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'O Neighbour, Where Art Thou?'

Spatial and social dynamics in wolverine and lynx, from individual space use to population distribution

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Abstract

The organisation of individuals in space and time influences population structure and dynamics, and is important for our understanding of animal ecology. The aim of this thesis is to gain an increased understanding of the mechanisms driving the abundance and distribution of solitary carnivores, from individual space use to population-level distribution. I used individual-level spatial and demographic data from Eurasian lynx (*Lynx lynx*) and wolverines (*Gulo gulo*), collected over more than 20 years in multiple areas within Scandinavia, to assess space use determinants and link territorial dynamics to dispersal patterns. For lynx, female total home range size declined as roe deer and lynx density increased. Male total home range size also declined with higher lynx density, while prey only became important for determining the size of more intensively used areas within the home range. There is also a positive effect of roe deer abundance on lynx survival in south-central Sweden. Roe deer is a predictable prey source compared to migrating reindeer, the main prey for lynx in northern Sweden. I found that home range overlap between neighbouring lynx increased with their relatedness (mother-daughter) for females in northern Sweden, but not for males nor females in the south. This finding suggests inclusive fitness benefits of sharing an unpredictable and highly seasonal food source with known relatives. The wolverine study population was characterized by a stable distribution of resident individuals with high territorial fidelity. When a territory became vacant in the study area, it was almost exclusively reoccupied by a female from the surrounding area. The availability of a young female’s natal territory substantially increased the probability of her establishing in the study area. Furthermore, the probability of a young female leaving the study area increased as the number of available territories decreased. This finding suggests that the study population is saturated, with limited room for dispersers to establish, which suggests that emigration to surrounding areas is related to survival of resident females. Wolverines in Sweden have expanded into boreal forests south and east of alpine areas. However, the recolonised areas with limited snow cover remain largely unmonitored. Most females gave birth in natal dens in mid-February, and rarely moved their cubs between den sites for the first two months, while lactating and while prey availability was low. After weaning, den shifting over longer distances increased, matching the seasonal increase in prey availability. Increased knowledge of spatial and social dynamics can give insights into how these populations are influenced by human activity, as well as the outcome of management actions.

Keywords: adaptive management, breeding dispersal, carnivore, conservation, dispersal, *Gulo gulo*, home range, *Lynx lynx*, Scandinavia, solitary, territoriality

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Dedication

To Jens, Glenn and Nora, you give me a reason to get up in the morning.

"I don't see much sense in that," said Rabbit.
"No," said Pooh humbly, "there isn't. But there was going to be
when I began it. It's just that something happened to it along the way."
A.A. Milne, The House at Pooh Corner (1928)

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Aronsson, M., Low, M., López-Bao, J.V., Persson, J., Odden, J., Linnell, J.D.C. & Andrén, H. (2016). Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. *Ecology and Evolution*, 6(9), 2957–2967.

II Andrén, H., Aronsson, M., López-Bao, J.V., Samelius, G., Chapron, G., Rauset, G.R. & Persson, J. Effects of prey density and human activity on Eurasian lynx survival in human-dominated landscapes. (*Manuscript*)

III Aronsson, M., Åkesson, M., Low, M., Persson, J. & Andrén, H. It´s relative: Resource dispersion and relatedness influence home range overlap in a solitary carnivore (*Manuscript*)

IV Aronsson, M. & Persson, J. Female breeding dispersal in wolverines; a solitary carnivore with high territorial fidelity. *(Manuscript*)

V Aronsson, M., Low, M., Andrén, H., Ordiz, A., Segerström, P. & Persson, J. The link between local territorial dynamics and dispersal patterns for female wolverines (*Manuscript*)

VI Aronsson, M. & Persson, J. 2016. Mismatch between goals and the scale of actions constrains adaptive carnivore management: the case of the wolverine in Sweden. *Animal Conservation,* 1–9. doi:10.1111/acv.12310.

VII Persson, J., Aronsson, M., Andrén H. & Low, M. Reproductive timing and denning behaviour of female wolverines in relation to resource availability and population monitoring (*Manuscript*)

Papers I and VI are reproduced in the thesis with the permission from Wiley, Paper I is published with open access.

The contribution of Malin Aronsson to the papers included in this thesis was as follows:

I Designed the study together with HA, ML, JP and JVLB. Performed spatial analysis. Performed statistical analysis with support from ML. Wrote the manuscript with contribution from co-authors.

II Designed the study together with HA and GS. Performed spatial analysis. Wrote the manuscript together with HA.

III Designed the study together with ML, HA and JP. Performed spatial analysis. Performed statistical analysis with support from ML. Wrote the manuscript with support from MÅ, JP and contribution from co-authors.

IV Designed the study together with JP. Performed spatial and statistical analysis. Wrote the manuscript with support from JP.

V Designed the study together with JP, ML and HA. Performed spatial analysis. Performed statistical analysis with support from ML and HA. Wrote the manuscript with support from JP and contribution from co-authors.

VI Designed the study and collected the data together with JP. Analysed the data. Wrote the manuscript together with JP.

VII Designed the study together with JP. Performed spatial and statistical analysis. Assisted JP in writing of the manuscript.

1 Introduction

The arrangement and movement of individuals in space and time influences population structure and dynamics, and are important aspects of our understanding of animal ecology (Sutherland 1996; Kernohan *et al.* 2001; Morales *et al.* 2010). Thus, the performance of populations is the result of individual performance. Many animals restrict their movements to a specific area, called a home range (Burt 1943), which is determined by access to critical resources for individual fitness (Börger *et al.* 2008; Morales *et al.* 2010). Furthermore, the organization of animals is determined within a complex social context of interactions between individuals (Hofman *et al.* 2014). Consequently, the spatial organization of animals results from individual interactions and the utilization of resources under various environmental conditions (Gomper & Wayne 1996; Maher & Lott 2000; Adams 2001; Morales *et al.* 2010). Intraspecific competition for limited resources may result in territorial behaviour (Brown 1964; Adams 2001), ranging from partial home range overlap to exclusive space use (Maher & Lott 2000), which could have important consequences for demography and population regulation. Landscapes consist of mosaics containing patches of various quality habitat that influence the fitness of animals (Wiens 1976; Pulliam 1988). According to despotic distribution theory (Fretwell & Lucas 1970), highest quality territories will be occupied first and result in an unequal division of resources between individuals, which might influence survival and reproductive success. Consequently, social and spatial dynamics and their determinants have important consequences for population dynamics; from individual home range size, fidelity and overlap, to regional and population level density and distribution.

For solitary, polygamous species, sex-specific space use patterns are expected to emerge when female fitness is largely determined by resources for offspring provisioning; hence a female is expected to use the minimum area required to sustain herself and her offspring, while male fitness and hence space use is primarily aimed at maximizing mating opportunities (Emlen & Oring

1977; Clutton-Brock and Harvey 1978; Sandell 1989). The importance of different resources, as well as individual interactions, might also vary within sexes on both a temporal scale (*e.g.* due to seasonal breeding and offspring rearing; Gittleman & Tompson 1988), and on a spatial scale (*e.g.* when factors that influence total area used do not determine more intensively used areas within the whole; Johnson 1980), resulting in spatio-temporal variation in space use pattern. Furthermore, important space use determinants may be strongly correlated in natural systems, making it difficult to disentangle their individual effects (*e.g.* food and conspecific density; Benson *et al.* 2006). Additionally, the effects of different determinants might vary within populations due to *e.g.* different environmental conditions causing important patterns to vanish at the population level (Maher & Lott 2000). Consequently, multiscale approaches are needed to understand how the relative importance of sex-specific space use determinants change in both space and time (Börger *et al.* 2006a; van Beest *et al.* 2011; Campos *et al.* 2014), as well as fine scale differences within populations, to improve our current understanding of the flexibility of animal spatial organization (Maher & Lott 2000; Hofman *et al.* 2014).

Because resource availability is often heterogeneous in space and time, the dispersion and predictability of resources are important factors influencing home range size, as well as overlap between neighbours (Maher & Lott 2000; Adams 2001; Macdonald & Johnson 2015). Resource predictability influences the degree to which an animal can depend on its environment over time, and larger home ranges are needed to account for higher spatiotemporal resource variability (Johnson *et al.* 2002; Eide *et al.* 2004). The area required to sustain an individual may support additional individuals during periods of high resource availability, increasing home range overlap (Johnson *et al.* 2002). However, the presence of additional animals may inflict high costs during periods of resource scarcity, resulting in strong year-round territoriality and constant overlap independent of temporal resource fluctuations (von Schantz 1984). Furthermore, the cost of competition may be offset by inclusive fitness benefits of sharing resources with related individuals (Hamilton 1964; Reyer 1984; Parker *et al.* 2002; Hatchwell 2010), and several recent studies have showed that relatedness is an important factor influencing space use pattern in non-cooperative, solitary species (Kitchen *et al.* 2005, Stoen *et al.* 2005, McEachern *et al.* 2007, Maher 2009, Meshriy *et al.* 2011, Messier *et al.* 2012, Innes *et al.* 2012, Quaglietta *et al.* 2014).

Individuals' fidelity to an area provides insight into the stability of the spatial and temporal organisation of animals. Site fidelity is generally associated to dispersion, predictability and depletion rate of resources, as well as reproductive success, age, and competition (Moorhouse & Macdonald 2005; Kirk *et al.* 2008; Edwards *et al.* 2009; Terraube *et al.* 2015). Home range fidelity is beneficial because it allows individuals to become familiar with resources in an area (Switzer 1993; Kirk *et al.* 2008) and for species that aggressively defend territories, movement into unfamiliar areas increases mortality risk (Isbell *et al.* 1990; Stamps & Krishnan 2001). Despite this benefit, some reproductive individuals may vacate an established territory to re-establish and reproduce elsewhere (*i.e.* breeding dispersal; Greenwood 1980). Breeding dispersal may be a consequence of reproductive failure, mate loss or an attempt to acquire a higher-quality territory (Wauters *et al.* 1995; Forero *et al.* 1999; Pasinelli *et al.* 2007). It can also result from intraspecific competition, both when resident individuals are evicted or disperse to take over a territory (Pasinelli *et al.* 2007; Mattisson *et al.* 2013). Breeding dispersal has also been considered as a form of parental investment when the territory is bequeathed to an offspring to enhance offspring survival and reproductive success when competition for available areas is strong (Lindström 1986; Berteaux & Boutin 2000).

Dispersal of individuals has direct consequences for population structure and dynamics, from individual fitness to species distribution, colonization and persistence (Kokko & López-Sepulcre 2006; Ronce 2007; Clobert *et al.* 2009; Benton & Bowler 2012). The dispersal process is divided into three stages – departure, transience and settlement – with potentially different factors affecting these stages (Bowler & Benton 2005; Clobert *et al.* 2009; Bonte *et al.* 2012; Matthysen 2012). Although natal dispersal (*i.e.* the departure from the natal site to an individual's first breeding site) is a commonly studied aspect of animal dispersal, the causes and consequences of natal philopatry (*i.e.* an individual remaining and breeding in its natal area, Greenwood 1980; Waser & Jones 1983) is an often-underestimated aspect, despite its importance for understanding the factors driving animal dispersal decisions (Clutton-Brock & Lucas 2012). Most polygamous species have a sex-biased dispersal pattern; consequently, population distribution is primarily limited by dispersal of the more philopatric sex. Dispersal can act as both a cause and effect of ecological patterns and processes (Starrfelt & Kokko 2012), and knowledge about the reciprocal relationship between local social dynamics and dispersal is needed to link individual level spatial and social organisation to population level density and distribution.

