown bears were eating the bones of the moose (probably to get access to the marrow fat) and tissue from stomach and mesenteries , in one case a bear dragged a piece of moose skin and legs away from the range of vision of the camera.

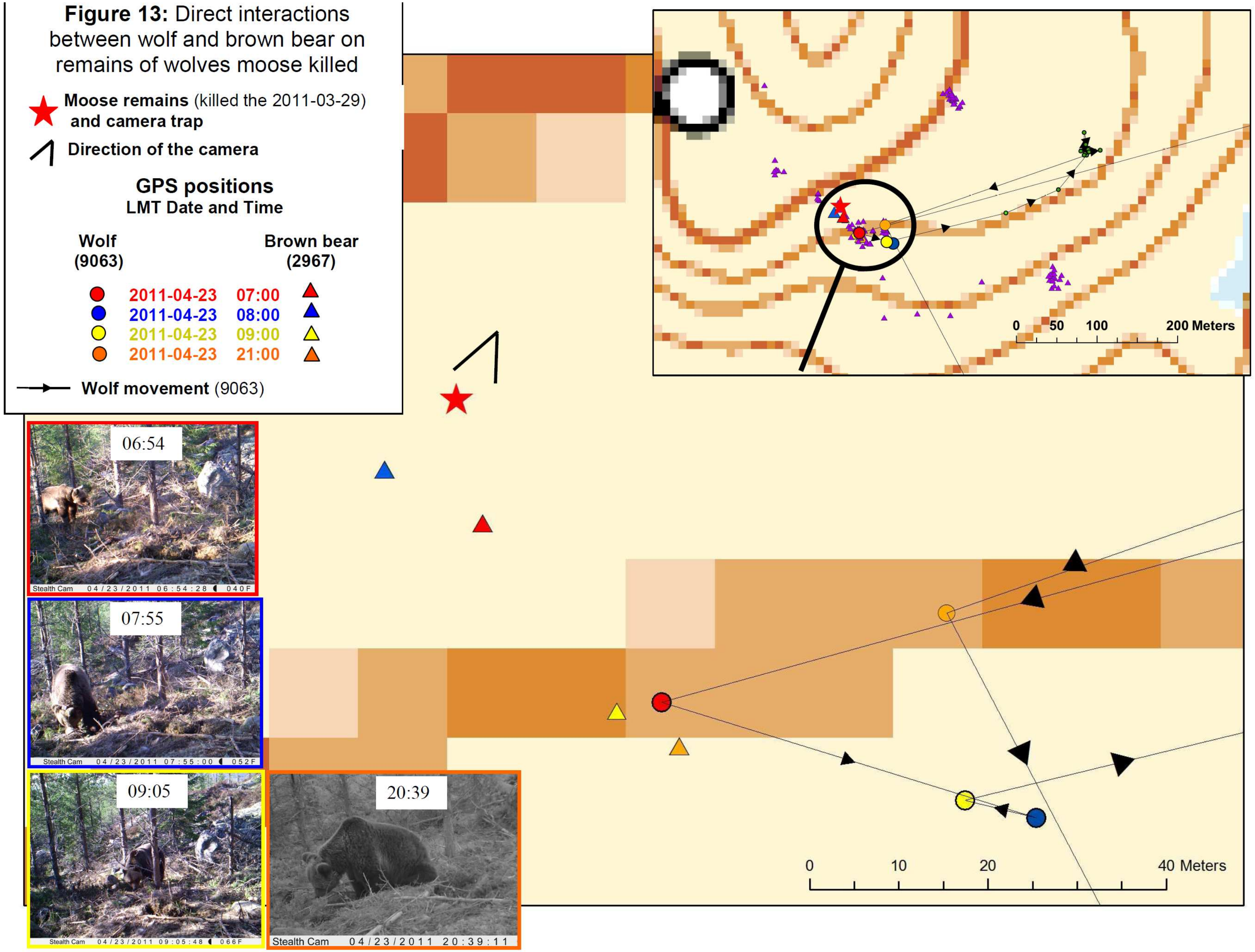
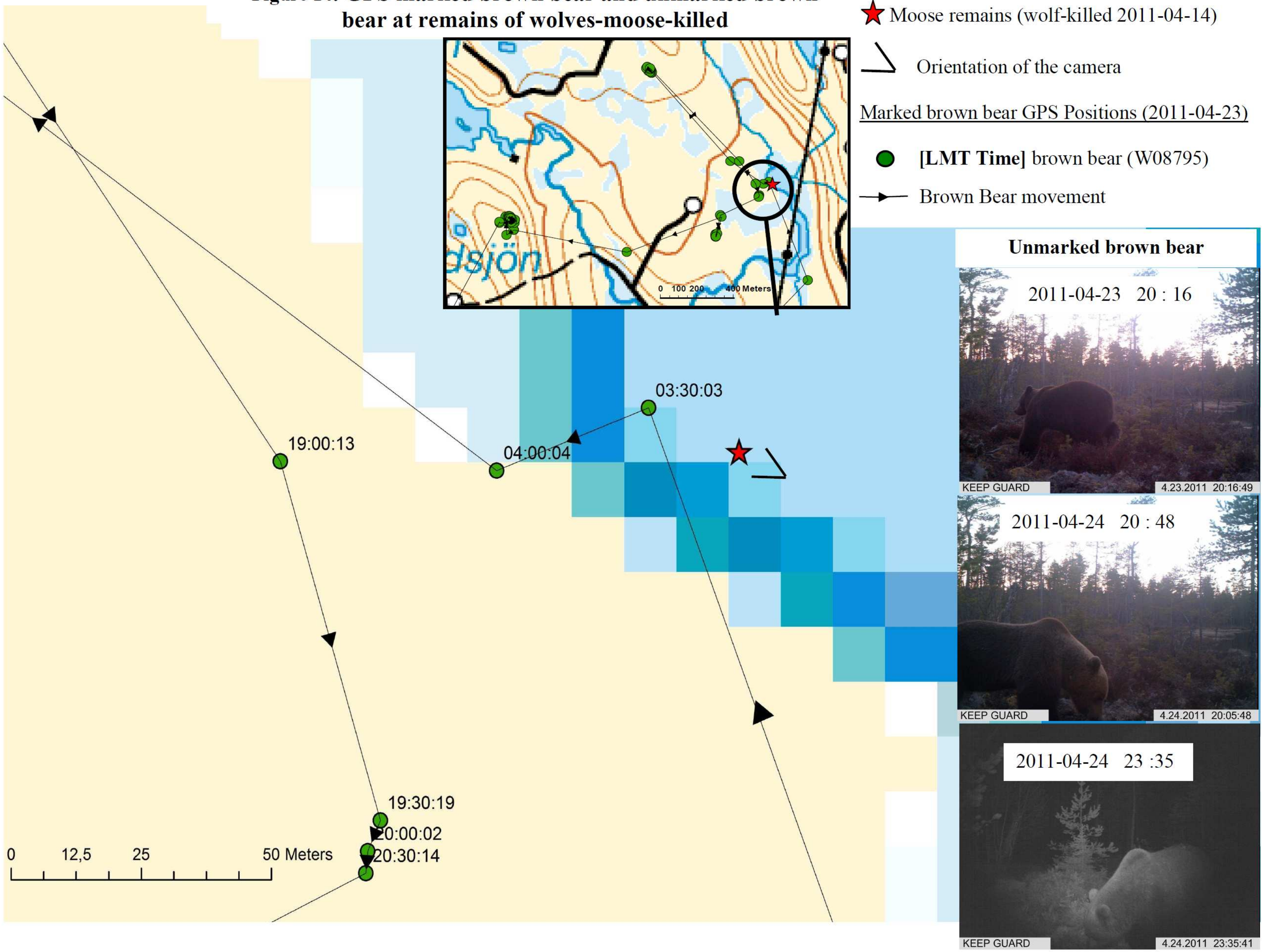


