Bachelor Thesis

Parental care and movement patterns of wolves (*Canis lupus*) during summer

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Van Hall Larenstein University of Applied Sciences

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Parental care and movement patterns of wolves (*Canis lupus)* during summer

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ABSTRACT

Wolves are territorial and social animals. Their activity patterns can be influenced by several factors, such as prey density, prey activity and human density. For all wolves parental care plays a significant role in their movements and territory use, because all activities are centred around the home sites. I analyzed positioning data of GPS-collared wolves to assess spatial and temporal differences between the breeding pair during the first 4 weeks of pre-denning and the first 19 weeks of pup raising. A total of four breeding pairs from the Scandinavian Peninsula were included in this study. The males travelled greater distances and the females spent more time at the den. Throughout the summer the movement patterns of the adults became more similar due to the females increasing their movement activity continuously. Females invested more time in direct pup care than males, independent of pup age. The female took part in food supplying when the pups were in the transition phase. The used proportion of annual home ranges was small for both parents, as long as pup dependency was high and pup mobility was low. The adults spent most time together during the pre-denning period. Interactions between the adults and the pups can be studied in detail when intensive GPS data is used. Further research should define if additional parameters are responsible for summer activity patterns of Scandinavian wolves.

Key words: Wolves (*Canis lupus)*, summer activity patterns, home sites, temporal and spatial patterns, attendance, GPS, parental care.

PREFACE

This Bachelor Thesis is the final part of my study Forest and Nature Conservation. My fascination for wolves started around the same time as I started with my studies in Velp. When I arrived to Evenstad I realized that this could be a good place to study wolves more in detail. Together with P. Wabakken we discussed different topics from which I could choose; my choice was to analyze movement patterns of breeding wolves. I joined snow-tracking to learn more about the movement patterns of wolves. We followed tracks, collected scats and visited kill sites. On the 12th of February I saw free ranging wolves for the first time and a month later I witnessed the capturing of a wolf in order to equip him with a GPS-collar. These experiences made me eager to know more about wolves.

I am grateful that I got the possibility to graduate in Norway. I would like to thank SKANDULV for giving me the possibility to work with their data. Thanks to Barbara Zimmerman for her support and help, and to Peter Wabakken for his comments. Mike Ferguson has done a great job to improve my English writing skills and I appreciate his support during my final work. I would like to thank Suzette Stumpel for her supervising role. Lastly I would like to thank my family and friends, special thanks to my parents because their advice and help was very valuable for me.

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1 INTRODUCTION

Wolves *(Canis lupus)* in general are known to be social and territorial carnivores. Their present geographical range covers most parts of the Northern Hemisphere which give them the status of one of the most widely distributed land mammals. However, they formerly inhabited a larger range but due to extirpation and habitat loss wolves became exterminated or classified as an endangered species in many countries (summarized by Mech & Boitani 2003). Nowadays we can observe a wolf come-back in Scandinavia, which results in conflicts with humans mostly concerning live stock predation (Wabakken et al. 2001). Most people still see the wolf as a wilderness species but this view is a result of the long history of persecution. Wolf territories may also be located in areas with a high human activity (summarized by Mech & Boitani 2003). Wolves have the tendency to cover great distances in short time and are therefore able to maintain large territories; however wolves are seasonally more restricted in terms of spatial distribution. Breeding wolves generally have a smaller home range in early summer due to restriction of providing parental care (Kolenosky & Johnston 1967; Jedrzejewski et al. 2001; Merril and Mech 2003; Hinton & Chamberlain 2010). The den is the centre of activities in late spring and early summer, thereafter activities become centred around rendezvous sites, which changes frequently (Fuller 1989; Jedrzejewski et al. 2001; Merril and Mech 2003). The parental role of males and females differ, resulting in space use difference. The female provides her pups with milk and body warmth and keeps the den clean, whereas the male's contribution is through foraging, territorial defence and food provision (summarized by Mech & Boitani 2003). Therefore the female reduces the proportion of the territory she uses during the first weeks after pupping (Jedrzejewski et al. 2001;Merril and Mech 2003;Theuerkauf et al. 2003-1 ;Potvin et al. 2004;Tsunoda et al. 2009;Hinton & Chamberlain 2010), while the male's movements increase (Tsunoda et al. 2009). Den attendance by the female decreases, and travel distances become greater, as her pups grow older (Jedrzejewski et al. 2001; Theuerkauf et al. 2003-1; Potvin et al. 2004;Tsunoda et al. 2009).

Movement patterns of free ranging wolves have been widely studied through observations (Murie 1944; Mech & Merril 1998; Potvin et al. 2004), tracking on snow (Pimlott et al. 1969, Wabakken et al. 2001), wolf howling techniques (Joslin 1967) and radio tracking (Kolenosky & Johnston 1967; Fuller 1989; Jedrzejewski et al. 2001; Theuerkauf et al. 2003-1; Potvin et al. 2004; Tsunoda et al. 2009; Hinton & Chamberlain 2010). With the introduction of GPS it became possible to analyse wolf movements in detail. Zimmerman et al. (2001) concluded that downloadable GPS in combination with GIS are helpful instruments to study the behavioural ecology of wolves. Merril and Mech (2003) and Frame et al. (2004) showed that GPS use increased the ability to determine the area use explained by time and distance.

However, little is known about the parental care investment by the male in comparison to the female during late spring and summer. Over the last few years, the Scandinavian Wolf Research Project (SKANDULV) has obtained data from downloadable GPS-telemetry from four breeding pairs of Norway and Sweden. We used GPS positions to examine the spatial and temporal patterns of the parents from 4 weeks before until 19 weeks after birth. In total four breeding pairs have been collared. I expect that home site attendance, movements and cohesiveness of males and females in breeding pairs changes between different life stages of pups. I hypothesize, that the males travelled greater distances than the females, and that the female invested more time around the home sites.

2 METHODS

2.1 Study area

This study was conducted in 4 wolf territories on the Scandinavian Peninsula. Two territories, Koppang and Gråfjell were entirely within Norway. The Kloten territory was located within Sweden, whereas the Gräsmark territory lies across the Swedish/Norwegian border. The latitude ranges were from 59°-61°, longitude 11°- 15°. The data were collected over seven years (2003-2009).

All territories are within the boreal forest zone, which is dominated by Scots pine (*Pinus sylvestris)* and Norway spruce (*Picea abies).* Birch (*Betula pendula, Betula pubescens),* aspen (*Populus tremula),* alder (*Alnus incana, Alnus glutinosa)* and willow (*Salix spp.)* are the most common deciduous species. The study area has extensive clear cuts, areas of young forest and a high number of gravel roads due to extensive forestry. The forest landscape is characterized by mouontains, lakes, bogs and streams. The human population averages <1 inhabitant km2 within the wolf territories (Wabakken et al. 2001). Moose (*Alces alces)* was the most abundant prey species. Although Scandinavian wolves mainly prey on moose (Sand et al. 2005, Sand et al. 2008) other potentiel prey species include roe deer (*Capreolus capreolus),* beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*). Red deer (*Cervus elaphus*) and wild reindeer (*Ragnifer ragnifer)* were also present in the northwestern parts of the contemporary wolf range (Wabakken et al. 2001, Alfredéen 2006).

2.2 Telemetry collars with Global Positioning System (GPS)

Wolves were tracked during winter on skis. When fresh tracks of the territorial wolves were found a helicopter took off to locate the animals. Immobilization of the individuals was done from the helicopter. After immobilization the wolves were measured, weighed and equipped with a GPS neck collar. All wolves were collared during January/February. Each collar was programmed to receive positions in certain time intervals. In this study, I used positions determined every four hours (i.e. 6 positions a day). The only exception was the Kloten male whose GPS was programmed for 12-hours intervals.
I analyzed data collected from 4 weeks before the birth date until the pups were 19 weeks old (approximately from the end of April to the end of September). To determine the birth dates of pups and the annual home range I used all positioning data available of these animals.

2.3 Territories

Koppang

Wolves became established in Koppang in 1997. Breeding was confirmed for four consecutive years (1997- 2000). In August 2000 a male was shot because of damage prevention, this was the dominant male and father of pups. In 2001 no breeding pair of wolves were tracked, but the female of the original pair was still present. A new male and thereby a new territory holding pair was confirmed in 2002 inside the same borders as the previous territory. They successfully bred in 2002, and in winter 2002-2003 the Koppang wolves consisted of a family group of five wolves. Until winter 2002 the boundaries of the Koppang territory have been stable, however the new breeding pair of 2002 started to expand their territory. Their territory was adjacent to, and partly overlapping with, the territory of the Gråfjell pack. In early spring 2003, a Gråfjell pup was found dead in the overlapping zone between the territories, possibly due to a territorial fight with the Koppang wolves. There were no signs of breeding in 2003 (Wabakken et al. 2004-1).

A new territorial pair was found in winter 2003-2004 and both wolves were GPS collared in January 2004. DNA analyses confirmed that they were the father and a daughter from the litter of 2002 (Wabakken et al. 2004-2).Gradually, the territory was significantly increased, the Gråfjell territory was almost entirely included in the Koppang territory. There were several occasions when the pair was near the centre of the Gråfjell territory and the male came close to the pups and dominant male of the Gråfjell pack. The Koppang couple was unusually solitary and they often travelled alone; a possible explanation is their close relatedness. In January 2005 both wolves were shot during a license hunt. The puppies of summer 2004 were confirmed, but could not be located anymore after August 2004 (Wabakken et al. 2005).

Kloten

The female of the Kloten territory was radio collared in March 2005 when she was a pup in the Uttersberg pack. When she was about two years old she was located in the territory in Kloten. During winter 2006-2007, she was tracked alone, and was recollared in February 2008. 2007-2008 was the first year when a territorial couple was present in Kloten; breeding was confirmed in 2008 (Wabakken et al. 2008). The pack consisted of 5-7 wolves during winter 2008-2009 (Wabakken et al. 2009).

Gråfjell

The Gråfjell territory was established in 2000 with the first breeding confirmed in spring 2001; however in late winter 2001-2002 no pups could be confirmed on snow anymore. In late spring of 2002 a new litter of pups were born. During winter of 2002-2003 4 individuals were collared; the parents and 2 pups. The two unmarked pups were found dead on Storsjøen Lake in March and April 2003. This was area overlapping the territory of the Koppang pack (Wabakken et al. 2004-1). In 2003, breeding was confirmed again, and in winter 2003-2004 the pack consisted of seven wolves. Another pup of the litter from 2003 was collared; giving a total of three pups equipped with GPS collars. All pups dispersed when they were about one year old. The 4th year of successful breeding was confirmed in 2004 (Wabakken et al. 2004-2),with 6-7 wolves being found in winter 2004-2005. One of the collared pups from 2003, a female, was shot in northeastern Finland on 1 March 2005, 10 kilometers away from the Russian border. She travelled 1100 kilometers but was killed because she preyed on semi-domestic reindeer. This is the longest dispersal distance ever recorded (Wabakken et al. 2007-2). The breeding female was shot in January 2005 during license hunt and the male was found dead 4 months later. The Gråfjell territory hereby discontinued (Wabakken et al. 2005).

Gräsmark

The Gräsmark territory was established in 2004-2005 (Wabakken et al. 2005). In spring 2005, the pair bred successfully for the first time, the pack counted 5 wolves in winter. Three wolves were equipped with GPS collars in February 2006, two adults and one pup. The pup dispersed at age of 1 (Wabakken et al. 2006). The pack consisted of 5-6 wolves in winter 2006-2007. The male received a new GPS collar due to failure of the previous collar (Wabakken et al. 2007-1). Mating again was successful in 2007 with 4-6 wolves being tracked on snow (Wabakken et al. 2008). In winter 2008-2009 the wolf pack consisted of 4-6 wolves. DNA analyses confirmed that the pack had a new dominant male. Breeding in 2009 was not sure (Wabakken et al. 2009).

2.4 GPS Success

Succesful determination of positions by GPS, or GPS success, depend on factors such as, canopy and ground cover, satellite cover, age, type of GPS, antenna position and age of battery. I calculated the weekly GPS success rate, defined by the number of locations divided by the hypothetical number of locations (Appendix 1). The GPS collar of the Gråfjell female failed on 04.04.2004; therefore she couldn't be included for the analysis in the 2004 study.

2.5 Identification of reproduction

To identify the birth dates of the Kloten and Gräsmark pups, I used the same method as Alfredéen (2006). Alfredéen selected five different approaches to estimate the birth date, which are ranked on their precision (Table 1). For the Koppang and the Gråfjell territories I used the birth date estimated by Alfredéen (2006).

Table 1: Approaches to identify birth dates defined by Alfredéen (2006) in ranked order

	Approach	Description
1	Number of received locations	When females are denning the GPS reception decreases significantly due to the use of a den site in the ground or under close canopy cover. Missing GPS positions for one to several days can indicate that the female started the denning period (Appendix 2).
2	Identified den site	The actual locations of the sites can be determined by field observations or radio tracking. The first visit of the female to this site is regarded to be the birth date.
3	Measured pup weight	Age assessment based on the measured pup weight. Through this method you can recalculate the birth date of the pups.
4	Mean Daily Movement	The females are expected to be stationary during the day of reproduction, with limited movements the days after. The average straight line distance per day will show the stationary behavior (Appendix 3).
5	Cluster Methodology	Reproducing wolves become stationary at the den site. Therefore, she will create clusters during her denning period and these can be defined as den sites (Appendix 4)

2.6 Identification and definitions of home sites

Den sites are used during the first weeks of pupping. Rendezvous sites are used after abandonment of den sites and are known as areas where adult wolves leave their pups and meet them again after e.g. hunting. Den sites and rendezvous sites are defined as home sites (summarized by Mech & Boitani 2003).

To identify the den sites I used four-hourly female positions. I placed a 25-meter buffer (ArcGIS 9.3) around positions to take into account a potential 25 meter error of the GPS positions. Eriksen et al (2009) summarized that GPS position accuracy is <20 m. To distinguish den sites from kill sites I categorized clusters of overlapping buffers that were used for at least 3 consecutive days as den sites (Alfredéen 2006). I expected the denning period to end around the beginning of the fifth week after birth, when pups usually become capable of walking long distances themselves (Chapman 1977) and eating solid food (Packard et al. 1992). Any clusters that started before five weeks but ended later were also categorized as den sites.

