Interactions between Eurasian Lynx and Wolverines in the Reindeer Husbandry Area

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Cover: Wolverine tracks to a lynx–killed reindeer
    (photo: J. Mattisson)

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Abstract

In conservation and management, carnivore species are often treated as isolated units, even though interspecific interactions can have important implications for the behaviour, demography and distribution of the species involved. In this thesis I used individual based GPS-location data to study interactions between two solitary predators in the reindeer husbandry area in Northern Scandinavia: The Eurasian lynx (*Lynx lynx*), an obligate predator, and the wolverine (*Gulo gulo*), an opportunistic predator and scavenger. Semi-domestic reindeer (*Rangifer tarandus*) is the main prey for both species, which creates a conflict with the reindeer management. I found no major competition between lynx and wolverines. The two species had completely overlapping home ranges, they moved independently of each other and they generally selected for the same type of habitat: steep and rugged terrain mainly in deciduous forest and heath. The lynx is an efficient predator on reindeer and I observed a high variation in individual kill rates depending on lynx status, season and reindeer density. Wolverine predation was lower than lynx predation and although reindeer dominated wolverine diet it was mostly attained through scavenging, predominantly on lynx-killed reindeer. Although, wolverines scavenged two thirds of available lynx-killed reindeer, wolverine scavenging had only minor influence on lynx kill rate. My result suggests that wolverines benefit from being sympatric with lynx through increased scavenging opportunities while the costs for the lynx seem to be limited. I studied the interactions between lynx and wolverines in an area with high densities of both predators and prey and the outcomes may look different in other ecological settings. Especially, low prey densities are likely to enhance the potential for competition. This knowledge of interspecific interactions between lynx and wolverines will be useful for management and conservation of the two species in an area of conflict: the reindeer husbandry area.

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Dedication

To all of you that made my day

Learn from yesterday, live for today, hope for tomorrow. The important thing is not to stop questioning

    Albert Einstein

Contents

Dissertation: SLU, Uppsala, Loftets hörsal, 11 March 2011, 10:00 am.

Chairman:	**Tomas Pärt**, SLU, Uppsala
External examiner:	**Eric Gese**, Utah State University, Logan, USA
Evaluation committee:	**Torkild Tveraa**, NINA, Tromsø, Norway
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Main supervisor:	**Henrik Andrén**, SLU, Grimsö
Assistant supervisor:	**Jens Persson**, SLU, Grimsö

List of Publications

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

I   Mattisson, J., Andrén H., Persson, J., & Segerström, P. (2010). Effects of species behavior on Global Positioning System Collar fix rates. *Journal of Wildlife Management* 14(3), 557-563.

II Mattisson, J., Persson, J., Andrén H., & Segerström, P. (2011). Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). *Canadian Journal of Zoology* 89 (2), 79-89.

III Rauset, G.R., Mattisson, J., Persson, J., Andrén, H., Chapron, G., & Segerström, P. Scale dependent differentiation in habitat selection between two sympatric predators. (Manuscript).

IV Mattisson, J., Odden, J., Nilsen, E.B., Linnell, J.D.C., Persson, J., & Andrén, H. Factors affecting lynx kill-rates on semi-domestic reindeer in northern Scandinavia: can ecological research contribute to the development of a fair compensation system? (Manuscript).

V   Mattisson, J., Andrén H., Persson, J., & Segerström, P. Top predator facilitates conservation of an opportunistic predator by increasing scavenging opportunities (Manuscript).

1 Introduction

Many large carnivore species are now recovering and expanding into new areas often in multi-use landscapes (Landa et al. 2000, Linnell et al. 2009), which challenge the current regimes for management and conservation of carnivores. Increasing carnivore populations often result in enhanced conflicts with humans. One of the most common causes of human-wildlife conflicts is livestock depredation by large carnivores, which can have a significant socio-economic impact on individual farmers (Thirgood et al. 2005, Zimmermann et al. 2010). In conservation and management, carnivore species are often treated as isolated units, even though interspecific interactions can have important implications for the demography and distribution of the species involved (Creel and Creel 1996, Linnell and Strand 2000, Caro and Stoner 2003, Berger and Gese 2007). Therefore, it is important to increase knowledge about interactions among coexisting carnivore populations to better understand what is limiting populations and to facilitate conservation and management in multi-predator systems. In addition, depredation levels may be influenced by interspecific interactions as cumulative predation on a common prey from two or more predators is not necessarily the sum of predation by each species separately (Sih et al. 1998).