Figure 13: Direct interactions between wolf and brown bear on remains of wolves moose killed

Figure 14. GPS marked brown bear and unmarked brown bear at remains of wolves-moose-killed



4. **Discussion**

This study aims to be a first step in the evaluation of wolf and brown bear interactions in Scandinavia, hence the amount of data was small, concerned only 2 years of study and comprised only one wolf pack. But it is already possible to discuss in a sound of ecological context the results obtained. The results supported the hypothesis that wolves modified their behaviour in spring, as coinciding with brown bear emergence, compared to winter (Manchi & Swensson, 2005).

However, estimating the true causes of the observed variation in wolves' movement patterns is complex because interference interactions add an extra level of complexity to the understanding on species behaviour (Linnell & Strand, 2000; Palacios & Mech, 2010 ; Wikenros et al., 2010; Mattisson et al., 2011).

In the study area, brown bear absence was synonymous with winter period and generally deep snow, and wolf kill rates are generally reported to be higher in late compared to early winter during February and March (Jedrzejewski et al., 2002, Smith et al., 2004), and in term of kg biomass available and consumed (Sand et al., 2008). However the wolf kill rate within the Tenskog pack was among the lowest observed in Scandinavia (Sand Håkan, Personal communication) with on average 0.8 moose killed per week per pack as compared to almost 2 moose usually killed by pack in Scandinavia (Sand et al., 2005).

Moose in Scandinavia are currently naïve to re-colonizing wolves and results in a high wolf hunting success (Sand et al., 2006b). Moose are also more vulnerable to predation by wolves at snow depths greater than 75cm (Perterson 1977 in Sand et al., 2006a) but not at snow depths of less than 60cm (Sand et al., 2006a). Snow depth in central Sweden is usually high in winter and reached 105cm in mid February 2011 in Tenskog territory (Weather station Hamra and Lillhamra, 2011). However the low kill rates observed during the winter study period did not support the hypothesis that moose get more vulnerable to wolf predation with increased snow depth. In winter, access to prey varies strongly within an area because moose in Scandinavia commonly aggregate in specific browsing areas (Zimmermann et al., 2007). Zimmermann et al (2007) reported a case where wolves killed four moose within 29 hours and a maximum distance of 4.4 km in an aggregation area. In contrast, the Tenskog wolf pack in the 2011 winter had an extremely small territory of about 75km² never observed so far in Scandinavia (Sand Håkan, Personal communication) with only one moose killed during a one month period.

Moose density estimated by pellet counts in spring (Sand et al. 2010), showed both a higher and a lower density than the one observed by aerial counting (on adjacent and to some extent overlapping areas with Tenskog territory) (Ahlqvist Per; Sand Håkan; personal communication). These two methods are relatively accurate to estimate population trends over years but pellet count surveys should be used with caution in areas where population structure changes over time, while aerial counting in winter gives an absolute population size at a certain point in time (Rönnegård et al., 2008). Hence a lower moose density in winter, due to moose migration 40-60km south from the Tenskog territory along the Voxna River (crossing wolf territory north to south) (Ahlqvist Per, Brunberg Sven, Personal communication), would result in a low encounter rate between moose and wolves (Sand et al. 2005) and a longer time between kills (Merrill et al., 2010). Wolves may choose the option to stay very stationary near a food source to minimize energy cost of travelling in a deep snow. However, that hypothesis was not supported by studies in Yellowstone National Park which showed increasing kill rates in winter even when prey density decreased due to winter migration (Smith et al., 2004) Furthermore if we consider that wolves were able to consume the amount of biomass of moose during fairly a long time period (30 days), results showed that the amount of biomass consumed was just at the limit of the minimum intake requirements for wild wolves (*fig. 3*) (Peterson and Ciucci 2003, Sand et al., 2008). This is supported by the observation during the winter 2011 when wolves started to move from their small territory (browsing 54.2km in 48hours) as soon as the snow became crusty on the upper layer, then wolves were able to walk on the top of the snow (Milleret Cyril, visual observation). Hence the shift between the two study periods were distinct regarding two different causes; brown bear emergence, wolf Tenskog pack killed 0.1 moose/day compared with 0.17 moose/ day after brown bear emergence when snow started to melt.

Although using GPS positioning is currently the most accurate method available to estimate wolf kill rates and prey consumption might be underestimated and has to be considered as a minimum estimate of the true kill rate, although using GPS positioning is currently the most accurate method available to estimates wolf kill rate (Sand et al., 2005). Nevertheless, Sand et al., (2005) reported moose found killed near single positions, the quality of results depending of cluster definition and intensity of positioning interval. Palacios & Mech (2010) reported difficulties in finding small prey during summer when small deer fawns may have been target: first because of low handling time of small prey and second because their results suggest that predation on small prey tended to be related to wolves travelling alone. Hayes et al (2000) mentioned than wolves might survive by killing small prey (snow hare *Lepus timidus).* In winter 2011 more than 1 single position out of 2 was checked in the field, and two capercaillies were found, one of which was found between 2 single positions while following wolves' tracks in the snow. Wolves in a same pack might split into several groups and the GPS collared wolf might not be present at the kill site for the entire time required to handle prey (Webb et al., 2008). However half of the study was done when snow was present, resulting in a better prey detection than during the snow free periods (Merrill et al., 2010).