Rendezvous sites were identified with the combined dataset of female and male positions. The male's attendance at the home site becomes more similar to that of the female after the first weeks (summarized by Mech & Boitani 2003). As for den sites I used a 25-meter buffer around each position. Rendezvous sites can be used for a couple of weeks but also for as few as 2 days (Chapman 1977). The parents can bring the pups to the kill and stay there for a day. Four hourly positions were not enough to define short-term clusters; this would result in guessing between kill sites or rendezvous sites (Sand et al. 2005, Sand et al. 2008). Therefore, I concentrated on clusters that contained a total of at least 10 locations and lasted for minimum three consecutive days. No time limit for the rendezvous period was defined since wolves can use the system of rendezvous sites until the pups are 8 months old (summarized by Mech & Boitani 2003).

2.7 Spatial patterns

For each identified home site, I calculated the average X and Y- coordinates to define the centre. The distances to the centre for all positions within the cluster period were calculated. I used the average weekly distances to show the spatial differences between the male and the female. In ArcGIS 9.3., I calculated cumulative Minimum Convex Polygons (MCP, Mohr 1947) by using weekly positions. Because territory size varied among the wolf packs I calculated annual MCP's (from 1 May to 30 April) to determine the proportion of the annual territory. The data did not cover the entire year for the Koppang pair, the Kloten male and the Gråfjell female in 2003 (Table 2).

Table 2 Period of annual MCP for 5 wolf pairs

Territory	Female Period of calculated annual MCP	Male Period of calculated annual MCP
Koppang	1 May 2005 – 16 January 2006	1 May 2005 – 22 January 2006
Kloten	1 May 2009 – 30 April 2010	1 May 2009 – 24 September 2009
Gräsmark	1 May 2006 – 30 April 2007	1 May 2006 – 30 April 2007
Gråfjell 2003	1 May 2003 – 4 April 2004	1 May 2003 – 30 April 2004
Gråfjell 2004	-	1 May 2004 – 30 April 2005

To assess how far each pair travelled I calculated the Mean Daily Movement (Appendix 5), the straight line distance between consecutive points. For each pair I calculated the average weekly straight line distance.

2.8 Temporal patterns

To assess how much time the adults spent on each home site I calculated the attendance rate, by dividing the number of positions in each cluster by the total number of positions during each period.

I also examined cohesiveness between the breeding pair i.e., how far they were from each other at a given time. I selected locations of male and female that were taken at the same time (+/- 5 minutes), and calculated the straight line distances for each pair between these positions.

2.9 Analyses

I defined three pup development phases during the study period, based on the dependency level from pups. According to Packard et al. (1992), wolf pups go through 3 developmental stages, namely a milk-dependency phase, transition-to-solid-food phase and milk-independency phase. At about 5 weeks of age, pups start to eat solid food. In the 10th week, pups usually do not suckle anymore. Therefore I defined week 1-4 as the milk-dependency phase, week 5-9 as the transition period and ≥10 weeks as the milk-independency phase. I assessed adult behavior in relation to these phases of pup dependency, in addition to the pre-denning period of four weeks.

The pup development phases and the sex of each member of each breeding pair were entered as explanatory variables in generalized linear mixed models (SAS 9.2). The responses were weekly data on: a) mean distance to current home site; b) the mean distance travelled per day; c) the cumulative MCP size; d) the proportion of cumulative MCP in relation to annual territory size; e) the attendance rate of home site; f) the cohesiveness of each pair and; g) the proportion of positions between adults being closer than 50, 100 or 250 m. For all proportional data (d, e, g), I used logistic mixed regression models with a logit function (Glimmix procedure in SAS 9.2). The continuous responses were transformed if residuals were not normally distributed. Territory was entered as random factor, and week number was nested in territory to correct for biased datasets. Explanatory variables and their interactions were considered significant at an alpha-level of $p < 0.05$.

I plotted model values and confidence intervals from least square means estimation. For a description of weekly tendencies of the same responses, I used the scatterplot function in Excel and added the trend lines and R^2.

3 RESULTS

3.1 Reproduction

The pups were born between April 26 and the May 20 (Table 3).

Table 3 Identification of reproduction based on the method by Alfredéen (2006)

Territory	Wolf	Sex	Year	Received locations	Identified den site	Measured Pup Weight	Mean Daily Movement	Cluster Method	Estimated date of reproduction
Gråfjell	U0110	F	2003	-	13-17 May	-	13-16 May	from 12 May	**13 May**[1]
Gräsmark	M0610	F	2006	-	-	-	26 - 30 April	from 25 April	**26 April**[2]
Kloten	KF2009	F	2009	27 April	28 April	-	29 April-1 May	from 28 April	**27 April**[3]
Koppang	U0403	F	2004	-	20 May	-	20-23 May	from 16 May	**20 May**[4]

[1] Determined by Alfredéen (2006)
[2] Determined by Wierda
[3] Determined by Wierda
[4] Determined by Alfredéen (2006)

3.2 Home sites

The number of identified den sites was either 2 or 3 per study (Appendix 3). The duration of denning varied from 4-7 weeks. The identified den sites were used for between 5 and 31 consecutive days. During a period of 6 days, no den site could be identified for Gråfjell 2003 because no cluster was identified.

Number of rendezvous sites ranged from 2 to 5 per pair (Appendix 6), and they were used between 5 and 24 days. The success of identifying rendezvous clusters was low with 14 to 91 days with the location of the pups unknown.

The distances between the centers of the identified den sites ranged from 96 to 3100 meter. The distance between the identified rendezvous sites ranged from 28 to 3680 meters. The distance between the last den site and the first rendezvous site was 1407 meters for Gräsmark, 1700 meters for Koppang and 5738 meters for Gråfjell.

3.3 Spatial patterns

Distances to home site

Female and male distances to the home sites differed during the three pup life phases (Figure 1), with a significant interaction of sex and pup life phase ($F_{2,55}$=4,81, P=0,0118).

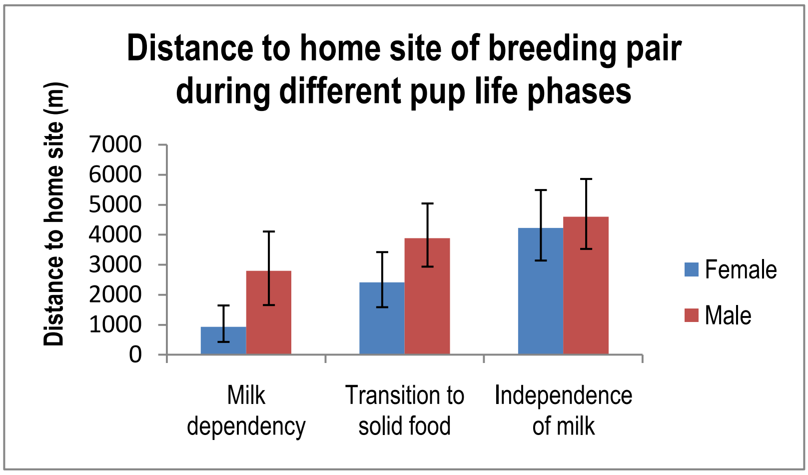

Figure 1 Distance to home site (LS means with confidence intervals)

The difference between male and female was most pronounced during milk-dependency, when males were on average 3 times further from the den than females. During the transition-to-solid-food, females more than doubled the average distance, but males were still 60% further from their home site. When pups became independent of milk, the distances of males and females to the rendezvous sites were about similar.

The increasing trend of distances to home sites was a continuous process, but most pronounced for females (Figure 2-5).

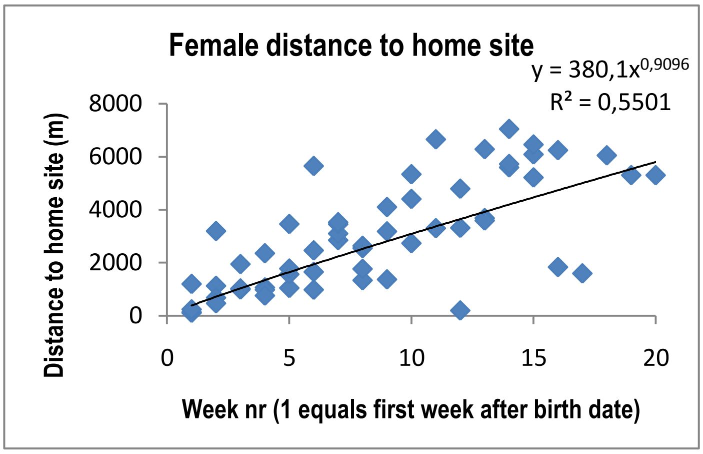

Figure 2 Weekly distances to home site of females

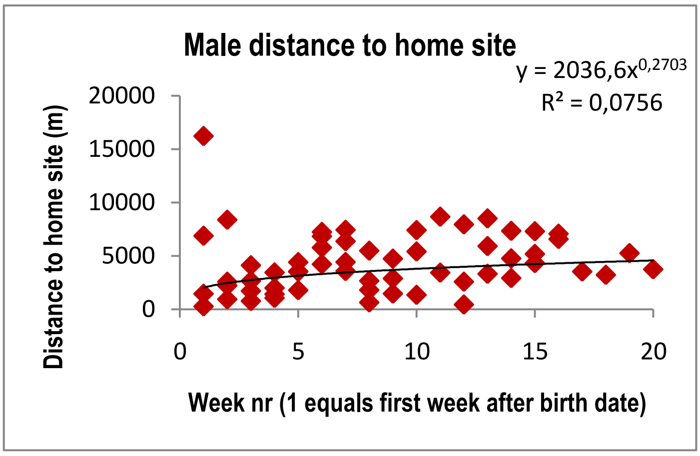

Figure 3 Weekly distances to home site of males

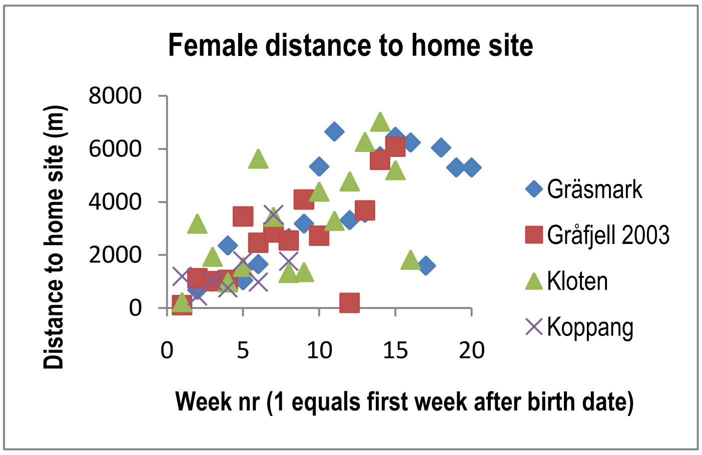

Figure 4 Weekly distances of females to home site categorized per territory

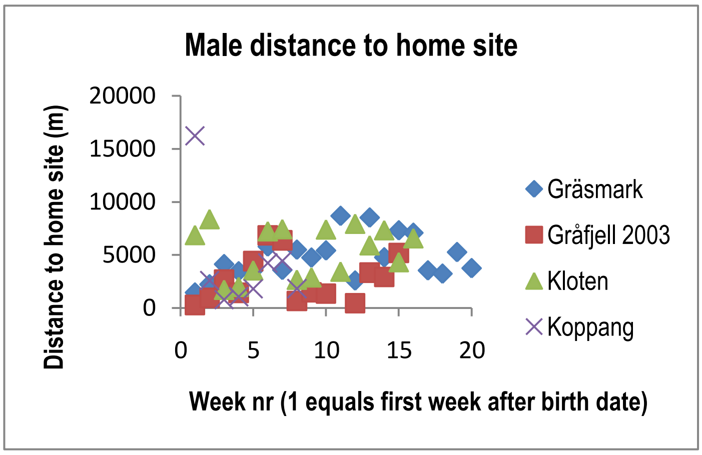

Figure 5 Weekly distances of males to home site categorized per territory

Mean Daily Movement

The Mean daily movements (Appendix 5) of the adults differed significantly (Figure 6) in the defined pup life phases ($F_{4,92}$=5,68, P=0,0004). The confidence intervals are overlapping in all pup life phases and show a trend for the defined pup life phases. Mean daily movements of both parents was lowest during the milk-dependency phase and highest during the milk-independency phase.

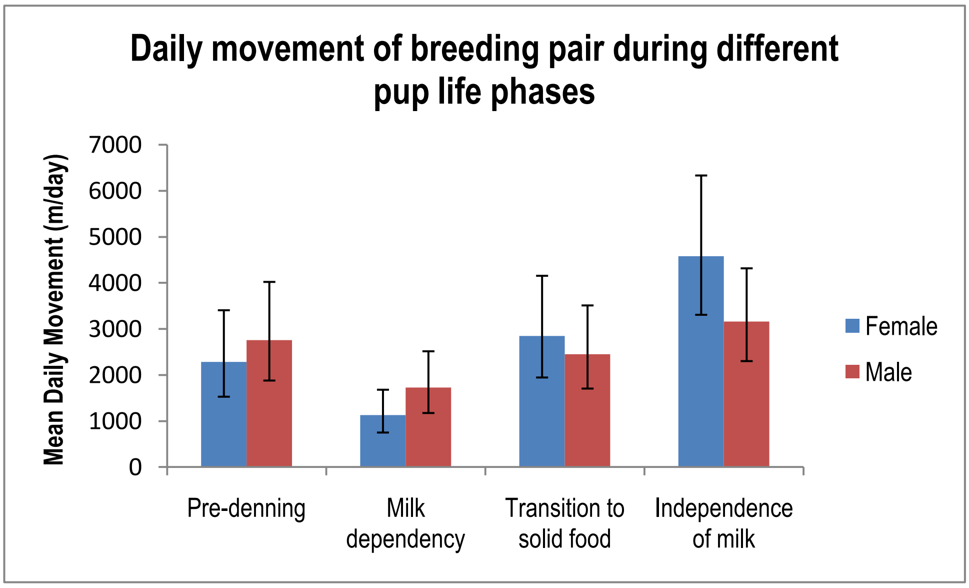

Figure 6 Daily Movement Pattern (LS means with Confidence Intervals)

Proportion of annual ranges

The absolute area covered by the wolves differed between the packs (Figure 7); however in this study I focused on the proportion of the packs' annual range they use after pupping.

