



# **Territorial dynamics of female wolverines**

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## Abstract

Spatial and social systems form the organisation of animals in space and time and are important aspects of animal ecology due to their effect on population dynamics and structure. In this study I investigate territorial dynamics of female wolverines, with particular focus on interannual territorial fidelity and reoccupation of territories vacated due to death of territorial females. To do this, I used location data and den site locations of adult female wolverines ( $n = 58$ ), collected from 1993-2008 in and around Sarek National Park, northern Sweden.

I found that female wolverines exhibited high interannual fidelity to territory. Resident females ( $n = 34$ ) were monitored for a total of 145.9 wolverine years, and only twelve females moved from their territories one or more times during the study, resulting in a total of 14 vacated territories. Hence, 9.6% of resident females moved from their territories annually. Fifty-eight percent of the females ( $n = 7/12$ ) that abandoned their territories established new territories, with a mean distance of 11.7 km between dens in their old and new territories.

Sixteen (70%) of territories vacated due to death of a resident female ( $n = 23$ ) were reoccupied by a replacing female. The mean territory overlap between the deceased female and her replacer was 75% (range 57-87). Sixty-nine percent of replacers ( $n = 16$ ) occupied vacated territories within a year. There was a new reproduction the first year after the territory was vacated in 30% of all the vacated territories ( $n = 23$ ). The time from reoccupation to first reproduction in the territory was significantly longer for juvenile and subadult replacers than for adult replacers. I found that 54% of the marked replacers were daughters and 15% were granddaughters of the deceased female. Every time a daughter was still present in the territory when her mother died, the daughter occupied the vacated territory.

My results suggest that the spatial organization of female wolverine territories in Scandinavia is characterized by long-term stability, as vacated territories are generally occupied by new individuals rather than absorbed by neighbours. Furthermore, in a population that is saturated with territories, deceased females are generally replaced by females from the local population, and primarily daughters if they are still present in the territory when their mother dies. Hence, local density of territorial females is resumed while emigration is decreased, which can have implications for adjacent populations. I also showed that the time from reoccupation to first reproduction for the replacing females varied considerably. This is important from a Swedish management perspective, as the local density, and possibly predation pressure, might recover quickly after removal of territorial females, while the amount of economical compensation, based on number of wolverine reproductions, to reindeer herding districts for predation losses is reduced until next reproduction in the territory. My study shows that the reoccupation process and time to next reproduction, effects on local density and emigration are important factors to consider when using removal of individuals to decrease predation pressure

The demographic importance of female survival for population growth is further emphasized by my results, which shows the strong influence of adult female survival on territorial dynamics and dispersal, and hence its effect on a larger scale.

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## Introduction

Spatial and social ecology are important aspects of animal ecology due to their influence on population structure and dynamics. Hence, understanding the organization of animals in space and time is essential because population dynamics are affected by the spatial arrangement and movements of individuals (Kernohan et al. 2001). With area requirements that exceed the size of most protected areas, large carnivore populations often coexist with humans in multi-use landscapes, and human-carnivore conflicts occur globally (Noss et al. 1996, Ginsberg 2001, Linnell et al. 2001). Hunting and lethal control (hereafter removal) are common tools for managing human-carnivore conflicts. Removal of individuals can affect not only carnivore demography, but also carnivore social systems (e.g., spacing pattern and dispersal) (Frank and Woodroffe 2001). Conversely, the social system can influence a population's response to removal of individuals (Tuytens and MacDonald 2000, Frank and Woodroffe 2001). Few studies have focused on the effect of removal on social systems and behaviour of the targeted carnivore species (Frank and Woodroffe 2001, Harding et al. 2001, Frey and Conover 2007). Thus, in addition to demographic studies, we need to study carnivore spatial and social ecology to increase our understanding of the effects of harvest. This understanding can help managers to find strategies to prevent conflicts with humans while maintaining viable populations of large carnivores.

Predation on livestock is one of the major and most common reasons for human-carnivore conflicts and can cause an economic burden for humans that coexist with carnivores (Nyhus et al. 2005, Thirgood et al. 2005). Predation conflicts appear to be particularly acute in areas where carnivore populations have re-established after being absent (Thirgood et al. 2005). The historical decline of carnivore populations in Scandinavia has resulted in husbandry systems where livestock are left unattended in grazing areas over long periods making them vulnerable to predation (Landa et al. 2000, Swenson and Andrén 2005). During recent decades, altered conservation policies have led to increases in numbers of wolverine (*Gulo gulo*), wolf (*Canis lupus*), brown bear (*Ursus arctos*), and lynx (*Lynx lynx*) and, consequently, increased depredation upon unattended livestock (Swenson and Andrén 2005). In northern Scandinavia, predation on semi-domestic reindeer (*Rangifer tarandus*) by mainly lynx and wolverine is the major human-carnivore conflict (Swenson and Andrén 2005).

Husbandry of free-ranging reindeer is an important cultural and economical component of the indigenous Sami culture in Scandinavia (Björvall et al. 1990, Landa et al. 2000). In contrast to that of other large carnivores in Scandinavia, the wolverine distribution is mainly limited to the reindeer herding area, where reindeer is the predominant prey (Persson et al. 2009). Hence, the predation conflict cannot be solved by complete protection of reindeer from predation because it would drastically influence the viability of the wolverine population (Swenson and Andrén 2005). The wolverine distribution also overlaps with summer grazing areas for domestic sheep in Norway (Landa et al. 2000), where sheep herding is of economic importance to farmers and rural communities (Bruteig et al. 2003). The present wolverine population consists of about 780 individuals in Scandinavia (Persson 2007). The species is listed as endangered in Sweden and Norway (Gärdenfors, 2000, Kålås et al. 2006). Thus, wolverine management in

Scandinavia faces a challenging task in preserving an endangered species in conflict with both sheep herding and an indigenous reindeer herding culture (Swenson and Andrén 2005, Persson et al. 2009).

The wolverine, known as a creature of the northern wilderness and remote mountain ranges, is the largest terrestrial member of the Mustelidae family (Banci 1994). This solitary mammal inhabits boreal forests and arctic and alpine tundra across Eurasia and North America (Banci 1994). Wolverines are generalist predators and scavengers with ungulates as the main diet component. Although most ungulates are obtained as carrion (Persson 2005), wolverines are capable of killing large prey such as moose (*Alces alces*) and reindeer (Björvall et al. 1990). Locally, livestock losses to wolverines are high in Scandinavia resulting in economic consequences for both reindeer and sheep husbandry (Swenson and Andrén 2005), and poaching comprises a significant portion of adult wolverine mortality in the Swedish reindeer area (Persson et al. 2009). Therefore, it is important to find management strategies that both reduce predation and enhance acceptance of wolverines.

Management strategies for the shared wolverine population differ between Sweden and Norway. In Norway, the compensation system is based on documented and assumed livestock losses, and wolverines are harvested both as quota-regulated hunts and lethal control (Swenson and Andrén 2005). The Swedish reindeer herding area is divided into 51 reindeer herding districts, and compensation is based on presence and reproductions of wolverines (and other predators) within each herding district (Swenson and Andrén 2005, Zabel and Holm-Muller 2007). Until now, the only legal harvest of wolverines in Sweden is limited lethal control targeting females with offspring to mitigate conflict in areas with high predation pressure (Persson et al. 2009.)

For a territorial species, such as the wolverine, vacant territories within the populations range are created by natural or human caused mortality. In addition, territories can become vacated due to abandonment by the resident animal. The population's response to these vacancies, (i.e. how they are reoccupied) depends on the social system of the species (Frank and Woodroffe 2001). Lidicker and Stenseth (1992) distinguish between resident animals that shift to a neighbouring territory and those that disperse to a new area secluded from the old. Animals that fail to establish territories after dispersal are called floaters and show more random movement over larger areas than resident animals (Lidicker and Stenseth 1992). A vacated territory could be occupied by a dispersing individual (Greenwood 1980), a neighbouring resident individual that expands or shifts into the vacated area (Lovallo and Anderson 1995, Benson et al. 2004), or by an offspring inheriting the area from the previous resident (i.e. natal philopatry [Waser and Jones 1983]). Space use and reoccupation of vacated territories can be affected by interactions between individuals (Kernohan et al. 2001). Thus, to examine how vacated territories are reoccupied, it is important to separate territories that are vacated due to death from those that are vacated due to abandonment by resident individuals, because the latter could be influenced by interactions between individuals.