The Tenskog wolf pack reproduced 5 days before the end of the study, and this could have affected the results (Palacios et al., 2010). Because the collar of the male was used for analysis and male travels longer distances during reproducing time (Alfredéen, 2006). Tenskog wolf male showed a small territory around the den and spent lot of time in the den cluster (43 hours). Before the entering in the den, the female changed her behaviour and split her movement with the male. On one of the female clusters, one unusual bed site was found, which could be considered as an indication of a pre-denning behaviour.

My results of the cluster analysis supported the results obtained by several studies in Scandinavia that predation events occur mainly during the night (Sand et al., 2005, Zimmerman et al., 2007) and carcass clusters contained more positions and more visits than others clusters (Zimmerman et al., 2007).
All GPS positions within a 200 meter buffer radius around the kill site may be generally considered as handling time of the prey (Webb et al., 2008). Sources of variation in killing and handling time are multiple but might be caused by other carnivores or scavengers using wolf kills (reviewed in Merrill et al., 2010). When brown bears were awake, cluster analysis revealed that wolves spent more time within carcass cluster and stayed closer to the prey carcass after killing it (<200m). In staying close to their killed prey, wolves may have adopted a protective behaviour, hence they may protect their food source against brown bears.

Wolf and brown bear interactions reported in Yellowstone national park showed that a bear usually are dominant against wolves at feeding site (Ballard et al., 2003). The only direct interaction detected during this study suggested that a brown bear gained access and was dominant at the same food resource. In 2010, Steyaert & Frank (2010) reported 2 direct interactions, but with the coarse GPS temporal resolution it was unclear how wolves and brown bears reacted to their encounter.

A resource unit consumed by one species cannot be consumed by another (Linnell & Strand, 2000; Ballard et al., 2003) and competition by scavengers can influence kill rates of other carnivores (Hayes et al., 2000). Previous work in Yellowstone National Park found that bears scavenged about half of wolf-killed carcasses during June and July and every wolf-kill from March through October in an area of high grizzly bear density, suggesting underestimates of the loss caused by scavengers (Hebblewite & Smith 2008; Metz et al, 2011). My results support those findings, because brown bear presence was detected at half of the wolf-killed moose carcasses detected, and on one occasion wolves used a brown-bear-killed moose carcass. But it is not obvious that wolves increased their kill rate as direct response of brown bear presence.

After direct interaction with brown bears where wolf likely did not get access to the food resource (*Fig. 13*), the wolf revisited two of his older kills. Because brown bears were found on wolf-killed moose two weeks after the date of death, should it then be considered brown bears possibly usurp wolf food? GPS data indicated that wolves returned on their old kill site, 65 days after kill it. Despite camera traps were set up on the main parts of left remains, wolves were captured in photographs in only one case. If the wolves did not intend to return to eat the moose remains, it is difficult to assess why they went close to left remains. Several explanations can be advanced:

First, wolves avoided the human smell left by the field worker near the carcass, but after more than 10 days, the smells of humans are not likely present.

Second, wolves did not feed on the main part of left remains.

Third, cameras did not detect their presence. Here again, the outcome of wolves and brown bear interactions is not obvious to analyse.

In 2010 June, Steyaert & Frank, 2010 found 3 interactions between wolves and brown bears with the brown bear being first at the carcass site, which was similar to the occasion in my study where wolves used the remains of a bear-killed moose. Because most predation by brown bears on moose calves is known to occur up to the age of 1 month (Swensson et al. 2007) and wolves generally increase their kill rates in terms of the number of individuals killed in summer due to the calving season (Sand et al., 2008), competition for food between brown bear and wolves may be intense.

Both camera traps and GPS positioning methods are likely underestimated the number and of interactions (*Fig. 13*). Only one camera trap was set up on the main part of prey remains found at kill sites and as observed with GPS data of brown bear (*Fig.14*), camera trap missed one brown bear visit. But camera traps adduced complementary information to GPS position alone.