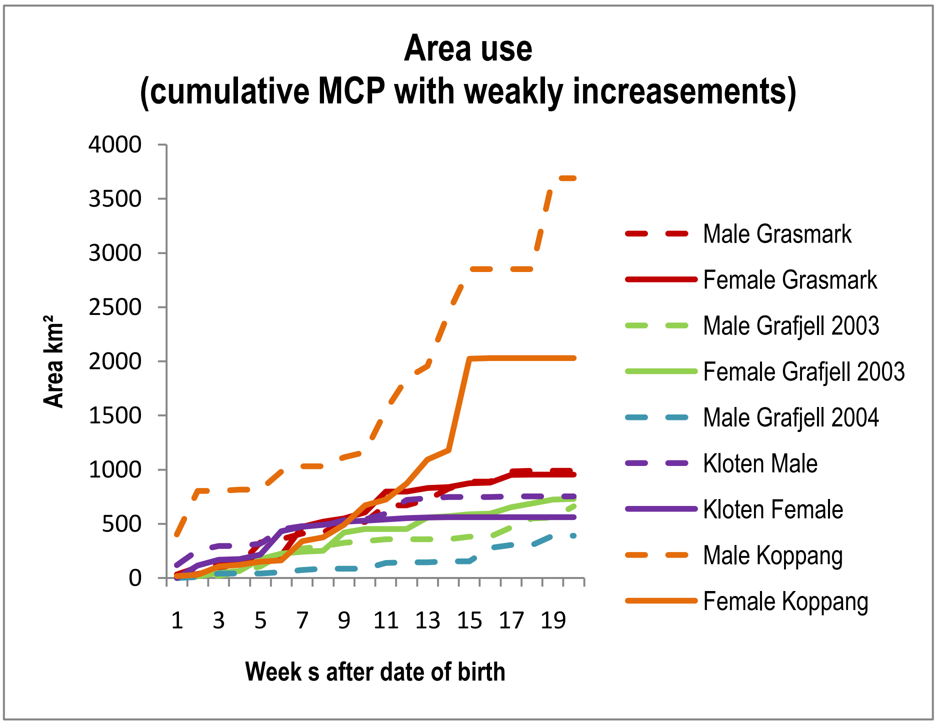

Figure 7 Area use (Cumulative MCP with weekly increasements)

I found a significant interaction between sex and pup life phase related to the used proportion of the annual territory ($F_{2,77}$=5,22, P=0,0075). The used proportions expanded with pup age (Figure 8). During the milk-dependency period, the females only used 3% of the annual territory (95% CI 1-11%) and the males used only 7% (95% CI 2-21%). Both adults used about 23% during the transition phase (Female 95% CI 8-48%, Male 95% CI 9-49%), and 56% during the milk-independency phase (Female & Male 95% CI 29-80%).

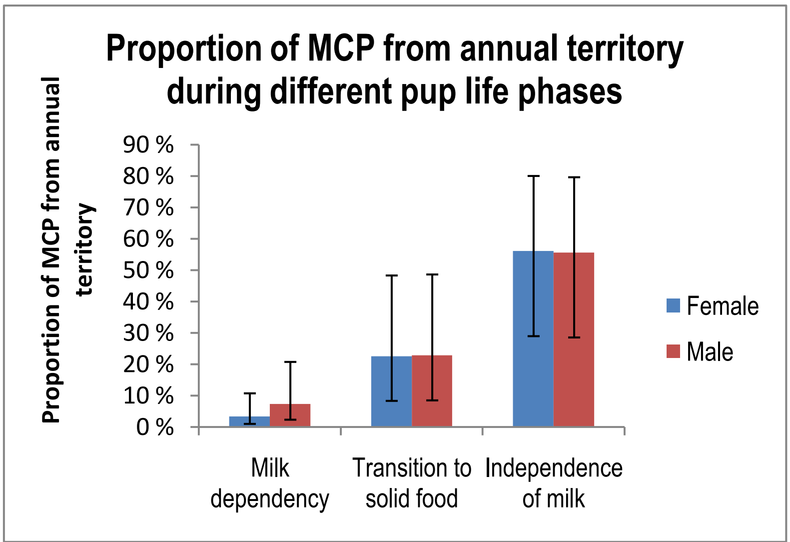

Figure 8 Proportion of MCP from annual territory
(LS means with Confidence Intervals)

3.4 Home-site attendance

The interaction of sex and development phase was related to the time parents spent at the home sites ($F_{2,55}$=11.09, p<0.001, Figure 9). The female-male difference in the home site attendance is the most profound during the milk-dependency phase. The female spent on average 44% more time at the home site than the male. The male visited the home site slightly more during the transition phase, but still the females' attendance is higher. During the milk-independency phase, the female and male showed a more or less equal attendance rate.

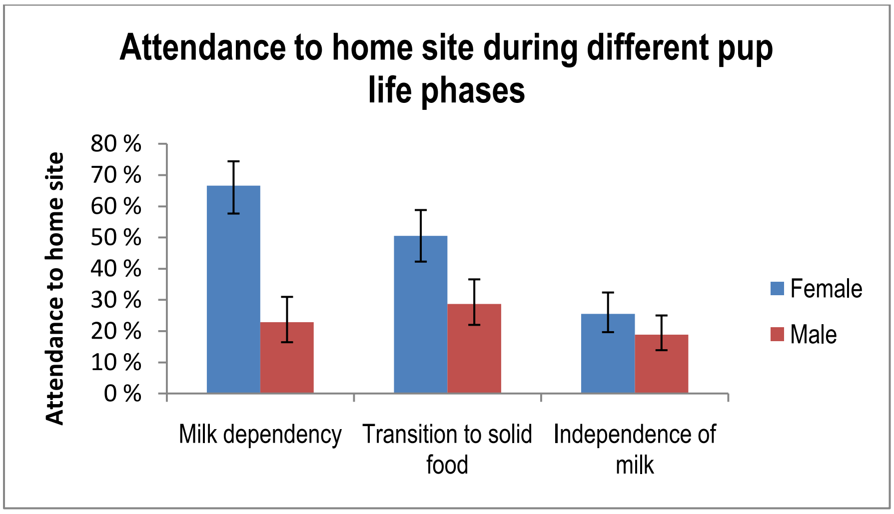

Figure 9 Attendance to home site (LS means with confidence intervals)

The female spents less time on the home site when the pups grew older; however, I did not detect differences in the males' attendance between phases (Figure 10-13).

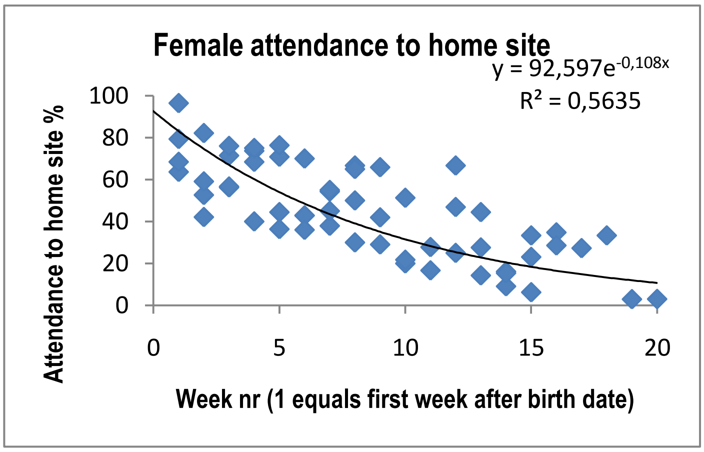

Figure 10 Weekly females attendance to home site

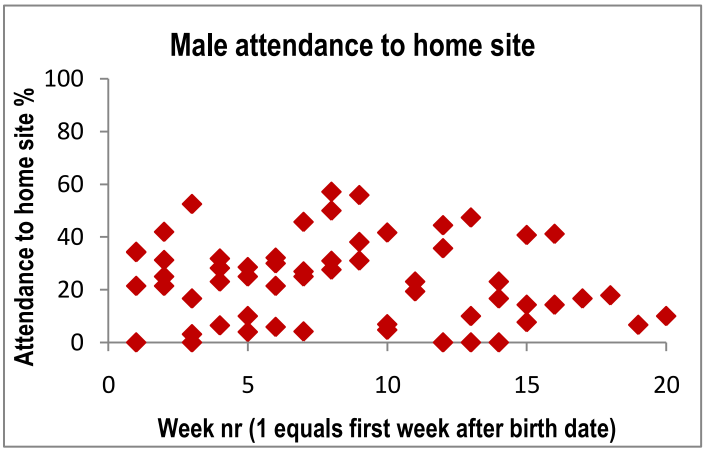

Figure 11 Weekly males attendance to home site

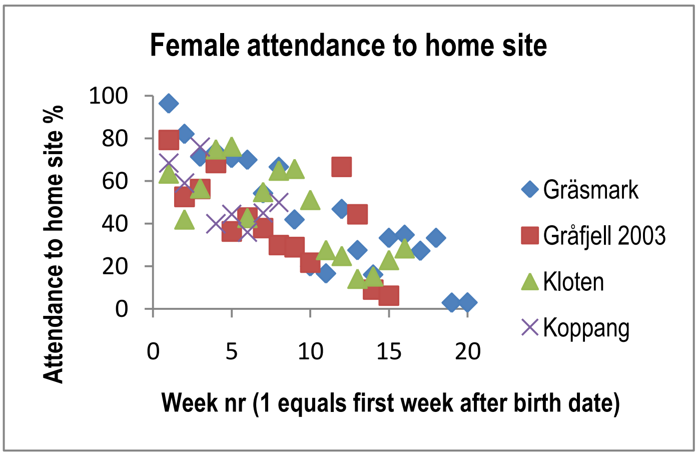

Figure 12 Weekly attendance of females to homesite categorized per territory

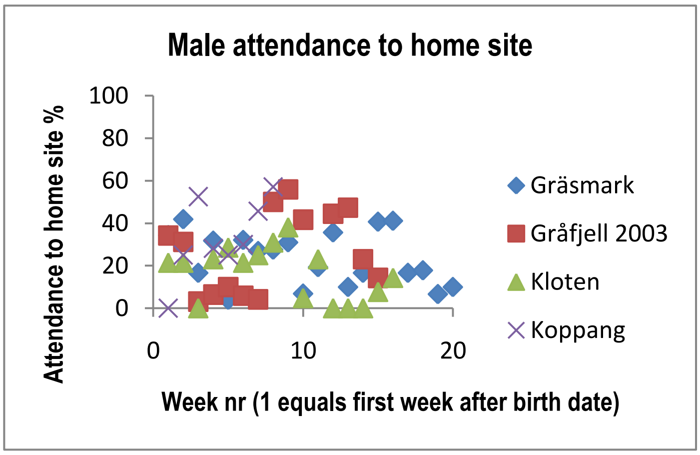

Figure 13 Weekly attendance of males to home site categorized per territory

3.5 Distance between concurrent positions for members of breeding pairs

The distance between concurrent positions of adults differed between pup-life phases ($F_{3, 79}$=12, 49, P=<0,001, Figure 14). During the pre-denning period the adults were closest to each other. The distance between the adults increased for each new pup life phase.

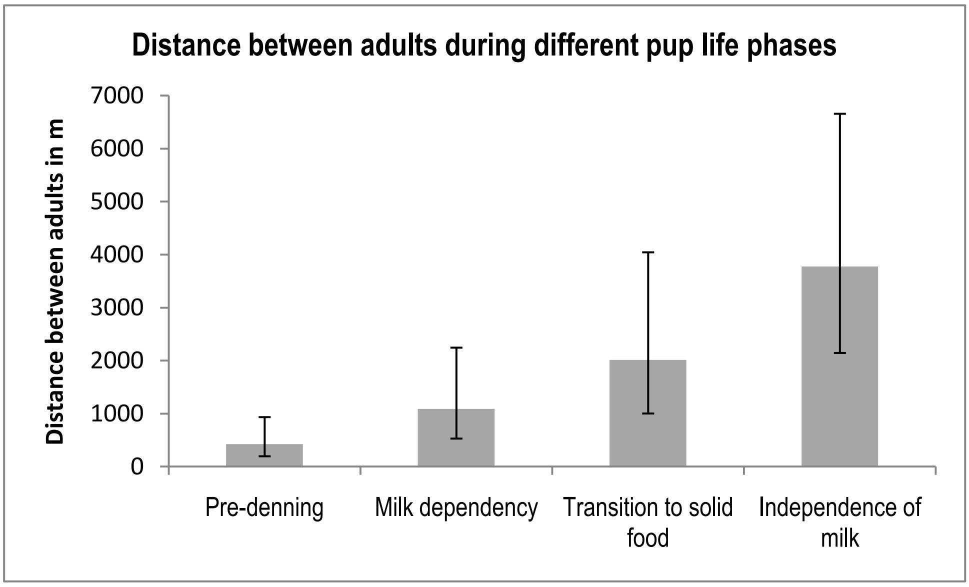

Figure 14 Distance between adults during different pup life phases (LS Means with Confidence Intervals)

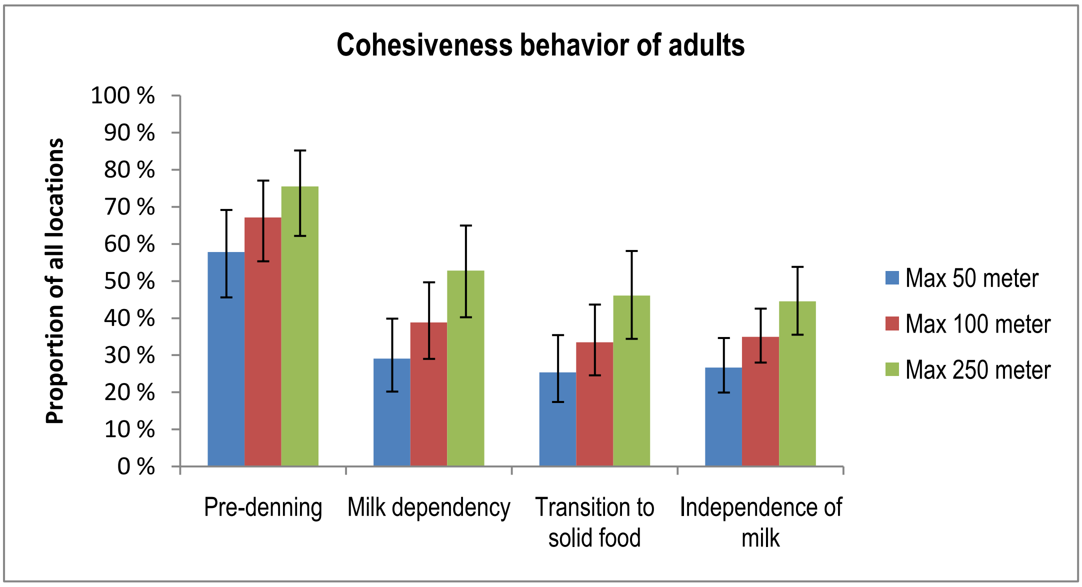

Figure 15 Proportion of distance between adults (<50m. <100m and< 250m) from all locations. Cohesive behavior is all kind of behavior that brings wolves together (e.g. playing, socializing, mating)

A significant relation was found between the life pup phases and the proportion of locations that parents were max 50 ($F_{3,97}$=11,29, P=<0,0001), 100 ($F_{3,97}$=9,32 P=<0,0001)and 250 meters ($F_{3,97}$=6,01 P=0,0010) away from each other (Figure 15). The breeding pair was closest to each other during the pre-denning period. From the milk-dependency period and onwards the cohesiveness was more or less stable.