1.1 Interactions among Carnivores

Interspecific interactions are often complex and can result in a great variety of outcomes (Thompson 1988, Glen and Dickman 2005) that seldom are constant even between the same pair of species (Linnell and Strand 2000). Interactions may be influenced by resource availability (Scognamillo et al. 2003, Belant et al. 2010, Henden et al. 2010), behavioural adaptations (Arjo and Pletscher 1999, Atwood and Gese 2008), landscape structure and

relative densities of the carnivores (Creel and Creel 1996, Berger and Gese 2007) and their prey (Creel 2001). Competition can be divided into exploitation or interference competition (Linnell and Strand 2000, Glen and Dickman 2005), but is often a combination of the two. Exploitation occurs when species are using the same recourses and thereby deprive each other of those resources. It is dependent on resource availability and is stronger when resources are limited. Interference competition involves antagonistic behaviour, which in the extreme cases can result in death i.e. intraguild killing, observed in many carnivore species (Palomares and Caro 1999). Aggressive interactions may totally exclude a species from a given habitat, while active avoidance can result in shifts of habitat use and reduce foraging opportunities. In contrast to exploitation competition, interference competition can occur when resources are not limited (Linnell and Strand 2000, Creel 2001). Similar ecology increases the risk of competition while mechanisms such as resource partitioning, temporal or spatial avoidance strategies (Arjo and Pletscher 1999, Mitchell and Banks 2005, Kozlowski et al. 2008), activity patterns (Fedriani et al. 1999), partitioning in prey size (Scognamillo et al. 2003), or different foraging strategies (Murray et al. 1995, Kunkel et al. 1999, Husseman et al. 2003) will facilitate coexistence.

Sympatric species do not necessarily influence each other negatively, and interspecific interactions may even be beneficial for one (commensalism) or for both species (mutualism; Thompson 1988, Polis et al. 1989, Dickman 1992). Beneficial associations can arise between species to improve foraging success (Minta et al. 1992, King and Cowlishaw 2009, Desbiez et al. 2010). Scavengers and opportunistic predators can benefit from being sympatric with an efficient hunter (van Dijk et al. 2008b) although the risk of interference competition may increase (Creel et al. 2001, Atwood and Gese 2008). Subordinate scavengers may feed when the predator is absent while dominant scavengers, like grizzly bears (*Ursus arctos horribilis*) can take over kills from the subordinate cougar (*Puma concolor*; Murphy et al. 1998). Dominant species stealing food can have large effects on the fitness, behaviour or kill rate of the subordinate species. For instance, African wild dogs (*Lycaon pictus*) need to spend more time hunting prey in areas with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), as they lose killed prey to these two predators (Gorman et al. 1998, Carbone et al. 2005). However, the hierarchy of species is not always consistent. For example, interactions between wolves (*Canis lupus*) and coyotes (*Canis lantrans*) is complex (Atwood and Gese 2010), where e.g. group size seems to play a crucial role to determine the outcome of interactions. Coyotes benefit from scavenging on remains of prey killed by wolves although wolves kill coyotes

(Arjo and Pletscher 1999, Berger and Gese 2007) and coyote density is negatively related to wolf density (Berger and Gese 2007).

1.2   Lynx, Wolverines and Reindeer

The Eurasian lynx (*Lynx lynx*) is found over large parts of Scandinavia while the wolverine (*Gulo gulo*) is mainly associated with the mountain region. In the latest Red list for Sweden, the lynx is listed as near threatened and the wolverine as vulnerable, but the conservation status has recently improved for both species (Gärdenfors 2005, 2010). The estimated population size within the Swedish reindeer husbandry area during the last 10 years was 500-900 lynx (Andrén and Liberg 2008) and 320-650 wolverines (H. Brøseth, pers. comm.).

The lynx is an efficient felid predator, largely specialized on medium sized ungulates (Pedersen et al. 1999, Odden et al. 2006, Molinari-Jobin et al. 2007). Semi-domestic reindeer (*Rangifer tarandus*) is the main prey of lynx in the reindeer husbandry area and roe deer (*Capreolus capreolus*) outside. The wolverine is an opportunistic mustelid predator that often depends on scavenging (van Dijk et al. 2008b, Dalerum et al. 2009). It is well adapted to find ungulate carcasses, which may be cached for later use (Haglund 1966). Wolverines are known to scavenge prey killed by other large predators (Haglund 1966, van Dijk 2008b). Although the wolverine is a less skilled hunter (Haglund 1966) it can be a significant predator on juvenile ungulates (Bjärvall et al. 1990, Landa et al. 1999, Gustine et al. 2006) and is fully capable of killing adult reindeer and even moose (*Alces alces*) when the conditions are right (Haglund 1966). Both lynx and wolverines are solitary and the only groups formed are adult females with young of the year. The lynx is slightly larger than the wolverine (lynx F: 17 kg, M: 22 kg; wolverine F: 10 kg, M: 14 kg) suggesting that the lynx may be dominant over the wolverine (Donadio and Buskirk 2006). Lynx are known to kill smaller carnivores like red fox (*Vulpes vulpes*), and pine martens (*Martes martes*; Okarma et al. 1997, Linnell et al. 1998, Helldin et al. 2006), but of 55 known wolverine mortalities none was killed by lynx (Persson et al. 2009). In contrast, wolverines have been killed by both wolves (Boles 1977, White et al. 2002), mountain lions (Krebs et al. 2005), and bears (Inman et al. 2007b). On the other hand, a young lynx may have been killed by a wolverine (Andrén et al. 2006) but this was only one possible incident in 33 known lynx mortalities.

