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Wolf movement patterns and the distribution of moose kills: implications for human harvest?

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Abstract

Most studies regarding wolf (*Canis lupus*) predation on moose (*Alces alces*) have focused on the total annual consumption of moose within a wolf territory but few have tried to describe the spatial impact of wolf predation on a local scale. In this study I have analyzed wolf movement data, wolf predation, moose hunting statistics and moose hunter observations to investigate how wolf predation affects the human harvest of moose in Scandinavia. Since wolves prey on mostly juvenile moose during summer, analysis of their summer movement patterns is crucial to understand its impact on the human harvest later during autumn. In this study both reproducing (n = 45) and non-reproducing wolves (n = 12) reduced their movement range during summer to 66% and 67% of their annual movement range, respectively. Reproducing wolves increased their movement range from early to late summer while non reproducing wolves did not. There where also a difference regarding the average distance between each moose carcass and the calculated centre of mass for all kills found during each summer study. Non reproducing wolves had an average kill distribution of 14510 m (± 7111, n = 45) while reproducing wolves had a much more restricted kill distribution of 7923 m (± 4809, n = 96). Wolf presence within moose hunting license areas during summer where negatively correlated to the distance between the area and the wolf den. Either wolf presence within the moose hunting license areas during summer or the distance between the license areas and the wolf dens where correlated to the human hunting success during autumn, with one exception. The total human hunting success where reduced in license areas where wolves had spent more time during summer. The number of cows followed by twin calves observed by hunters was the only observation variable that where significantly negatively correlated with the distance to the wolf den. These results show that pup-rearing and denning behavior has an impact on the wolves hunting behavior during summer. It also shows that this central place foraging behavior during the reproductive season influences the local human hunting success only at a small scale. The human outtake of the moose population within the wolf territories was 3.8 ± 1.6 moose per 1000 hectares. In areas where moose densities are lower wolf predation may affect the local human harvest more negatively. The long term impact of wolf predation on the local scale may be higher if wolves choose to locate their den in the same area year after year.

Sammanfattning

Syftet med denna studie var att analysera om vargpredation på älg är knuten till lyans placering och vargars rörelsemönster, samt om detta har någon lokal negativ inverkan på antalet älgar som fälls eller observeras under älgjakten. För att göra detta har jag analyserat GPS-positioner från totalt 28 sändarförsedda vargar, data insamlat vid vargpredationsstudier (13 sommarstudier och 16 vinterstudier), avskjutningsstatistik på älg från 80 licensområden samt data från 91 älgobsområden. Avskjutningsstatistik och älgobsdata kommer ifrån vargrevir i Dalarnas, Västmanlands, Värmlands, Västra Götalands och Örebro län.

Vargarnas genomsnittliga revirstorlek var 1299 km² och 1631 km² för reproducerande respektive icke reproducerande vargar, men denna skillnad var inte signifikant. Både reproducerande och icke reproducerande vargar minskade sina rörelseområden sommartid ner till mindre än 70 % av den årliga revirstorleken. Något som sannolikt möjliggörs av en ökad födotillgång i form av älgkalvar. Reproducerande vargar expanderade sitt rörelseområde under sommaren med 26 % i takt med att valparna blev mer mobila. Detta mönster återfanns inte hos de icke-reproducerande vargarna. Sommarpredationsstudierna visade att den genomsnittliga radien mellan älgkadavren och den geometriska centrumpunkten var 7923 m för reproducerande vargar och 14510 m för icke reproducerande vargar. Detta tyder på att storleken på de reproducerande vargarnas jaktområde reglerades av deras behov att återvända till lyan med jämna mellanrum medan icke reproducerande vargar jagade mer slumpmässigt över sommarområdet.

Andelen GPS-positioner sommartid inom olika licensområden ökade ju närmare lyan området var beläget. Den totala avskjutningen av älg per 1000 ha var lägre i licensområden där vargarna var frekventa besökare under sommaren. Det fanns även en tendens till att avskjutningen av älgkalv per 1000 ha var lägre i frekvent besökta licensområden men denna koppling var ej statistiskt signifikant. Det fanns dock ingen säkerställd koppling till avståndet mellan lyan och den registrerade avskjutningen (antalet kalvar fällda per fälld ko, antalet kalvar fällda per fällt vuxet djur, antalet kalvar fällda per 1000 ha och total avskjutning per 1000 ha) i de olika licensområdena. Andelen kor med dubbelkalv som registrerats i älgobsen var signifikant lägre ju närmare lyan området låg. Det fanns dock ingen koppling mellan andelen kor med enkelkalv, antalet kalvar per ko eller antalet kalvar som observerats per mantimme och avståndet mellan licensområdet och lyan.

Även om vargarna begränsade sina rörelseområden och därigenom koncentrerade predationstrycket kring lyan under sommaren påverkade detta den lokala avskjutningen marginellt. Avskjutningsstatistiken avslöjar inte arbetsinsatsen bakom resultaten vilket innebär att två licensområden med olika älgtätheter kan producera liknande avskjutningssiffror (i synnerhet fördelningen mellan kalvar och vuxna djur) även om tidsåtgången har skilt sig åt sinsemellan. Denna faktor, tillsammans med skilda förvaltningsplaner i olika licensområden (samt slumpen) påverkar också avskjutningen av älg. Den observerade andelen kor med dubbelkalv visade sig vara kopplat till lyans placering medan de andra kategorierna inte var det. Andelen kor med dubbelkalvar är mindre än andelen kor med enkelkalv vilket kan ha lett till att vargpredationen påverkade den förstnämnda kategorin starkare.

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Introduction

Little is known about wolf predation on ungulates during summertime due to difficulties to follow wolf movements on a fine scale. The introduction of GPS technology into wildlife research has changed that in just a few years and it is now possible to follow the movements of wolves in great detail (Sand *et al* 2004a). Several studies has been performed to estimate kill rates of wolves on ungulates (Demma *et al* 2007, Gundersen *et al* 2008, Sand *et al* 2008) and homesite attendance patterns (Potvin *et al* 2004, Alfredéen 2006, Demma & Mech 2009). However, few have tried to describe variations in the spatial patterns of predation pressure within the boundaries of a wolf territory (Wam & Hjeljord 2003).

A wolf pack is usually a family group consisting of a male and a female and their offspring of different ages where the parents share the leadership and provision of food for the group (Mech 1999). The daily mean movement range of individual wolves is highly affected by the stage of the reproductive cycle including the mating season, denning season and juvenile rearing season (Jedrzejewski *et al* 2001, Alfredéen 2006, Schmidt *et al* 2006). The male and the female divide the chores so that the female is in charge over the rearing of the pups while the male mainly focuses on food provision for the family (Mech 1999, Shmitd *et al* 2006, Tsunoda *et al* 2009). Early in the breeding season females are present at the homesite almost every day even though they do leave the area on a regularly basis (Demma & Mech 2009). The spatial utilization of the territory of reproducing wolves increases towards the autumn along with the ageing of pups (Jedrzejewski *et al* 2001, Schmidt *et al* 2006). The denning period for Scandinavian wolves has been estimated to last for on average six weeks (44 days) and the family (pups) is usually stationary within a 3000 m radius from the den for another six weeks (Alfredéen 2006). The reduced movement range during summer may partly be made possible due to an increase in the availability of prey in terms of increased density of juveniles (Jedrzejewski *et al* 2001). Non-breeding wolves, on the other hand, shows high variation in foraging bouts and higher movement rates over the territory in a less predictable way compared to breeding individuals (Demma & Mech 2009).

Moose is the main prey for wolves in Scandinavia and wolves show a preference for calves (Sand *et al* 2005, 2008).The average kill rate in summer on moose in Scandinavia has been estimated to 0.58 kills per day but decrease throughout the summer season, reflecting the increase in body mass of moose calves. Wolf kill rate on moose in Scandinavia is not correlated to the number of individuals in the wolf pack (Sand *et al* 2008).