The time delay between the positions taken at the same time averaged 20-33 seconds in the different phases and ranged from 0 to 139 seconds.

4 DISCUSSION

4.1 Time of breeding

Wolf pups were born between 26th April - 20Th May. The breeding season of wolves' starts earlier in the most southern parts of their geographical range. The parturition dates of the four studied territories support this latitudinal difference (Fuller 1989).

4.2 Home sites

GPS reception can be strongly affected by the type of den site used by wolves such as excavated holes, hollow logs, rock caves (Fuller 1989). Wolves move their pups to other den sites because of prey abundance, human and predator disturbance, den deterioration, sanitation and pup-size changes (Chapman 1977). Pups younger than four weeks are mostly carried, whereas older pups can follow the parents, but the process may take several days (Chapman 1977). The number of den sites used during the breeding seasons varied from 2-3 among the territories; however, the number of den sites may have been overestimated because a minimum distance between the identified sites was not set.

Joslin (1967) characterized rendezvous sites as sites with playing areas, feeding grounds, beds and tracks. At the activity center, the vegetation is usually leveled. Rendezvous sites can be selected based on habitat type, presence of water and human activity (Capitani et al. 2006). Selection may also vary geographically. Rendezvous sites are often located near kills (Fuller 1989). In this study den sites were easier to identify than rendezvous sites, possibly due to the infrequent use and short-term use of rendezvous sites (Fuller 1989, Potvin et al. 2004). I did not increase the buffer size around positions or shorten the time for identifying clusters because this would lower the reliability of detecting true rendezvous sites. Four hour intervals may have been too short to identify some kill and rendezvous sites. In addition, there was no data available of other pack members, but they could have temporarily taken over parental care. The dependency of pups decreases over time. Pups have travelled up to 11 km with their parents when just older than four weeks, and from week 9 they are capable of travelling greater distances by themselves (Chapman 1977). At about ten weeks old, pups start to accompany the parents while hunting (Packard et al. 1992). The parents therefore do not need to attend the home sites as often, resulting in fewer clusters of positions over time. Fuller (1989) reports that rendezvous sites were used less frequently towards the end of the summer; the same pattern was found in this study. Additionally GPS success rate for two out of the four territories decreased throughout summer, resulting in fewer positions to identify clusters and gaps with missing data of the pups' location.

4.3 Spatial and temporal patterns

Mech and Boitani (2003) summarized that there is variation in the way that wolf packs use their home sites in summer. The results of this study are in accordance to that. Differences in use of home sites can be caused by prey densities and disturbance by humans. Jedrzejewski et al. (2001) also found a significant relationship with activity patterns and food abundance. When prey density was low, wolf mobility increased; however, Potvin et al. (2004) found that home site attendance was not dependent on prey density, in that study, patterns varied even though prey densities and pack size were constant. Other factors that may influence attendance patterns includes differences in individual health, nearness of prey carcasses, loss of key pack members and hunting skills (Potvin et al. 2004).

I hypothesized that the males would travel greater distances and that initially the female would spent more time at the den site, then later females gradually move further away from home sites as the pups matured. The results confirm this hypothesis. Female activity was centered around the den for about four weeks after birth. Other studies showed similar results. Potvin et al. (2004) reported that both breeding and yearling females have a high home site attendance rate, while yearlings and breeding males show the opposite pattern. Individuals that attended the home site less frequently hunted to supply food for the individuals that were centered around the home sites (Potvin et al. 2004).

Tsunoda et al. (2008) found the same activity patterns for males and females. Jedrzejewski et al. (2001) found that the male's behavior did not change much during the breeding period. Although males were more centered around the den their movements were 80% of those in winter.

4.4 Spatial and temporal patterns related to pup development

By dividing the study period into three different pup phases (i.e. milk dependent, transition-to-solid-food and milk-independency) I assessed relationships between pups development and parental behavior. The mean daily movement of both parents was lowest during the milk dependency period. The proportion of the annual range used during the milk-dependency phase was the smallest for both females and males, although smaller for females. In the subsequent two periods proportions used by males and females were similar. This indicates that females took more responsibility in food gathering after pups started eating solid food. Male attendance at the home sites was highest during the transition period. Males may have cared more for pups during the transition phase, allowing females to go out hunting herself. When a higher amount of food per day is necessary for pup growth and survival, females may become more active in food supplying (Potvin et al. 2004). When pups come into the transition phase, they suckle less, start eating solid food, and beg for regurgitation (Packard et al. 1992). Breeding males mostly regurgitate to both the female and the pups, while breeding females merely regurgitate to the pups (Mech et al. 1999). Nevertheless female attendance at home sites is higher during all phases, which implies that she took most of the responsibility for direct parental care throughout the summer.

4.5 Cohesiveness of adults

The distance between adults increased with every new phase of pup development. However, when the proportional relationship was shown it was clear that the parents were closest to each other during the pre-denning phase. The other three subsequent phases show an equal proportion. This implies that when pups are born the parents had to spend more time in pup care (different tasks for male and female) and therefore could not spend so much time together as in the pre-denning phase.

Differences in movement patterns of males and females are influenced by pack size and by dissimilar parental roles (Tsunoda 2008). Other pack members can take over hunting obligations from the breeding male, which allows the male to stay closer to the pups. This study didn't take in account the role of other pack members, therefore no statements could be made about the role of other pack members and their influence on adult behavior. In smaller packs the alpha female is able to spend less time at the den. She can therefore show a more active role in providing food. Breeding males in a pack can show the same movement patterns as the female because the other pack members take over the food supplying (Tsunoda et al. 2008).

4.6 Recommendation for further research

An underlying assumption of my cluster methodology was that pups were present in each cluster. The probability that this assumption was valid during the first four weeks was high, but as the pups grow older, the probability decreased. Their mobility increased and their need for full time care decreased. In addition, the probability of pup mortality also increased with time. GPS locations with a time interval of 4 hours turned out to be too coarse to define clusters. Merril and Mech (2003) also claimed that daily patterns of wolf activity cannot be showed when GPS interval is >3 hours. In addition, I did not know if yearlings or other wolves were still members of the pack. If one wants to know more about the interactions and the behavioral patterns short interval positions (i.e. ≤3 hours) are necessary, and all pack members (incl. pups and yearlings) need to be equipped with GPS collars. Beside parental care, wolf activity patterns can be influenced by factors, such as prey availability, prey migration, prey activity, activity of neighboring wolf packs and human activity (Tsunoda 2008). To assess what causes certain patterns, it is necessary to collect data on these parameters as well. In this study, Scandinavian wolves showed similar patterns as to those in North America. Further research should determine the role of additional parameters on the activity patterns and the interactions between the parents, pups and other pack members during the critical pup-rearing periods.

5 MANAGEMENT IMPLICATIONS

In order to define the importance of my study for wolf management I made a literature review about wolves in Scandinavia. I would recommend reading this review first, because it includes information about the wolf population in Scandinavia, management goals and management challenges (Appendix 7).

The Scandinavian wolf population is an isolated, inbred population, with 213-252 individuals during winter 2008-2009 (Wabakken et al. 2009), not enough, according to several scientists, to ensure a viable population in the future (Appendix 7).

Immigrants rarely reach the population on the Peninsula, so immigration may not have a significant direct influence on population size. Therefore, pup survival is important for the viability of this population. Pup survival on average is high during summer, due to high densities of prey. It is mostly viruses that lower the survival chances of pups. Autumn is claimed to be a more difficult period, because the pups' food requirements increase while prey abundance decreases (summarized by Mech & Boitani 2003). Especially during the milk-dependency and transition periods pups are highly dependent on their parents. Studies have shown that some wolves can survive on their own when they are about four months old, but that statement is not applicable to all wolves (summarized by Mech & Boitani 2003). As shown in this study, breeding wolves change their activity patterns significantly during pup raising, however, pup survival depends on more factors than parental care itself.
By identifying attendance and movement patterns of breeding wolves', wildlife managers could for example set restrictions to protect wolves during this period. Contemporary wolf management in Scandinavia does not include such measures yet (Appendix 7), but I believe that this could become important in the future.

If the Scandinavian wolf population is allowed to grow (e.g. to increase the viability of the population), then new territories could be established. Consequently, more people will be living in new wolf territory and the chance of resistance is likely. In order to include the inhabitants, managers should discuss what to expect. Most people have problems with wolves arriving in their living areas. If these wolves induce negative attitudes, then there is a higher risk for illegal killing (Appendix 7). The most effective way to prevent wolves' expansion is to kill the adults with the litter. Managers therefore need to know how breeding wolves use the area in order to prevent illegal killing and to facilitate management of wolves in current and new territories.
Managers may also decide to translocate Russian/Finnish immigrants; ensuring pup survival would be of enormous value for the genetic variation in the population (Appendix 7).

Frame et al. (2005) mentioned that managers in North America are bending their heads over the impact of human disturbance on wolf home sites. Human disturbance can cause wolves to change their home sites more frequently (Fuller 1989), however Theuerkauf et al. (2003-1) showed that human activity doesn't influence wolf activity patterns where wolves can avoid humans. Theuerkauf et al. (2003-2) also concluded that the suitability of an area depended on both human activities and spatial distribution of the forest and less to habitat characteristics. A possible management implication is to lower the effects of human disturbance by closing areas when pups are most fragile. Whatever managers decide it is important to know what affects pup survival and their parents' movement patterns.

There are several situations in which it is important to know more about movement patterns of wolves in summer. Demma and Mech (2009) found that wolves travel in rotations (around the home site) during summer. In order to control an entire pack that is preying on livestock, it is important to take in account their rotational use. Demma and Mech advised that hunters should wait until they are sure that all pack members can be killed. As far as I know it is not studied if Scandinavian wolves move similarly. As for all species that are hunted, it is important to know more about their ecology and movements. This will be very important in the near future, since Sweden has started hunting to manage the wolf population (Appendix 7).

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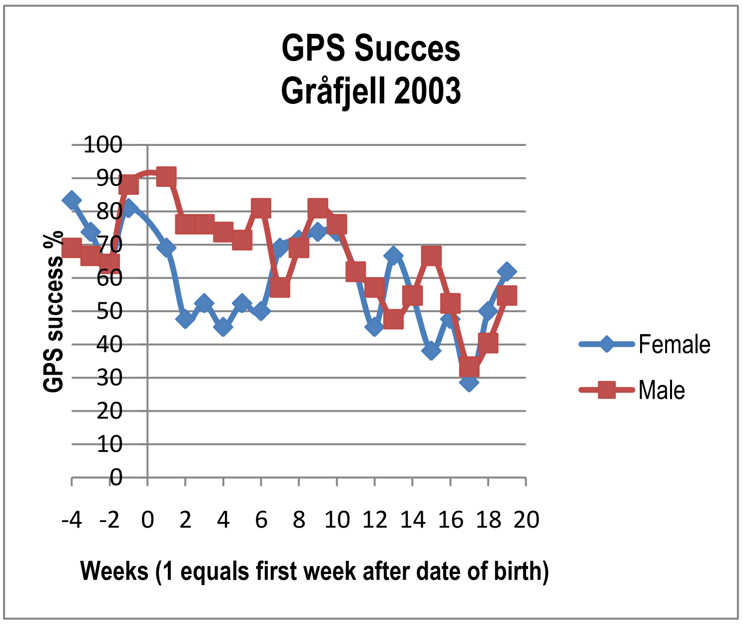
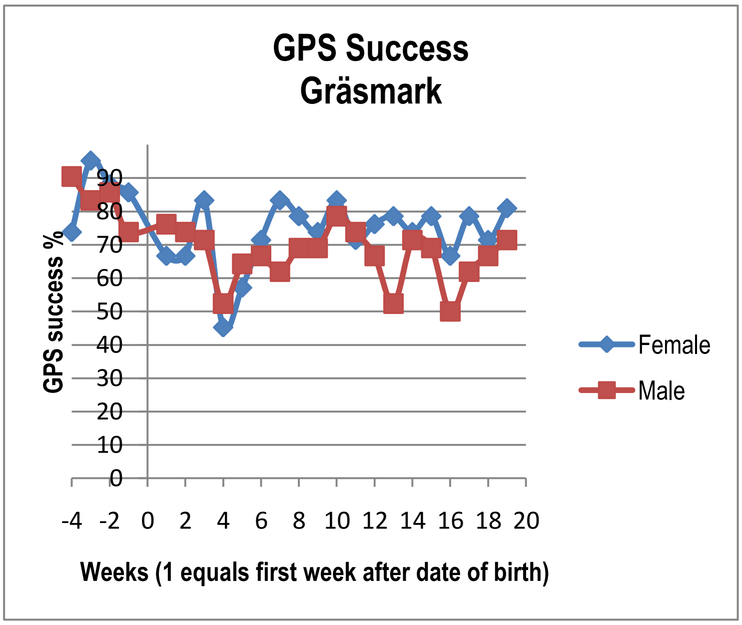
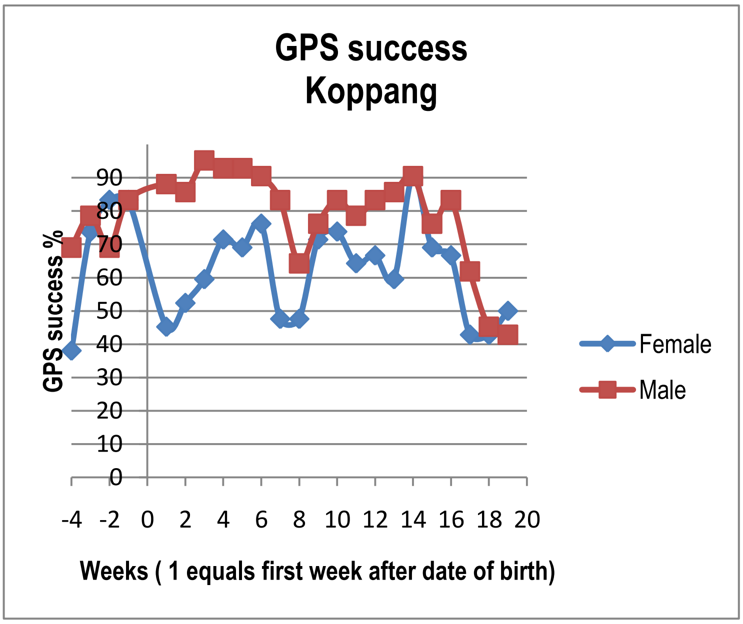
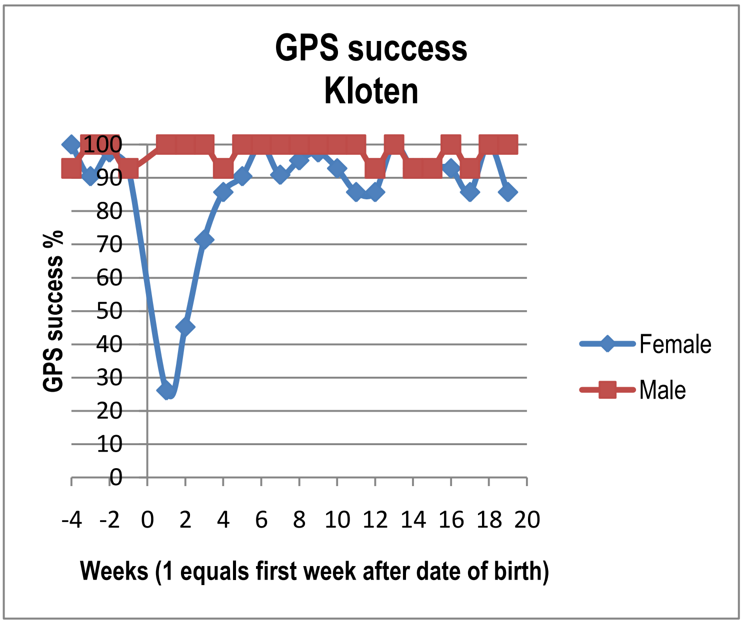
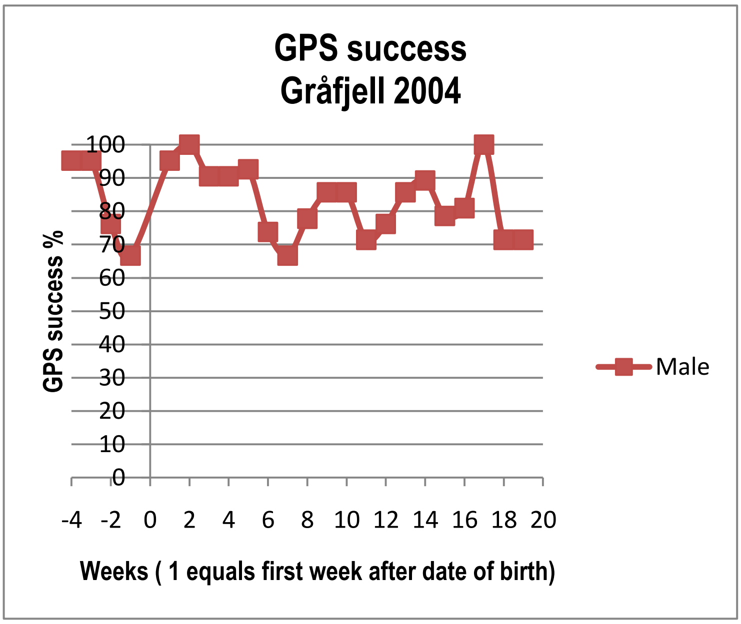
Appendix 1 GPS success rate