Definition of the two periods without brown bear presence (in den) and with brown bear presence have been done with literature and data of the study area available (Friebe et al., 2001; Manchi & Swensson 2005, Scandinavian brown bear project). Even if that data is really accurate, the ranges of intra-individual emergence among brown bears might have biased the estimation. I considered 14 April as the date of brown bear emergence but before this time some brown bears, in particular adult males, were already out of the den while female adult (≥4 year old) without cubs emerged 10 days later my definition of the period of brown bear presence (Source: Scandinavian brown bear project). Friebe et al. (2001) reported large range in the date of brown bear female emergence, female with cubs emerged the 23 May and female pregnant the 14 June. Because the number of brown bears active differed over the spring, intensity of interactions might have varied over time.

To conclude, wolves and brown bears interactions have been detected in this study and seemed to be mainly indirect. However the conjunction of all ecological factors affecting the species' behaviour (snow condition, moose density, individual behaviour) makes interpretation of the results difficult.
Wolves showed a very low kill rates among the lowest observed in Scandinavia and brown bear feed on the half of all carcasses found. Even if the method has bias it was the more accurate method available and was appropriate for the study.

The same study should be conduct in autumn because intensity of interactions between brown bear and wolf could vary. First because that period coinciding with pre and denning period of brown bear (Friebe et al., 2001; Manchi & Swensson 2005) and second because diet of brown bears in spring comprising mainly ungulates switches to berries in autumn making up half of the brown bear's estimated dietary energy (Persson et al. 2001)

The small dataset comprising only one year of study and only one pack was not enough to employ powerful statistical methods to discuss and find a strong correlation between brown bear emergence and modification of wolf behaviour. More data is necessary to implement a better understanding of brown bear and wolf interactions. Further studies should involve predation studies on moose by brown bears and wolves (several pack) throughout the year, and especially during June, when moose calves are new born. Both wolves and brown bears might increase ungulate killing with the pulse in neonate availability in early summer. (Swensson et al., 2007; Sand et al., 2008; Knopff et al., 2010) Camera traps have proved to be a complementary method to analyse and estimate brown bear and wolf interactions. For further study I recommend an increase in the number of brown bears GPS marked within Tenskog wolf territory, and using a higher resolution of GPS-positions from wolves over the year. Selection of GPS fixes intervals is a trade off between battery lifetime of the GPS collar and the data accuracy (Merrill et al., 2010). Wolf GPS collar used (Vectronic GPS PRO Light, battery 1D), allowed taking on average 7100 position, resulting in about 19 positions/ day for one year (Vectronic Aerospace, GmbH, , Berlin, Germany). To maximise the quality of study it would be preferable to target some periods with a high positioning rate per day and other with low position per day. Hence it will be possible to save the life of the battery and allow the wolf recapture the following year.

Estimation of moose density and distribution by several methods would be preferable (Rönnegård et al., 2008). A high density of GPS collared moose, especially female moose (Swensson et al., 2007) will also permit a better understanding of wolves-brown bears predation and interaction with moose.

5. Implications for management and other studies

5.1. Hunter, wolves, brown bears harvest on moose

Even if estimating predation is not evident because many factors interfere and are difficult to estimate (Gundersen et al., 2008), as an example of implications of this study, I calculated roughly the yearly impact of predation by wolf, brown bear and hunting harvest on moose in the Tenskog territory.

Sustainable hunting harvest on moose should not exceed the annual production of moose defined as 40% of the total number of moose in the winter population (Sand Håkan personal communication). Although brown bear and wolf predation is mainly done on moose calves (Sand et al., 2005; 2008), I based my estimation of hunting harvest and predation on the annual moose production. Parameter using for estimation are summarized in *Table 4*. Wolf and brown bear predation on moose are thought to represent an almost total additive mortality source in the moose population (Sand et al., 2005; 2008; Swensson et al., 2007) Hunting harvest thus needs to be adjusted in order to maintain a sustainable moose management plan. The figure 15 shows the relative importance of brown bear and wolf predation compared to the hunting harvest and the variation of results highlights the importance of accurate estimation parameters.