Moose hunting is considered to be of great economical and recreational value in Sweden. Approximately 250 000 of the 300 000 Swedish hunters participate in moose hunting every year. The average hunter spends approximately nine days hunting moose every autumn and approximately 100 000 individuals or 30% of the total moose population is harvested by hunters every year (Swedish Association for Hunting and Wildlife Management 2010a). Nilsen *et al* (2005) recommends that since wolf predation on moose is mostly additive, hunters within a wolf territory must reduce the annual harvest in order to maintain a stable moose population.

The number of calves per cow observed by hunters in Scandinavia is often lower inside a wolf territory compared to the outside but the opposite has also been recorded (Gundersen *et al* 2008). This may have to do with the human harvest of moose calves within the wolf territory when the hunters have reduced their harvest in order to compensate for wolf predation (Gundersen *et al* 2008). Wam & Hjeljord (2003) found that wolf predation on moose had the highest impact during the first year after a wolf

territory had been established. After the first year the moose population had recovered to levels similar to before the wolf introduction. They suggest that this may have been caused by an increase in fecundity among the moose cows that had lost their calves during the last year (Wam & Hjeljord 2003). The proportion of calves killed by wolves may vary between different territories even if the moose density is the same (Bernelind 2006). This is probably due to differences in hunting strategies among wolf packs that may be independent of the age distribution of the prey species (Gundersen *et al* 2008). In general a high proportion of calves killed instead of adults within a wolf territory have less impact on the annual population growth of moose (Sand *et al* 2004b).

The aim of this study was to investigate how wolves utilize their territories over the year, the spatial distribution of wolf predation and if these patterns are reflected in the size of human harvest of moose within the territory. In order to do this I have analyzed i) wolf movement data, ii) data on the spatial distribution of kills during studies of predation (both summer and winter), and iii) statistics on human harvest rates and hunters observations of moose during autumn.

I predict that:

1. Reproducing wolves has a smaller movement range during summer compared to non-reproducing wolves.
2. Kills of moose made by reproducing wolves are less evenly distributed within the territory as compared to kills made by non-reproducing wolves.
3. Reproducing wolves expand their movement range during the summer as the pups are getting more and more mobile, while non-reproducing wolves do not.
4. There should be no difference in the movement range between reproducing and non-reproducing wolves during winter.
5. There should be no difference between reproducing and non-reproducing wolf regarding the distribution of moose kills during winter.
6. Human harvest rate and hunters observations of moose (calves per cow) are lower in areas with higher proximity to the wolf den.
7. Human hunting success (no. of moose shot per license area size unit) is negatively affected by the presence of wolves in the area during summer.

Methods

Study area

Wolves are nowadays present in Sweden and Norway mainly in an area between 58º-62º N and 12º-17 º E (Wabakken *et al* 2007). Coniferous forest with scattered deciduous stands in various combinations covers most of the region. The predominant species of trees are scots pine (*Pinus sylvestris*), norway spruce (*Picea abies*), aspen (*Populus tremula*) and birch (*Betula sp*.) The forests are managed which means that dirt roads built for logging transports makes most of the areas available to the public (Wabakken *et al* 2001). Moose is the predominant prey species within the current distribution area of the Scandinavian wolves, but also roe deer (*Capreolus capreolus*), beaver (*Castor fiber*), badger (*Meles meles*), grouse species (*Tetrao* sp.) and hares (*Lepus* sp.) are consumed when available (Sand *et al* 2008).

Wolf data collection

Since 2002 a number of wolves have been fitted with GPS (Global Positioning System) collars within the Scandinavian Wolf Project (SKANDULV) (see Sand *et al* (2006) for a more detailed description of capture and handling of wolves). The data from the GPS collars have either been downloaded in the field through a VHF (Very High Frequency) device (Sand *et al* 2006) or sent as a text message via the GSM (Global System for Mobile communication) system directly into a computer database (Sand *et al* 2005, Sand *et al* 2007).

Wolf data

Wolf movement data and spatial analysis of land units (hereafter referred to as license areas) used for calculation of moose harvest rates has been made in ArcView 3.3 (with extensions Animal movement SA v2.04 beta, Center of mass v. 1.b, Geoprocessing, Home range analysis, Spatial analyst, Spatial tools 3.3 and XTools). To analyze the movements of reproducing wolves in comparison to non-reproducing wolves on a one year basis, I divided a year into different time periods (Table 1). A "complete year" starts on the 1 of May and runs to the 30 of April the following year since the average birth date of wolf pups in Sweden is the 5 of May +/- approximately 14 days (Alfredéen 2006). By choosing this date as the start of the annual cycle, wolf movements of the following winter period are influenced by the addition of pups to the pack. This distinction may be important when comparing movements by reproducing individuals and non-reproducing individuals. The 1 of October was used as the start of the winter period (Sand *et al* 2008). I divided the summer category into two additional categories, named "early summer" that spans between the 1 of May and the 15 of July and "late summer" that spans between the 16 of July and the 30 of September. The 15 and 16 of July is used to make the two summer sub-categories about equal in length. This was done to study differences in movement of reproducing individuals at different time periods during the reproductive season and compare to non-reproducing individuals. In order to quantify wolf presence within the different moose hunting license areas during the calving season, a time interval called "calving season" was added. Moose calves are most often born between the 19 of May and the 8 of June (Sigouin *et al* 1997). The "calving season" is therefore defined as 1 of June until the 9 of October. The annual moose hunting starts on the second Monday of October in south-central Sweden (Swedish Association for Hunting and Wildlife Management 2010a). In order to quantify the proportion of wolf movements made (and any attendant wolf predation on moose calves) on the different moose hunting license areas during the calving season, I chose the 9 of October as the end date.

Table 1. The different time periods used to analyze wolf movements. The different columns display the name of the time period, when it starts and when it ends. The x represents the year when the time period starts and the x + 1 represents the following year

Name	Starts	Ends
Complete year	1 May year x	30 April year (x + 1)
Summer	1 May	30 September
Winter	1 October year x	30 April year (x + 1)
Early summer	1 June	15 July
Late summer	16 July	30 September
Calving season	1 June	9 October

Movement range of reproducing and non-reproducing wolves.
I used MCP (Minimum Convex Polygon) to calculate the movement range for both reproducing and non-reproducing wolves in the different time periods. On a few occasions the data does not span over a full time period but has been included into the data set if the time span has been estimated to be sufficiently large (Appendix 1). I have chosen the 1 of March as the minimum end date for winter data when the data ends before the 30 of April. This was done in order to obtain winter movement ranges that reach the reproduction period that occurs in late February – early March (Sand *et al* 2007). A wolf may be represented in both categories if it is reproducing one year but not the following year, or vice versa. In some cases data from both adult collared individuals in one territory were available and were both used in the analyses. The number of wolves included in this section is 21 reproducing wolves (12 females and 9 males, Appendix 1) and 7 non-reproducing individuals (3 females and 4 males). The average number of positions for wolves used in the analyses over the entire year was 1485 ± 1093 (mean ± SD).

To investigate how wolves used their territory over the year regarding potential differences between reproducing and non-reproducing individuals I calculated the following parameters:

- *Annual movement range*. MCP-s were calculated to estimate the range used for every individual during a complete year. This total annual movement area is later on used to compare seasonal movements in relation to the total annual movement range.
- *Summer movement range*. MCP-s for each wolf was calculated using only positions within the summer period. I divided the size of the summer movement range with the size of the complete year movement range in order to find the proportion of the complete year range that were used during the summer. I used a t-test to look for differences between the different categories in this and in both of the following range calculations.
- *Winter movement range*. MCP-s for each wolf was calculated using only the winter category positions. The size of these winter polygons were then divided with the size of the complete year movement range in order to find the proportion of the annual movement range that is used during winter.
- *Early and late summer movement range*. MCP-s for every wolf were calculated using early and late summer positions respectively to investigate differences in how the territory is used during the reproduction season. I divided the size of both the early and late summer movement range with the corresponding total summer movement range to get the proportion of territory use of the two time periods.