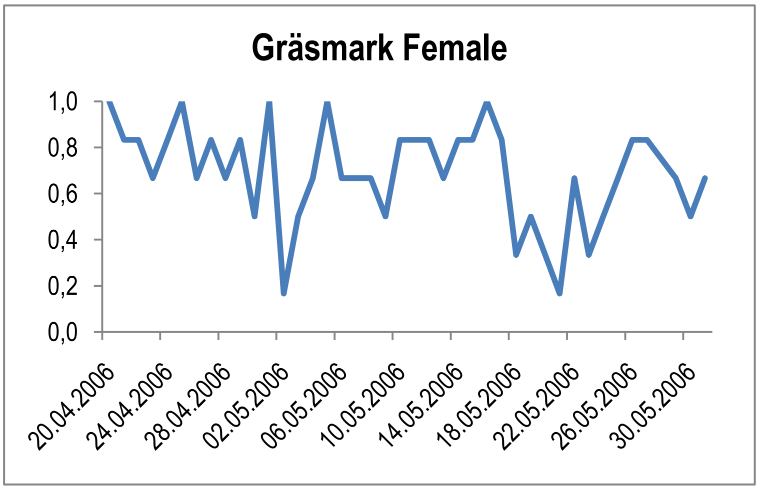


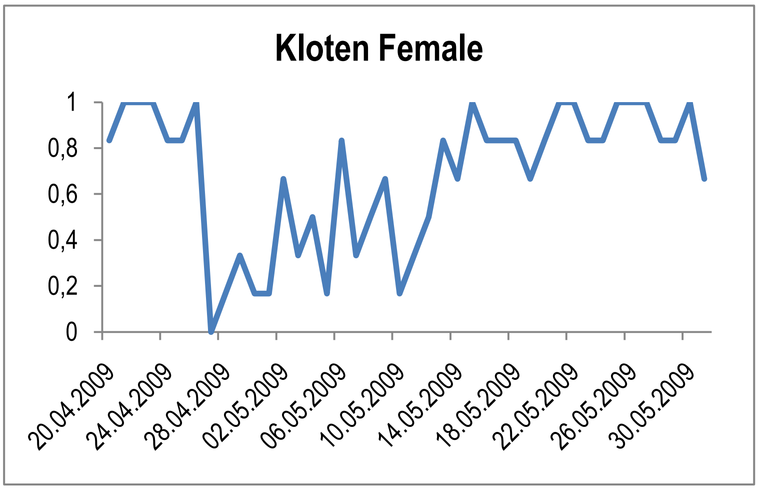

GPS success
Koppang
GPS success %
90
80
70
60
50
40
30
20
10
0
-4 -2 0 2 4 6 8 10 12 14 16 18 20
Weeks (1 equals first week after date of birth)
Female
Male


GPS success
Kloten
GPS success %
100
90
80
70
60
50
40
30
20
10
0
-4 -2 0 2 4 6 8 10 12 14 16 18 20
Weeks (1 equals first week after date of birth)
Female
Male

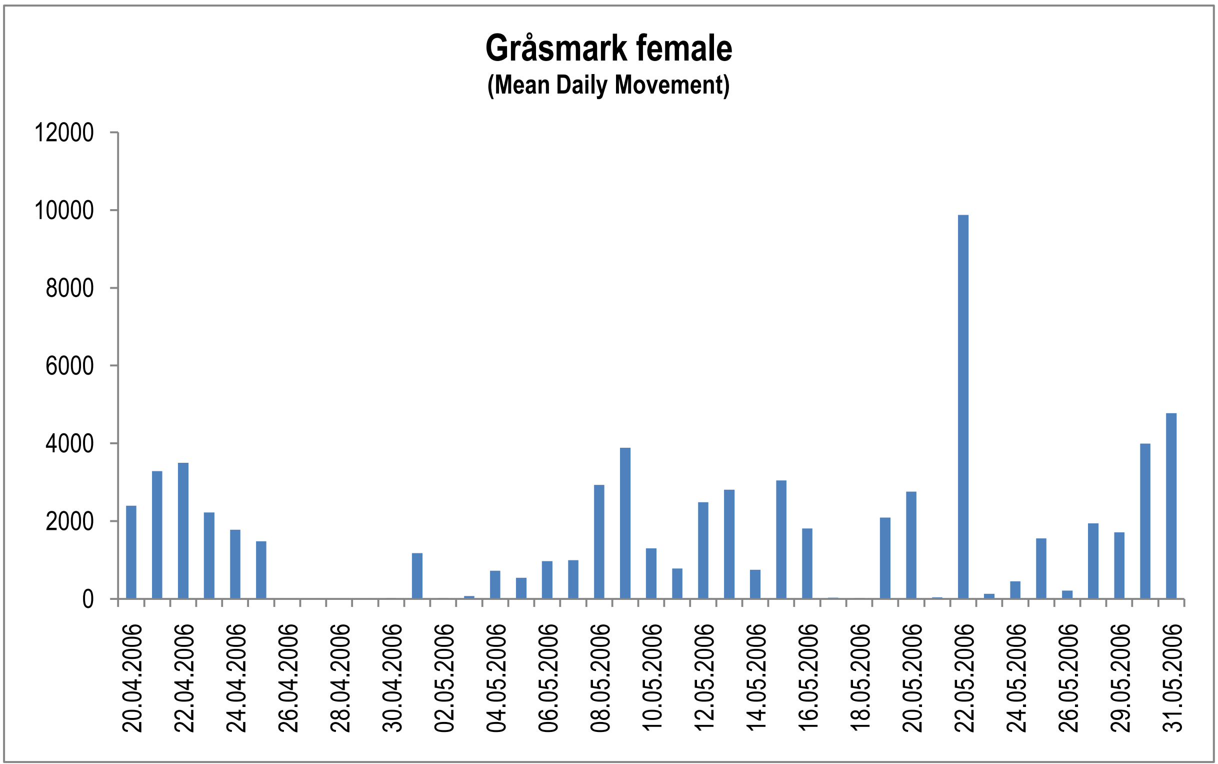

GPS success
Gråfjell 2004
GPS success %
100
90
80
70
60
50
40
30
20
10
0
-4 -2 0 2 4 6 8 10 12 14 16 18 20
Weeks (1 equals first week after date of birth)
Male

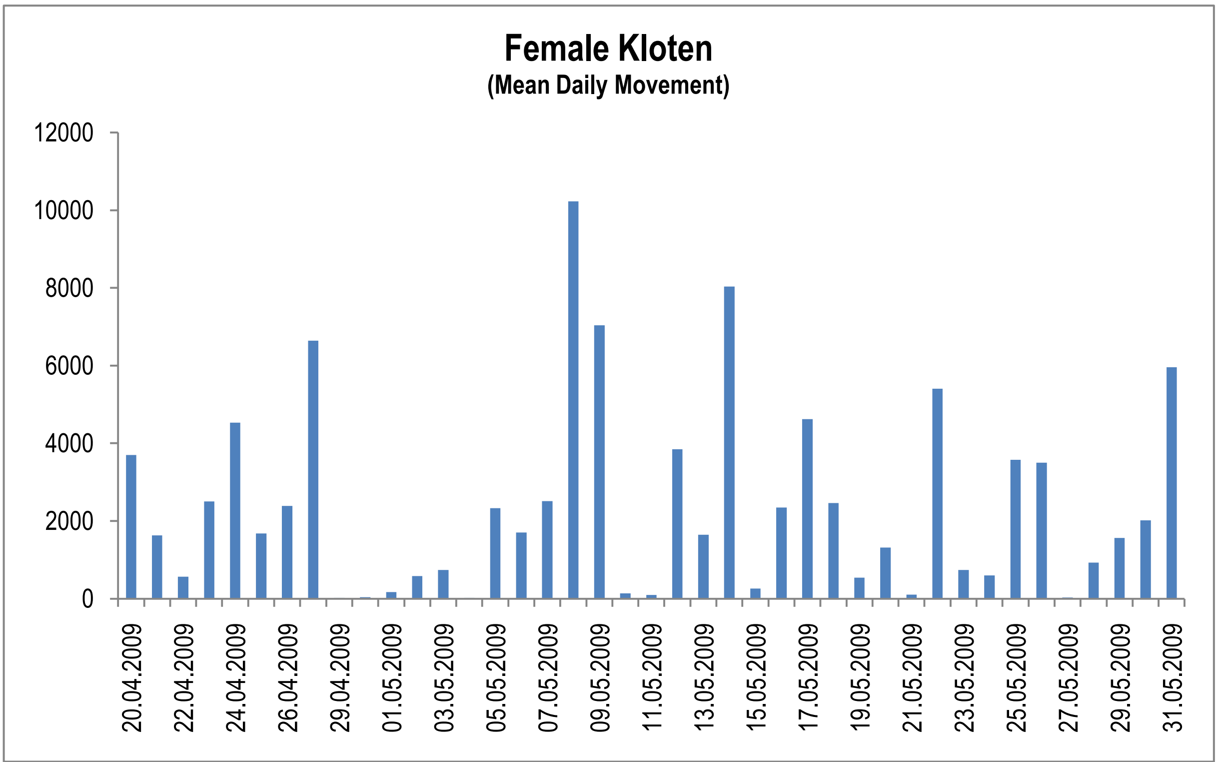
Appendix 2 Frequency of received positions during the period 20 April- 31 May





Appendix 3 Mean Daily Movement (MDM) in meters/day during the period 20 April- 31 May