Large carnivores in Scandinavia had been hunted almost to extinction by the early 20th century, but have substantially increased due to subsequent legal protection, largely outside of protected areas (Chapron *et al.* 2014). The conservation of large carnivores is often challenging because they use large areas, compete with hunters for game, and prey upon domestic animals (Woodroffe 2000; Treves & Karanth 2003; Thirgood *et al.* 2005; Redpath *et al.* 2013). Because individual spatial and social organisation has a strong influence on population dynamics and distribution, it is important for our understanding of how carnivores are influenced by human activity. Large carnivores have large area requirements, often very high dispersal capacity, and therefore wide distributions across habitats of different quality. Different levels of human activity may often also result in spatial differences in survival of individuals across landscapes (*e.g.* Delibes *et al.* 2001; Basille *et al.* 2013). Furthermore, licensed hunting and/or lethal control are commonly used tools to decrease damage caused by carnivores, often based on the general assumption that this will reduce local population density (Herfindal *et al.* 2005; Robinson *et al.* 2008; Minnie *et al.* 2016). However, the effect of harvest on local population density depends on species-specific factors such as life history, social structure and dispersal patterns, as well as general population density (Frank & Woodroffe 2001; Milner *et al.* 2007; Robinson *et al.* 2008; Cooley *et al.* 2009; Minnie *et al.* 2016). Consequently, knowledge from individual-based studies of space use and dispersal at different scales will increase our understanding of the reciprocal interaction between harvest and spatial dynamics, and thus facilitate management at the appropriate scale. Questions that are important to address in this context include what factors influence size, overlap, and stability of home ranges; spatial differences in survival; and how these differences could influence dispersal patterns. In addition, individual-based studies of space use can also add valuable information for the proper design of population monitoring programs for the focal species.

2 Objectives

The aim of my thesis is to increase our understanding of the mechanisms explaining the abundance and distribution of solitary carnivores, from individual space use, at the home range level, to the distribution of animals at the population level. I also assess the implications of the gained knowledge for management of carnivores. To achieve my aim, I used individual-level spatial and demographic data from two solitary carnivores, the Eurasian lynx (*Lynx lynx*) and the wolverine (*Gulo gulo*), collected during a period of more than 20 years from multiple study areas within the Scandinavian populations of these two species.

My thesis is composed by the following seven objectives:

1. To disentangle the spatiotemporal influences of the two main drivers of space use patterns, prey and conspecific density, on lynx sex-specific home range size. (*Paper I*)

2. To assess lynx survival in relation to habitat, and investigate the relative importance of human vs. non-human-caused mortality for the spatial distribution of risk in the landscape. (*Paper II*)

3. To investigate how genetic relatedness influences lynx spatial organization, and whether this effect is universal or changes with environmental conditions, such as resource dispersion. (*Paper III*)

4. To examine the stability of wolverine spatial organisation by assessing internal territorial fidelity in relation to age and reproductive success. (*Paper IV*)

5. To investigate the link between female territorial dynamics and dispersal patterns in wolverines, and how this affects local and regional population density and distribution. (*Paper V*)

6. To assess wolverine population size and distribution with specific focus on recent recolonization of forest landscapes outside high-conflict areas, and to evaluate how well current monitoring methods document this range expansion. (*Paper VI*)

7. To determine the timing of reproduction and denning behaviour of wolverine females in relation to foraging strategies and resource distribution, and assess how this knowledge could be implemented in population monitoring and management. (*Paper VII*)

3 Study system

3.1 Eurasian lynx (*Lynx lynx*)

The Eurasian lynx is the largest of the world's 4 lynx species (females: 16 kg, males: 22 kg), present in 11 populations across Europe, from the 'Balkan′ and 'Carpathian' in the south-east to the 'Karelian' and 'Scandinavian' populations in the north (Chapron *et al.* 2014). In Scandinavia, lynx were almost hunted to extinction by the early 20th century, but due to legal protection and hunting restrictions, they have recovered during the last decades and are now widespread throughout Sweden and Norway (Fig. 1; Chapron *et al.* 2014).

The lynx is a solitary and territorial felid, with a polygamous mating system where 1 male overlaps several females (Breitenmoser-Würsten *et al.* 2007; Mattisson *et al.* 2011*a*). Approximate home range sizes are 300–700 km^2 for females and 600–1700 km^2 for males (lower range in the south and upper range in the north of Scandinavia; Herfindal *et al.* 2005; Mattisson *et al.* 2011*a*). Lynx mate in March (Mattisson *et al.* 2013) and females give birth to ~2 kittens in late May/early June (Gaillard *et al.* 2013). Juveniles become independent at 8–10 months and they have a male-biased dispersal pattern where all young males disperse while approximately one third of the young females establish in the vicinity of their natal range (Samelius *et al.* 2012). Most male and female subadults have settled by 18 months of age (Samelius *et al.* 2012). The lynx is an ambush predator, specialized on medium-sized ungulates (Jedrzejewski *et al.* 1993). In south-central Scandinavia, their main prey is roe deer (*Capreolus capreolus*; Nilsen *et al.* 2009; Odden *et al.* 2013; Andrén & Liberg 2015), whereas semi-domestic reindeer (*Rangifer tarandus*) is the main prey in northern Scandinavia. Additionally, in Norway lynx prey on free-ranging domestic sheep during the summer (Odden *et al.* 2013). The main mortality causes for lynx in the Scandinavian multi-use landscape are legal hunting, poaching and vehicle accidents (Andrén *et al.* 2006; Basille *et al.* 2013).

Lynx populations are monitored on a yearly basis in both Sweden and Norway, through a joint monitoring program (SEPA 2014*a*). The main monitoring unit is family groups, based on snow tracking of ≥2 animals tracked together (*i.e.* females with kittens born the preceding summer; Linnell *et al.* 2007). The monitoring takes place from 1st October to 28th February and is mostly carried out by snow tracking during December to February. Total population size estimates are calculated for both countries based on the counts of family groups (Andrén *et al.* 2002); in 2016 the estimate was ~1,600 individuals (1,300 in Sweden and 300 in Norway; Tovmo *et al.* 2016). Based on the monitoring results in relation to national population size goals (870 and 390 family groups in Sweden and Norway, respectively), quota hunting takes place in late winter/early spring in one or both countries. Lethal control is used as a management tool to decrease depredation conflicts in both Sweden and Norway.

3.2 Wolverine (*Gulo gulo*)

The wolverine is the largest terrestrial mustelid (females: 10 kg; males: 15 kg), with a circumpolar distribution occupying tundra and taiga habitat in the northern hemisphere (North America and Eurasia; Copeland 2010). In Europe, the wolverine distribution is limited to Fennoscandia and Russia, where they are divided into the ‘Scandinavian’ and ‘Karelian’ population (Chapron *et al.* 2014). Due to intense persecution, the Scandinavian wolverine population was reduced to a very low level and in 1960s it was restricted to restricted to northern alpine areas (Haglund 1965; Flagstad *et al.* 2004). Wolverines became protected 1969 in Sweden, 1973 in southern Norway and 1982 in remainder of Norway (Persson 2003), and have now recolonized large parts of central to northern Scandinavia (Fig. 1; Chapron *et al.* 2014; Persson & Brøseth 2011; Aronsson & Persson 2012).

The wolverine is a solitary carnivore with a polygamous mating system and is highly territorial within the sexes (Hedmark *et al.* 2007; Persson *et al.* 2010; Inman *et al.* 2012*a*). Approximate home range sizes are 200 km^2 for females and 700 km2 for males (Persson *et al.* 2010; Mattisson *et al.* 2011*a*). Wolverines have low reproductive rates, female rarely reproduce before 3 years of age and mean number of cubs per adult female per year is 0.84 (Persson *et al.* 2006; Rauset *et al.* 2015). Female reproductive success is influenced by winter food availability as well as age-related reproductive costs, where the probability of successfully reproducing two years in a row declines with age (Persson 2005; Rauset *et al.* 2015). Wolverines give birth in February-March, earlier than other non-hibernating northern carnivores (Inman *et al.* 2012*b*), and female keeps their cubs in a snow-covered den, often in steep and rugged terrain (Magoun &

Copeland 1998; May *et al.* 2012; Makkonen 2015). Young wolverines exhibit a male-biased natal dispersal pattern, and both males and females generally disperse at 13 months of age (Vangen *et al.* 2001; Flagstad *et al.* 2004; Inman *et al.* 2012*a*). The wolverine is a generalist predator and scavenger, often scavenging for extensive periods and caching food for later use (Haglund 1965; Mattisson *et al.* 2011*b*; Inman *et al.* 2012*b*, Mattisson *et al.* 2016). In Scandinavia, wolverines primarily prey on semi-domestic reindeer and free-ranging domestic sheep in Norway during the summer (Mattisson *et al.* 2016). They frequently scavenge kills made by other more efficient predators such as the lynx (Mattisson *et al.* 2011*b*), and wolves (van Dijk *et al.* 2008). The worldwide distribution of wolverines is hypothesized to be limited by the spatial extent of persistent spring snow cover due to its importance for reproductive success (*i.e.* den site suitability; Magoun & Copeland 1998; Copeland *et al.* 2010) and/or limited by cooler conditions that are favourable for caching, especially during the lactation period (Inman *et al.* 2012*b*).

The yearly monitoring of wolverine populations in Sweden and Norway is primarily based on minimum counts of reproductive events (*i.e.* documentation of active den sites and females with cubs). The monitoring period is from 1st February until 31st July, and is mostly carried out by snow tracking during the denning season. A suspected den site is classified as a reproductive event depending on criteria in the monitoring protocol (SEPA 2014*b*). In addition to monitoring of reproductive events, observations of wolverines (*i.e.* visual observations or tracks) validated by authorized personnel are recorded, and wolverine scats are collected for DNA-analysis. Coordinates for reproductive events as well as scat samples and observations are stored in the joint Swedish and Norwegian database Rovbase (rovbase30.miljodirektoratet.no). National population estimates are calculated each year, using a population model that includes the average number of registered reproductions in the last 3 years (Landa *et al.*, 1998; Brøseth *et al.*, 2010; Anon, 2015*a*). In 2016, the population size estimate was 850 individuals > 1 years old (500 in Sweden and 530 in Norway; Brøseth *et al.* 2016). In Sweden, the number of wolverines is below the national goal (at least 600 individuals; SEPA 2014**b**), hence only strictly regulated lethal control is implemented to reduce depredation conflict (SEPA 2014*b*). In Norway, on the other hand, there is a yearly quota hunt for wolverines from mid-September to mid-February, to reduce the population to the national goal of 39 reproductions (Ministry of Environment, 2003).