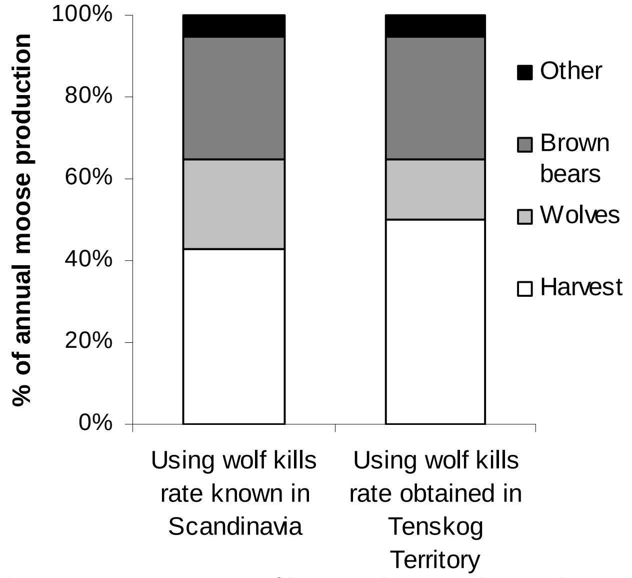


Figure 15 : Proportion of hunting harvest, brown bear and wolves predation of the annual total moose production in Tenskog territory using Scandinavian wolf kill rate and Tenskog wolf kill as estimations

Table 4: Estimating wolf, brown bear and hunting harvest in Tenskog territory based on annual estimating kill rates obtained in Tenskog in winter and in a low moose density territory obtained in summer and winter in Scandinavian (Sand et al., 2005, 2008; unpublished data). Summary of estimating parameters for kill rate calculation. Sustainable hunting harvest was obtained by annual moose harvest (wolf bear) and other mortality causes minus yearly moose production. Other mortality causes included traffic accident, disease, starvation etc (Sand .pers.com)

*Sand et al., 2010; **estimated by double winter kill rates observed (Sand et al., 2008); *** Scandinavian brown bear project, unpublished data; ****Solberg et al., 2006 [5] Sand, unpublished data**;** [6] Sand et al., 2005; Sand et al., 2008; Sand unpublished data**.**

Estimated parameters		**Using wolf kills rate obtained in Tenskog Territory**	**Using wolf kills rate, assuming a hypothetical functional response with a low moose density in Scandinavia[6]**
Wolf territory		1043,9 km²	1043,9 km²
		Estimating number	
Moose density (Pellet count)*	0,87km²	908,2	908,2
Wolf-moose winter predation		27,0	-
Wolf-moose summer predation**		27,6	-
Wolf-moose predation total		54.6	80
Adult bear-moose predation***	7 /adult bear / year	109,6	109,6
Bear density****	0,03/km²	31,3	31,3
Adult bear proportion ***	50%	15,7	15,7
Annual production of moose [5]	40%	363,3	363,3

Moose density in Scandinavia is typically above 1/km², at such density there are moose enough for large predators and hunters, but at low moose density, below 1/km² (i.e. in Tenskog territory) (Liberg et al., 2008), the competition between hunters, wolves and brown bears might be intense. The data obtained do not solve conflicts between predators and hunters, but they give guidelines and factual baseline for management to reach compromises. Because wolf often scared population by his presence (Boitani 2003, Schwartz et al., 2003), popularization of the scientific results obtained by research might help to decrease the fear caused by this predator.