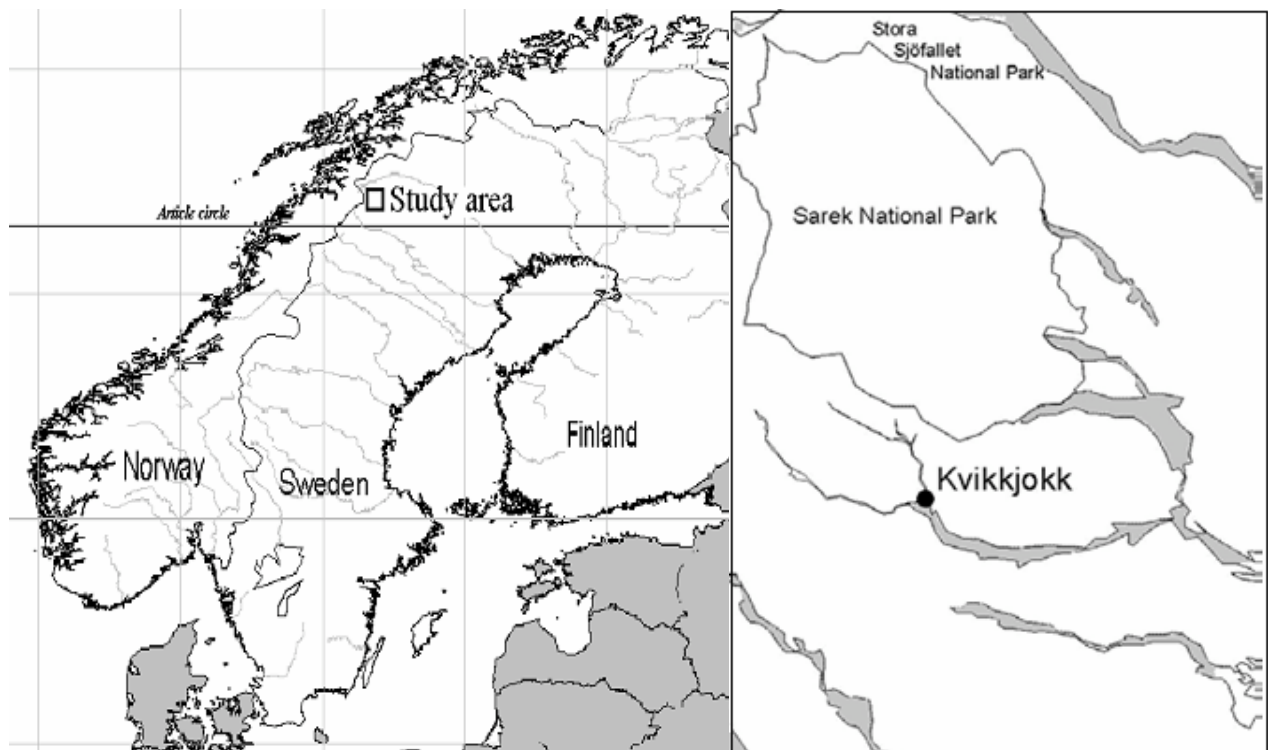
Because there are conservation concerns regarding the Scandinavian wolverine populations and individuals are being removed to decrease predation pressure on livestock, it is important to examine patterns of reoccupation of vacated areas after removal. Previous studies have consistently found that wolverines exhibit intrasexual territoriality and that the territory of one male encompasses the territories of several females (Banci 1994, Hedmark et al. 2007, Persson et al. 2010). However, information on territorial dynamics, e.g. stability and reoccupation patterns of vacated territories, is lacking. Because not all female wolverines reproduce each year (Persson et al. 2006), the next reproduction within a vacated territory does not necessarily occur in the year of reoccupation. Vangen et al. (2001) suggested that young female wolverines remained in their mother's territory if it was vacated before they reached dispersal age. This philopatric behavior could affect the reoccupation of vacated territories.

Long-term data from the Swedish Wolverine Project provides a unique opportunity to expand our understanding of spatial and social ecology of wolverines. My objective for this study was to examine the territorial dynamics of female wolverines. In particular, I examined the reoccupation of territories vacated due to death of resident females. To do this, I first analyzed territorial fidelity of female wolverines to identify territories that were vacated due to death of the resident female. Secondly, I examined the reoccupation of those vacated territories in terms of time to replacement, time to first reproduction following reoccupation, and degree of territorial overlap between the deceased female and her replacer. Thirdly, I examined the role of relatedness (e.g. mother-daughter) in territorial dynamics and reoccupation of vacated territories. Finally, I discuss implications of my results for wolverine management in Scandinavia.

## Material and method

### Study area

The study was carried out in a 7 000 km<sup>2</sup> area in and around Sarek National Park in northern Sweden above the Arctic Circle (Kvikkjokk 67°00'N, 17°40'E) (Figure 1). The climate is continental with cold winters (-10 to -13°C in January) and medium warm summers (13-14°C in July). The ground is usually snow covered from November to May and annual precipitation is 500-1 000 mm but higher (around 2500mm) in the western part (Påhlsson 1984). The area is characterized by deep valleys, glaciers, and high alpine plateaus with peaks up to 2000 m. The valleys are dominated by mountain birch (*Betula pubescens*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), with mountain birch forming the tree line at 600-700 m a.s.l. (Grundsten 1997). Semi-domestic reindeer are managed extensively by indigenous Sámi people. Moose is the only wild ungulate, but it occurs at low densities. There are breeding populations of both Eurasian lynx and brown bear. Wolves visit the area infrequently. The approximate wolverine density was 1.4/100 km<sup>2</sup> in the study area (Persson et al. 2006).



**Figure 1.** Scandinavian Peninsula with the study area in and around Sarek National Park (Kvikkjokk 67°00'N, 17°40'E), northern Sweden. (redrawn from Wedholm 2006)

## **Data collection**

I used telemetry and GPS data from 58 adult female wolverines (19 marked as juveniles) collected during 1993-2008. For details on capture, marking, and transmitters, see Persson et al. (2003), Persson et al. (2006), and Arnemo and Fahlman (2007). From 1993-1995, VHF-collars were used but during 1996-2008, all animals were equipped with implanted VHF-transmitters. In addition, 14 females were equipped with GPS-collars from 2004-2008. All transmitters had mortality sensors that detected the death of an animal. For animals that were not captured as juveniles (i.e. known age), we estimated approximate age using tooth sectioning (Matson 1981). The study was approved by the Animal Ethics Committee for northern Sweden, Umeå.

Radio-marked females were relocated from fixed-wing aircraft, helicopter, or from the ground using triangulation (White and Garrot 1990). Location precision was given as an estimated error-radius of 100 m around the location. I divided the study period into 3 periods based on monitoring intensity: From 1993-1998, females were relocated with high intensity (at least weekly) during the denning season (mid-February to the end of May) and bi-weekly thereafter. From 1999-2003, radio tracking was still intensive during the denning season but less frequent during rest of the year, focusing on detecting mortality instead of gaining exact locations. From 2004-2008, both VHF-transmitters and GPS-transmitters were used. Location intensity from the GPS transmitters was high (1-48 locations/day), but the animals were only periodically equipped with GPS-collars (1-12 months/year). Females with VHF transmitters were relocated following the same schedule as period two. Data on survival and mortality causes were obtained from Persson et al. (2009).

I used den site locations of marked and unmarked females. Den sites of marked females ( $n = 127$ ) were located with the combined use of radio tracking, GPS-locations, snow tracking, and visual observations (see Persson et al. 2006). Den sites of unmarked females ( $n = 86$ ; 1996-2008) were collected by County Administration personnel during the annual den surveys (cf. Landa et al. 1998).

### ***Interannual fidelity to territory***

I included females in the fidelity analysis at the time of their first known reproduction, which confirms they have established a territory. To analyze interannual fidelity to territory, I used distance between consecutive den sites as the overriding method. For years without a den site, I used interannual territory overlap or percentage of annual locations within the territory of previous years (Philips et al. 1998, Gorman et al. 2006, Breitenmoser-Würsten et al. 2007). I calculated distance between den sites using ArcGIS 9.2 (ESRI, Redlands California) and Hawth's Tools extension (Beyer 2004). I calculated annual territory using Minimum Convex Polygon (MCP; Mohr 1947) with Home Range Extension 0.9 (Rodgers and Carr 1998) for ArcView 3.3 (ESRI, Redlands, California). Year was defined as calendar year. I used 95% MCP to account for temporary excursions and I only used locations with a triangulation error < 1,000 m. If an animal's total territory is calculated from an insufficient number of locations, the estimation is not likely to show the animal's true territory (White and Garrott 1990, Kernohan 2001). Therefore, the sufficient number of locations required for home range estimations (the asymptote) should be known before analysis begins. However, some animals never reach an asymptote depending on their biology and behaviour (Harris et al. 1990). Linnell et al. (2007) suggested that when animals are monitored with low intensity, total sample size could be increased by decreasing location requirements, while still providing an approximated territory size. Persson et al (2010) were unable to find an asymptote and suggested that 20 locations were sufficient to estimate wolverine territory, based on regression analysis. Thus, I included animals with  $\geq 20$  annual locations for the annual territory estimation. I calculated the interannual territory overlap as a static interaction (Kernohan et al. 2001):

$$HR_{t,t+1} = A_{t,t+1} / A_{t+1}$$

where  $HR_{t,t+1}$  is the proportion of the territory for year  $t$  that is overlapped by the territory the following year ( $t+1$ ),  $A_{t,t+1}$  is the area of overlap between year  $t$  and  $t+1$ , and  $A_{t+1}$  is the territory for year  $t+1$ . Because territory size does not differ for females with or without cubs (Persson et al. 2010), overlap between years with and without reproductive events was calculated. For years when a female, included in the study, had < 20 but  $\geq 10$  locations, I calculated the percentage of locations contained within the range from previous years. For females that died during the study period, I examined if their death location was within their estimated territory from previous years. Additionally, for females that disappeared or had an unknown death location, I examined if their last known location was within their estimated territory from previous years. I excluded females with < 20 locations/year and no known den site from this analysis. Additionally, females followed for < 1 year were excluded.