3.3 Study areas

The studies included in my thesis are conducted within the Scandinavian Lynx Research project SCANDLYNX (http://scandlynx.nina.no) and The Swedish Wolverine Research Project (http://www.wolverineproject.se). Both projects have been going for ≥20 years and consequently for my thesis I have used data collected during different time periods from different study areas on the Scandinavian Peninsula (Fig. 1, Table 1).

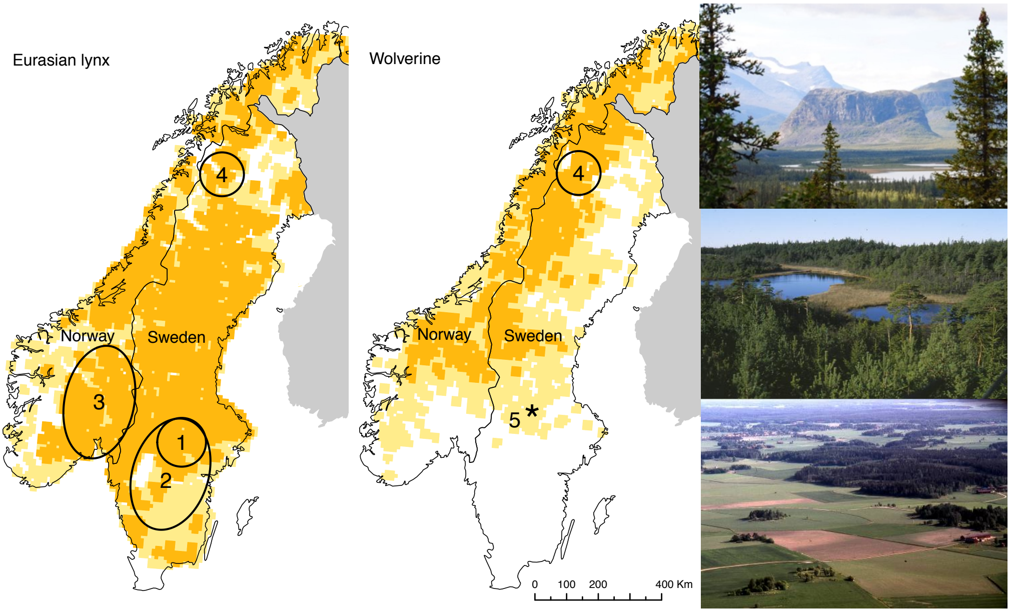


Figure 1. The distribution of the Eurasian lynx (left) and wolverines (centre) in Scandinavia in 2011, dark cells indicated areas of permanent occurrence, light cells indicate areas of sporadic occurrence (Chapron *et al.* 2014). Numbers indicate the different study areas included in this thesis (see Table 1). Photos to the right shows examples of the habitat characteristic in Sarek (top), Bergslagen (middle) and southern Sweden (bottom).

Table 1. *Study areas, study period study species and main data type used in the different chapters included in this thesis.*

	Name	Study species	Paper	Main data type	Study period
1	Bergslagen	Lynx	III	Collared individuals	1996-2010
2	South-central Sweden	Lynx	I, II	Collared individuals	1996-2010
3	Southern Norway	Lynx	I	Collared individuals	1996-2012
4	Sarek	Lynx, Wolverine	III–V, VII	Collared individuals	1993-2014
5	Southern Dalarna	Wolverine	VI	Camera trapping	2013-2014

3.3.1 Bergslagen and South-central Sweden

Lynx research started in 1996 in the Bergslagen study area (8000 km^2), located mainly in Örebro and Västmanland counties, centred around Grimsö Wildlife Research Station (59°30′ N, 15°30′E). The area is dominated by coniferous forest (*i.e.* Norway spruce [*Picea abies*] and Scots pine [*Pinus sylvestris*]), interspersed with birch (*Betula pubescens* and *B. pendula*) and aspen (*Populus tremula*) (Esseen *et al.* 1997). The forest is intensively managed for timber and pulp, creating a mosaic of even-aged forest stands of different age classes. Agricultural land covers about 5% of the landscape (< 1% in the north and increasing to the south). Roe deer is the main prey for lynx in the area (Andrén & Liberg 2015). Roe deer are solitary or living in small groups, and in south-central Sweden they are stationary within <1 km2 home ranges (Hewison *et al.* 1998; Cagnacci *et al.* 2011; Morellet *et al.* 2013). Consequently, at the lynx home range scale, roe deer are relatively evenly dispersed and predictable, although there is some local variation since roe deer abundance is positively correlated to agricultural land (Bouyer *et al.* 2015). Alternative prey species in the area include hares (*Lepus spp.*), grouse (*Tetrao spp.*) and rodents (*Rodentia*) (Andrén & Liberg 2015). Moose (*Alces alces*), wolves (*Canis lupus*) and foxes (*Vulpes vulpes*) are also present.

In Sweden, the lynx population is expanding southward, after year 2000 lynx started to colonise areas south of Bergslagen (Andrén *et al.* 2010). To study this colonisation, the lynx research project started to capture and collar lynx also south of the Bergslagen study area, forming the south-central study area. During this period, lynx were continuously captured and collared in Bergslagen until 2010; hence depending on the study question I use the Bergslagen study area or the whole south-central Sweden study area. The south-central study area reaches down into the hemiboreal zone, which is still dominated by coniferous, birch and aspen but also interspersed with temperate broad leaved species such as ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), lime (*Tilia cordata*) and oak (*Quercus robur*) (Esseen 1997). Altitude ranges from 30 to 500 m a.s.l. and primary productivity, human density, road density increases to the south, as well as the proportion of agricultural land. Roe deer is still the main prey for lynx in the whole area, although red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) occur in the central and southern parts.

3.3.2 Southern Norway

In Hedmark county (northern part of the southern Norway study area Fig. 1) lynx research started in 1995. In 2001 the study was moved to the central and south-eastern part, and from 2006 in the southern and western part (Odden *et al.* 2013).

The southern Norway study area encompasses several environmental gradients from north to south. The northern part is characterized by several river valleys at around 200–300 m a.s.l., separated by hills reaching to 700–800 m a.s.l. The forest is mainly managed coniferous forests (*i.e.* Norway spruce and Scots pine). The western part resembles the northern part, but with deeper valleys, steeper terrain and higher mountains between the valleys. In the central and south-eastern part the altitude is ≤ 300 m and there is both coniferous and deciduous forests (mainly birch). The landscape is more human-modified compared to the northern part and the forest is fragmented by cultivated land. In the southern part the landscape is increasingly human-modified. Environmental productivity increases to the south, whereas winter snow cover increases to the north. Roe deer is the main prey for lynx in the whole area and roe deer density is lowest in the north and north-western parts and increases to the south. Alternative prey species are hares, grouse, rodents and some occurrence of red deer in the south-western parts as well as some wild mountain reindeer at higher altitudes in the northern part. The whole study area has free-ranging sheep (*Ovis aries*) grazing in forest and alpine-tundra habitats during summer. Moose, wolves and foxes are also present in the area.

3.3.3 Sarek

This study area (~7 000 km2) is located in and around the Laponia UNESCO World Heritage Site in northern Sweden (Kvikkjokk 67º00′ N, 17º40′ E) and named after Sarek National Park (contained within the study area), one of the first national parks in Europe, created in 1909 (Rauset *et al.* 2016). The area is characterized by deep valleys at about 300 m a.s.l. and high mountainous plateaus of bare rock and glaciers with peaks up to 2000 m a.s.l. Tundra represents 57% of the study area and forest 36% (Mattisson *et al.* 2011*a*). The vegetation at lower elevations mainly consists of mixed conifer forest (*i.e.* Norway spruce and Scots pine) interspersed by bogs and lakes, followed by hillsides where mountain birch (*Betula pubescens*) forms the tree-line at 600–700 m a.s.l. Above the tree-line, dwarf birch (*Betula nana*) and willow (*Salix spp.*) shrubs, lower growing heaths, grass and meadows form the alpine tundra, followed by bare rock, and glaciers. The climate is continental with distinct seasons (mean temperature during the study period ranged from -13 ºC (Jan) to 12 ºC (July)), and the ground is usually snow-covered from November until May.

Lynx and wolverine research in the study area started in 1993 (wolverine) and 1994 (lynx). The area includes important spring to autumn grazing pastures for semi-domestic reindeer (see *reindeer husbandry* below), which is the most important prey for both lynx and wolverines in the area. Reindeer are highly mobile, herd-living and migratory, and in spring and summer reindeer are aggregated in large herds within the study area, whereas they are more patchily distributed during autumn (Bjärvall *et al.* 1990; Danell *et al.* 2006). During late autumn/early winter, most reindeer are moved to grazing areas in coniferous forests 100-300 km south-east of the study area (Danell *et al.* 2006). Consequently, the distribution of reindeer in the area is highly seasonal as well as heterogeneous and unpredictable in time and space. Alternative prey species are moose, mountain hare (*Lepus timidus*), ptarmigan (*Lagopus spp.*), grouse, and rodents. Apart from lynx and wolverines, other predators and scavengers present in the area are brown bears (*Ursus arctos*), golden eagle (*Aquila chrysaetos*), white-tailed eagles (*Haliaeetus albicilla*), common ravens (*Corvus corax*) red fox, and occasional arctic fox (*Vulpes lagopus*).

Previous studies have shown that lynx in the Sarek study area have lower reproductive rates, higher age at first reproduction and larger home ranges compared to lynx in the Bergslagen study area (Mattisson *et al.* 2011*a*; Nilsen *et al.* 2012). The main source of mortality for adult lynx in the study area is human-caused (legal and illegal killing; Andrén *et al.* 2006; Rauset *et al.* 2016). For wolverines, the main mortality cause is poaching for adults and intraspecific predation for juveniles (Persson *et al.* 2003, Persson *et al.* 2009; Rauset *et al.* 2016).

3.3.4 Southern Dalarna

This small study area (350 km^2) is located in the southern part of Dalarna county (60°17′ N 14°58′ E). The Swedish wolverine project started working in the area in 2013 to study wolverine ecology at the southern periphery of their distribution. The area mainly consists of managed coniferous forest (*i.e.* Norway spruce and Scots pine), interspersed with mires, lakes and smaller settlements. Elevation ranges from 150 to 500 m a.s.l, and mean temperature ranges from -6 °C (Jan) to 17 °C (July). Average dates for first and last day with snow cover ($\geq$ 5 cm) are November 17 and March 31. Wolves, brown bears, lynx, and red fox also occur in the area. Potential prey species for wolverines are moose, roe deer, grouse, beaver (*Castor fiber*), mountain hare and rodents.

3.4 Reindeer husbandry

In northern Scandinavia, semi-domestic reindeer are exclusively and intensively managed by the indigenous Sámi people. Within the reindeer husbandry area (~50% of Sweden and ~40% of Norway) reindeer graze freely and unattended as a part of an indigenous reindeer-herding culture. The Swedish reindeer husbandry area is divided into 51 reindeer-herding districts, and consists of areas designated for winter-only or year-round reindeer grazing (Hobbs *et al.* 2012). Reindeer migrate between summer pastures in the west to winter pastures in the east; today most reindeer are actively moved by their owners.