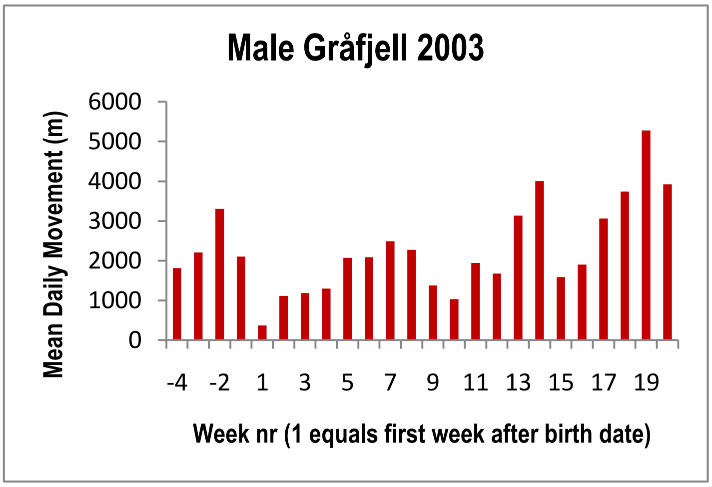


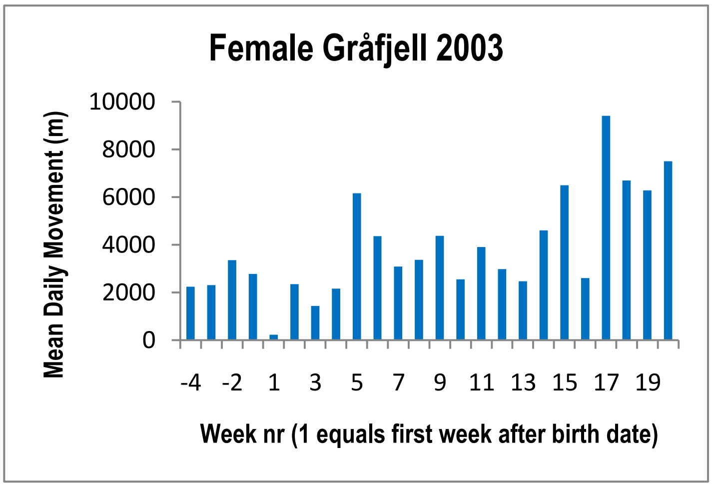
Appendix 4 Den site specifics

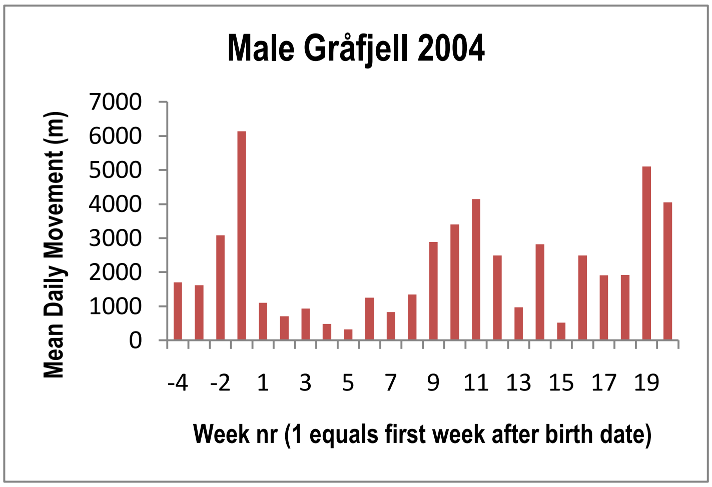
	Gråsmark	Gråfjell 2003	Kloten	Koppang
Birth date	26.04.2006	13.05.2003	27.04.2009	20.05.2004
Den site specifics				
Number of den sites	3	3	2	3
End denning period	23.05.2006	30.05.2003	11.08.2009	22.06.2004
Duration of denning (days)	27	47	106	33
End date den site 1	01.05.2006	25.05.2003	18.05.2009	27.05.2004
Duration of den site 1	5	12	21	7
End date den site 2	07.05.2006	30.06.2003	11.08.2009	10.06.2004
Duration of den site 2	6	31	85	14
End date den site 3	23.05.2006			22.06.2004
Duration den site 3	16			12
Missing dates		25.05.2003-30.05.2003		
Distance between sites				
Distance between den site 1+2	96	3100	2061	399
Distance between den site 2+3	169			1598
Age of pups				
Age of pups den site 1 (weeks)	1	1--2	1--4	1--2
Age of pups den site 2	1--2	3--7	4--16	2--4
Age of pups den site 3	2--4			4--5
Female				
Attendance to den site 1	96 %	69 %	55 %	68 %
Attendance to den site 2	78 %	44 %	37 %	69 %
Attendance to den site 3	74 %			35 %
Average Distance from den site 1	142	532	1960	1053
Distance from den site 2	322	2353	3014	730
Distance from den site 3	1468			1348
Max. Distance from den site 1	3462	8067	16284	12695
Max. Distance from den site 2	3777	14648	20641	14382
Max. Distance from den site 3	19112			8337
Male				
Distance from den site 1	1525	405	5627	16662
Distance from den site 2	1520	4624	4939	937
Distance from den site 3	3760			1547
Max. Distance from den site 1	7527	8173	18101	38788
Max. Distance from den site 2	6575	16178	23053	14848
Max. Distance from den site 3	19110			10231

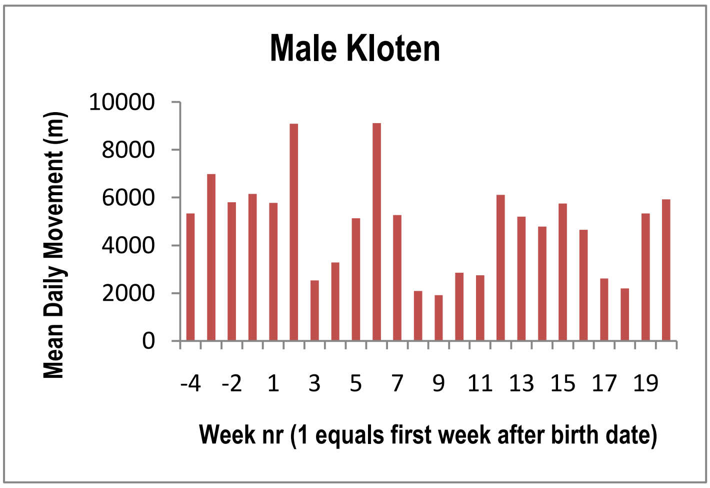
Appendix 5 Mean Daily Movement Weekly Average

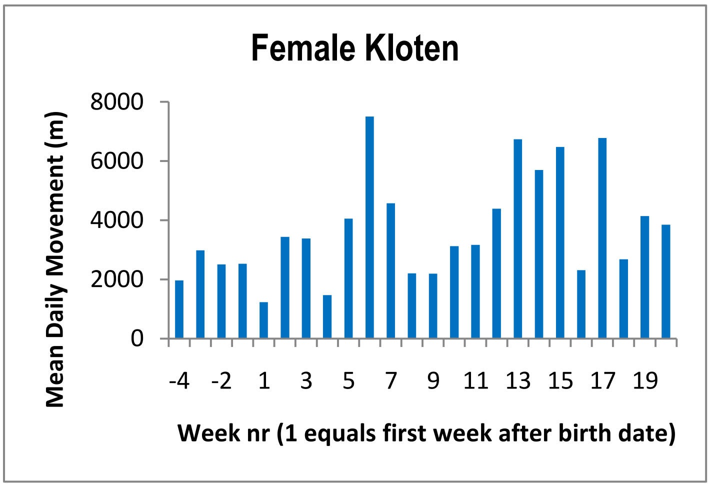
(Average straight line distance per day between two consecutive locations)

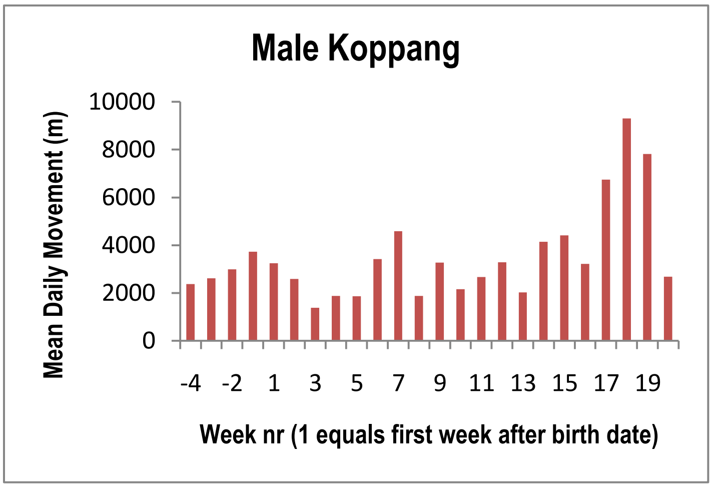


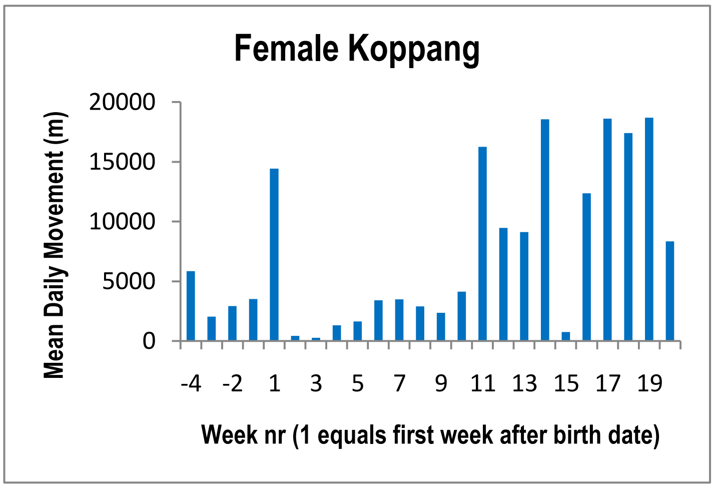


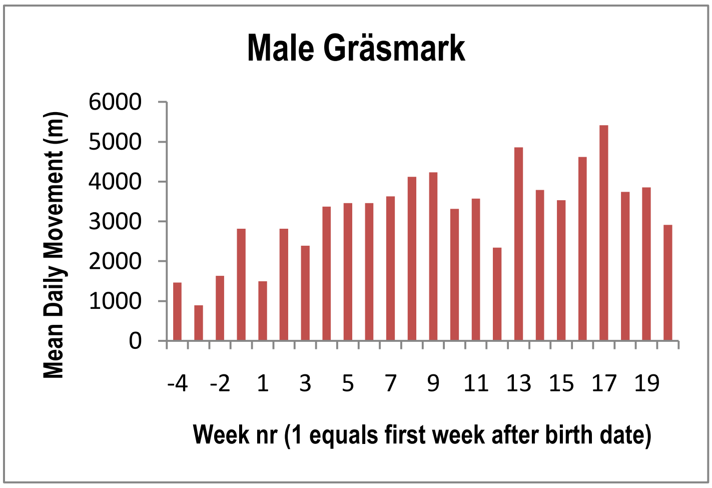


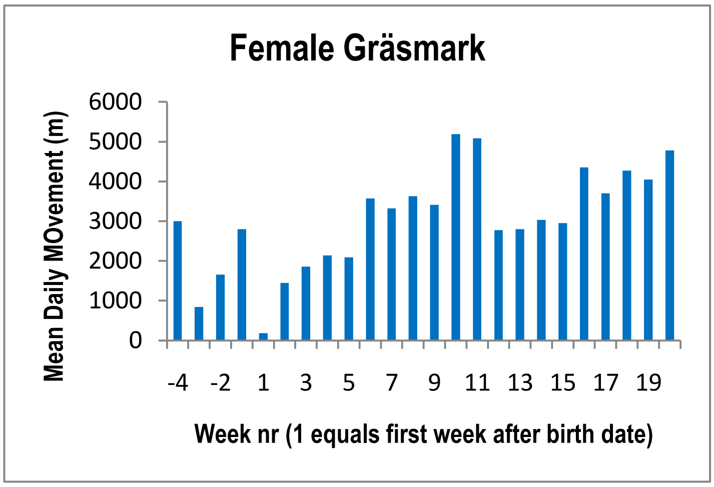





Male Koppang
Mean Daily Movement (m)
10000
8000
6000
4000
2000
0
-4 -2 1 3 5 7 9 11 13 15 17 19
Week nr (1 equals first week after birth date)


Female Koppang
Mean Daily Movement (m)
20000
15000
10000
5000
0
-4 -2 1 3 5 7 9 11 13 15 17 19
Week nr (1 equals first week after birth date)


Male Gräsmark
Mean Daily Movement (m)
6000
5000
4000
3000
2000
1000
0
-4 -2 1 3 5 7 9 11 13 15 17 19
Week nr (1 equals first week after birth date)


Female Gräsmark
Mean Daily MOvement (m)
6000
5000
4000
3000
2000
1000
0
-4 -2 1 3 5 7 9 11 13 15 17 19
Week nr (1 equals first week after birth date)

Appendix 6 Rendezvous site specifics

	Gråsmark	Gråfjell 2003	Kloten	Koppang
Birth date	26.04.2006	13.05.2003	27.04.2009	20.05.2004
End denning period	23.05.2006	30.06.2003	11.08.2009	22.06.2004
Start use of rendezvous sites	24.05.2006	06.07.2003		25.06.2004
Age of pups (days)	28	54		36
Days between denning and first rendezvous site	1	6		3
Total number of identified clusters	5	4	0	2
Rendezvous site 1				
Start	24.05.2006	06.07.2003		25.06.2004
End	29.05.2006	11.07.2003		29.06.2004
Number of days	5	5		4
Age of pups (weeks)	5--10	8--9		6
Male attendance	25 %	58 %		21 %
Average distance away from site	4688	1491		4128
Maximum distance away from site	18322	9220		14856
Female attendance	57 %	31 %		32 %
Average distance away from site	2632	4957		890
Maximum distance away from site	20302	21410		3925
Rendezvous site 2				
Start	30.06.2006	12.07.2003		29.06.2004
End	21.07.2006	19.07.2003		10.07.2004
Number of days	21	7		11
Age of pups (weeks)	10--13	9--10		6--8
Male attendance	21 %	43 %		48 %
Average distance away from site	5408	2405		4082
Maximum distance away from site	20966	14210		14811
Female attendance	32 %	48 %		41 %
Average distance away from site	4462	3044		2765
Maximum distance away from site	19836	14505		14722
Rendezvous site 3				
Start	22.07.2006	03.08.2003		
End	05.08.2006	11.08.2003		
Number of days	14	8		
Age of pups (weeks)	13--15	12--13		
Male attendance	16 %	36 %		
Average distance away from site	8236	1179		
Maximum distance away from site	30185	5552		
Female attendance	16 %	23 %		
Average distance away from site	6719	2042		
Maximum distance away from site	28924	19765		

	Gråsmark	Gråfjell 2003	Kloten	Koppang
Rendezvoussite 4				
Start	06.08.2006	15.08.2003		
End	14.08.2006	26.08.2003		
Number of days	8	11		
Age of pups (weeks)	15--16	14--16		
Male attendance	48 %	21 %		
Average distance away from site	4952	4271		
Maximum distance away from site	22397	11591		
Female attendance	39 %	14 %		
Average distance away from site	4839	5478		
Maximum distance away from site	22521	14640		
Rendezvoussite 5				
Start	20.08.2006			
End	13.09.2006			
Number of days	24			
Age of pups (weeks)	17--21			
Male attendance	15 %			
Average distance away from site	3924			
Maximum distance away from site	16647			
Female attendance	14 %			
Average distance away from site	5110			
Maximum distance away from site	24029			
Distances between sites				
1--2	955	1570	28	
2--3	3680	1683		
3--4	558	3155		
4--5	1397			

INTRODUCTION

The Scandinavian (Swedish-Norwegian) wolf population is a small population and still categorized as critically endangered (Artdatabanken 2010, Artsdatabankene 2010). As in many of the countries located on the Northern Hemisphere, wolves were persecuted until they were virtually extinct (summarized by Mech & Boitani 2003). However, a new population managed to recolonize on the Scandinavian Peninsula, as they again became a part of the Scandinavian fauna (Wabakken et al. 2001). Nowadays, humans still decide the future of this large predator. What are the factors that influence Scandinavian wolf management? This review will zoom in on the historical aspects, the human dimension, the management and the management challenges of wolves in Norway and Sweden.