I defined females as stationary if they remained in the same territory between years. I defined females as moving if they shifted or dispersed to a new territory, became floaters, or abandoned the territory and died or disappeared before their fate could be determined. Moving females were considered re-established in a new territory when they reproduced or when their continued interannual territory overlap showed that they became stationary

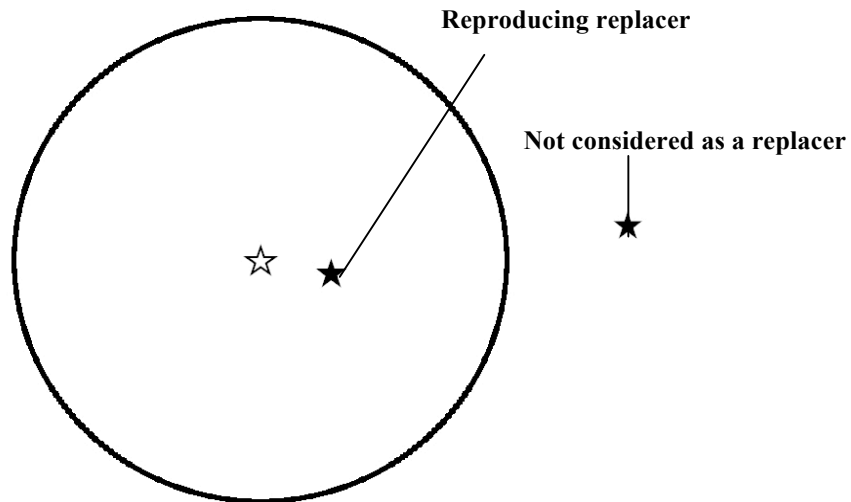
in a new area. To identify threshold values to separate stationary females from moving, I used distances between dens and amount of territory overlap between neighbouring females in this study area. The closest distance between known neighbouring females' den sites ( $n = 74$ ) during 1993–2008 was 5.7 km (cf. Wedholm 2006). The amount of territory overlap between neighbouring females was small (mean = 9%), and the largest overlap observed was 24% (Wedholm 2006, Persson et al. 2010). Therefore, I used 5.5 km between den sites and 25% interannual territory overlap as threshold values (i.e., if the distance between dens was  $\geq 5.5$  km or territory overlap was  $\leq 25\%$ , a female could have shifted to a neighbouring territory and was no longer considered stationary). For years without den site or territory estimations, I defined females as stationary if  $\geq 50\%$  of their locations occurred within the estimated territory for previous years. I considered females that died or disappeared as stationary their last year in the study if their death location or last known location was within the estimated territory from previous years.

### ***Reoccupation of territories vacated due to death of stationary females***

Only reoccupations of territories vacated due to death of a female that was considered stationary the year she died were included in this analysis. Reproducing females monitored for  $\leq 1$  year were considered stationary if their location of death was within 5.5 km of their den site and their vacated territories were included in this analysis. A female that occupied a vacated territory was defined as a replacer. I identified replacers by searching the database for den site locations of marked and unmarked females and locations of marked females. I refer to marked females that reproduced within vacated territories as marked reproducing replacers. They were considered replacers from the date their first location was detected within the vacated territory. I refer to unmarked females that reproduced within the vacated territory as unmarked reproducing replacers. They were considered replacers from when their den site occurred within the vacated territory. Additionally, I refer to marked females that occurred within a vacated territory but did not reproduce at any time as non-reproducing replacers. They were considered replacers from the date their first location was detected within the vacated territory. I analyzed reoccupation of vacated territories in two steps: 1) I identified replacers and estimated time to their first reproduction within the reoccupied territory, and 2) I calculated territorial overlap between the deceased female and her replacer.

### ***Identifying replacers and time to next reproduction***

I created a 5.5 km buffer zone around the last den site for the dead female using ArcGIS 9.2 (ESRI, Redlands, California) and Hawth's Tools (Beyer, H. L 2004). The first den found within the buffer zone after the territory became vacated was considered to belong to the reproducing replacer (Figure. 2).



**Figure 2.** To find the reproducing replacer a 5.5 km buffer zone was calculated around the deceased female's last den site (white star). The first den site found within the buffer zone was considered to belong to a reproducing replacer.

For marked reproducing replacers, I calculated the time from when the territory was vacated to their first location within the buffer zone ( $\text{time}_{\text{loc}}$  [months]). If  $\text{time}_{\text{loc}}$  was  $> 12$  months, I searched the database of marked females for an individual that occupied the vacated territory before the reproducing replacer. If  $> 50\%$  of the locations for a marked female occurred within the buffer zone during the period of interest, she was considered a non-reproducing replacer.

I divided marked replacers into two groups depending on where they were first marked: 1) females that were marked within the vacated territory and 2) females that were marked outside and later occupied the vacated territory. Furthermore, marked replacers were divided into juveniles (0-12 months), subadults (12-24 months), or 3) adults ( $> 24$  months) based on their age when they first occurred within the vacated territory.

I defined time to next reproduction ( $\text{time}_{\text{repr}}$  [year]) as the time from when the first reproduction could occur after the territory was vacated (i.e., March 1 after the death of the stationary female) to when it did occur. Additionally, I recorded distance and time from the last den site of the deceased female to the first den site of the reproducing replacer

### ***Proportion of the vacated territory occupied by the replacer***

I estimated the size of the vacated territory using the deceased female's locations from when she was considered stationary in a territory until she died. To estimate the territory for the replacer, I used locations from when she first occurred within the vacated territory until she moved, died, or disappeared from the study. All territories were estimated from  $\geq 20$  locations using Fixed Kernel (FK; Worton 1989) and Least Square Cross Validation to select smoothing parameters (Seamen et al. 1999). All calculations were done using Animal Movement extension (Hooge and Eichenlaub 1997) for ArcView 3.3 (ESRI, Redlands, California). When successive locations are dependent (i.e., autocorrelated),



they generate less information about movement pattern and range use than the same number of dependent locations (Swihart and Slade 1985). For spatial studies, Otis and White (1999) recommended that the biology of the animal is considered when the sampling interval is set. To avoid biological autocorrelation, I used one randomly selected location/day for territory estimations because wolverines can travel across their home range in less than one day (unpublished data). For individuals with both VHF and GPS locations from the same day, VHF locations were excluded. Additionally, Schoeners' Index (SI; Schoener 1981, Swihart and Slade 1985) was used to test for statistical independence. Location data were considered statistically independent for  $SI > 1$  (Kenward 2001).

The proportion of the vacated territory occupied by the replacer was calculated in the same way as interannual territory overlap:

$$HR_{1,2} = A_{1,2} / A_1$$

Here,  $HR_{1,2}$  is the proportion of the vacated territory that is overlapped by the replacer's territory,  $A_{1,2}$  is the area of the overlap, and  $A_1$  is the area of the vacated territory. When vacated territory estimates were known but the number of locations for the replacer was  $< 20$ , I calculated the percentage of locations for the replacer within the vacated territory. If the vacated territory could not be estimated, the overlap analysis was not carried out, even if the replacer had  $\geq 20$  locations.

### ***Natal philopatry and reoccupation of vacated territories***

To study the role of natal philopatry for the reoccupation of vacated territories, I examined the kinship between deceased females and their replacers. For replacers marked as juveniles, the mother was known. For the remaining replacers, I used DNA data analyzed by Hedmark et al. (2007). I considered the deceased female and her replacer to be mother and daughter when they had a relatedness value  $> 0.31$  (Hedmark et al. 2007). If a daughter replaced her deceased mother, the time from when the replacer was born until the territory became vacated (month) was recorded. If a deceased female was not replaced by a daughter, the entire dataset was searched to see if she had any daughters remaining within the study area when she died.

I examined if females that were defined as moving in the fidelity analysis had given birth to daughters sometime during the study before they moved. If a marked daughter was present within the study area when her mother moved, her locations and den sites were examined to determine if she had replaced her mother.

### ***Distance between natal den and first own den***

I determined if females marked as juveniles and monitored until their first reproduction had inherited their natal territory or had dispersed before reproducing. I calculated the distance between their natal den (i.e. the den they were born in) and their first den as a

reproducing female (hereafter first own den). I also examined if their mothers were still stationary or had moved, died, or disappeared from the study at the time the daughter reproduced for the first time. The distance between the daughter's natal den and first own den, combined with residency status for her mother, was used to determine if a daughter inherited her natal territory. If the distance between a female's natal den and first own den was  $< 5.5$  km, and her mother was not still stationary there, she was considered established within her natal territory. If the distance was  $< 5.5$  km but her mother was still stationary, both location and den site data for the two females were further examined to determine if the territory could be considered inherited by the daughter. In contrast, if the distance between a female's natal den and first own den site was  $\geq 5.5$  km she was considered to have dispersed.

## Result

During the study period, a total of 49 reproducing female wolverines were monitored for a mean of 3.7 years (0.1-11.4 years). Only four females were monitored for < 1 year. The remaining 45 individuals were monitored as reproducing adult females for a mean of 4.0 years (1-11.4). Fifteen (31%) of the reproducing females were marked as juveniles.

### *Interannual fidelity to territory*

Sufficient data for interannual fidelity analysis were available for 34 females. Seventeen (50%) of these were analyzed using only distances between consecutive den sites. For the remaining 17 females, den distances were combined with interannual territory overlap and percentage of annual locations within the territory of the previous years. For 13 females (38%), I used death location or last known location to examine if they were stationary their last year in the study. The distances between consecutive dens for individual females ( $n = 78$ , mean = 2.8 km, CI 2.1-3.6 km) were significantly shorter than the distances between dens for neighboring females ( $n=74$ , mean = 13.5 km, CI 12.4-14.5 km) (Mann-Whitney U;  $p < 0.01$ ).