Within the reindeer husbandry area, reindeer are the main prey for both lynx and wolverine and, consequently, they (together with other predators, *e.g.* brown bear) cause significant economic losses for the reindeer-herding communities (Hobbs *et al.*, 2012). In Norway, economic compensation is paid in relation to documented and assumed damage on both reindeer and sheep (Swenson and Andrén 2005), whereas in Sweden, a conservation performance payment system (CPP) has been implemented since 1996 (Persson *et al.* 2015). In the CCP, economic compensation is paid to each reindeer herding district in relation to carnivore presence within the district. The main unit for compensation for lynx and wolverines is reproductions (*i.e.* same unit as for the national monitoring program). The current compensation is 200,000 SEK per reproduction and the mean annual number of reproductions within the reindeer-husbandry area between 2002-2014 was 110 for lynx and 86 for wolverines (2002-2016, range: 65-150 and 55-125 for lynx and wolverines, respectively). Consequently, the monitoring system is not only important for assessing population size in relation to national and regional goals, but is also of critical importance for the CCP system. For example, the CPP has had a positive effect on wolverine female survival, which has contributed to a considerable population increase within the reindeer-husbandry area (Persson *et al.* 2015).

4 Material and Methods

4.1 Capture and monitoring

Both lynx and wolverines were captured and immobilized using strict ethics-approved handling protocols (see Arnemo *et al.* 2012). Lynx were captured using walk-through box-traps, foot-snares, trained hounds or darted from helicopter (Andrén & Liberg 2015; Mattisson *et al.* 2011*a*; Odden *et al.* 2013). Lynx were fitted with VHF transmitters (1994–2008), or GPS-collars (2003–2014). Wolverines were captured on the ground or darted from helicopter and equipped with VHF-collars (1993-1995), or intraperitoneally implanted VHF-transmitter (1996-2014) and GPS-collars (2003-2014). From all animals, a small tissue biopsy and a hair sample were taken at capture for genetic analysis.

Animals equipped with VHF-transmitters were radio-tracked on average every second week by air or from the ground (Persson *et al.* 2010; Samelius *et al.* 2012), although the location schedule varied extensively through the study period and study area (*i.e.* some individuals were intensively monitored for 1-2 months). GPS-location frequency varied from 3 to 48 locations/24h (Mattisson *et al.* 2011*b*), depending on study objectives.

Reproductive success and number of offspring were assessed annually for collared lynx and wolverine females. Lynx females were located as often as possible in late May and early June and kittens were found because females adopt a central place movement behaviour, centred at the natal lair for the first 6–8 weeks after parturition (Gaillard *et al.* 2013). Wolverine females were intensively monitored to evaluate whether they displayed denning behaviour during the spring (Persson *et al.* 2006). Because wolverines den in deep snow (Magoun & Copeland 1998) we could not observe the number of cubs at parturition. In May-June females that had reproduced were located to count the number of cubs after den emergence (Persson *et al.* 2006). At this time the cubs are 3–4 months old and can be equipped with an intraperitoneally implanted

VHF-transmitter. Thus, the number of monitored wolverines with known age increased along the study period (Persson *et al.* 2006; 2009; Rauset *et al.* 2015).

Radio-collars were equipped with mortality sensors, which allowed us to find the dead animals in the field to determine the cause of mortality. In addition, all dead animals were sent to the Swedish National Veterinary Institute for necropsy. Poaching is the mortality cause most difficult to determine, see Andrén *et al.* (2006) and Persson *et al.* (2009) for criteria used to classify mortality as poaching or suspected poaching for lynx and wolverines.

4.2 Spatial analysis

To estimate home ranges for lynx and wolverines, I used the fixed-kernel method (Worton 1989) with the *'adehabitatHR'* package (Calenge 2006) in R (R Core Team 2014). The kernel method estimates a utilization distribution (UD); consequently, home range estimations are obtained as a function of an individual's relative use of space (Marzluff *et al.* 2004). From the UD, the home range is defined as the smallest area that accounts for a specific proportion (isopleth) of the individual's total use of space. Thus, intensity of use of the area increases with decreasing isopleth values (Fig. 2). During the study period, the number of locations acquired per individual generally increased as radio-tracking technology developed. To reduce biases from different sampling regimes between animals and years (Börger *et al.* 2006x), I randomly sampled 1 location/24h/individual for home range estimations (Papers I–V). I defined lynx annual (*i.e.* 1st February year *t* to 31st January year *t* + 1 [Paper I and III], or 1st June year *t* to 31st May year *t* + 1 [Paper II]) and seasonal home ranges as the 90% isopleth using the reference bandwidth (*'href'*) multiplied by 0.8 (Kie *et al.* 2010, 2013). Furthermore, I calculated the 80%, 70%, 60%, and 50% isopleths to examine how the effect of roe deer abundance and lynx density on area use changes with increasing intensity of use within the home range (Paper I).

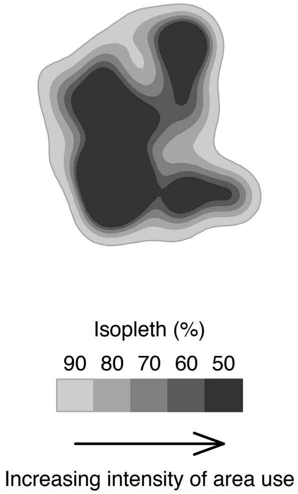


Figure 2. Home range estimation obtained as a probability density function of intensity of area use. Intensity of use increases with decreasing isopleth level within the home range (*i.e.*, darker areas = higher use)

Seasonal home ranges (Paper I) were estimated for: mating (February 1 to April 15), non-mating (April 16 to January 31), suckling (female only, May 20 to September 30, representing birth to end of lactation) and rearing season (female only, May 20 to January 31 representing birth to independence). I only estimated home ranges for lynx with ≥25 locations (based on simulations using ≥ 100 annual locations; see Paper I) collected during ≥ 7 months (annual) or ≥ half the season (seasonal).

For wolverines, I calculated annual (90% isopleth) and core (50% isopleth) home ranges using the reference bandwidth, and defined years as calendar years. Home ranges were only calculated for individuals with ≥ 20 locations (Rauset *et al.* 2015). To assess site fidelity and yearly residency status (*i.e.* stationary, moving or expanding; Paper IV) I only included individuals monitored for ≥6 months during ≥ 2 years. To assess the number and distribution of wolverine territories within the core Sarek study area (Paper V) I calculated home ranges for the time periods when females were defined as stationary in paper IV. For females with insufficient numbers of locations for home range analysis (*i.e.* < 20) I used a 4.6 km buffer zone (*i.e.* the closest distance between neighbouring females den sites, see Paper VII) centred on their den sites to approximate their home range. I defined unique female wolverine territories as the smallest spatial unit possessed for ≥1 year by one successfully reproducing female. Based on space use for 53 females, the core study area consisted of 26 territories (Fig. 3), monitored for a total of 321 territory years (mean time monitored per territory 12.5 years ±1.1 SE; range: 2-22).

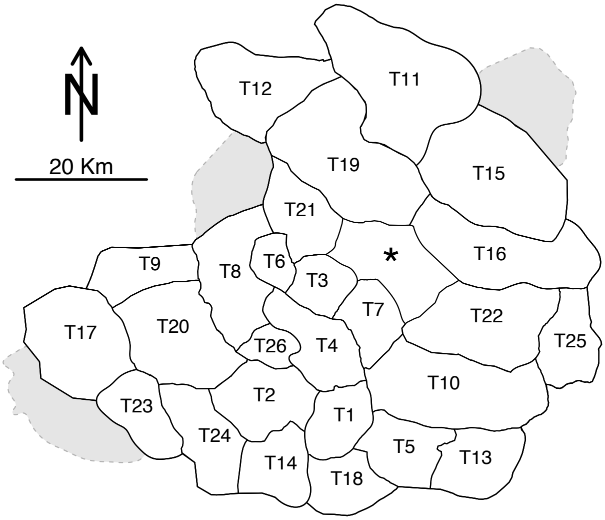


Figure 3. Approximate territorial boundaries for female wolverines within the Sarek study area, based on home ranges for resident females from 1996 to 2014.

To assess wolverine territorial dynamics (Paper V), I estimated the time until a vacated territory (*i.e.* due to death or movement by the territory holding female) was reoccupied in relation to the origin and status of the replacing individual (*e.g.* young dispersing individual or adult established individual).

I used two methods to quantify home range overlap between neighbouring individuals (Paper III) and between years for the same individual (Paper IV); overlap index (OI; Ginsberg & Young 1992) and volume of intersection (VI; Seidel 1992; Millspaugh *et al.* 2004). OI is calculated as the sum of locations for individual/year A and B in the overlap area divided by the sum of the total number of locations. VI measures the three-dimensional overlap between the utilization distributions (UDs) for individual/year A and B. Both measurements ranged from 0 (no overlap) to 1 (identical locations or UDs). I used distances between simultaneous (≤ 3 min) GPS locations to assess interactions between neighbouring lynx (Paper III) in different seasons based on reindeer abundance (low in winter (*i.e.* December-April); high in summer (*i.e.* May-July), and intermediate in autumn (*i.e.* August-November). I compared distances between neighbouring females to distances between simultaneous, random locations and random locations within the same area and overlap.

Land cover was obtained from a 25 m x 25 m digital land cover map (Swedish Land Cover [SMD], National Land Survey of Sweden). To assess lynx survival in relation to habitat (Paper II), We initially focused on two land cover classes: agricultural land and forest, and calculated the proportion of these two classes within each annual lynx home range. Proportion of agricultural land and proportion of forest within a lynx home range were highly correlated (r = - 0.80). Therefore, I only included the proportion of forest in the analyses since previous studies have shown that lynx occurrence is positively related to forest cover (Sunde *et al.* 1998; Basille *et al.* 2009). Length of secondary roads (unpaved forest roads) within each lynx home range was obtained from the Swedish Transport Administration database (www.trafikverket.se). I calculated the density of secondary roads by dividing the length of roads in the home range by the total area of the home range.

4.3 The use of indexes for prey abundance, conspecific density and territory quality

I used reported yearly number of hunted roe deer at the hunting district level in Sweden and municipality level in Norway as a proxy for roe deer abundance (Paper I and II). Roe deer hunting bag statistics is related to several other measurements of roe deer density (*i.e.* pellet counts, estimated population size, traffic-killed roe deer and sightings at feeding stations; Andrén & Liberg 2015;

Grøtan *et al.* 2005). Furthermore, there is an open hunting season for roe deer in Sweden since the 1980s, with no hunting bag limits, and local hunting bag records has been collected using the same reporting system over time. In Norway, the roe deer harvest is regulated through a quota system, but only a low fraction of the annual quota is actually harvested and harvest rate is not influenced by roe deer density (Grøten *et al.* 2005; Melis *et al.* 2013). Lastly, yearly hunting bag statistics are obtained on a much smaller spatial scale than lynx home ranges, thus there are multiple hunting districts/municipalities within each lynx home range. For each home range, I calculated the yearly area-weighted average roe deer bag size across the hunting districts or municipalities overlapping the home range.