1 HISTORY

1.1 Persecution

The wolf is an animal that has been loved and hated through history. The Greeks and the Celts admired the wolf and the story of Romulus and Remus shows us that the wolf was considered as a social animal. Domestication of animals and Christianity changed human attitudes. The Roman Catholic Church characterized the wolf as evil and The Bible described the wolf as a symbol of rapacity, wantonness, cunning and deceit. For centuries the wolf was portrayed negatively in literature. People no longer lived with nature but felt superior to it and dominated it (summarized by Mech & Boitani 2003).

To exterminate the wolf, the king initiated a system of bounties (Elgmork 2000). Each hunter that killed a wolf received a certain amount of money. By 1647 the first wolf bounty was paid in Sweden (summarized by Mech & Boitani 2003). In South-Central parts of Norway for instance a total of 1507 bounties were paid in the period of 1733-1845. A majority of the wolves were killed in remote forested areas, which still today is the wolf's preferred habitat (Elgmork 2000). Protection reasons and economical motives were seen as important to participate in the bounty hunt. For instance an adult wolf was approximately worth half of a cow in 1720 in Norway (Elgmork 2000).

The winter was the most successful season for wolf hunting. When snowmobiles were introduced the hunt became so efficient (summarized by Mech & Boitani 2003), that wolves in Norway and Sweden became functionally extinct in late 1960's (Wabakken et al. 2001).

1.2 Wolves in Scandinavia

The Scandinavian wolf population was on its lowest during the 1930s-1980's. Bounties were paid until the mid 1960s. The wolf was protected by law in 1966 in

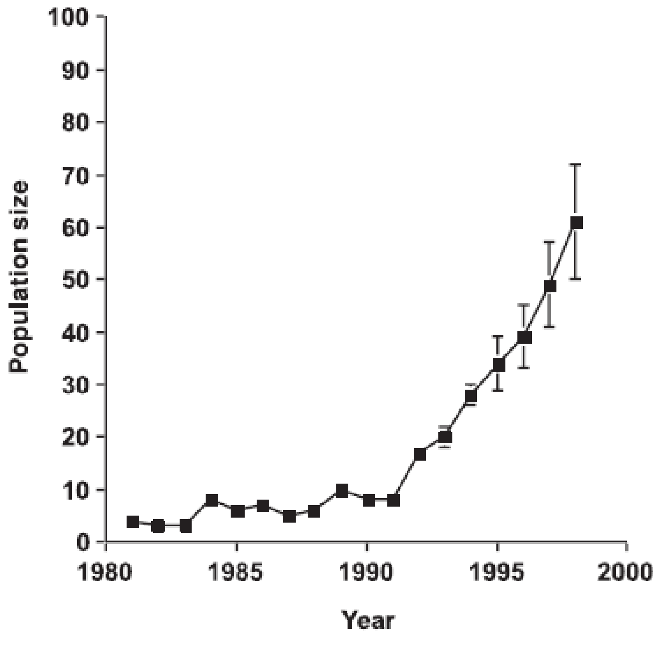


Figure I Population trend and minimum, maximum and average annual numbers of wolves in Scandinavia during winters 1980-1981 to 1997-1998
Source: Wabakken et al. 2001

Sweden and in 1972 in Norway. At that point the wolf was categorized as functionally extinct, with the last confirmed reproduction in 1964. Wolf observations have been reported between1965-1977 but remained mostly unconfirmed. During the winter of 1977-1978, several observations were made; and in northern Sweden, 8-9 wolves were tracked on snow. In the summer of 1978 reproduction was recorded in the same area. More wolf tracks were observed during the following years, but most of them further south. Therefore it was not too surprising that the next successful reproduction (in 1983) occurred in the south central part of Scandinavia (Wabakken et al. 2001).

<u>1983-1998</u>

With the start of the breeding in south central Scandinavia in 1983 the population gradually expanded. However, until 1991 the total number of wolves did not pass 10 individuals (Fig.1). One litter a year within the same territory (except for 1986) was recorded until 1990 (Wabakken et al. 2001).

In 1991 two reproductions were confirmed. From that moment the wolf population increased exponentially. The population existed of approximately 50-72 individuals in the winter of 1997-1998. The peak growth, during the 1990's had an annual growth rate of 29% (Wabakken et al. 2001).

<u>Present</u>

The number of wolves in winter 2008-2009 was estimated about 213-252 individuals in Scandinavia, whereas 25-26 individuals were restricted to Norway and 6-9 were located on both sides of the national borders. A total of 28 packs were established and the pack size varied between 3-8 wolves in each pack (Wabakken et al. 2009). Another 11-15 scent marking pairs, a minimum of 9-11 stationary wolves and 27-47 wolves categorized as others were present. At present, the Scandinavian wolf population is still increasing with an annual growth rate of 10-15% (P.Wabakken pers.comm.)

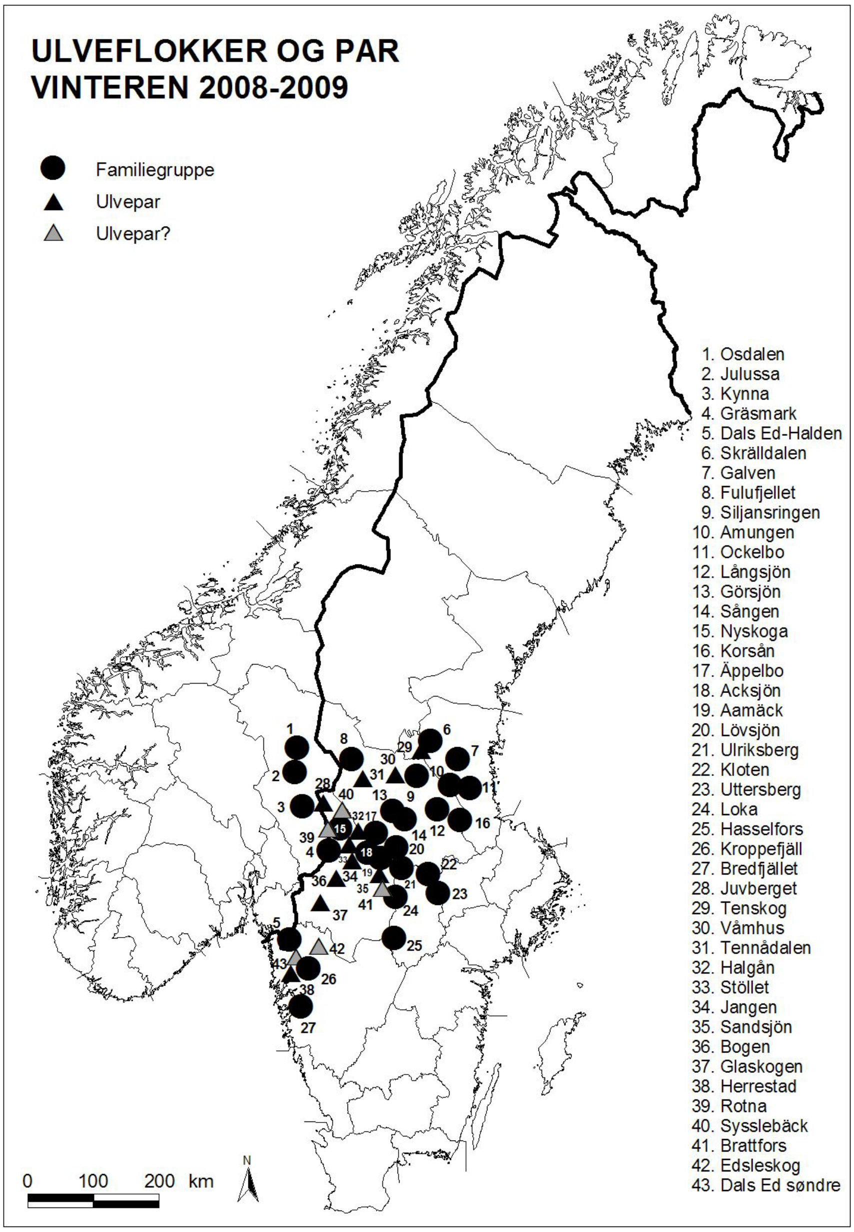


Figure II The distribution of wolf packs and scent-marking wolf pairs that have been recorded during October through February in 2008-2009.
Source: Wabakken et al. 2009

2 MANAGEMENT

2.1 Legislation

Wolf management in Scandinavia is mostly decided through politics. In Norway it has been like this since the wolf acquired a protective status by law in 1972, however, in Sweden it wasn't until 2001 when politicians became implicated in decisions making (T. Strømseth pers.comm). Before, it was the management that determined how to manage wolves, but due to an increase in conflicts it became a political issue as well. Next to the politicians there is a governmental organisation (Directorate for Nature Management (DN) in Norway and Swedish Environmental Protection Agency (EPA) in Sweden) which has the management role (e.g. check hunting quotas). At the bottom of the hierarchy are the regions or counties. In Norway, the parliament has established a wolf conservation zone (Linnell 2004). This zone is located across parts of two out of eight large carnivore management regions that can make decisions. Within this zone the management is only allowed to make decisions when the management goal is reached, otherwise DN is responsible (T. Strømseth pers.comm). The Norwegian wolf management goal was political decided to be a total of three annual reproducing wolf packs within the wolf zone totally inside Norway, and in addition an unlimited number of packs across the border (Linnell 2004). So far, the management goal within the zone has not been reached. In cooperation with DN, the eight regions can decide themselves and act when wolves are outside the wolf management zone.

In 2009, The Swedish Parliament decided to give the wolf counties permission to decide how to manage wolves within the framework of the management plan, more or less in a similar way as Norway. They activated a new management plan in autumn 2009. Since 2001, there was a target of 20 yearly breeding pairs but now they added an upper limit of maximum 210 wolves. The new plan decided to translocate and release up to 20 Finnish-Russian wolves within the next 5 years in order to bring new genes into the inbred Scandinavian population (T. Strømseth pers.comm). Beside population targets, predation compensation and hunting rules, no special goals are present in the management plans in attempt to take the wolves out of the endangered category (T. Strømseth pers.comm).

Norway and Sweden have population control through license hunting (T. Strømseth pers.comm). The hunting quotas are based on the national population goals for wolves and yearly official status reports. Biologists from Hedmark University College, together with the Norwegian Nature Inspectorate (SNO), are responsible for population monitoring in Norway (Wabakken et al. 2009). In Sweden the fieldwork is performed by each County administrative board whereas the Wildlife Damage Center (VSC) at Grimso Research Station evaluates and summarizes the results (Wabakken et al. 2009). License hunting is damage-control motivated and the quota is set every year by DN and EPA, it is only allowed in certain periods. Additionally there is direct damage control; this includes culling of specific problem individuals to prevent damage to livestock and semi-domestic reindeer (Rovviltportalen 2010). Wolves in Scandinavia are not restricted by prey densities but by human interference (T. Strømseth pers.comm).

2.2 Management Challenges

2.2.1 Inbreeding

The Scandinavian wolf population from today is founded by the breeding pair of 1983 (Vilà et al. 2003). It took eight years before another immigrant arrived and seventeen years before two other immigrants were added to the population, which brings it to a total of five founders. The female from the breeding pair of 1983 was killed in 1985, which thereafter resulted in mating between siblings. Thus, until 1991 the wolf population was more or less an inbred family (Liberg et al. 2005).However, the arrival of the male immigrant in 1991 decreased the risk of an inbreeding depression and it is claimed that he saved the population (Vilà et al. 2003). With his arrival, new genes were brought into the population, and as a result, the population started to grow exponentially. In 2008 and 2009, two new eastern male immigrants reproduced successfully (Wabakken et al. 2009). Future research may determine the effects of the additional two immigrants on the population gene diversity.

Many researchers express their worries concerning the viability of the population. In general inbreeding affects the viability of populations or individuals, especially small isolated populations are more vulnerable (Keller & Waller 2002). According to several studies the present Scandinavian population is not sure of long term viability. Ebenhard (2000) found that when a population is totally isolated a minimum of 500 wolves is needed to maintain 95% of the genetic variation in the upcoming 100 years. Soulé (1980) calculated that at least 200 individuals with an effective size of 50 are necessary to avoid the acute risk of inbreeding. Franklin (1980) claimed that long term viability is ensured when a population exists out of 2000 wolves with 500 breeders.

The present inbreeding coefficient is about 0.25, which implies mating between full siblings. Bensch et al. (2006) showed that the genetic loss in the Scandinavian population does not happen as fast as expected. They found that the most heterozygous wolf reproduced despite an increase of the inbreeding coefficient among the population. This shows a certain selection mechanism in the population. However, although inbreeding effects are hard to detect in wild populations (Räikkönen et al. 2006) a few studies already present negative impacts on the Scandinavian population. Liberg et al. (2005) showed a correlation between inbreeding and winter litter size of first time breeders; the litter size born and/or pups' survival decreased with an increasing inbreeding coefficient. Räikkönen et al. (2006) found malformations that could be due to inbreeding, e.g. lumbosacral transitional vertebrae.

A genetic depression can be prevented in only one way, namely by continuous immigration which brings us to the most important management challenge; the connection to the eastern populations (P. Wabakken pers.comm).

2.2.2 Connection to the Finnish/Russian populations

Looking at the geography of Sweden and Norway, we can conclude that wolves can only enter the Scandinavian Peninsula from Finland or Russia. Not many wolves accomplish to disperse successfully to the Scandinavian Peninsula, I summarized the main causes hereafter.