Predation data
The predation data has been obtained through GIS cluster analysis of wolf GPS locations with additional field investigations. Coordinates of carcasses found and classified as killed by wolves were registered along with additional information (Sand *et al* 2005, 2008, Zimmerman *et al* 2007). Predation studies has been carried out both in summer (13 periods in 10 territories, Appendix 2) and during winter (16 periods in 13 territories, Appendix 3) between 2001 and 2009. During summer, the interval was 30 minutes and in winter 60 minutes between consecutive locations.

Den location
The approximate location of the den in all of the reproducing territories was calculated. To do this I used a technique similar to the cluster-methodology described by Alfredéen (2006). If one of the adult collared wolves in a territory had been stationary for some time (more than a week) at the beginning of May, the den was assumed to be located at the first position in this cluster. Females are less mobile during the denning period when compared to males (Potvin *et al* 2004, Tsunoda *et al* 2009) so the male must return to the den on a regular basis to provide food for the female and their offspring (Mech 1999). This made it possible to calculate the spatial location of the den even in cases where only the male were collared. For some of the packs the date for reproduction and spatial location of the den had been established previously (Alfredéen 2006). Alfredéen (2006) used female locations exclusively in order to calculate the date of reproduction.

Patterns of predation
Data on the location of wolf-killed moose were compared for reproducing and non-reproducing wolves. MCP-s were calculated for wolf killed moose found during predation studies in both summer and winter and the mean position of the mass of the polygons (hereafter referred to as the centre of mass) estimated for each study. The distance between the centre of mass and each moose carcass were then calculated. This was done for both reproducing and non-reproducing wolves during summer and winter. These distances (hereafter referred to as kill radius) were then used to test (nested ANOVA) for differences in patterns of predation between the reproductive categories within seasons and also for differences within each reproductive category between the two seasons.

Moose hunting statistics.
Every team of hunters has to follow directions given by the local County Administration Board regarding moose bag limits. The moose hunting statistics used in this study has been provided by the County Administration Boards. In this study only those that allow hunting of both adult moose and calves are included in order to get a calf per cow ratio. All teams of hunters are obliged to report the number of bulls, cows and calves that are shot within a license area. I have used GIS maps provided by the County Administration Board, consisting of the license areas within the counties of Dalarna, Västmanland, Värmland, Västra Götaland and Örebro to relate human moose harvest statistics to wolf GPS locations. License areas showed large variation in size and ranged from 256 ha to 36187 ha with a mean value of 5079 ± 7002 (mean ± SD). For each license area I calculated the centre of mass in order to compare hunting statistics of each area in relation to the distance to the wolf den. Only license areas that overlap a complete year wolf movement range with more than 90% were included in the analysis.

Hunter observations
The number and type of moose observed during the first seven days of the hunting season is registered in a voluntarily system that is controlled by the Swedish Association for Hunting and Wildlife Management (Ericsson & Wallin 2001). The number of bulls, cows and calves that has been observed

during hunting is summarized along with the time spent and the number of observers. Hunter observations of the number of calves per cow may be used to estimate wolf predation rate (Gundersen *et al* 2008). The observation data used in this study may come from several teams that hunt within a defined license area and the exact location of each report is not specified. The fact that all teams within a license area do not report their observation data is a potential source of error. In this study I therefore made the assumption that all reports represented random samples of the total license area. Only reports where the number of man-hours (sum of the number of participants and hours each individual spent hunting) in the observation exceeded 100 were included. The hunter observation data has been provided by the Swedish Association for Hunting and Wildlife Management (2009).

Wolf presence within moose license areas

To standardize the data I have chosen to use only two positions per day per wolf to analyze how much time the wolves have spent in the different license areas within their territories. If possible the positions used were 00.00-01.00 AM and 12.00-13.00 PM. On some occasions the time interval has been skewed a few hours due to gaps in the position sequences but the formula one position during daytime and one per night have still been used if possible. I then calculated the number of wolf positions in each license area. I divided the number of positions in a specific license area with the total number of positions from each wolf or pair of wolves to estimate the proportion of time that the wolf/wolves spent within that area. This estimate was then divided with the size of the license area to get the presence as a proportion of the total time that wolves spent in a particular size unit (hectare). The proportion of the total time that wolves spent per ha was then multiplied by 1000 to get the index in 1000 ha which is a standard size when, for example, counting the number of game animals per area unit. This index (hereafter referred to as wolf presence) makes it possible to compare a theoretical predation pressure between license areas of different sizes regardless of the sample size (number of locations). The number of locations within the calving season (1 June – 9 October = 131 days) ranged between 63 to 262 locations after the standardization of locations.

Analysis of the impact of wolf predation on human hunting success

I used two parameters as a proxy for local variation in wolf predation rate that may be correlated to human hunting success. Those are 1) the distance between the wolf den and the centre of mass for the license areas and 2) to what degree a wolf have spent time within each license area during the calving season. I used regression analysis to analyze the relation between these two variables and human hunting success. Since the distance to the wolf den is a radius without any given direction, the probability of wolf presence within a certain license area must be non-linearly correlated to the distance to the den. A doubling of the radius leads to a quadrupling of the surface area ($\pi * r^2$) and in theory a quadrupled decrease in the probability that a certain wolf by random events visits an area twice the distance from the den. With that in mind every analysis regarding the distance to the den has been made using logarithmic regression. Wolf presence in the license areas, on the other hand, is an index based on actual presence and should be linearly correlated to any predation event. I have therefore analyzed human hunting success to wolf presence using linear regression. I included only license areas where the bag limit was two or more moose in order to get a reasonable calf per cow/adult ratio harvested within each license area.

The following response parameters were included in the analysis of proximity of an active wolf den:

- *The number of calves per cow shot* (n = 55 license areas, 238 cows, 420 calves).
- *The number of calves per adult shot* (n = 66 license areas, 594 adults, 453 calves).

- *The number of calves shot per 1000 ha* (n = 60 license areas > 1000 ha, 448 calves).
- *Total human harvest per 1000 ha (n* = 60 license areas > 1000 ha, 1032 moose).

The following response parameters were included in the analyses of wolf presence, including both reproducing and non-reproducing wolves:
- *The number of calves per cow shot* (n = 73 license areas, 531 cows, 832 calves).
- *The number of calves per adult shot* (n = 89 license areas, 1222 adults, 874 calves).
- *The number of calves shot per 1000 ha* (*n* = 80 license areas > 1000ha, 866 calves).
- *Total human harvest per 1000 ha* (*n* = 80 license areas > 1000ha, 2072 moose).

I also examined the relation between the two parameters wolf presence versus distance to wolf den. The minimum size of the license areas are 1000 ha and only reproducing individuals were included.

Analysis of the impact of wolf den proximity on hunter observations The following response parameters of moose observations were included in the analyses of proximity of an active wolf den (the total number of man hours where 118355):
- *The number of calves per cow observed* (n = 3073 cows, 1762 calves)
- *The number of calves observed per man-hour* (n = 1762 calves)
- *The fraction of cows with single calf observed* (n = 3073 cows, 1237 cows with single calf)
- *The fraction of cows with twin calves observed* (n = 3073 cows, 203 cows with twin calves)

The significance level used for all of the statistical analyses was 0.05.

Results

Movement range
The size of the annual wolf movement range was 1299 km² ± 1067 (mean ± SD, n = 47, range = 275-4981, Appendix 1). Non-reproducing wolves had a slightly larger average movement range (1631 km² compared to 1185 km² for reproducing wolves) but this difference was not significant (two tailed t-test, df = 45, t = 1.26, p = 0.21). There were no difference between reproducing (66% ± 19 [mean ± SD, n = 35]) and non-reproducing (67% ± 27 [mean ± SD, n = 12]) wolves in the percentage of the annual movement range used during summer (two tailed t-test, df = 45, t = 0.06, p = 0.96). However, there were a significant difference between the early (mean = 458 km²) and the late (mean = 695 km²) summer movement range for reproducing wolves (two paired sample t-test, df = 36, t = 5.81, p < 0.01) with the late summer range being 26% ± 28 (mean ± SD, n = 37, range = -25-+88%) larger than the early summer range. This difference between early (mean = 809 km²) and late (mean = 671 km²) summer movement range was not significant for non-reproducing wolves (two paired sample t-test, df = 11, t = 0.23, p = 0.83). There was also a difference between reproducing and non-reproducing wolves regarding the percentage of their annual movement range that where used during winter (t-test, df = 45, t = 2.97, p < 0.01). Reproducing wolves used 92% ± 10 (mean ± SD, n = 35, range = 62–100%) of their annual movement area during winter while non-reproducing wolves used 81% ± 14 (mean ± SD, n = 12, range = 48-95).