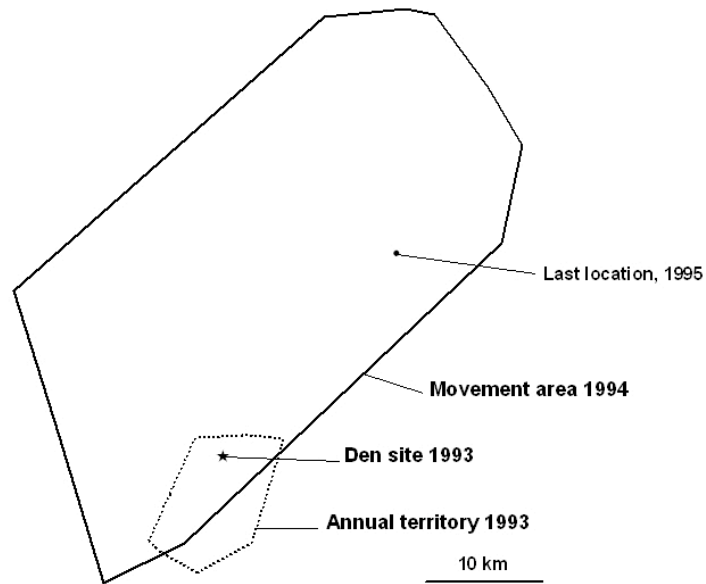
The 34 females were monitored for a total of 145.9 wolverine years. Twelve females moved from their territories one or more times during the study resulting in a total of 14 vacated territories. Hence, 9.6% of resident females moved from their territories annually. Age was known for 1 and estimated for 8 of the moving females. Mean approximate age at the time they moved was 5.5 years (SE 0.5), ranging from 3 to 8.

One female (F9869) was considered stationary although she had  $\geq 5.5$  km between successive den sites (5.8 and 7.2 km). All her den sites were within the territory estimated by her locations from her first year as marked. She placed consecutive dens at opposite sides of her territory resulting in these large distances.

Six of the 12 moving females reproduced after they moved and were considered re-established in new territories. Additionally, 1 female (F9525) did not reproduce but remained in the same area after she moved was considered re-established (Appendix 1). A total of 58% of the moving females re-established. Mean distance between the last den of a moving female in her old territory and her first den in her new territory was 11.7 km ( $n = 8$ , CI 10.3-13.1 km). In contrast, the mean distance between successive dens of stationary females was 1.8 km ( $n = 70$ , CI 1.5-2.2 km). Female 9530 moved 2 times, 1996 and 1998, she re-established both times and the distances between her den sites in the old and new territories were 12.2 km and 10.3 km, respectively. In 2003, F9762 expanded into a vacated neighbouring territory where she reproduced. After the expansion she maintained her previous territory where she reproduced again in 2005. Her new territory included the former territories of two females; due to this, the distance between her den sites indicated that she had moved two times (Appendix 1).

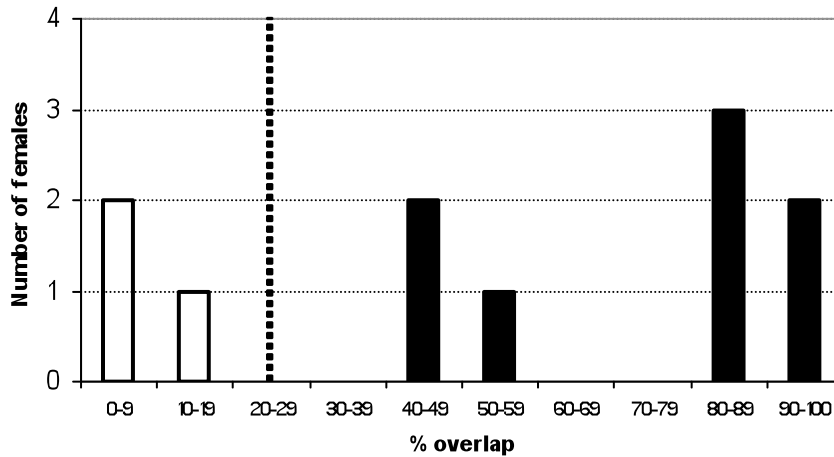
Three of the five females that did not reproduce after they moved had insufficient locations to determine their continued fate. The remaining two females (F9315 and

F9312) exhibited floating behaviour. In 1993, when F9315 reproduced, her territory was 85 km<sup>2</sup>, corresponding to average territory size of resident females (Persson et al. 2010). After she abandoned her territory in 1994, her locations covered 1 151 km<sup>2</sup>. She died in 1995 and the distance between her last den site and last known location was 22.8 km (Figure. 3). The locations for F9312 the year after she moved covered an area 10 times larger than her territory her last year as stationary (445 vs. 45 km<sup>2</sup>).



**Figure 3.** Spatial history for F9315. She was established in a territory where she reproduced in 1993. After she abandoned her territory in 1994, she ranged over an area 13.5 times larger than her 1993 territory .

The interannual territory overlap for all stationary females ranged from 41 to 100%, with an average of 72.4 % (n = 8, SE 7.8). For females that shifted territories, the average interannual territory overlap was 5.9% (n = 3, SE 4.4) ranging from 3.2 to 10% (Figure 4). Data from two females were analyzed using percentage of annual locations within their territories from previous years. Based on this analysis, one was considered stationary (77%) and the other moving (12.5%).



**Figure 4.** Interannual territory overlap ( $n = 11$ ) for female wolverines in and around Sarek National Park. I used the largest overlap observed between neighboring females (24%) to set a threshold value at 25% overlap (vertical, dashed line) to separate stationary (black bars) from moving (white bars) females.

### ***Reoccupation of territories vacated due to death of stationary females***

Twenty-six females were considered stationary when they died: 20 (77%) based on site fidelity analysis, 5 (19%) were monitored for <1 year and died within 5.5 km from their den site, and 1 (4%) that was assumed to be stationary because she remained within the same area even though her exact locations were not registered (J. Persson, pers.comm. 2009). Mortality cause for the 26 females were classified as natural ( $n = 5$ ), lethal control ( $n = 5$ ), marking ( $n = 2$ ), unknown ( $n = 3$ ), poaching ( $n = 4$ ), and assumed poaching ( $n = 7$ ) (Persson et al. 2009 and unpublished data).

### ***Identifying replacers and time to next reproduction***

Because 3 of the 26 females died at the end of the study period, I could not identify their replacers. Of the remaining 23 females, 16 (70%) were replaced by a reproducing replacer before September 2008 (Table I). Only 2 of 16 reproducing replacers were unmarked, although one of these was presumably an unmarked daughter of the deceased female (see section Natal philopatry and the reoccupation of vacated territories).

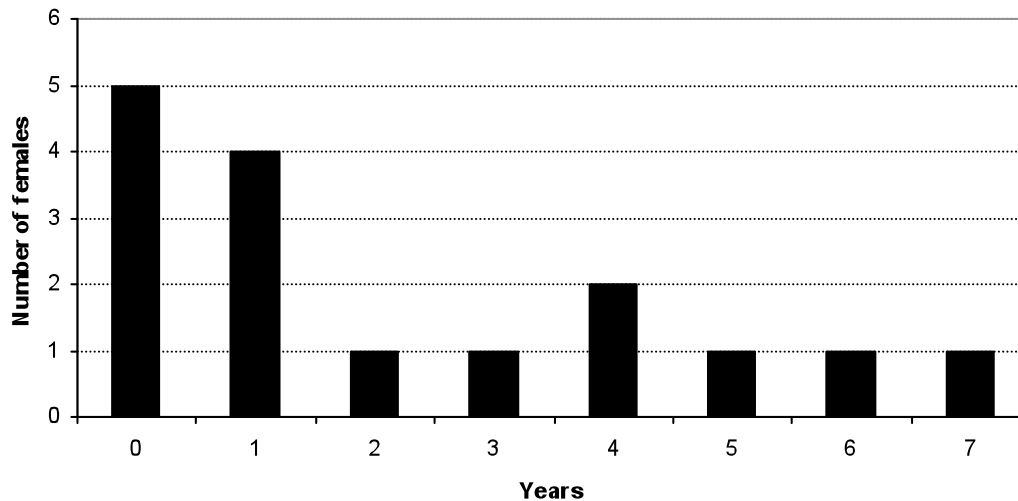
I estimated  $time_{loc}$  for 13 of the 14 marked reproducing replacers, ranging from 0 to 6 years (Table I). For 9 (56.2%) of the marked reproducing replacers  $time_{loc}$  was  $\leq 1$  year. For the 4 females with  $time_{loc} > 12$  months I searched for non-reproducing replacers. I found two non-reproducing replacers, F9525 in the territory vacated by F9648 and 9986 in the territory vacated by F9995 (Table I). F9648 was replaced by F9525, a female that moved into the territory the year after it was vacated and stayed there until she disappeared 3.5 years later. The first reproducing replacer to occupy this territory was F9762, the daughter of F9525 born before F9529 replaced F9648 (Appendix 1). F9995 was replaced by her daughter, F9986, marked as a juvenile 1 year prior to the death of F9995. F9986 remained for 4 years in her mother's old territory until she expanded into a vacated neighbouring territory where she started to reproduce. At her first reproduction

F9986 gave birth to a daughter (F04189) who became the reproducing replacer in the territory vacated by F9995 (Appendix 2). Both non-reproducing replacers (F9525 and F9986) occupied the vacated territory within a year after the death of the resident female.