<u>Distance</u>

Wolves coming from the Kola/northern Karelia (Russia) and dispersing to the contemporary Scandinavian population have to travel about 1100 kilometres (Linnell et al. 2005). Although wolves are known as extremely good dispersers (summarized by Mech & Boitani 2003), this still is a big distance to cover. There are extreme dispersal distances reported, 1092 km straight line distance of a GPS collared wolf (Wabakken et al. 2007). Wabakken et al. (2007) mentioned that those long distance travellers are of huge importance for the gene flow between populations, however, many barriers exist for long distance dispersers. Aspi et al. (2009) summarized from former studies that Finnish wolves have an average dispersal distance smaller than 100 km.

Linnell et al. (2005) examined the possibility of dispersal over the Baltic Sea, as this would decrease the travel significantly to a maximum of 230 kilometers. Several studies show that wolves are capable of travelling over ice, but this concerns merely tundra dwelling wolves whereas Scandinavian wolves are forest dwelling (Linnell et al. 2005). It is therefore uncertain if wolves disperse over ice to Scandinavia. Kojola et al. (2006) found that most Finnish wolves disperse approximately at the age of 11-12 months (peak in April to June). If a dispersing wolf during this period would reach the Baltic Sea the ice would be melted. In the future, global warming may decrease the possibility to cross the Baltic Sea as well.

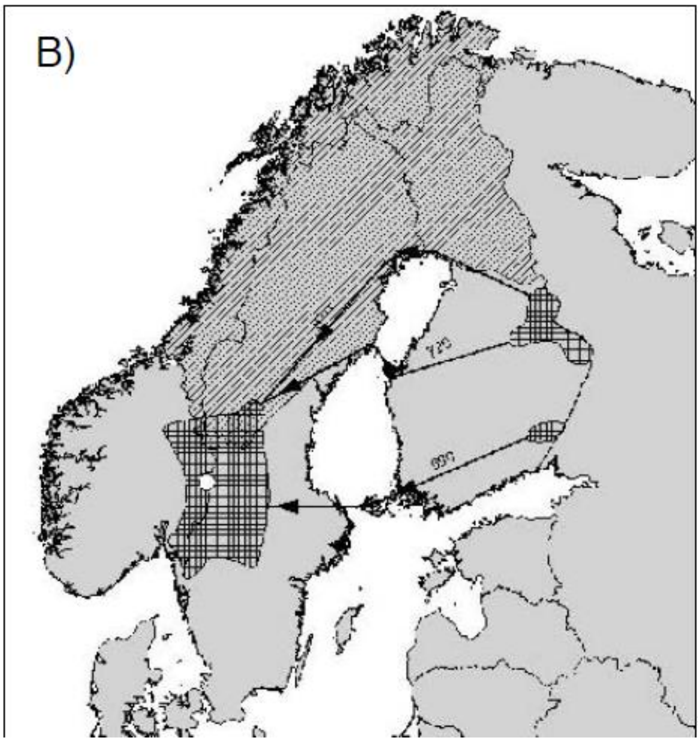


Figure III Wolf distribution in Finland and Scandinavia (cross hatched) in 2005. (Reindeer areas are marked with diagonal hatching. The open circle represents the reproduction site of 1983). Source: Linnell et al. (2005).

Reindeer herding

Big parts of Finland, Norway and Sweden are pointed out as reindeer areas where wolves are not allowed to establish (Figure III). The distance between the Finnish and the Scandinavian population is therefore at least 500 km (Linnell et al. 2005). Kojola et al. (2006;2009) showed that Finnish dispersers that cross reindeer areas are most likely to be shot (in their studies all wolves that crossed the area were killed). This prevents the development of a continuous population.

Wolf populations in Finland and Russia

New immigrants from Finland and Russia could prevent a further inbreeding depression in the Scandinavian population. However, there is the possibility of animal translocation, but what is the current situation for natural dispersal towards the peninsula? The Finnish population counted >> 200 individuals in 2009 (Wabakken et al. 2009). The northern part of Finland is dominated by reindeer herding areas, therefore wolves mainly establish in the central east part of the country. However, wolves recently have recolonized parts of western Finland, which may imply more dispersal and immigration to the Scandinavian peninsula due to decreased travel distance (Kojola et al. 2009). The distance that Finnish wolves need to travel towards Scandinavia is minimum 700 km, if crossing the Bothnian Bay (Kojola et al. 2009) and over land will be approximately 800 km. As already mentioned the average dispersing distance of Finnish wolves is mostly less than 100 km (Aspi et al. 2009), which indicates that human induced barriers and geographical barriers are of significant influence on dispersing possibilities.

For a long time the interaction between the Russian Karelian wolf population and the Finnish wolf population was high, and Finland received many immigrants from Russia (Pulliainen 1980). However in the 1990s this connection disappeared (Aspi et al. 2009). It seems that the Finnish population is starting to differentiate from the Russian population which implies that the migration rate between these two is low. The distance between these populations is small and there are no geographical boundaries as between the Finnish and Scandinavian population, however, Aspi et al. (2009) indicated that fences dating from the Soviet Era possibly prevented wolf migration. Additionally, Aspi et al. (2009) pointed out that the effective available space on the eastern Finnish border (south of the semi-domestic reindeer area) is occupied by territories, which prevent immigration to the Finnish population. Earlier studies showed that the survival of dispersing wolves is most often very low, and approximately 3 individuals per generation migrate to Finland, thus nowadays there is more migration from the west to east. Both the Finnish and the Russian population have an effective size of 40 individuals, which could be too few to avoid negative effects of inbreeding (Aspi et al. 2009).

2.2.3 Human dimension

After years of absence from large carnivores, people adapted to a place where no carnivores existed (Zimmerman et al. 2001). Society changed and new traditions and activities were created. With the protection of wolves in Scandinavia today, it was inevitable that humans would face problems with this predator. In this paragraph I attempt to characterize the human relation with wolves in Scandinavia.

<u>Hunting</u>

Norway and Sweden are countries where hunting is a popular activity. Different game species, such as moose *(Alces alces)* and hare *(Lepus timidus, Lepus europeaus)* are hunted with the use of unleashed dogs, which can chase game kilometres away from the owner. Around 100.000 hunting dogs are registered in each country (Backeryd 2007).

Backeryd (2007) reported that wolf attacks on hunting dogs is a serious problem for hunters. Nowadays, this is a bigger conflict in Sweden than in Norway, but an increase of attacks is recorded for Norway (Backeryd 2007, T. Strømseth pers.comm). During a period of ten years (1995-2005) 152 dogs were attacked in whole Scandinavia, of which 71% died (Backeryd 2007). Why wolves attack and kill domestic dogs is not entirely understood, there are though some hypotheses. It can be an inherited behavioural aspect or an accidental encounter that ends up with a territorial fight, but predation and competition could also be of importance (Backeryd 2007). Especially when prey densities are low, dogs can be an easy prey. Backeryd showed that 72% of the killed dogs were consumed by wolves, which implies that dogs are regarded as food.

Losing a hunting dog is an emotional and economical loss and the owner has the right to receive compensation. Most hunters would like to be able to defend their own dog against predators and they want legal protection in order to do this. Swedish hunters are allowed to kill a predator when the predator injure or kill their dog, Norwegian hunters are not allowed to kill wolves to defend their dogs (Backeryd 2007). The main reason for this difference is the management goals of breeding wolves; this is much lower in Norway, which implies larger wolf population consequences of shooting a territorial wolf in Norway than in Sweden (P. Wabakken pers.comm). Debates about changing the legislation are vivid at present. Backeryd (2007) examined the effect of new hunting rules on the wolf population. When a hunter can shoot a wolf 1) when it moves towards a dog to attack 2) during an attack 3) after the attack or 4) a combination of the above then a maximum of 3 % of the Scandinavian wolves gets killed each year. This will save on average one dog per year from being killed; this number is low because few hunters really witness the attack. According to Backeryd (2007) abuse of these rules can therefore be easily detected.

Hunting has a strong tradition in both countries and the political influence of hunters is large (Heberlein & Ericsson 2008). Since wolf management is determined by politicians, arguments by hunters have been well represented in the decision making.

<u>Livestock</u>

Norway is famous for its traditional sheep farming system. More than 2 million sheep are free ranging in the Norwegian mountains and forests during summer, allowing the farmers to collect winter fodder on their small patches of agricultural land down in the valleys below. Norway doesn’t have many rich pastures. An additional benefit of this system is the decreased risks of parasite related diseases because sheep densities are lower (Asheim & Eik 2005). A disadvantage is predation by carnivores, and in particular large predators, because the free ranging livestock is mostly unattended during the whole summer, and thereby vulnerable, especially the lambs. Sheep and lambs that graze on outfield pastures are collected and counted in September, which gives the farmer the possibility to calculate the total sheep loss. An increase in sheep losses was documented; in the 1980's around 80 000 sheep and lambs were reported lost on outfield pastures, whereas in 2003 this numbers increased to around 130 000. Similarly, predator numbers increased as well. Although the documented losses were not only a result of predator attacks, significant losses were attributed to them. Asheim (2005) pointed out that the welfare conditions of sheep are negatively influenced by predator attacks. Sheep experience fear and great pains while under attack, and in case of survival they have to deal with wounds and infections, however, the sheep owners receive compensation for their losses.

Beside free ranging sheep there are free ranging domestic reindeer. Sweden has a compensation system that depends on the reproduction number of predators and not on the number of killed reindeer (Zabel & Holm-Müller 2008). Norway also has a compensation system for Saami reindeer loss to large predators (P. Wabakken pers.comm).

Wolf hunting

In Norway and Sweden the wolf population is controlled through license hunting. This management tool has been under debate for many years since the legal protection of the species, within both countries as well as on a worldwide level. The most recent case was in January 2010 when such hunting was allowed again for the first time in Sweden, after a 45-year period ban. A total of 237 wolves was estimated for Sweden, representing a surplus of 27 individuals following the Swedish management goal. An enormous high number of hunters (12 000), signed up to take part in this hunt and within four days the target was reached (Icenews, 25th January 2010). The hunt was controversial and Mikael Karlsson, the head of the Swedish Society for Nature Conservation (SSNC), claimed that the hunt was approved in order to please the hunters that had been asking for a hunt for years (Icenews, 25th January 2010) and he lodged a complaint with the European Commission. Similar commotion occurred in 2005, when Norwegian managers (DN) gave permission to shoot the first wolves by 426 licensed hunters, and all wolves were killed within during 15 days (Wabakken et al. 2005). At that time, the five wolves culled represented more than 40 percent of the next summer's potential breeders in Norway (Wabakken et al. 2005).

Illegal killing

Liberg et al (2008) used data of 76 radio collared wolves during the period 1998-2006 to study the causes of death. A total of 42 wolves died during this period, of which 15 (36%) were presumably illegally killed and 6 (14%) confirmed as illegally killed. 17% died of natural causes, 12% by car/train collisions, 14% during license hunt and 7% during research activities. P. Wabakken mentioned in an interview with the Norwegian newspaper that the disappearance of wolves caused stagnation in the population's growth in the beginning of this century; illegal hunting was suspected to be the cause (Aftenposten, 2004). The Swedish Environmental Protection Agency reports that 25% of the wolves are killed illegally (Swedish Environmental Protection Agency, 2007).

Human attitudes

Wolf acceptance in Scandinavia is lower than in many other parts in the world (Williams et al. 2002). In general negative attitudes towards wolves are found more with women, elderly people, less educated and rural inhabitants. Zimmerman et al. (2001) showed that people accept large carnivores more when they are used to live in the same area as the carnivores and when they live far away from them. Acceptance is lowest when carnivores arrive to human populated areas for the first time.

Many Swedes have weak attitudes to wolves (Ericsson & Heberlein 2003) and are therefore more shaped by cases that receive a lot of media attention. Since wolves are expanding in Sweden, more and more people will live in a wolf area. If people become more negative because of negative cases, such as live stock predation and the killing of hunting dogs, a change in human behaviour can occur (Ericsson & Heberlein 2003). Zimmerman et al. (2001) mentioned that re-establishing wolves can be negatively affected by local resistance and poaching .

Karlsson & Sjöström (2007) also stated that indirect negative experiences have a great effect on public acceptance. Although not many people experience a negative encounter with a wolf, if one does then the story spreads itself easily. Ericsson & Heberlein (2003) showed in his study that human attitudes can change strongly in time. In the mid 70's hunters were the most positive about wolf reintroduction in Sweden. However in 2003 their view was more negative, due to the fact that people expected wolves to settle down in mountainous areas and not in their own living areas. Thus, it is easier to support a hypothetical wolf than a wolf in reality (Heberlein & Ericsson 2008).

Røskaft et al. (2003) showed that Norwegians are mostly afraid of the larger carnivores in their country, namely bears (*Ursus arctos)* and wolves (*Canis lupus).* According to Linnell et al. (2002) it is not surprising that humans have become afraid of wolves. In Europe numerous wolf attacks have been reported, but only a few have been officially confirmed in Scandinavia. In the 19th century 31 people were attacked in Sweden during a 3 month period, of which 12 attacks were lethal. All of the victims were children with the exception of two young adults (18 and 19 year). When the wolf was shot the attacks stopped. Research determined that this wolf was kept by humans but managed to escape. Four other cases have been reported in Sweden in the 18th century. In Norway there is only one trustworthy case reported, this concerned a young girl on 28th December 1800 (Linnell et al. 2003). Linnell et al. (2003) pointed out that wolf attacks are rare and that one should put them in the right perspective. The number of attacks in Europe drastically decreased, mainly because of changed conditions. Rabies is more or less under control, children are barely used to herd a flock of sheep, wild prey availability increased, wolves or hybrids are not held captive outside zoos anymore and the heavy extirpation of wolves made them fearful of humans. Still, Linnell pointed out that wolf attacks should be taking into account as a possible event. Reduce the risk of rabies, prevent wolves from getting used to people and habitat/prey management represents the most important management responsibilities in this matter. Although fear is maybe not rational it should not be neglected in management.

Heberlein & Ericsson (2008) suggested that public acceptance can increase if urban citizens explore the countryside more often and initiatives to support this would be beneficial for future wolf acceptance. He also pointed out that it is important that wolves are not only considered as harmful by hunters, but that they could become a valuable asset. Sport hunting would be the most plausible possibility and in this way the hunter could become the protectors of the species that hunt. Hunting would also decrease the feeling of urban dominance. In many cases wolf restoration by rural citizens has been seen as a way of suppressing people that lives in the country side. Some feel that decisions were made, without any interaction with the local citizens. By giving them the ability to manage the population, could decrease this feeling of being powerless, and thereby help to increase the acceptance of wolves within the wolf distribution range (Heberlein & Ericsson 2008).

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