Predation patterns
There was a tendency for reproducing wolves to distribute moose killed less widely (7923 m ± 4809, n= 96) (Nested ANOVA, df = 1, Fs = 4.03, p = 0.09, figure 1) compared to non-reproducing wolves

(14510m ± 7111, n= 45) during summer. There was no differences between reproducing and non-reproducing wolves regarding the distribution of moose kills during winter (Nested ANOVA, df = 1, Fs = 1.19, p = 0.29, reproducing wolves 14681 m ± 7630, n = 123, non-reproducing wolves 11854 m ± 6587, n = 67).

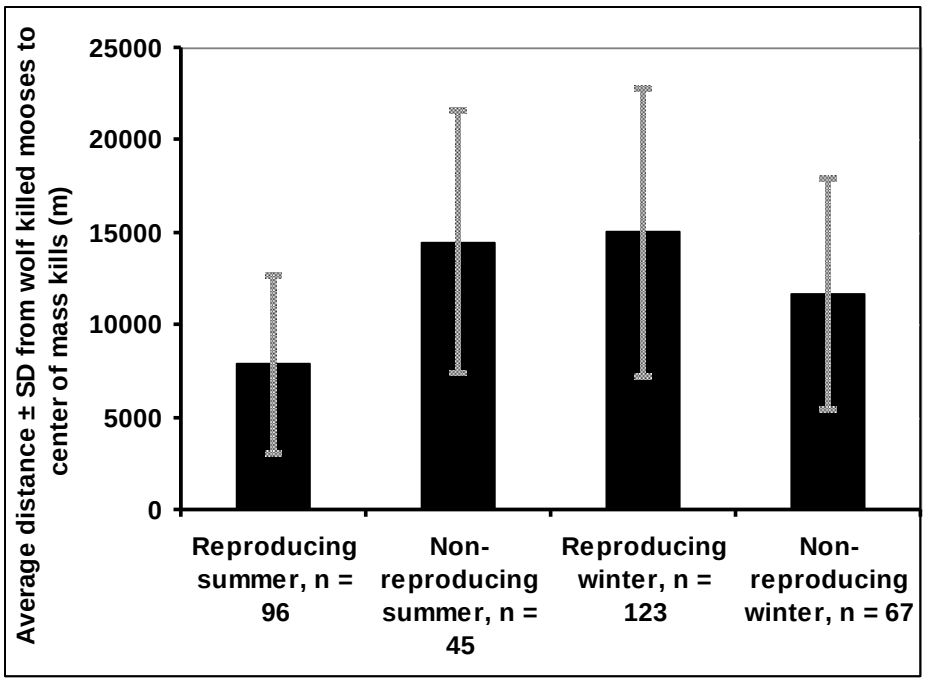

Figure 1. The columns and bars represent the average kill distribution ± SD.

There was a significant difference between the summer and winter kill radius for the reproducing wolves (Nested ANOVA, df = 1, Fs = 10.1, $p < 0.01$) but not for non-reproducing wolves (Nested ANOVA, df = 1, Fs = 0.6, p = 0.47, figure 1).

Wolf presence in relation to wolf den proximity

There were a strong negative relation between the index of wolf presence within different license areas (i.e. number of GPS locations) and the proximity to the wolf den (figure 2). However, there was large variation in the time spent by wolves in different license areas even for areas with a high degree of proximity to a wolf den.

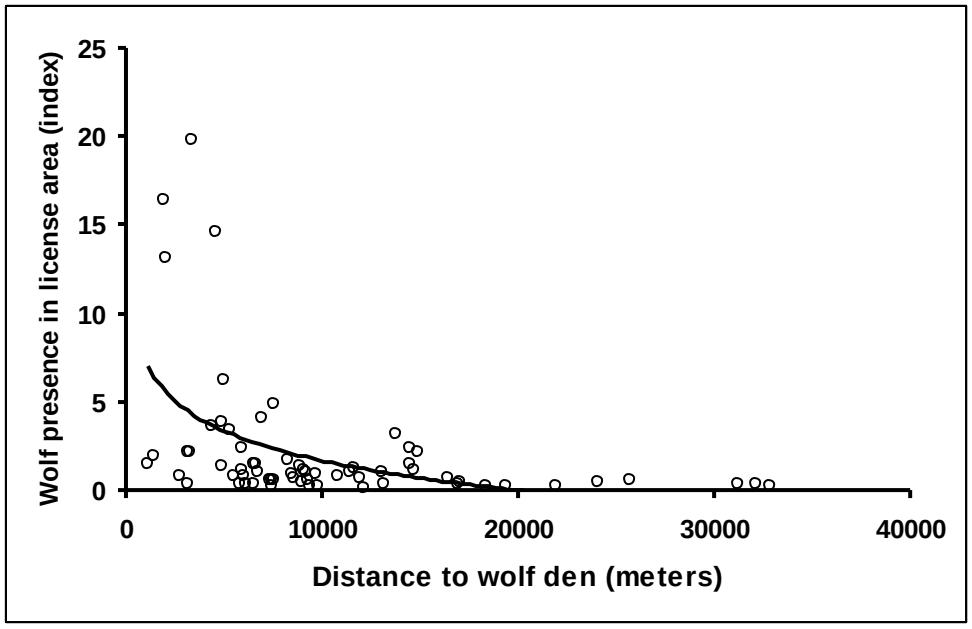

Figure 2. The relation between the wolf presence index and the distance between the license area and the den. $y = 23.955 - 2.419 * \ln(x)$; $R^2 = 0.21$; $n = 65$; $p < 0.01$.

Hunting statistics

No statistical relationship was found between the number of calves per cow shot by hunters and the distance from the license area to the den ($n = 55$, $R^2 < 0.01$, $p = 0.30$), nor to the index of wolf presence ($n = 73$, $R^2 < 0.01$, $p = 0.88$). There were also no relation between the number of calves per adult shot in relation to either wolf den proximity ($n = 66$, $R^2 < 0.02$, $p = 0.86$) or to the index of wolf presence ($n = 89$, $R^2 < 0.01$, $p = 0.54$). Similarly, the number of calves shot per 1000 ha showed no significant relation to wolf den proximity ($n = 60$, $R^2 < 0.01$, $p = 0.83$) whereas there was a slight tendency to a negative relation to the index of wolf presence ($n = 80$, $R^2 = 0.03$, $p = 0.10$). The same pattern was also found for the total number of moose shot per 1000 ha with no significant relation to the wolf den proximity ($n = 60$, $R^2 < 0.01$, $p = 0.25$) but a significant negative relation to the index of wolf presence ($n = 80$, $R^2 = 0.07$, $p = 0.02$, figure 3).