Eleven (79%) of the 14 marked reproducing replacers were marked within the vacated territory, four were daughters of the deceased females and marked at birth, i.e., marked before the territory became vacated. Two of the 3 remaining marked reproducing replacers moved into the vacated territory. The remaining marked reproducing replacer, F9869, was a neighbour to F9873. The year after the death of F9873, F9869 placed her den at the edge of her territory, which overlapped with the buffer zone for F9873. F9869 did not expand into the vacated neighbouring territory, but were considered as the reproducing replacer after F9873 because her den site was the first found within the buffer zone. Both non-reproducing replacers (F9525 and F9986) were marked outside the vacated territory.

Age data were available for 13 of 14 marked reproducing replacers and both non-reproducing replacers. At the time when they first occurred within the vacated territory, two (15%) of the marked reproducing replacers were juveniles, 3 (23%) were subadults, and 8 (62%) were adults. Of the non-reproducing replacers (F9525 and F9986), 1 was juvenile and 1 was adult.

The first reproduction by replacers occurred within 0-7 years (mean  $\text{time}_{\text{repr}} = 2.19$  years) from the first possible denning season (March 1) after the territory was vacated (Figure 5). Mean distance between the last den of the deceased females and the first den of the reproducing replacers was 2.9 km ( $n = 16$ , CI 2.0-3.8) ranging from 0 to 5.3 km (Table I). There was a new reproduction the first possible year in 30% of all the vacated territories ( $n = 23$ ). The dens for 5 (31%) of the 16 reproducing replacers occurred within the buffer zone the first year possible (i.e.,  $\text{time}_{\text{repr}} = 0$ ).



**Figure 5.** Time to next reproduction ( $\text{time}_{\text{repr}}$ ) within a territory vacated by the death of the resident, calculated from March 1 after the death to the first reproduction of the known reproducing replacers ( $n=16$ ).

The time from when a reproducing replacer first occupied the vacated territory ( $time_{loc}$ ) to her first reproduction ( $time_{repr}$ ) was significantly longer for juvenile and subadult replacers (pooled; mean = 3.33 years) compared to adult replacers (mean = 0.25) (Mann-Whitney U;  $p = 0.003$ ).

### ***Proportion of the vacated territory occupied by the replacer***

The number of locations per individual for the 26 females defined as stationary when they died varied from 2 to 146. Fifteen (58%) had a sufficient number of locations to estimate the vacated territory (mean = 65; range 22-146). I found six pairs of deceased females and reproducing replacers for which both had sufficient numbers of locations for territory estimates (mean = 100, range 26-315). For three additional pairs, I calculated the percentage of locations for the reproducing replacer within the vacated territory. Mean proportion of the vacated territory overlapped by the reproducing replacer's territory was 75% ( $n = 6$ , SE 4.8,) ranging from 57 to 87% (Table I). Mean percentage of locations for the reproducing replacers within the vacated territory was 72% ( $n = 9$ , SE 7.5) ranging from 35 to 100% (Table I).

**Table I.** Replaced females that were stationary at time of death in Sarek National Park, northern Sweden, during 1993-2008. Reproducing replacer refers to the first female that placed her den < 5.5 km from the deceased female's last den before her death. Proportion of a vacated territory overlapped by the replacer's territory is expressed as either percentage of territory overlap (Overlap Territory) and/or percentage of the replacer's locations in the vacated territory (Overlap Locations). Non-reproducing replacers occupied the vacated territory before the reproducing replacer.

Dead female	Time of death	Reproducing replacer	Distance between dens (m)	$Time_{repr}$ (year)	$Time_{loc}$ (month)	Overlap		Non-reproducing replacer
						Territory	Locations	
F9419	Jun-98	F9983	921	4	11	57	51	
F9533	Apr-97	F9870	4080	0	13	87	76	
F9643	May-97	F9646	921	3	0	84	97	
F9651	Feb-00	F9879	4561	1	0	76	89	
F9540	May-03	F9986	1627	0	1	83	75	
F9648	Jan-97	F9762	2580	6	6 *	67	35	F9525
F9987	Dec-02	F02156	536	4	0		75	
F9647	Feb-00	F01148	4504	1	16		100	
F9873	Nov-04	F9869	5263	0	3		50	
F9869	Feb-07	F05192	4409	0	0			
F9993	Aug-00	F03171	223	2	32			
F9530	May-99	F01130	3132	1	24			
F9995	May-00	F04189	3715	7	48			F9986
F01130	May-01	F07216	5298	5	-			
F9538	nov-98	Unmarked	4800	0	-			
F9424	dec-94	Unmarked	0	1	-			

\*The mother of F9762 was the non-reproducing replacer after F9584, therefore the large difference between  $time_{loc}$  and  $time_{repr}$  (Appendix 1).

## ***Natal philopatry and reoccupation of vacated territories***

The kinship was known for 13 of 14 pairs of deceased females and marked reproducing replacers. Seven marked replacers (54%) were daughters of the deceased females, two replacers (15%) were granddaughters, and the remaining 4 (31%) were not closely related to the females they replaced (i.e., not daughter or granddaughter). The unknown replacer following F9538 was presumably a daughter (F9541) that lost her transmitter in 1996 but was recaptured within her mother's vacated territory in 2001. Of 2 deceased females with non-reproducing replacers, one was replaced by her daughter and one was unrelated to her replacer (Appendix 1 and 2)

Five of the 8 daughters that replaced their mother were marked as juveniles and remained in their natal territory on average 17 months (SE 2.8) before the mother died (Table II).

**Table II.** Length of time (months) wolverine mothers and daughters remained together in the mother's territory before the mother died. All daughters remained in the territories after the death of their mother.

Mother	Daughter	Time together (months)
F9987	F02156	9
F9643	F9646	15
F9651	F9879	23
F9869	F05192	24
F9995	F9986*	14

\* Non-reproducing replacer.

All daughters that replaced their mother were the only female in the litter the year they were borne and the only daughter alive within the study area when their mother died. Three of the deceased females (F9541, F9873, and F01142) had a daughter remaining within the study area but were not replaced by them. However, their daughters had already dispersed and established in a new territory when their mother died. When two of the 12 (17 %) moving females left their territory, their daughters were still present within the study area. In both cases the daughters inherited the territory vacated by their mother where they later reproduced.

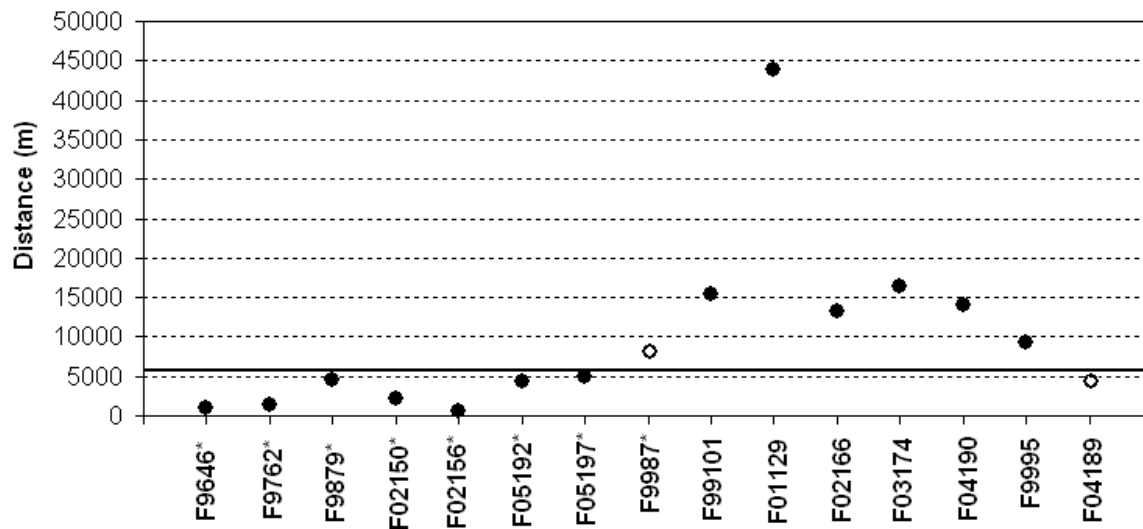
## ***Distance between natal den and first own den as a reproducing female***

Fifteen (30%) of the 50 study females were marked as juveniles and monitored to their first reproduction and distance between their natal den and first own den ranged from 0.5 to 44 km (mean = 9.5 km, SE 2.8 km; Figure 6).

Except for F04189, all 8 females with a distance < 5.5 km between her natal den and first own den replaced their mother after the mother died, moved, or disappeared. When F04189 reproduced, her mother (F9986) was still alive and stationary and data suggest that F9986 and F04189 split F9986's old territory (Appendix 2). All seven females with a distance  $\geq$  5.5 km between their natal den and first own den dispersed to a new territory before they reproduced. For all but F9986, the mother was still alive by the time her daughter first reproduced. F9986 remained in her natal territory after the death of her



mother but she did not reproduce until she expanded into a neighboring territory (vacated by her grandmother), resulting in a distance between dens of  $> 5.5$  km (Appendix 2). Average distance between the natal den and first own den for females occupying their mother's old territory was 3.4 km ( $n = 9$ , SE 0.8). For females that dispersed before reproducing, but remained within the study area, average distance between the natal den and first own den was 18.7 km ( $n = 6$ , SE 5.1).



**Figure 6.** Distance between natal den and first own den as a reproducing female for wolverines marked as juveniles. The black line indicates 5.5 km between natal den and first own den. Female with  $< 5.5$  km between natal den and own den inherited their natal territory. F04189 did not replace her mother even though she had  $< 5.5$  km between her natal den and first own den, F9987 did replace her mother even though she had  $> 5.5$  km between her natal den and first own den (white circles) (Appendix 2). \* indicates that, before the female reproduced for the first time, her mother either died, moved, or disappeared from the study.