To get a proxy for lynx density (Paper I) I calculated the yearly area-weighted monitoring results for the biogeographical regions (Sweden) or carnivore management areas (Norway) overlapping each home range.

To assess wolverine territory quality (Paper IV and V) I used the average reproductive output from each territory during the time it was monitored (Garshelis 2000; Johnson 2007; Stephens *et al.* 2015). Rauset *et al.* (2015) showed that both female age and reproductive cost influence wolverine reproduction in our study area. Consequently, to calculate the average number of reproductive events in each territory I only included years when the resident females were in prime age (3-9 years of age). To account for some females that reproduced but lost their young during the denning period, I also used the average number of cubs produced in each territory during the same period. Consequently, I used an important fitness component (reproductive output) to describe territory quality and only used territories monitored during ≥ 5 years, held by ≥ 2 females to reduce the influence of between-year environmental conditions, and variation within and between individuals.

4.4 Parturition date and denning behaviour

18 adult wolverine females were intensively monitored with GPS-collars during 54 denning seasons to assess parturition date and denning behaviour (Paper VII). Den sites were identified using GPS locations in GIS (ArcMap 9.3, ESRI), complemented with VHF radio tracking from the ground or by helicopter. The natal den site (*i.e.* where the cubs were born), was defined as the place where the female remained within a very restricted area for several consecutive days. Reproduction was confirmed by observation of cubs later during the denning season, and the date for parturition was defined as the first day at the natal den site (see Walsh *et al.* 2016). I calculated two different distances between den sites used by individual females during the denning season: the daily distance

between natal den site and subsequent den sites, and the distance from the currently used den site to the most distant of the previous dens (Fig. 4). Furthermore, I calculated daily distances between den sites for neighbouring females.

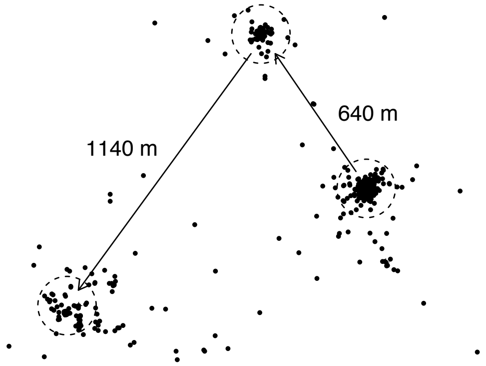


Figure 4. Example of GPS-locations for a wolverine female showing 3 different den sites.

4.5 Camera monitoring

From 15th February 2013 to 15th January 2015 I used six camera stations to document wolverine presence, and to identify and sex different individuals. Camera stations were constructed following Magoun *et al.* (2011) and consisted of two cameras and a run pole where wolverines are supposed to stand and reach for overhanging bait, showing the abdominal and chest area. Sites for camera stations were selected based on information from locals about frequent observations of wolverine tracks to maximize the chance of visitation by a wolverine; because my aim was to evaluate if wolverines used the camera stations and not to estimate population size (Magoun *et al.* 2011). The cameras (PC800; RECONYX Inc., Holmen, WI, USA) took one picture per second when triggered by movement and I defined all wolverine photos taken within 30 min as belonging to a single visit. I visited all camera stations at least once every second month during the study period (2–8 weeks) to retrieve photos, check battery status and change bait.

4.6 Genetic analysis

Genetic analyses for papers III and V were performed by the laboratory at Grimsö Wildlife Research Station, SLU. Genomic DNA for lynx tissue and hair samples (Paper III) were extracted using standard phenol/chloroform–isoamylalcohol extraction, and precipitated using two volumes ethanol-sodium acetate solution. After removal of the ethanol solution the precipitated DNA was solved in distilled water. DNA samples were genotyped on 17 microsatellite loci (*i.e.* FCA001, FCA008, FCA031, FCA043, FCA045, FCA090, FCA126, FCA149, FCA272, FCA275, FCA391, FCA506, FCA559, FCA567, FCA573, F026, F115; Menotti-Raymond & Obrien 1995; Menotti-Raymond *et al.* 1999). Genomic DNA from wolverine tissue and hair samples (Paper V) were extracted and analysed using 20 microsatellite markers following Hedmark *et al.* (2007).

The maximum likelihood estimates of relatedness (r) between individuals was calculated using the program ML-RELATE (Kalinowski *et al.* 2006). The existence of close genealogical kinship (*i.e.* half siblings, full siblings or parent-offspring) was tested by likelihood ratio tests using the maximum likelihood estimates of a pair being unrelated or having relationship. The relationships with likelihood values within the 95% confidence interval were calculated in ML-RELATE using 10000 randomizations to get the sample distributions for the null hypothesis.

4.7 Statistical analysis

4.7.1 Generalised linear mixed models

For papers I, IV and V, I used generalized linear mixed models (GLMM) in the *'lme4'* (Bates *et al.* 2014) or *'glmmADMB'* package (Skaug *et al.* 2012) in R. To model home range size (Paper I) I used log-transformed home range size as the response variable and a Gaussian error distribution. For models with home range overlap as response variable (Paper IV), I used a Beta error distribution and logit link-function. For models with time (months; Paper V) as response variable I used a Poisson error distribution and log link-function. Individual identity was included as random effect in all model to account for repeated measurements. I used a bootstrap method implemented in R using the *'ez'* package (Lawrence 2013) to calculate 95% confidence intervals for predictions from GLMMs. Model residuals did not violate assumptions for normality, homogeneity of variance, and structure relative to predictors (Zuur *et al.* 2010).

4.7.2 Survival analysis

We estimated lynx survival using Kaplan-Meier staggered entry (Pollock *et al.* 1989), and used the Andersen-Gill formulation of the Cox proportional hazards model (Andersen & Gill 1982) in the 'survival' package for R (Therneau 2015) to examine how lynx mortality varied with sex, seasons (*i.e.* during and outside hunting season) and environmental variables (Paper II). Because most lynx were monitored during multiple years, we included individual identity as a random effect. When the assumption of proportional hazards was not fulfilled, we followed Diaz (2013) recommendation and divided the exposure time into appropriate time periods. We modelled lynx survival in relation to all mortality causes, and for human-caused mortality (*i.e.* vehicle accidents, legal hunting, poaching and suspected poaching) and non human-caused mortality (*i.e.* disease and unknown mortality causes) separately. When analysing lynx survival for only human-caused mortality, all lynx with non human-caused mortality were right-censored and vice versa.

4.7.3 Multistate mark-recapture models

I used Multistate mark–recapture models in program MARK (version 5.1; White and Burnham 1999) to estimate age-related probabilities that young wolverine females, born within the core Sarek study area, would establish within the study area or disperse from the area (Paper V). I focused on two state transitions; a young unestablished female present in the core study area in month m (state P) would establish in a territory in the study area (state ES, state transition $\Psi_{P\rightarrow ES}$) or leave (state L, transition $\Psi_{P\rightarrow L}$) in the following month ($m + 1$). The models were based on 67 females monitored between 6 and 36 months of age. The survival parameter for state P (Φ_P) was estimated as a constant parameter, while survival in the other states was fixed at zero ($\Phi_{ES} = \Phi_L = 0$) to remove individuals from analysis once they settled or left the study area.

I first examined the influence of time since birth (age; months) on each transition probability separately by comparing constant probability of transitioning versus a linear change in transition probability over time. Based on AICc support, the highest-ranked parameter structure for each transition state was then used as the basis for fitting additional covariates (Low *et al.* 2010). These included the following: (1) number of available territories, (2) distance from the natal den site to the closest available territory, excluding the natal territory, (3) if the natal territory was available or not, and (4) the distance from the natal den site to nearest study area border, as well as multiple pairwise interactions that I considered likely to influence the transition probabilities.

4.7.4 Bayesian modelling

To model space use overlap between neighbouring lynx in Bergslagen and Sarek in relation to relatedness value or most likely genealogical relationships (Paper III), I used a zero-inflated beta regression (Ospina & Ferrari 2012) that incorporates a two-step process to account for (i) non-overlapping neighbours, and (ii) the degree of overlap when overlap >0, using the following Bayesian models:

$$\gamma_i = \alpha_{j[i]} + ax_i$$

$$y_i \sim \text{Bernoulli}(\gamma_i)$$

and

$$\mu_i = \beta_{j[k]} + bx_k$$

$$u_i \sim \text{beta}(p_k, q_k)$$

where γ_i and μ_k are the deterministic model predictions of the probability of no overlap and the amount of overlap, respectively, y is the binary overlap value (*i.e.* 1 for overlap = 0 and 0 for overlap > 0), u is the non-zero overlap measurement, a and b are vectors of regression coefficients and x is explanatory variables. The subscript *i* indexes total overlap estimates and *k* indexes non-zero overlap measurements. To account for individuals with multiple neighbours included in the dataset, I included the focal individual for each overlap measurement as a group level effect on the intercept in each model (α and β, individual indexed by subscript *j*), using a normal distribution. All prior distributions were chosen to be minimally informative. Lastly, I combined the two models to generate predictions for overlap using:

$$\text{Overlap} = (1 - \gamma) \times \mu$$

To model the probability that two den sites separated by more than certain threshold distances (*i.e.* 0.5, 1, 2, 3, 4 and 5 km), during the same denning season, belongs to the same wolverine female (Paper VII), I used to the binary model above (*i.e.* Bernoulli).

For Bayesian models, I used a Gibb's sampler (*i.e.* JAGS; Plummer 2003) called from R using the *'rjags'* package (Plummer 2014) to estimate final model parameters and generate predictions. Convergence was assessed by visual inspection of trace plots to assure stability and homogeneous mixing and by using the Gelman and Rubin diagnostic (< 1.1; Gelman & Rubin 1992). To make probability statements on differences between different categories I subtracted the posterior distributions from each other within the JAGS model structure.

4.7.5 Model selection

For GLMMs I used sample-size corrected Akaike information criterion (AICc), AIC weights (w_i) and relative variable importance weights (RVI) (Burnham and Anderson 2002) using the *'MuMIn'* package (Barton 2013) in R. For Bayesian models, I used the Watanabe-Akaike Information Criterion (WAIC) based on the posterior predictive distribution generated within the JAGS model structure (Hooten & Hobbs 2015).

In the following summary section, CI is used for Confidence Intervals and CRI for Bayesian Credible Intervals.