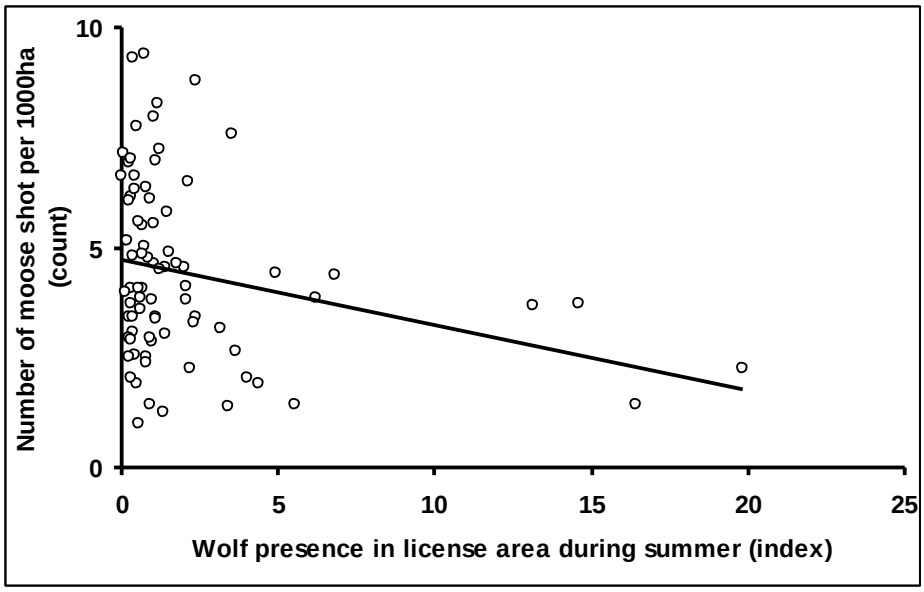

Figure 3. The relation between the number of moose shot per 1000 ha and the wolf presence index. y = -0.15x + 4.73.

Hunter observations

There was no significant relation between either the total number of calves per cow observed (n = 91, $R^2 = 0.05$, p = 0.58) or the number of calves observed per man-hour and the distance to the wolf den (n = 91, $R^2 = 0.03$, p =0.39) However, even if there were no relation between the total proportion of cows followed by a single calf (n = 91, $R^2 < 0.01$, p = 0.31) there was a positive relation between the total proportion of cows followed by twin calves and the distance to the wolf den (n = 91, $R^2 = 0.07$, p = 0.05, figure 4).

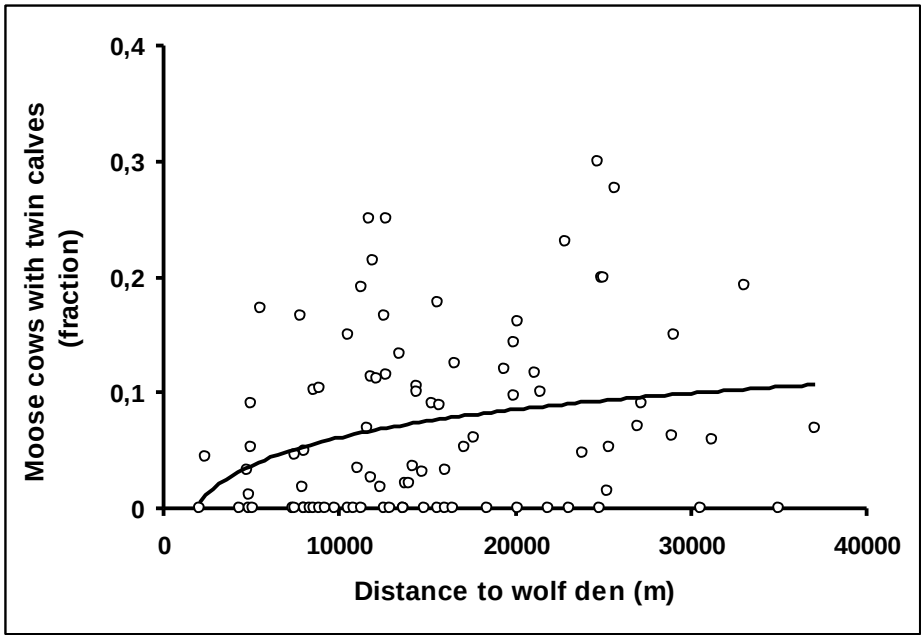

Figure 4. The observed fraction of cows that was followed by two calves in relation to the wolf den proximity. y = -0.261 + 0.035 * ln(x).

Discussion

Territory use during summer

Aggregation of moose kills in combination with movement range analysis among reproducing and non-reproducing wolves are key components to understand the spatial impact of wolf predation within wolf territories. My first prediction was that reproducing wolves would have a proportionally smaller movement range during summer compared to non-reproducing wolves. Since both reproducing and non-reproducing wolves used the same fraction of their complete year movement range during summer, my first prediction was not confirmed. Instead, wolves restricted their summer movement range regardless of their reproductive status. In a Polish study both the stage in the reproductive cycle and prey density had a strong influence on wolf movements (Jedrzejewski *et al* 2001). Since non-reproducing wolves also restricted their movement range during summer, prey density might be a more important factor than reproduction to influence wolf movement ranges during summer (see Appendix 4 for examples).

However, non-reproducing wolves tended to distribute their kills over a wider area during summer compared to reproducing wolves. This is in line with my second prediction that kills made by reproducing wolves would be less evenly distributed over the territory compared to kills made by non-reproducing wolves during summer (see Appendix 5 for examples).

Even if the two reproductive categories of wolves used the same fraction of their annual movement range during summer only reproducing wolves expanded their movement range significantly from early to late summer and this supports my third prediction. Since kill rate on moose calves is highest in the beginning of the summer in terms of prey individuals (Sand *et al* 2008) predation pressure will be proportionally higher in the surroundings of the den in that period. In late summer kill rate is reduced in the terms of prey individuals (since the moose calves have grown larger) at the same time as reproducing wolves may expand their movement range and distribute their central place foraging behavior around several rendezvous sites instead of a single den. This phenomenon will result in a dilution effect of the predation pressure per area unit compared to the early summer period. Reproduction occurs annually in most of the wolf territories (Wabakken *et al* 2009), and this makes this pattern common within the majority of the Scandinavian wolf territories. Thus, concentration of kills will be less pronounced in non-reproducing territories during summer since the average kill radius, although not significant, where on average 1.83 times longer than the radius for reproducing wolves. This will result in a more than three times larger surface area where kills are distributed over in a non-reproducing territory.

Territory use during winter

During winter reproducing wolves moved over a larger proportion of their annual movement range compared to non-reproducing wolves and this did not support my fourth prediction that there would be no difference. The size of a wolf territory is dynamic and may change from year to year due to wolf preferences, random events and dynamics of neighboring territories. The reproducing wolves used 92% of their territory during winter while non-reproducing wolves used 81%. This difference in winter territory use may be an effect of differences between reproducing and non-reproducing wolves regarding the maintenance of territory borders during the mating season that occurs in late February – early March (Sand *et al* 2007).

There was no significant difference in the kill radius between reproducing and non-reproducing wolves during winter and this supported my fifth prediction (see Appendix 6 for examples).

Hunting statistics

Wolves spend significantly more time during summer in license areas close to the den compared to areas that are more distant and this is in line with my sixth prediction. However, contrary to prediction six, hunting statistics in terms of the calf/adult ratio or number of killed moose per 1000 ha did not show any relation to the distance to the den. Hunting statistics may be a good way to follow long term trends in moose populations and is useful on a larger scale (Crete & Dussault 1987, Courtois & Crête 1993, Gundersen *et al* 2008). However, despite high numbers of animal counts, the ratio is utterly restricted by the bag limit within the different license areas. A comparison between the numbers of killed moose of different age classes may therefore be affected by to many things to be a reliable census method of wolf predation. The ratio between the bulls, cows and calves that ought to be harvested every year in order to reach a certain goal is a subject of debate and is to some extent also affected by the management strategies currently in use within each license area. The same license area may produce different calf/cow or calf/adult ratios in two adjacent years due to a change in the management plan, or by random variation in human hunting success, even if the ratio for the total area is consistent. The variation caused by this human/random factor may possibly be overcome if the data set is large enough. There is currently no estimate to reveal the effort that has been used to reach the game bag limit and this may make it difficult to compare game bags from several separate license areas. The average number of moose shot per 1000 ha has been 3.8 ± 1.6 (mean ± SD) which indicate that the moose population in these license areas have relatively high density but also large variation. This makes wolf predation less influential than it would be if the moose population where at lower densities (Sand 2004b).