There was no significant difference in the distance between a deceased females' last den and the replacers' first den (Mann-Whitney U;  $p = 0.29$ ) for replacers that were daughters (mean = 2.2 km) versus those that were not (mean = 3.2 km).

## Discussion

My study shows that wolverine females in Scandinavia exhibit high fidelity to territory and that their spatial system show long term stability. The death of a territorial female creates vacated areas that are occupied by new individuals rather than absorbed by neighbours, hence the local density of territorial females resumes when vacated territories are reoccupied. The time to reoccupation was usually less than 1 year and a majority of the replacers were daughters to the deceased female. This territorial inheritance reduces the time to reoccupation, while it generally increases the time to next reproduction within the vacated territory. Because deceased females are primarily replaced by females from the local population, local density is resumed whereas emigration/dispersal to adjacent areas would likely decrease with decreased adult female survival.

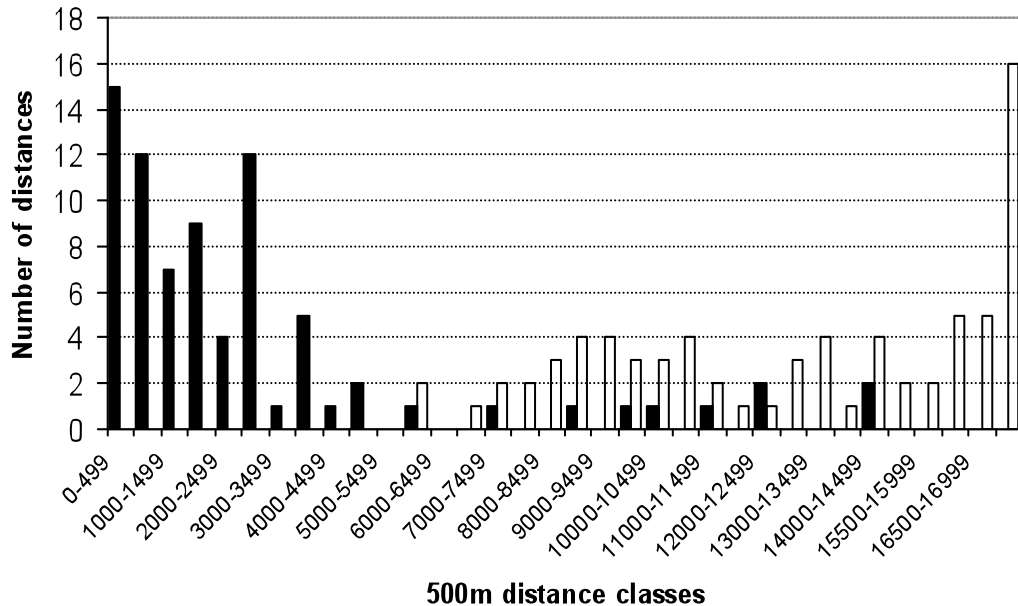
### *Interannual fidelity to territory*

I suggest that the high fidelity to territory observed for female wolverines is a result of their intrasexual territoriality, which is maintained by territory marking and aggressive behavior (Persson et al. 2010). Furthermore, the population density and territorial saturation in the study area is high (Persson et al. 2010) and increased competition for territory reduces the possibilities to shift territory (Moorhouse and Macdonald 2005). Similarly, females in other Mustelid species exhibit high fidelity to home range (Gorman et al 2006; Zalewski and Zędrzejewski 2006).

Although interannual fidelity to territory was high in this study, 9.5% of resident females abandoned their territories annually. To understand territorial dynamics in wolverines, it is crucial to reveal the underlying factors that lead to abandonment. Abandoning an established territory in an area that is saturated with established territories is associated with potential costs (e.g. aggressive behavior from territorial females, traveling through unfamiliar areas, establishing and defending boundaries of a new territory, and the risk of not finding a potential territory in which to reproduce). For females to abandon their territories, the costs associated with abandoning a territory should be less than the cost of staying (Switzer 1993). Possible reasons for females to abandon established territories are 1) resources within the existing territory are not sufficient for successful reproduction and the ability to increase territory size is hindered by neighboring territories at high population density (Persson 2005), 2) another female forces the territory owner to vacate her territory (Switzer 1997), or 3) females vacate an established territory in favour of her offspring (Waser and Jones 1983). Additionally, understanding territorial dynamics requires an examination of interactions between females that result in altered territorial ownership. Knowledge about age, reproductive success, survival, and kinship for both moving and replacing females would provide important insight into territorial dynamics of female wolverines.

Distances between consecutive den sites for individual females were significantly shorter than the distances between den sites of neighboring females. Distance between dens provided a means of measuring territorial fidelity for female wolverines, and the threshold value used was adequate, as a high proportion (86%) of distances between

consecutive dens for individual females were shorter than distances between dens of neighboring females (Figure. 7). However, to be able to use the same distance criteria for different populations it is important to consider the need for similar territory and movement patterns resulting from similar ecology and habitat characteristics (Linnell et al. 2007). For wolverine populations that differ in home range size, territorial saturation, or other factors, a threshold value must be found using data from the population of interest.



**Figure 7.** Distances between consecutive dens of individual females (filled bars) and all dens of neighboring female' (blank bars) within Sarek National Park, northern Sweden, from 1993 to 2008. Because the closest distance between neighboring females' dens was 5.7 km, a threshold value at 5.5 km (vertical, dashed line) was used to differ between stationary and moving females.

The interannual overlap threshold value used to distinguish between stationary and moving individuals varies greatly among other studies. Breitenmoser-Würsten et al. (2007) classified lynx with 55 and 58% interannual overlap as moving, while Nielsen and Woolf (2001) required that annual territories had to be exclusive for bobcats (*Lynx rufus*) to be classified as moving. Additionally, Phillips et al. (1998) used  $\leq 10$  locations within the range of previous years to classify martens (*Martes americana*) as moving. Because my main concern was to distinguish established territories vacated due to death from territories abandoned by the resident female, I used the maximum territorial overlap between neighboring females as the threshold value to avoid classifying moving females as stationary. The interannual overlap for females classified as stationary ranged from 48-95 %, while the range for females classified as moving was 4-10% (Figure 4). The gap between 10 % and 48% indicates a clear distinction between interannual overlaps for stationary and moving females and that a threshold value of 25% is adequate, and even conservative. The use of MCP, which likely underestimates total territory size with few

locations (White and Garrot 1990), is a conservative method compared to Fixed Kernel which likely overestimates territory size with few locations (Seaman et al. 1999). If annual territory size is underestimated, I would be more likely to underestimate the overlap area (i.e. classify stationary individuals as moving) than vice versa. By choosing both a conservative threshold value and range estimator, I risked classifying stationary females as moving. However, the highest interannual overlap for females classified as moving (10%) was far below the threshold value and, therefore the number of moving individuals was not overestimated.

Other methods used for fidelity analysis are distance between home range centroids and multi-response permutation procedures (White and Garrot 1990, Kernohan 2001). Both these methods use distances between individual locations; the former calculates a mean location for the yearly location distribution and compare those between years, while the latter examines if yearly sets of locations originates from the same distribution. Because the data used in this study was skewed towards the denning season, the location distribution would be influenced by the den location, complicating comparison between years with and without reproducing events. I used distance between dens to compare between years with reproductions, and annual MCP to compare the total area used in years with and without reproductions, thereby avoiding the bias toward locations around dens in reproduction years.

In this study, I focus only on the site fidelity of female wolverines. Because the underlying factors affecting spatial structure and territoriality differ between males and females (Sandell 1989), their site fidelity might differ. For example, Phillips et al. (1998) found that female martens either maintained a high degree of fidelity between seasons or completely abandoned their home ranges, while the spatial structure of males was more flexible at adapting to altered resources and space availability. For better understanding of the spatial structure of wolverines, the results from this study should be combined with studies of territorial fidelity of males.

### ***Reoccupation of territories vacated due to death of stationary females***

I found reproducing replacers in 70% of the vacated territories. Although some territories were probably not reoccupied during the study period, this is presumably a minimum estimate, because I did not expect to find all replacers in vacated territories before the end of the study. Reasons for this include; 1) den sites of unmarked females were not found, or 2) a territory could have been reoccupied by a non-reproducing replacer not followed by a reproducing replacer, and hence are missed with the method used. I found replacers in all territories vacated before 2002. Thus, the maximum number of consecutive years any of the vacated territories without replacers could have been empty was six years. The maximum time from when a territory was vacated until a reproducing replacer was first located in the territory was also six years. Hence it is possible that there were still no reproducing replacers in the empty territories at the end of the study.

Eleven of the 14 marked reproducing replacers and 1 of the non-reproducing replacers were either daughters of marked females or were captured before the territory they occupied was vacated. Hence, only 4 (25%) of the identified reproducing replacers had no known connection to the study population. Depending on the number of vacated territories without identified replacers that were actually reoccupied, and the proportion of those replacers that had previous connection to the study population, the proportion of the deceased females that were replaced by individuals from the local population ranged from 52-75%. That a majority of replacers had a known connection to the study population is probably explained by shorter time to detection of vacated areas or that previous experience of the area increases the settlement chances (Bruinzeel and van de Pol 2004). Similarly, vacated territories are re-occupied by individuals from the vicinity in cougar (*Felis concolor*) and stone marten (*Martes foina*) populations (Laing and Lindzey 1993, Genovesi et al. 1997).