5 Results and discussion

5.1 Factors affecting lynx home range size and survival in the Scandinavian multiuse landscape (Paper I, II)

Based on 157 home range estimates for 77 lynx I found that males have larger home ranges than females in all seasons, and that female lynx have larger home ranges in Norway compared to in Sweden. This was not surprising considering that previous studies have found sex difference in home range size for lynx, as well as decreasing home range size with increasing habitat productivity (e.g. Herfindal 2005; Mattisson 2011*a*). However, I found that female home range size decreased with both increasing roe deer abundance and lynx density (Fig. 5) and the Norway-Sweden difference was completely explained by differences in roe deer abundance and lynx densities. This suggests that females adapt their space use relative to the resources needed to survive and successfully reproduce (Sandell 1989). For males, I found that roe deer abundance did not affect total home range size (Fig. 6). This was contrary to a previous study that did not account for the confounding negative effect of lynx density and found that both male and female home range sizes were negatively affected by roe deer (Herfindal *et al.* 2006).

By examining the sex-specific effects of range size determinants as intensity of space use increased within the home range, I showed that the negative effect of prey abundance on female range size decreased with increasing intensity of space use (Fig. 6). This suggests that although food availability is a key driver of total home range size, factors other than food define female space use in the more intensively used areas (e.g. availability of den sites, or habitats that provide protection; Kelt and Van Vuren 2001; Basille *et al.* 2013; Rauset *et al.* 2013), and that less intensively used areas (i.e. those relating to the total home range size) might be critical for food provisioning. Males, on the other hand, showed the opposite pattern and a negative effect of prey abundance on range size becoming evident for high intensity of space use (Fig. 6), possibly due to energetic requirements. Interestingly, for the isopleth level when male area-use was of similar size as female total home ranges, males and females range size were equally influenced by roe deer abundance.

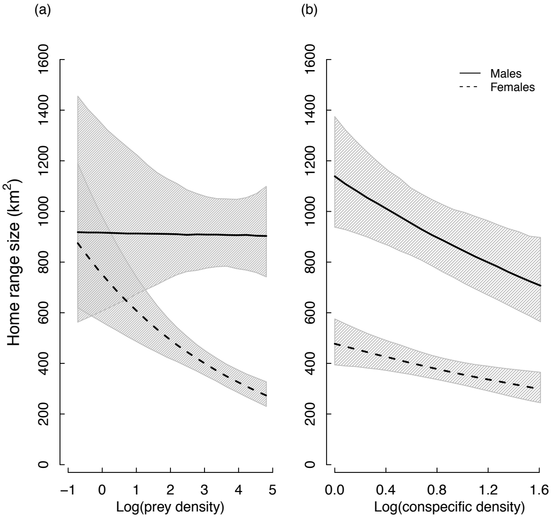
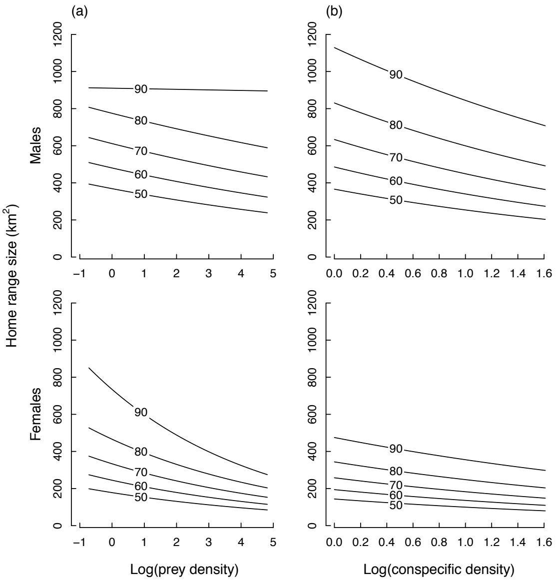


Figure 5. Sex-specific relationships between annual lynx home range size (km^2; 90% fixed- kernel isopleth) and (a) roe deer abundance, and (b) lynx density, for lynx in south-central Scandinavia during 1996-2012. Model-averaged predictions (solid lines = males, dashed lines = females) with associated 95% CIs (shaded area).

Figure 6. Sex-specific relationships between annual lynx home range size (km^2) and (a) roe deer abundance, and (b) lynx density for a range of isopleths (90, 80, 70, 60, and 50%) that represent increasing intensity of use within the home range (see Fig. 2 in methods). Lines show model-averaged predictions for the different isopleth levels while all other explanatory variables are kept at their mean value.



Males did not adapt their home range size to encompass a constant number of females when female home range size decreased. This suggests that males maximize their home range size to an upper bound; presumably set where the energetic costs of maintaining a large territory outweighs any additional fitness benefits of encountering more females (Kelt & Van Vuren 2001). However, male range size was smaller during the mating season compared to non-mating season. This is probably because lynx, contrary to many other smaller felids, are strict seasonal breeders (Jewgenow *et al.* 2014; Painer *et al.* 2014) and males stay close to receptive females (mate guarding), instead of roaming (Sandell 1989), during the mating season.

Apart from being an important determinant for lynx space use, I also found that roe deer abundance positively influences lynx survival. Lynx have an average yearly survival of 0.79 (± 0.04 SE) in south-central Sweden and average monthly survival decreased during the hunting season (0.943 ± 0.018 compared to 0.985 ± 0.004 during the rest of the year). Human-caused mortality dominates for lynx in south-central Sweden (Fig. 8). There is a similar risk of human-caused mortality throughout the landscape, while the non-human caused mortalities appears to shape the landscape of risk for lynx, since both overall mortality and non-human caused mortality was associated to functional habitat within lynx home ranges (e.g. roe deer).

Previous studies from Norway show that lynx hunting mortality increased with road density and that lynx were shot closer to roads than expected (Sunde *et al.* 1998; Bunnefeld *et al.* 2006; Basille *et al.* 2013). I did not find the same effect in Sweden, probably because of higher and less varying road density within lynx home ranges in Sweden, which makes the entire landscape highly accessible for hunters. Furthermore, I did not find indications of attractive sinks for lynx, as human-caused mortality was not higher in areas with high resource abundance, contrary to in the Norwegian landscape (*cf.* Bunnefeld *et al.* 2006; Basille *et al.* 2013). This might be explained by the higher hunting pressure in Norway compared to Sweden (Andrén *et al.* 2006; Linnell *et al.* 2010).

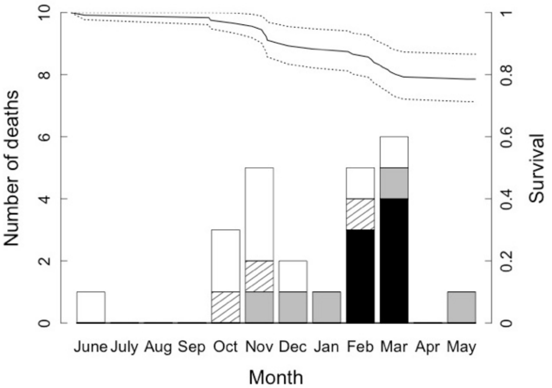


Figure 7. Survival with 95% CI (dotted lines) and mortality cause for in lynx in relation to month. Mortality caused by legal hunting (black), poaching (grey), traffic (hatched) and disease or unknown causes (white).

5.2 The effect of relatedness and resource dispersion on lynx home range overlap (Paper III)

By comparing home range overlap between neighbouring lynx, I found that home range overlap increased in Sarek compared to Bergslagen for both sexes, although the increase in overlap for females was larger than for males resulting in a smaller difference between sexes in Sarek compared to Bergslagen. In Sarek, overlap between neighbouring females increased with increasing relatedness, whereas there was no effect of relatedness on female overlap in Bergslagen, nor for males in any area. Interestingly, by separating the analysis into different kinship categories I found that the positive influence of relatedness on home range overlap was restricted to mother-daughters and did not include the similarly related full-siblings (Fig. 8). In fact, increased home range overlap between mother-daughters explained most of the observed differences between females in Sarek compared to Bergslagen, because there was little or no difference in overlap between study areas for other kinship categories (Fig. 8).

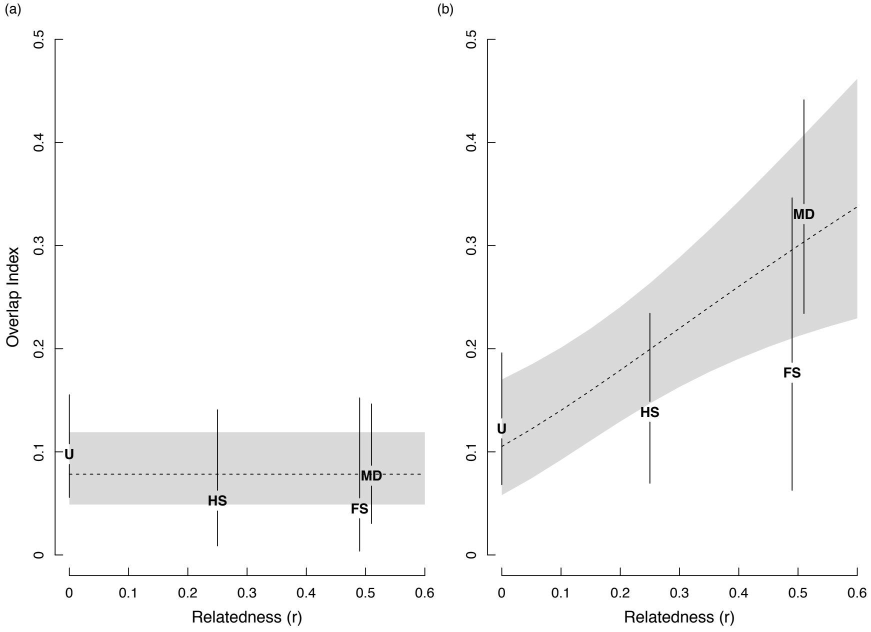


Figure 8. The effect of genetic relatedness on female lynx home range overlap (Overlap Index) in the Bergslagen (a) and Sarek (b) study areas. Model predictions (dashed line) with associated 95% CRI (shaded areas). Additionally, the predicted overlap values for each relationship category is showed at corresponding relatedness values (i.e. unrelated (U) at r = 0, half-siblings (HS) at r = 0.25, full-siblings (FS) at r = 0.5, and mother-daughter (MD) at r = 0.5). Vertical lines are 95% CRIs.

That relatedness did not influence home range overlap for males was not surprising, as the average relatedness between neighbouring males was very low compared to females and highly-related neighbouring male pairs were uncommon (i.e. parent-offspring, full siblings). This is expected because the male-biased dispersal pattern (Samelius *et al.* 2012) should result in a low occurrence of closely-related neighbouring adult males. For females on the other hand, average relatedness between neighbours and the existence of close kin were high in both study areas; thus, the different effects of relatedness on home range overlap was not explained by study area differences in relatedness per se. Instead, I suggest that the observed female space use pattern is explained by an interaction between kin selection and resource dispersion.