Wolf presence during summer proved to have some predictive power to estimate the total human hunting success within an area. However, the calf per cow ratio and calf per adult ratio was not influenced by the wolf presence and this was against my seventh prediction. Calf per cow or calf per adult ratios are an attempt to describe the current situation while the total number of animals shot per area unit may include long term effects of wolf predation. A study in Poland performed by Schmidt *et al* (2006) showed that wolves have a preference for choosing a den site in a nearby area to where they reproduced in the previous year (but rarely reuses the same den). The average distance between dens used in consecutive years for the same female was 2.4 km (Schmidt *et al* 2006). It is not investigated if Scandinavian wolves also prefer to locate the den in the near surroundings of last years den site. If so, the predation from the last year (and perhaps even from previous years) may negatively affect the number of reproducing moose cows in the near den region. Wam & Hjeljord (2003) found that the wolves in a territory in south eastern Norway moved the location of the den 17 km between two adjacent years. They speculate that if this is common within wolf territories, moose living in the areas surrounding the den will experience high predation pressure one year but will have a chance to recover in the following year when the den is moved to another site. Since their observation is based on data from a single wolf territory it is difficult to draw any general conclusions about den preferences among Scandinavian wolves.

In this study, wolf presence was used to select which license areas to include in order to find which license areas that are within the wolves summer movement range. This wolf presence is based on, at best, two GPS locations for every 24 hour period during summer. The license areas were selected depending on if one of these locations ended up within the area or not. This was made with the intention of making various levels of wolf presence a common nominator between the different license areas and excluding areas where there had been no wolf presence during the summer. Wolves may move across several license areas during one night and one GPS location per night may be too few to

describe the *true* presence. If one out of 100 positions ends up within a quite small area and this position is a transport position, the wolf presence index will be skewed upwards in that specific area even if no actual predation has occurred. I suggest that in future studies one should include more (or perhaps even *all* of the) GPS locations during summertime. The more license areas that can be included into the study the larger the data set, which will give an even more detailed image of wolf movements during summertime.

Hunter observations

The hunter observation data were related to the distance to the wolf den and not against the wolf presence. These license areas where simply selected depending on if they fall within the limits of a wolf territory or not. This means that the moose observation data was correlated directly to the proximity of the wolf den without accounting for GPS-data. In this study only the observation data regarding the fraction of cows followed by twin calves was significantly correlated to wolf den proximity. Moose cows alternates between giving birth to none, one or two calves between years and a 12 year study in a moose enclosure (that effectively excluded predators) showed that the percentage of moose cows giving birth to twin calves where approximately 17% while 47% of the cows gave birth to a single calf (Sand & Bergström 2004). Two calves may be harder to defend for the cow, easier to scent for the wolf during its foraging bouts or triggers the wolf to attack more determined compared to a single calf. In this study a total of 3073 cows were observed, but only 203 cows were observed followed by twin calves. If, for example, one hundred calves have been killed in each category, the outcome will have made a much higher impact in the twin calves category than in the total number of calves observed category. One thing to consider is that a cow that have had one of her two calves killed by wolves during the calving season will be registered as a single calf rearing cow during hunter observations.

Wam & Hjeljord (2003) did not find any reduction in the human hunting success in the summer movement range surrounding a wolf den in Norway when compared to the same areas before the wolf establishment. Since their movement data was obtained through radio telemetry, the movement range in their study may very well be compared to the wolf presence category in this study. I found that wolf presence where negatively correlated to human hunting success and this is not in line with Wam & Hjeljord (2003). However, they discovered that both the number of calves per cow observed and the number of calves observed per cow with calves where significantly lower within the summer movement range when compared to the years before the establishment of the wolf territory. This is partially in line with my results even if there were no relation between the numbers of calves observed per cow and the distance to the wolf den. The category they called calves observed per cow with calves includes both single and multiple calves observed per cow. This category includes and is to some extent comparable with the category observed fraction of cows followed by two calves that where significantly correlated to the distance to the wolf den. Since Wam & Hjeljord (2003) obtained their data in a single wolf territory it is difficult to distinguish between the certain preferences and hunting behavior among the pack members in this specific wolf territory and general wolf behavior.

Conclusion

Both reproducing and non-reproducing wolves restrict their movement range during summer. Reproducing wolves expands their movement range from early to late summer while non-reproducing wolves do not. The central place foraging behavior that occurs among reproducing wolves during the denning period will focus the predation on moose mainly to an area within a 10 km radius from the den. Since wolf presence is strongly correlated to the wolf den, it is more likely that a nearby area will

experience a proportionally higher wolf predation pressure than a more distant area. But, since the moose / wolf ratio is high in Scandinavia, this locally increased predation pressure will likely have minor effects on the human harvest within this hunting range. It does not affect the ratios of adults or calves that may be harvested within the close proximity to the den. It may on the other hand have potential long term effects on the total annual harvest in the near den areas. Wolves may, by preference or by random events, spend their time differently in equally distant license areas which make it difficult to predict in advance where the predation pressure will be highest during the denning season. The observation data regarding the fraction of cows that where followed by twin calves seem to be a better way to witness the local impact of wolf predation than game bag recordings, even if there are large variations in the data.

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Appendix

Appendix 1. A summary of the id, status and movement range of the different wolves included in this study. All data below the season headlines is movement ranges in km². The number of positions is for a complete year. If any of the studies has been shortened, the end date is presented to the right.

Wolf id	Year	Sex	Repr.	Wolf year	Summer	Winter	Early summer	Late summer	n positions	Data ends
Amungen 0512	2005-2006	F	yes	1475	1122	1419	648	1097	818	
Amungen 0512	2006-2007	F	yes	1243	997	1193	567	858	460	2007-01-19
Bograngen 0009	2000-2001	M	No	493	364	381	317	220	140	
Bograngen 0009	2001-2002	M	No	684	381	573	141	354	118	
Bograngen 0009	2002-2003	M	No	1211	585	1128	492	407	3015	
Bograngen 0009	2003-2004	M	No	4981	1689	4751	1610	1181	2470	
Bograngen 0009	2004-2005	M	No	1350	1249	959	745	1106	3896	2005-03-14
DalsEd 0208	2002-2003	M	yes	674	280	657	96	224	403	
Djurskog 0209	2003-2004	F	yes	336	318	301	243	305	1578	
Djurskog 0209	2004-2005	F	yes	343	193	337	144	160	297	2005-03-12
Djurskog 0209	2002-2003	F	No	379	101	333	81	59	320	
Djurskog 0306	2004-2005	M	yes	355	320	222	260	271	1677	
Forshyttan 0509	2005	F	yes	x	842	x	703	698	957	Summer only
Glaskogen 0213	2002	M	No	3350	2903	1593	2832	718	2846	2002-12-21
Gråfjell 0109	2001-2002	M	yes	2224	1771	1447	1057	961	2271	
Gråfjell 0109	2003-2004	M	yes	1226	891	1131	714	573	2182	
Gråfjell 0109	2004-2005	M	yes	975	481	975	239	397	1572	
Gråfjell 0110	2001-2002	F	yes	1452	1051	1438	385	809	4205	
Gråfjell 0110	2002-2003	F	yes	1304	1096	1129	894	1023	2240	
Gråfjell 0110	2003-2004	F	yes	1253	1060	1177	964	728	2356	
Gräsmark 0610	2006-2007	F	yes	1810	1054	1802	852	1010	2624	
Gräsmark 0611	2006	M	yes	x	1036	x	691	1010	1095	Summer only
Gräsmark 0611	2007-2008	M	yes	1818	1164	1818	684	1142	1518	2008-03-29
Halgån 0206	2004-2005	F	yes	830	494	801	320	385	652	
Halgån 0206	2005-2006	F	yes	784	588	756	272	564	599	
Halgån 0206	2006-2007	F	yes	1056	554	1053	326	554	710	
Halgån 0206	2007-2008	F	yes	1360	711	1315	577	658	802	
Halgån 0206	2002-2003	F	No	2102	595	1972	410	434	170	
Halgån 0206	2003-2004	F	No	738	726	502	456	675	1756	
Hasselfors 0105	2001-2002	M	yes	793	559	750	397	511	2154	
Hasselfors 0105	2002-2003	M	yes	766	522	641	243	476	2555	
Hasselfors 0105	2004-2005	M	yes	275	246	198	104	240	136	2005-01-23
Jangen 0405	2004	F	yes	x	489	x	269	426	222	Summer only
Kilsbergen 0504	2005-2006	M	yes	750	494	748	466	417	617	2006-03-02
Kloten 0507	2008-2009	F	yes	576	381	575	351	255	1155	
Koppang 0402	2004-2004	M	yes	4639	4065	3623	1347	3921	3783	2005-01-22
Koppang 0403	2004-2005	F	yes	3036	2447	2693	922	2124	3336	
Nyskoga 0007	2000-2001	M	yes	996	587	826	83	567	257	
Nyskoga 0007	2001-2002	M	yes	1561	344	1561	22	327	287	
Nyskoga 0007	2002-2003	M	yes	2017	446	1959	84	429	179	
Nyskoga 0007	2003-2004	M	yes	1423	414	1353	x	x	1687	2004-03-16
Tyngsjö 0204	2002	F	yes	1131	780	979	499	733	892	2002-11-13
Ulriksberg	2004-2005	M	No	3492	2587	2770	1980	2241	574	
Ulriksberg 4506	2006-2007	F	yes	905	576	894	349	531	1833	
Ulriksberg 4506	2007-2008	F	yes	904	633	874	530	572	750	
Uttersberg 0506	2005-2006	M	yes	399	333	382	229	320	3378	2006-02-07
Uttersberg 0506	2008-2009	M	yes	457	210	457	175	180	767	
Uttersberg 0506	2007-2008	M	No	395	369	357	340	311	909	
Uttersberg 0601	2006-2007	F	yes	329	300	315	246	275	1251	
Uttersberg 0601	2007-2008	F	No	398	362	357	304	354	571	