The majority (69%) of the replacers (both reproducing and non-reproducing) were present in the vacated territory within a year after the resident female died. However, there was a new reproduction in only 30% of all the vacated territories the year after they were vacated. A delay from reoccupation to reproduction is expected because not all adult wolverine females reproduce each year (Persson 2006). In addition, age of the replacer affects time until next reproduction as shown by the significantly higher time from occupation to first reproduction for young (juvenile and subadult) compared to adult replacers. Persson et al. (2006) showed that the mean proportion of adult females that reproduced annually in this study area was 0.53. Hence, if the original female had survived (i.e. the territory was not vacated), a new reproduction next year was expected in 53% of the territories. Factors that affect time to next reproduction in a vacated territory include the time it takes for a replacer to occupy the territory, reproductive frequency, age of the replacer and the presence of non-reproducing replacers.

Removal of predators can have different short and long term effects on local population density (Côté and Sutherland 1993, Harding et al. 2001, Frey and Conover 2005). To study long term effects, the underlying factors contributing to the spatial distribution of individuals is important as these affect reoccupation of vacated areas and therefore the local density (Frey and Connover 2005). If spatial distribution is mainly affected by competition for food or other habitat resources, neighbouring individuals would increase their territories by expanding into vacated areas, resulting in decreased local population density (e.g., Baker et al. 2000). On the other hand, if spatial distribution is not primarily affected by competition, the removal of resident individuals does not affect the distribution of neighbouring individuals. Hence, removal creates opportunities for dispersing individuals to establish in the local population, thereby maintaining density of territory holding individuals at the same level. In this study, deceased female wolverines were replaced by a new female that occupied a large proportion of the vacated territory. Several studies of other carnivore species have found that vacated territories are reoccupied by dispersing individuals of the same sex (Smith et al. 1987, Laing and Lindzey 1993, Benson et al. 2004, Breitenmoser-Würsten et al. 2007). I observed two occasions when a female wolverine expanded into a neighbouring territory after it was vacated. However, one of these expanded territories was later divided between mother

and daughter, and the spatial distribution of territories was resumed. In conclusion, my results suggest that the spatial structure of wolverine females shows long term stability.

In major parts of my study area the territorial saturation is high (Persson et al. 2010). Spatial dynamics might be different in a less saturated population where vacancies exist prior to removal of individuals. Territories vacated due to the death of resident females may not be reoccupied if there are more suitable areas available, furthermore the time to reoccupation will probably increase. While this study suggests that vacancies in a saturated population will mainly be occupied by individuals from the local area, vacancies in a less saturated population would be reoccupied by immigrants more often.

That most of the removed individuals in this study were replaced suggest that the long-term density of wolverine females does not decrease following removal at the rate observed in the study area. However, removal might affect the wolverine population in Scandinavia on a larger scale. Because most vacated areas are reoccupied by individuals from the same area, emigration rate to adjacent areas would likely decrease with increased removal. A more generalized view of the effects of removal on wolverine social systems and spatial structure requires a comparison of the reoccupation process in populations with different local densities, territory saturation, and removal rates.

### ***Natal philopatry and reoccupation of vacated territories***

In this study 67 % of the replacers (n=15) were closely related to the deceased female (i.e., 8 daughters and 2 granddaughters). In all cases where a daughter was still present within the territory when her mother died or moved, the vacated territory was occupied by the daughter. This suggests that the mother-daughter relationship is an important aspect of territorial dynamics of female wolverines, and that kinship is important in the reoccupation process. Territorial inheritance affects the reoccupation of vacated territories by reducing the time to reoccupation, while the time to next reproduction might increase. Potential reasons for the observed natal philopatry are that female offspring benefit from remaining in a familiar area (Haugland and Larsen 2004) and that the cost of dispersing is high (Waser 1996). Similarly, other studies have shown that daughters replace their mothers; in some species daughters inherit their natal territory when the mother dies (Breitenmoser-Würsten et al. 2007, Laing and Lindzey 1993), some species form matrilineal assemblages when daughters establish in proximity to their mother (Smith et al. 1987, Zedrosser et al. 2007), additionally, in some species mothers bequeath their territory in favour for their offspring (Berteaux and Boutin 2000).

In this study, 47% of females monitored from birth to their first reproduction occupied their natal territory. Additionally, one female occupied her natal territory as a non-reproducing replacer for 4 years before she expanded into a vacated neighbouring territory. However, I did not analyse true dispersal pattern because I only included females that remained within the study population. Therefore, the proportion of non-dispersing juveniles is most likely an overestimation and the dispersal distance (18.7 km) is probably an underestimation. Accordingly, an earlier study showed that 30% of juvenile wolverine females in this study area did not disperse (Vangen et al. 2001). The

distance between the natal den and first own den for females that did not inherit their natal territory indicates that they disperse beyond neighbouring territories which suggests that wolverines do not generally form matrilineal assemblages.

The main type of territorial inheritance was that a daughter remained in her natal territory after the death of her mother. This suggests that wolverine females exhibit opportunistic philopatry (Waser and Jones 1983), where individuals disperse to the nearest vacated area, which happens to be their natal territory if the mother dies before the offspring reaches dispersal age. Average age at the time of their mother's death for daughters that inherited their natal territory was 17 months, corresponding to the dispersal age of young females (13 months [Vangen et al. 2001]). Interestingly, for 2 mother-daughter pairs the time spent together (23 and 24 months) well exceeded the average age for dispersal, indicating underlying factors that prolong the time to dispersal for some young females. Examinations of interactions are needed to find if this is a form of philopatry by parental consent (Waser and Jones 1983), or a result of parent-offspring competition. I observed one case where a territorial female (F9651) was killed by intraspecific strife and replaced by her daughter (F9879), however, it was not possible to identify which individual killed F9651. I observed two other types of territorial inheritance: 1) the mother moved while the daughter remained (i.e., bequeathal) and 2) the mother abandoned a part of her territory, which was subsequently occupied by her daughter (i.e. splitting). One possible explanation for bequeathal is that the mother abandons her territory in favour of her offspring because a young individual faces greater risks while dispersing than an adult would, and an adult is more likely to establish a new territory than a younger animal (Waser and Jones 1983). On the other hand, competition between mother and daughter might force the mother to abandon her territory. By 8-10 months of age, there is no obvious size difference between young and adult female wolverines (unpublished data). Every time a daughter was present in the territory at the time a female moved, the daughter remained and became the replacer. However, 83% of the moving females did not have a daughter present in the territory when they moved (unpublished data). Therefore, bequeathal to an offspring is not the main reason for females to abandon their territories. The one case of splitting that I observed (Appendix 2) occurred following the expansion of a resident female into a neighboring territory. After the expansion she gave birth to a daughter and the expanded territory was subsequently divided between mother and daughter, resuming same territories as before the expansion. A mother might expand her range beyond her own survival needs before sharing with an offspring to reduce the costs of splitting a territory (Waser and Jones 1983). Additionally, I observed one other occasion when a female (F9762) expanded into a vacated neighboring territory (Appendix 1). At the end of the study, F9762 still maintained the expanded territory and she had not given birth to any daughters.

To further understand patterns of territorial inheritance in wolverines, it is important to examine factors that could reveal whether natal philopatry is a consequence of parental consent or of daughters conquering their natal territories. One approach would be to examine the interactions between mothers and daughters during the time they are together.

## Management implications for Scandinavia

Removal of female wolverines might have only a short-term effect on local density and distribution of territorial females as long as the recruitment of female offspring and/or immigration exceeds the removal rate. Furthermore, Landa et al. (1999) found that removal of wolverines led to decreased lamb losses shortly after the removal but this effect declined quickly when new individuals established in the vacated territories. The local density might recover quickly after removal of territorial females, while time to next reproduction is prolonged. This is interesting from a reindeer herding perspective, as the economical compensation for predation losses in the Swedish reindeer herding area is mainly based on number of reproductions. Therefore, on a small scale (e.g. reindeer herding district), this might cause reductions in the amount of compensation even if the local density of territorial females is resumed after removal. Hence, when removal of territorial females is used to decrease predation pressure it is important to consider the reoccupation process and its effects on local density and time to next reproduction.