Kin selection theory predicts a positive relationship between intrasexual space-use overlap and genetic relatedness (Hamilton 1964); accordingly, we would expect a positive effect of relatedness on overlap in both study areas. However, the two study areas are very different in regards to prey dispersion and predictability. In Bergslagen, the main prey (roe deer) is evenly dispersed and predictable compared to Sarek where the main prey (reindeer) is highly clumped and with large seasonal differences in abundance (see study areas, section 3.3). The resource dispersion hypothesis predicts space use overlap to increase during periods with high resource availability (Macdonald 1983; Johnson *et al.* 2002); thus, if the increased overlap in Sarek is solely due to high prey abundance in the summer this should be similar for all kinship categories. However, in Sarek there are regularly occurring periods with low prey abundance (winter), and given that home range overlap is accompanied by a fitness cost during periods with low resource abundance, one way to reduce this cost for an individual is to be ‘less territorial’ towards related individuals, since this may provide inclusive fitness benefits (Hamilton 1964). Consequently, relatedness influences the cost-benefit ratio of sharing space where the net fitness benefit from sharing with related individuals when food is abundant is higher than the cost of sharing with anyone when food availability is low. That the effect of relatedness on home range overlap is mediated by resource dispersion is also supported by the lack of effect in Bergslagen, suggesting that the cost of sharing space when resources are predictable and homogenously distributed is always high, independent of relatedness.

If the increased home range overlap between mother-daughters is due to increased tolerance and sharing of prey resources during seasons with high prey abundance, the individuals should also interact more during this period. Consequently, by using distances between simultaneous locations I found that mother-daughter neighbours were closer to each other than expected from random locations during the summer, whereas distances between other kinship categories were close to random in all seasons.

5.3 Wolverine territorial fidelity and the link between territorial dynamics and natal dispersal (Paper IV, V)

Wolverines are highly territorial (Persson *et al.* 2010), and by comparing space use overlap between years for the same individual I found that wolverines show high territorial fidelity resulting in a stable distribution of resident individuals. Interestingly, territorial fidelity in general is predicted to be low in habitats where food resources are low, variable, unpredictable or deplete fast (Wauters *et al.* 1995; Kirk *et al.* 2008; Edwards *et al.* 2009), which corresponds to the characterization of wolverine habitat in general (Inman *et al.* 2012*b*), and particularly in this study area (Person 2005). However, scavenging and caching are integral parts of wolverine biology (Inman *et al.* 2012*b*; Mattisson *et al.* 2016), which increase resource predictability, decrease depletion rate and create a valuable resource (*i.e.* cache sites) to defend, promoting high territorial fidelity despite the unpredictable environment (Tye 1986; Eide *et al.* 2004). In addition, occurrence of more efficient predators, such as the Eurasian lynx (Lynx lynx), provide carcasses for direct consumption and caching (Mattisson *et al.* 2011*b*). Furthermore, both males and females showed higher between-year fidelity at the territory level (*i.e.* 90% isopleth) compared to the core areas (*i.e.* 50% isopleth). That fidelity was lower at the core area compared to territory level suggests that it is critical to maintain the outer territory boundary to secure long-term resources, while the most used area within the territory may vary between years due to spatial fluctuations in key resources, or, for females, location of den sites may vary between years.

I determined residence status from one year to the next for 42 females in 122 territories; in 86% of these the female remained stationary, while 8% were vacated and 6% expanded. I found 6 occasions of female breeding dispersal (Fig. 9), a rarely documented behaviour in long-lived, large mammals (Jerina *et al.* 2014). Most females successfully reproduced prior to leaving their territory. In fact, for breeding dispersal females the reproductive frequency before and after dispersal were higher than average in the study population, indicating that these females were in prime condition and reproductive failure was not the reason for moving. However, other females exhibited floating behaviour after leaving, suggesting that they might have been forced to abandon their territory. Consequently, the abandonment of established territories could be due to competition for high-quality territories in this saturated population (Wauters *et* *al.* 1995), creating infrequent, but interesting, exceptions to the stable spatial organisation of resident wolverine females.

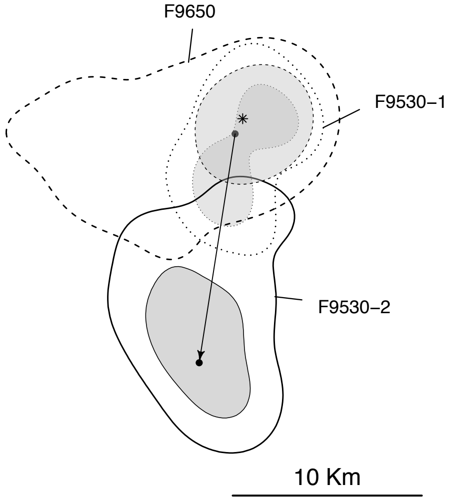


Figure 9. Breeding dispersal by wolverine female F9530. F9530 reproduced successfully in a territory (F9530–1; dotted line) in year 1. She subsequently left her first territory and re-established and reproduced in a new territory (F9530–2; solid line) in year 2. Den sites of F9530 are represented by filled circle (•), arrow show dispersal direction. Simultaneously, F9650 established a territory (dashed line) and reproduced (✳) in the former area of F9530. Core areas are shown in grey with the same outline as corresponding territory

During the study period, nearly all established females and their offspring were monitored within the study area. Thus, I could to assess both female territorial dynamics and natal dispersal in relation to detailed information on territory availability, territory quality, individual age, presence of kin, and seasonal effects. That established females rarely leave their territories is further illustrated by the fact that of 51 territories that became available in the core study area during the study period only 18% became available because a resident female left, while the remaining 82% was due to death of resident females. I found a replacing individual in 46 of the available territories, and at least 93% of the replacers came from the local area. The most common types of replacer were young female offspring that remained in the natal territory after the mother died or moved (natal philopatry; 30%) and neighbouring adult females that expanded into the available territory (expanding; 26%). This suggests that females benefit from being present in or nearby a territory when it becomes available (Sutherland 1996). The advantage of fast detection is further illustrated by the fact that, apart from natal philopatric females who replaced instantly, time to replacement was shorter for expanding females compared to the other categories (e.g. moving females and young dispersing females). I did not find any effect of territory quality on time to replacement, however, established females only moved to available territories with higher-than-average quality, indicating that resident individuals will only voluntarily abandon a territory when they can occupy a high-quality territory.

The observed pattern of territorial replacement in this study has several implications. The first is that there are very limited opportunities for immigrants to establish in saturated areas like our study area because almost all replacers were from the immediate surrounding. This leads to the second implication; by following 67 young females born in the study area to assess the probability that they will establish within the study area or leave, I show how territorial dynamics influence departure and settlement for young dispersing individuals. The availability of the natal territory is of fundamental importance for the probability of young females to remain and establish in the local area (Fig. 10a), and the probability for young females to leave the study area decreased with the number of vacant territories (Fig. 10b). This, together with estimated closed population growth (λ) of 1.06 (Persson *et al.* 2015), while the number of reproductive females was stable, suggests high competition for available territories and that our study population most likely acts as a source population because a surplus of young females have to disperse from the area. Consequently, the emigration to surrounding areas is related to the survival of resident adult females.

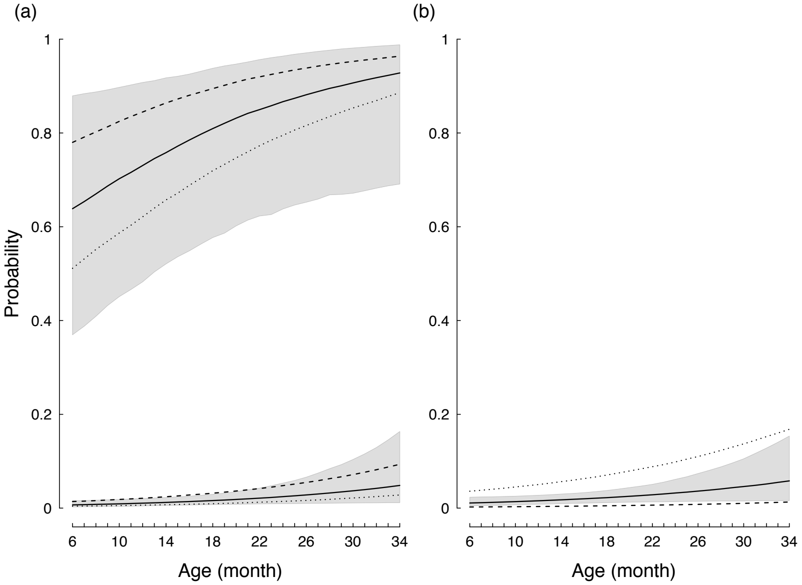


Figure 10. Monthly probability of a young wolverine female establishing in or leaving the core study area relative to her age. (a) shows the probability of establishing in the core area if the natal territory is available (upper curve) versus if the natal territory is not available (lower curve); (b) is the probability of leaving the core study area. Solid lines are mean model predictions (from Table 3, at mean number of available territories) and shaded areas 95% CIs. The dashed and dotted line shows how the mean model prediction changes when the number of available territories is reduced to the minimum (dotted) or increased to the maximum (dashed).

5.4 Wolverine population expansion, monitoring, denning behaviour and parturition date (Paper VI & VII)

When the wolverine monitoring started in 1996, wolverine reproductions in Sweden were almost exclusively registered in northern alpine areas. Thereafter wolverine distribution has increased considerably and wolverine reproductions are now found in the boreal forest landscape east of alpine areas (Fig. 11). Since 2002 wolverine observations have also been registered within the yearly monitoring program and these show the same eastward expansion. However, the southward distribution of reproductions ends at the southern limit for the reindeer husbandry area whereas wolverine observations continues southward for an additionally ~170 km (Fig 11). Based on observations, wolverines are currently recolonizing what is believed to be their historical distribution in Sweden (Persson & Brøseth 2011).

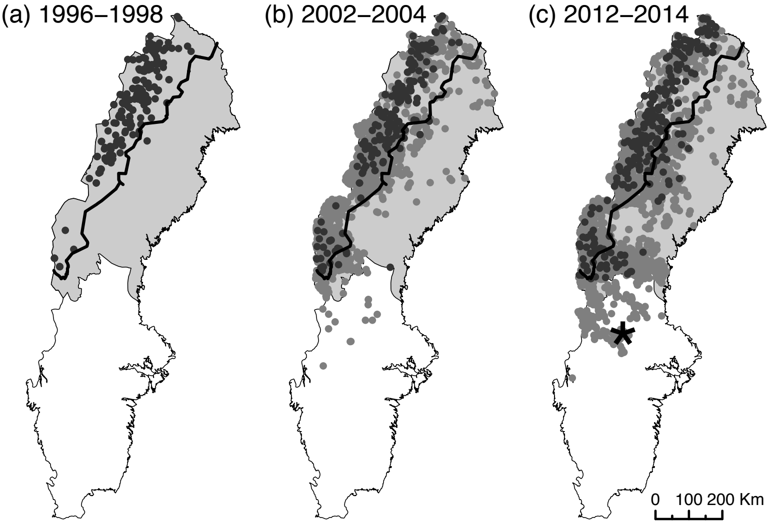


Figure 11. Wolverine population distribution trend in Sweden based on reproductions (black dots) and observations (grey dots) registered within the national monitoring program. Monitoring results are presented for 3-year periods; (a) start of the monitoring program, (b) wolverine observations started to be registered and (c) current distribution range of reproductions and observations. The star (★) shows the location of the pilot study. Shaded area shows the reindeer-husbandry area and black line shows the border used to differentiate alpine areas and boreal forest landscape.