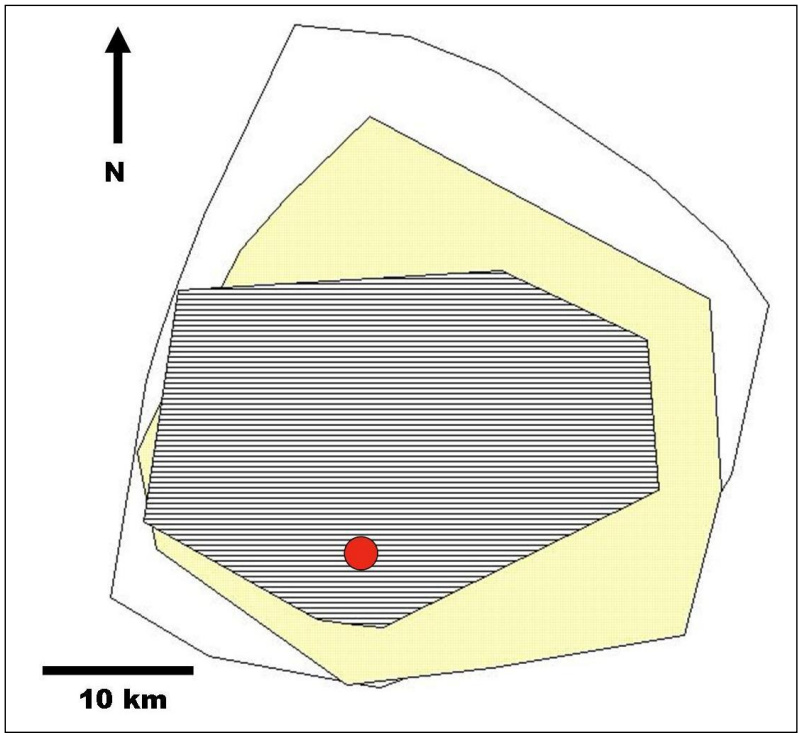
Appendix 2. A summary of the summer predation studies included in this study. The start and stop date for all of the studies are included, as the number of kills and the average distance between the kills and the center of mass for the kills.

Territory	Repr.	Wolf in study	n wolves last winter	n wolves following winter	Start	End	n kills	Average distance c.o.m.to kills
Bograngen	No	Male	3	?	2003-06-02	2003-07-12	25	17962
Djurskog	Yes	Male	5	8 or 9	2004-06-22	2004-07-08	13	7759
Djurskog	Yes	Male	5	8 or 9	2004-08-06	2004-08-18	9	8815
Forshyttan	Yes	Female	2	2 or 3	2005-08-09	2005-08-24	7	15514
Glaskogen	No	Male	8	2	2002-06-28	2002-07-02	3	4999
Gråfjell	Yes	Both	6	7	2003-06-02	2003-07-12	28	7355
Gråfjell	Yes	Both	7	6 or 7	2004-06-13	2004-06-28	7	4807
Halgån	No	Female	0	2	2003-06-22	2003-07-09	9	13544
Halgån	No	Female	0	2	2003-08-02	2003-08-19	8	8378
Kloten	Yes	Both	?	?	2009-06-15	2009-07-10	13	7701
Koppang	Yes	Both	2	2	2004-06-14	2004-06-29	7	5762
Nyskoga	Yes	male	5 to 7	4	2003-06-02	2003-06-09	4	6670
Uttersberg	Yes	Male	5 or 6	9	2005-09-16	2005-10-01	4	5010

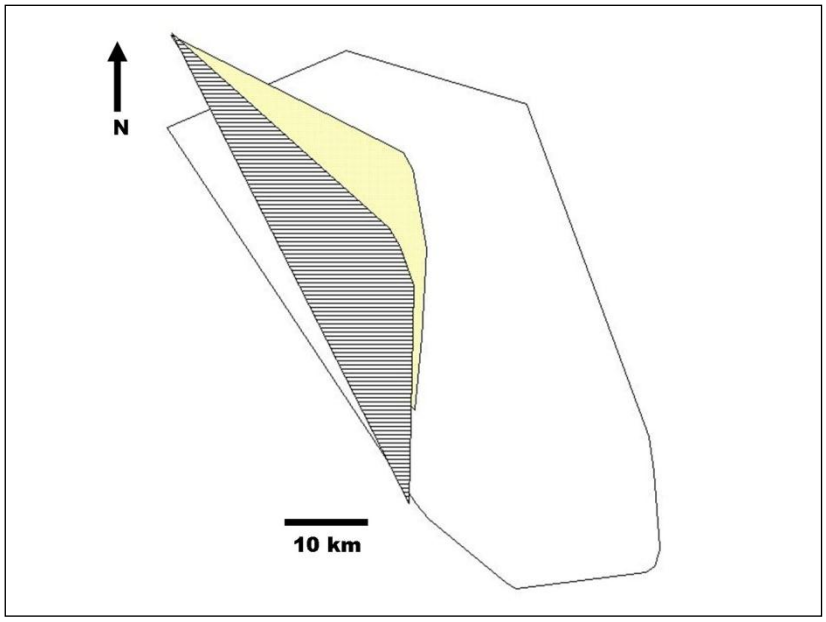
Appendix 3. A summary of the winter predation studies included in this study. See appendix 2 for further explanations regarding the data.