Removal of individuals can be used to temporary reduce predation pressure even if long-term local density is not reduced. Harding et al. (2001) used demographic models to evaluate how removal of red fox (*Vulpes vulpes regalis*) affected the predation pressure on California Clapper Rail (*Rallus longirostris obsoletus*) and found that, to have a long-term effect, effort should be made to control juvenile and immigrant foxes to decrease the reoccupation rate. For wolverine management in Scandinavia, it is important to examine factors influencing reoccupation rate and to understand how different removal strategies influence the type of replacers and the time to first reproduction in the vacated territory, to target the desired categories in removal programs. The success of removal programs on reducing predation also depends on predation rates by targeted categories of individuals and on timing of the removal programs. For instance, Conner et al. (1998) suggested selective targeting of individuals causing high predation losses to reduce coyote (*Canis latrans*) predation on domestic sheep. However, Linnell et al. (1999) hypothesized that, when livestock is free ranging, most individuals have the opportunity to kill livestock because encounter rates are high so problem individuals that cause a high proportion of the predation are not likely to appear. Identifying areas, rather than individuals, with a high predation rate or where the prey species are more vulnerable is an alternative. Thus, to decrease wolverine predation on reindeer, we need more information on predation rates for different categories and different areas. Furthermore, timing of removal should be considered (Conner et al. 1998). To have the highest effect, predators should be removed shortly before the predation peak to minimize replacement before the sensitive period. For summer-grazing sheep in Norway, the predation peak is in late summer (Landa et al. 1999, May et al. 2008). Predation on reindeer calves is highest in the late summer and autumn (Björvall et al. 1990, Landa et al. 2001). Wolverine predation on adult reindeer is lower than predation on calves (Björvall et al. 1990) and there are no studies that show a predation peak for adult reindeer. In Sweden, lethal control is mainly carried out in May-June when resident females with young are removed from presumably sensitive areas (e.g. calving areas). This control targets resident individuals before the predation peak on reindeer calves. When using less selective quota-regulated harvest, removed individuals are more likely to be nonresidents with higher movement rates than residents (Waser 1996). Removal of territorial females before potential daughters have



dispersed might promote instant reoccupation by daughters, if they are old enough to survive on their own, which would increase the time until next reproduction. Wolverine cubs display independence when about 6-months-old (Landa et al. 2005). Furthermore, Vangen et al. (2001) reported that a 7-month-old female dispersed and I found that a 9-month-old female replaced her mother. This suggests that juvenile females would survive on their own from early-autumn, while mean dispersal age is 13 months (March-April) (Vangen et al. 2001).

Importantly, when considering the effects of harvest and lethal control, it is essential to consider different spatial scales. Because removal reduces emigration from the targeted area, this can affect population densities in adjacent areas. Hence, there might be a negative effect in more sensitive populations outside the targeted area. Additionally, removal of individuals does not result in long-term reduction in local density of territory holding females if removal does not exceed the recruitment of female offspring or immigration (Lindzey et al. 1992). Therefore, increased removal would eventually lead to decreased local density. Adult female survival is the most important demographic parameter for population growth (Persson et al. 2005). This importance is further emphasized by my results, showing the strong influence of adult female survival on territorial dynamics and dispersal, and hence its effect on a larger scale, not only the targeted area.

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### **Personal comments**

Persson, Jens. 2009. Project leader of the Swedish Wolverine project. Grimsö.



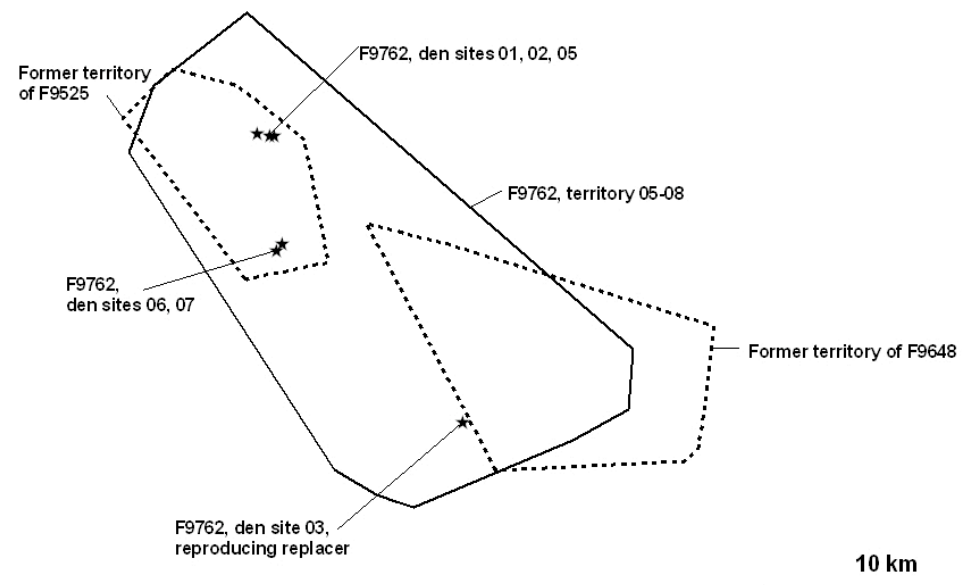
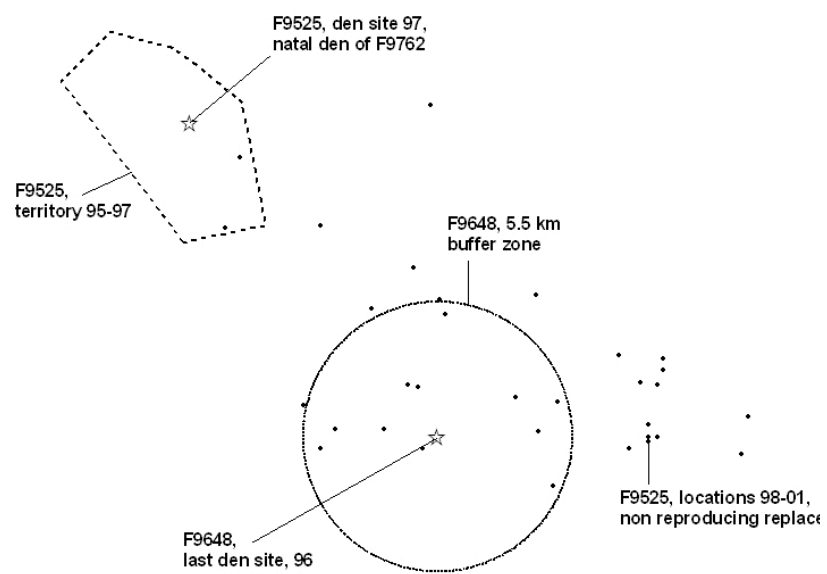
## Appendix 1

### ***Non reproducing replacer, territorial inheritance and expansion into a vacated neighboring territory***

F9648 died in January 1997 and the next reproduction within the vacated territory belonged to F9762 in 2003, 6 years later. The first location for F9762 occurred within the vacated territory 6 months after the death of F9648. At that time F9762 was approximately 5 months old. Additionally, F9762 first reproduced within her natal territory before she became the reproducing replacer in the territory vacated by F9648. I searched the dataset to find an explanation for the time gap between the first location and first den site for F9762 within the territory vacated due to the death of F9648.

The mother of F9762 (F9525) was a neighbour to F9648. The distances between den sites for F9525 from 1995 to 1997 suggest that she was stationary during that time. When F9648 died the locations for F9525 indicates that she shifted to the vacated neighboring territory. Because 32% of the locations for F9525 from 1998-2001 (n=32) occurred within the vacated territory (i.e. buffer zone) and while only 6% occurred within her old territory from 1995-1997, F9525 abandoned her old territory. F9525 never reproduced within her new territory, and was therefore considered a non-reproducing replacer after F9648. This explains the early locations for F9742 within the territory vacated by F9648, as she was still following her mother. After her mother moved, F9762 inherited her natal territory, where she reproduced 2001 and 2002.

After the death of F9525 in the summer 2001 the locations for F9762 and her den site 2003 indicates that she expanded to the west, into the area vacated by her mother. The den site for F9762 in 2003 was the first reproducing replacer after F9648. After her expansion, F9762's territory included both her natal territory and the old territory of F9648. Locations from 2005-2008 shows that F9762 still inhabit an area that was earlier divided into two territories. In 2006, F9762 again placed her den at the east end of her expanded territory, leading to a distance between dens >5.5 km even though she remained within the same territory. After her expansion in 2003, F9762 only gave birth to males.



## Appendix 2

### ***Mother-daughter relationship affecting territorial dynamics across 4 generations; influencing non-reproducing replacer, territorial expansion and territorial split***

F9995 died in year 2000 and the time to next reproduction within the vacated territory was 7 years. Because the time until the first location for the reproducing replacer occurred within the vacated territory was 48 months, I searched the dataset for a non-reproducing replacer. In 1999, one year prior to her death, F9995 gave birth to a daughter (F9986). The distance between the den sites 1999 and 2000 for F9995 was 1.7 km, showing that F9995 was stationary until she died. I created a 5.5 km buffer zone around the last den site for F9995 and found that 86% (n=22) of the locations for her daughter (F9986) from 2000-2003 occurred within the buffer zone. This suggests that F9986 was the non-reproducing replacer after F9995. The neighboring female (F9540) remained stationary during the entire period.

After the death of F9540 in May 2003, F9986 started to expand into the vacated neighboring territory. At the time of her first reproduction in 2004 the territory of F9986 included the old territories of both F9995 and F9540 and her den site was located 1.7 km from the last den of F9540. Location data for 9986 from 2003-2005 indicates that she remained possession of her old territory 5 years after the expansion. Due to her territorial expansion, F9986 was not considered to have dispersed from her natal territory (see section Distance between natal den and first own den) even though the distance between her natal den and first own den site was >5.5 km (i.e. 7.8 km). F9540 was the mother of F9995 (borne 1995 and dispersed to a neighboring territory) and consequently the grandmother of F9986 who now occupies both her mother's and grandmother's old territories.

In 2004, F9986 gave birth to a daughter (F04189). The distance between following den sites for F9986 shows that she is stationary in the west side of her expanded territory until today. At the time of the first reproduction of F04189 her den site was located in the eastern half of her mother's territory. Examination of GPS positions for both F9986 and F04189 illustrates that the old territory of F9986 was split between mother and daughter in 2006. Consequently, after the territorial split both F9986 and F04189 occupied the territories earlier inhabited by their grandmothers respectively. Due to this territorial split F04189 was counted as dispersing female (in section "Distance between natal den and first own den") even though the distance between her natal den and first own den site was <5.5 km (i.e. 4.3 km).