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	Type and time of death						Type of carcass			Carcass characteristics			
Carcass number	Wolf killed	Probably wolf-killed	Not wolf killed	Unknown	Killed within study period	Date of founding	Species	Age	Sex	Estimated date of death earliest	Estimated date of death latest	Time of first GPS-position*	Proportion (%) consumed of carcass
							2011						
1	X				no	17/03/2011	Moose	Juvenile				14/03/2011 01:00	100%
2		X			X	17/03/2011	Capercallie	?	Female	03/03/2011	16/03/2011	14/03/2011 01:00	100%
3		X			X	23/03/2011	Capercallie	?	Female	07/03/2011	22/03/2011	19/03/2011 09:00	100%
4	X				no	24/04/2011	Moose	Adult	?	01/02/2011	10/03/2011	14/03/2011 19:00	100%
5	X				X	29/03/2011	Moose	Juvenile	?	25/03/2011	27/03/2011	25/03/2011 09:00	75%
6	X				X	01/04/2011	Moose	Yearling	Male	27/03/2011	31/03/2011	29/03/2011 02:00	60%
7	X				X	14/04/2011	Moose	Juvenile	?	01/04/2011	10/04/2011	07/04/2011 14:00	100%
8		X			X	14/14/2011	Roe deer	?	?	01/04/2011	10/04/2011	11/04/2011 07:00	100%
9		X			X	14/14/2011	Roe deer	?	?	01/04/2011	10/04/2011	11/04/2011 05:00	100%
10	X				X	19/04/2011	Moose	Juvenile	?	04/04/2011	16/04/2011	14/04/2011 23:00	100%
11	X				X	22/04/2011	Moose	Juvenile	?	13/04/2011	19/04/2011	18/04/2011 11:00	98%
12	X				X	01/05/2011	Moose	Juvenile	Male	25/04/2011	30/04/2011	27/04/2011 21:00	90%
13	X				X	07/05/2011	Moose	juvenile	?	29/04/2011	06/05/2011	02/05/2011 06:00	95%
14			X		X	09/05/2011	Moose	Juvenile	?	25/04/2011	02/05/2011	05/05/2011 00:00	95%
15	X				X	05/09/2011	Moose	Juvenile	?	06/05/2011	13/05/2011	09/05/2011 03:00	80%
							2010						
1	X				X	18/02/2010	Moose	>1	Female	08/02/2010	09/02/2009	10/02/2010 14:00	94%
2				X	X	21/02/2010	Roe deer	?	?	December	?	17/02/2010 21:00	100%
3	X				X	02/03/2010	Moose	1 or 2	?	21/02/2010	26/02/2010	21/02/2010 23:00	95%
4				X	?	13/03/2010	Black grouse	?	?	Before winter	February		100%
5			X		no	17/03/2010	Moose	>1	Female	?	?	12/03/2010 04:00	?
6			X		no	23/03/2010	Moose	>1	?	From 2009 hunting	From 2009 hunting	12/03/2010 21:00	100%
7				X	no	24/03/2010	Moose	1	?	01/12/2009	13/02/2010	20/03/2010 05:00	100%
8	X				X	30/03/2010	Moose	1	?	23/03/2010	28/03/2010	23/03/2010 12:00	100%
9				X	X	31/03/2010	Snow hare	?	?		30/03/2010		95%
10	X				X	31/03/2010	Roe deer	>1	?	29/03/2010	29/03/2010	28/03/2010 01:00	95%
11			X		no	09/04/2010	Moose	>1	Bull	01/11/2009	01/12/2009	19/03/2010 22:00	0%
12		X			X	10/04/2010	Moose	0	?	31/03/2010	10/04/2010	31/03/2010 08:00	98%
13		X			X	11/04/2010	Moose	0	?	31/03/2010	10/04/2010	30/03/2010 06:00	98%
14		X			X	11/04/2010	Moose	>1	Female	10/04/2010	11/04/2010	07/04/2010 17:00	15%
15				X	no	19/04/2010	Moose	0	?	01/12/2009	15/01/2010	16/02/2010 21:00	100%

Appendix 1: Summary of carcass list and carcass characteristics found during the two study periods (2010-2011) within a 200m radius buffer around carcass. Definition of criteria defined in paragraph 2.4

Appendix 2: Clusters of hourly wolf positions using 50m buffer radius, defined by cluster type and characterized by the number of positions and visits, the ratio of positions to visits, the cluster area (ha), the movement linearity when entering at cluster, the distance cluster form last kill (meters) the distance from previous cluster (meters), the distance from next cluster(meters). Movement linearity ranges from 0 (back and fourth to the same site) to 1 (straight line movement).

Clusters	N		Positions		Visits		Positions/ visits		Distance from last kill (m)		Linearity		Distance previous cluster (m)		Distance next cluster (m)	
Period	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
Type	Number		Average													
Carcass	7	8	25,6	39,1	9,6	5,6	3,1	7,26	3115,5	3047,5	0,95	0,82	2510,4	2979,5	1354,5	2890,5
Bed site	33	24	20,8	8	3,25	1,36	5,7	5,9	5441,863	11960	0,88	0,9	2306,9	4014,8	2913,1	2646,9
Den	0	2	-	30,7	-	5	-	5,3	-	3115,8	-	0,96	-	2038,1	-	2065
Negative	5	24	3,4	4	1	1,64	3,4	3,15	14037,3	9809,9	0,78	0,84	3852,7	3557,2	2989,5	4724,5
Track	6	0	2,2	-	2,2	-	1	-	2211,736	-	0,9	-	2352,1	-	3317,5	-
Unknown	21	2	4,7	2,5	1,7	1	3,52	2,5	8540,8	15628,9	0,86	0,98	3251,9	1527	3677,9	8846,2