I suggest several explanations for the observed range expansion. The wolverine population has increased considerably in alpine areas (Persson *et al.* 2015), with increasing density leading to an increased number of dispersers (Paper V). Furthermore, remains from the autumn moose hunt provides a substantial amount of food for scavengers in the forest landscape (Wikenros *et al.* 2013) and the Scandinavian wolf population is now overlapping with most of the wolverine distribution south of the reindeer husbandry area (Anon, 2015*b*). This provides year-round remains from wolf kills (van Dijk *et al.* 2008) that provide scavenging opportunities that might buffer any negative effects of reindeer absence.

The southward expansion also shows that wolverines today are present in areas with non-persistent spring snow cover (see Fig 3. in Copeland *et al.* 2010). This provides a challenge for management because the wolverine monitoring protocol was developed for northern alpine areas and is to a large extent based on snow tracking. Furthermore, south of the reindeer husbandry area wolverines are subject to low levels of human conflict. Consequently, management efforts are focused on the more controversial wolf and lynx, and wolverine monitoring is limited to opportunistic documentation of tracks and scats (Aronsson & Persson 2012). As a consequence, during 2012-2014, wolverines present within 30% of the distribution are not included in population estimates because monitoring is based on reproductions, which were only found in 70% of the area with recurrent wolverine observations. Consequently, there is a need for snow-independent monitoring methods to monitor the southern part of the wolverine population.

I tested camera stations (Magoun *et al.* 2011; Fig. 12) to document wolverine presence in the southern periphery of the distribution (Southern Dalarna study area). From only 6 camera stations distributed within 200 km^2 (corresponding to one female territory) I got ~10,000 photos, in which wolverines were the most frequently photographed species (59% of photos). Based on unique chest patterns I identified 5 individuals and a total of 66 visits. Identifying individuals was time consuming because there was little individual variation in chest colour patterns. However, when wolverines used the climbing support with the back legs to reach the overhanging bait it was easy to determine their sex. Thus, camera stations could be used to locate resident females to direct the search for den sites in southern areas with early snowmelt.

Another important aspect for wolverine monitoring within the entire Scandinavian range, and not only in areas with limited snow cover, is female denning behaviour. For a suspected den site to be classified as a reproductive event, certain pre-defined criteria have to be fulfilled (i.e. photographs of cubs or their tracks, or documented regular wolverine activity at the den site during 3-4 weeks; SEPA 2014*b*). Consequently, the possibility to document regular activity will decrease if the female changes den site during the denning period. Furthermore, the ability to determine if two different den sites belong to the same female (i.e. one reproductive event) or different females (i.e. two reproductive events) might influence population size estimates, and even a few potential errors could negatively influence trust in management as reproductive events are the basis for the conservation performance payment system to the reindeer herding districts.

Figure 12. Wolverine checking the information sign describing use of a camera station (seen in the background) to monitor wolverines.

Based on GPS-locations from wolverine females in the Sarek study area, I found that females change den sites earlier and more often than previously suggested (Magoun & Copeland 1998; Inman *et al.* 2012*b*), and assumed when the Scandinavian monitoring system was implemented (Andersen *et al.* 2002). Most wolverines gave birth in mid-February (Fig. 15) and spent very little time outside of the den site the first 1-2 weeks. Although there was much variation both between individuals and years, females rarely shifted den site, or only moved short distances, during the first 1.5 months of the denning period (Fig 15, 16). Later during the denning period (after 15th April), females start to move more often and further between den sites (Fig. 16). These results suggest that searching for tracks to document regular activity at den sites should be initiated in early March, when females start to move outside of the den, and focus until the second half of April when females start moving more frequent and longer distances than before. Furthermore, observed distances between neighbouring females and sequential dens of individual females suggest that a distance criterion that is dynamic over time could be used to separate different females' den sites. From February to mid-April a distance criterion between 2.5 and 4 km would minimize erroneous conclusions. Thereafter, in the first part of May and particularly during the latter part of May, distance criterion should be larger (i.e. 5-10 km) when the difference between individual females' den site movements and neighbouring den sites decreases and the overlap between these distances increases.

The timing of birth and temporal pattern of den site use in relation to current knowledge about temporal aspects of offspring development, resource availability, and foraging strategies can shed light on wolverines' adaptation to its northern habitats. During the first period, 2-2.5 months from mid-February, when most females give birth, the females spend extended time at each den site and move short distances between den sites. This corresponds with the lactation period, when females do not need to bring back food to the cubs in the den site (Inman *et al.* 2012*b*). Also, available prey is generally rare and females presumably rely mainly on cached food, scavenging and opportunistic predation on reindeer. This early period also coincides with a persistent snow cover that provides for den sites that gives protection for cubs (e.g. against predators and cold weather), as well as favourable conditions for food caching. After this first period, from late April, the females shift den sites more frequently and over longer distances. The cubs are now more mobile and rely more on solid food brought by the mother. This coincides with a drastic increase in prey availability, primarily due to the return of migrating reindeer and their calving period (Mattisson *et al.* 2016), which presumably reduces the females´ need to bring food long distances back to the den. The timing of parturition and temporal change in denning behaviour presumably reflects wolverines' adaptation to match birth time and offspring development to changes in resource availability and foraging strategies in this area. Considering that similar seasonal shifts in resource abundance are observed at multiple locations at different latitudes within wolverine range (Inman *et al.* 2012*b*), indicate that the observed pattern is general within the distribution of this solitary carnivore.

6 Management Implications

In large parts of Europe, carnivores coexist with people in multi-use landscapes outside protected areas (Chapron *et al.* 2014). However, management strategies often differ between areas, within and between countries. Scandinavian lynx and wolverine populations are both subject to different management strategies in Sweden and Norway. Population goals for both species are considerably lower in Norway compared to Sweden, resulting in higher hunting pressure in Norway (Andrén *et al.* 2006; Linnell *et al.* 2010; Gervasi *et al.* 2015). For example, in south-central Sweden legal hunting caused 29% of lynx mortality (Paper II), compared to 51% in Norway (Basille *et al.* 2013). In Paper II, I show that lynx survival in south-central Sweden is primarily influenced by functional habitat characteristics. However, the risk of human-caused mortality was the same throughout the landscape, and was not higher in areas with high resources density. Thus, I did not find indications of attractive sinks in south-central Sweden, contrary to previous studies in Norway (*cf.* Bunnefeld *et al.* 2006; Basille *et al.* 2013). Although lynx persist in the human-dominated landscape of south-central Sweden, contrasting management regimes within the same population can result in large-scale source-sink dynamics (*e.g.* Gervasi *et al.* 2015). Consequently, the effect of human activity on habitat use, different management strategies, and consequences for population dynamics need to be further evaluated at the population level. Moreover, the influence of roe deer abundance on lynx survival (Paper II), in addition to its importance for space use patterns (Paper I and III), emphasize the importance of accounting for variation in prey abundance for lynx monitoring and management (*e.g.* Gervasi *et al.* 2013).

Our understanding of carnivore abundance and distribution at the population level benefits from detailed long-term studies of individual space use over time. Accordingly, in Paper V, I show that a in saturated wolverine population with relatively low adult female mortality, vacant territories are quickly reoccupied by females from the area, while there were limited opportunities for dispersers to settle. Females born in the area often remain philopatric if they have the opportunity to inherit their natal territory or settle in a neighbouring territory. Together, these findings suggest that saturated areas are most likely to act as a source, providing emigrating females to surrounding areas. This dynamic has consequences for the resulting harvest, as management actions take place at different scales.

On a local scale, lethal control of carnivore is used to decrease conflicts on a local level, *e.g.* reindeer calving areas. However, my findings in Paper V suggest that this management action likely has a limited effect on the local density of resident individuals in saturated populations of territorial species, like the wolverine. Instead, my results suggest that fewer young females disperse when there are vacancies available in the immediate surroundings. Consequently, the primary effect of limited harvest will be to decrease emigration to surrounding areas, while the number of resident individuals will remain relatively constant, possibly with an increasing proportion of young established individuals in the local area, resulting in a changed age structure.

On a larger scale, source populations can be important for sustaining the persistence of threatened populations (Clobert *et al.* 2009). However, source-sink dynamics can also complicate management strategies, which differ between areas. The Scandinavian wolverine population is an example, as it is subject to very limited harvest in Sweden compared to Norway. Accordingly, wolverine numbers have increased in Sweden the last decades (Persson *et al.* 2015; Paper VI). At a large scale, this has resulted in a net flow of wolverines from Sweden (source) to Norway (sink; Gervasi *et al.* 2015). This dynamic may hinder both countries in achieving their respective management goals (*i.e.* increase in Sweden, decrease in Norway). On the other hand, my findings also suggest that the recent increase in wolverine numbers, and density, along the Swedish mountain range has presumably resulted in an increasing number of young females dispersing to surrounding areas. This dispersal, in turn, is an important driver behind the recent recolonization of the forest landscape east and south of the alpine areas (Paper VI).

Moreover, this recent expansion further illustrates the importance of matching management to ecological processes at the appropriate scale. The wolverine population expansion is in alignment with the Swedish management goal to increase wolverine distribution outside the reindeer husbandry area (SEPA 2014*b*). However, I show that ~30% of the current wolverine distribution remains largely unmonitored. Thus, management decisions are currently based on incomplete information about the status of the population. This scale mismatch between monitoring practices and population goals can hinder implementation of management actions in high-conflict areas, which would be possible with appropriate information about the entire population. This situation could have negative consequences for the credibility of management and for wolverine conservation. One reason is that the current monitoring protocol is not adapted to conditions without persistent snow cover, as in the newly colonized areas. Therefore, it is important to adapt the current monitoring protocol for different conditions, *i.e.* lack of persistent snow cover for snow tracking to find den sites to document reproductive events, or to find scats for genetic analysis. It is still essential to maintain the current monitoring of reproductions in the Swedish reindeer husbandry area, due to its importance for the conservation performance payment system, which in turn is facilitates wolverine conservation (Persson *et al.* 2015)

Even in areas with persistent snow cover, monitoring can be improved with more knowledge about individual females' space use. In Paper VII, I show that denning females give birth in mid-February, and start moving outside the den more often from late February onward, and change den sites infrequently and over short distances until mid-April. This activity pattern implies that documentation of den sites (*i.e.* consistent activity at suspected sites), is most efficient from early March to mid-April, conditional on snow conditions. This finding, in combination with observed distance between neighbouring females' den sites, implies that the distance criteria for separating simultaneously documented den sites should be dynamic over time, during the denning season. Furthermore, the fact that wolverine females give birth as early as January 29, with a peak in mid-February, is important information for setting harvest season limits for the species.

In conclusion, my findings underline the importance for management of carnivores to consider the appropriate scale of management in relation to the scale of ecological processes (Cumming, Cumming & Redman, 2006; Guerrero *et al.*, 2013; Hermoso *et al.*, 2016). This is relevant for management from a very local scale (*e.g.* lethal control of single individuals; Linnell *et al.* 1999) to management across national borders (Bischof *et al.* 2015).

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