Territory	Repr.	Wolf in study	n wolves in pack	Start	End	n kills	Average distance c.o.m.to kills
Bograngen	No	Male	3	2003-02-18	2003-04-19	16	12290
Djurskog	Yes	Male	5	2004-02-09	2004-03-18	10	10600
Gråfjell	No	Both	3	2001-02-18	2001-04-17	16	17020
Jangen	No	Both	2	2004-02-03	2004-03-26	10	7397
Stadra	No	Male	2	2003-01-27	2003–03-16	4	9855
Ulriksberg	No	Female	2	2006-02-21	2006-04-05	7	12500
Kloten	No	Female	?	2008-02-11	2008-03-31	14	8885
Gråfjell	Yes	Both	2	2001-12-11	2002-04-17	27	17733
Gråfjell	Yes	Both	3	2003-02-17	2003-04-08	19	21410
Gräsmark	Yes	Both	?	2007-02-18	2007-04-06	12	12633
Hasselfors	Yes	Male	4 or 5	2003-02-19	2003-04-04	7	6031
Nyskoga	Yes	Male	4	2004-02-13	2004-03-11	10	17121
Tyngsjö	Yes	Female	6	2002-01-31	2002-04-21	18	14245
Ulriksberg	Yes	Female	?	2007-01-20	2007-03-04	9	13381
Uttersberg	Yes	Male	9	2005-12-12	2006-01-18	7	6583
Uttersberg	Yes	Female	?	2006-10-11	2006-12-11	4	6555

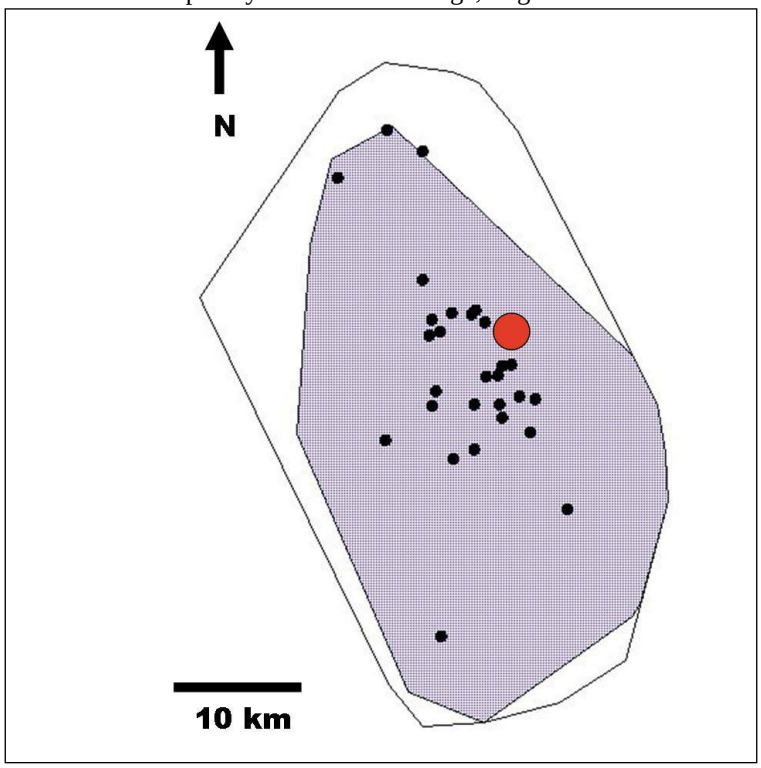
Appendix 4A. An example image of early and late summer movement ranges of a reproducing wolf, the Amungen female in 2005. Dark area = early summer movement range, colored area = late summer movement range, white area = winter movement range, red dot = den location.



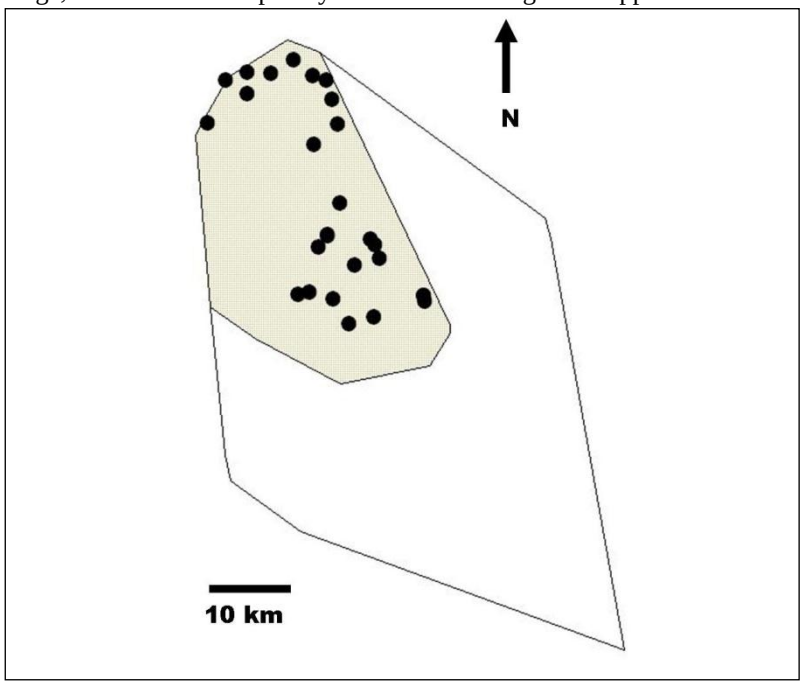
Appendix 4B. An example image of early and late summer movement ranges of a non-reproducing wolf, the Halgå female in 2002. Dark area = early summer movement range, colored area = late summer movement range, white area = winter movement range.



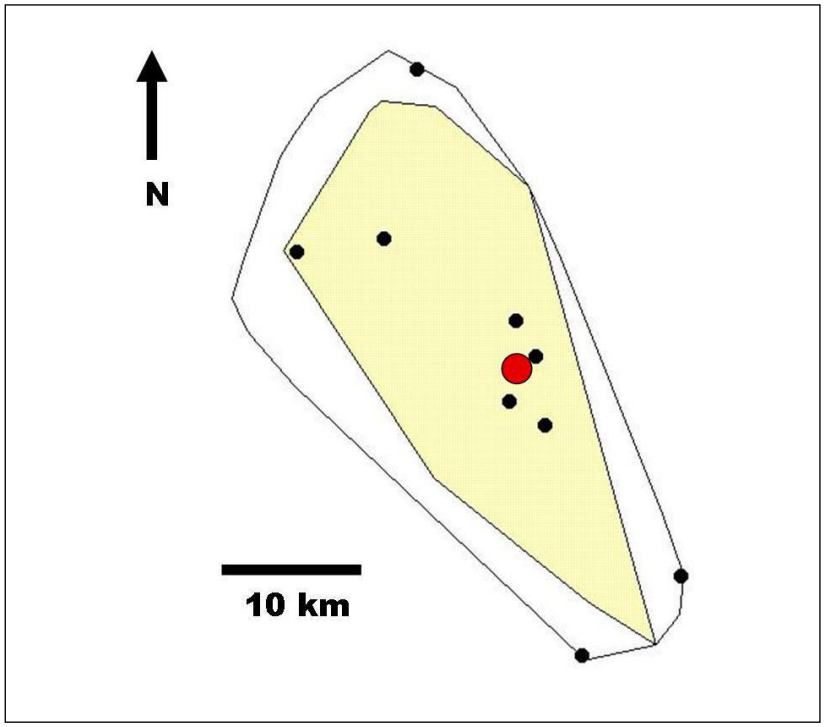
Appendix 5A. An example of kill distribution during summer in a reproducing pack. The study has taken place in the Gråfjell territory between 2003-06-02 and 2003-07-12 (n = 28 kills (black dots)). Colored area = summer movement range, white area = complete year movement range, large red dot = den location. See appendix 2 for more information.



Appendix 5B. An example of kill distribution during summer in a non reproducing pack. The study has taken place in the Bograngen territory between 2003-06-02 and 2003-07-12 (n = 25 kills (black dots)).Colored area = summer movement range, white area = complete year movement range. See appendix 2 for more information



Appendix 6A. An example of kill distribution during winter in a reproducing pack. The study has taken place in the Ulriksberg territory between 2007-01-20 and 2007-03-04 (n = 9 kills (black dots)). Colored area = summer movement range, white area = complete year movement range, large red dot = den location in 2006. See appendix 3 for more information.



Appendix 6B. An example of kill distribution during winter in a non-reproducing pack. The study has taken place in the Bograngen territory between 2003-02-18 – 2003-04-19 (n = 16 kills (black dots)). Colored area = summer movement range, white area = complete year movement range. See appendix 3 for more information.