In Scandinavia, reindeer are managed exclusively and extensively by indigenous Sámi people. The reindeer husbandry area covers ~ 50% of

Sweden and ~ 40% of Norway, where 250 000 and 230 000 reindeer respectively, graze freely and mainly unattended. The natural seasonal migration of reindeer between winter and summer pastures is maintained but governed by the owners and land use restrictions. The reindeer husbandry today is forced to adapt to environmental changes due to e.g. land use, forestry, hydropower development, and to decreased forage availability as an effect of changing weather conditions (Lundqvist 2003). In addition to this, there is a constant depredation pressure from carnivores. In contrast to the other impacts, carnivore depredation is direct and perceptible and the potential for changes is within reach by decreasing the number of carnivores. The extent of depredation on semi-domestic reindeer is unknown but rough estimates indicate that the losses, at least locally, can be as large as the harvest (Swenson and Andrén 2005). Lynx and wolverines are held responsible for a major part of the depredation on semi-domestic reindeer (Bjärvall et al. 1990, Nybakk et al. 2002) but locally, brown bear (*Ursus Arctos*; Bjärvall et al. 1990) and golden eagles (*Aquila chrysaetos*; Nybakk et al. 1999, Nordberg et al. 2006) can be the main predator on small calves.

Both Sweden and Norway have signed the UN's International Covenant on Civil and Political Rights, and are thereby committed to sustain the Sami culture in which reindeer management is an important part. Likewise both countries are signatories of the Council of Europe's Bern Convention, and Sweden is bound by the European Union's Habitats Directive and is thereby committed to preserve lynx and wolverines in viable populations. Consequently, management need to compromise between the conservation of carnivores and the sustainability of reindeer husbandry (Nilsson Dahlström 2003). Depredation losses should be fully compensated in both countries. In Sweden, the compensation scheme for reindeer losses is based on presence and density of carnivores rather than the actual losses. Yearly national surveys of lynx family groups and wolverine reproductions are conducted by the county administration in collaboration with the reindeer management districts (Landa et al. 1998, Andrén et al. 2002, Linnell et al. 2007) and compensation is paid per lynx family group and wolverine reproduction to each district. The compensation for the different species is added independently of one another. In Norway, compensation is based on documented and probable losses (as the detection rate of carnivore-killed reindeer is very low) and is paid directly to the owners. To reduce depredation, lynx are hunted on a quota system in both countries while wolverines are subject to very limited lethal control in Sweden but hunted on a quota system in Norway. Lethal control is undertaken in addition to

quota hunting when damage gets to severe. Poaching occurs on both species in both countries (Andrén et al. 2006, Persson et al. 2009).

The current level of compensation is based on uncertain and limited information on individual kill rates. There is an urgent need of increased knowledge on lynx and wolverine predation on reindeer and an understanding of the ecological factors that cause variation in kill rates, including effects of interactions between the species. This information is essential in order to reach a fair compensation scheme.

1.3 Objectives

The aim of this thesis was to investigate the relationship between lynx and wolverines and predation on semi-domestic reindeer. To do this, I used individual based data from GPS-collared lynx and wolverines to study interactions in space and time and their foraging behaviour. The main questions were:

Paper I   Do species' behaviour affect the performance of GPS-collars?

Paper II   Do spatial and temporal interactions between lynx and wolverines influence their use of space?

Paper III   Does species ecology or interspecific interactions influence habitat selection in lynx and wolverines?

Paper IV   How many reindeer do lynx kill and which ecological factors affect variation in kill rates?

Paper V   Is lynx-killed reindeer an important resource for wolverines and does wolverine scavenging affect lynx kill rate on reindeer?

2 Material and Methods

2.1 Study Areas

This thesis is a part of the Swedish Wolverine Project and Scandlynx (a collaboration between the Swedish and the Norwegian lynx projects). The thesis is mainly based on data collected in and around Sarek National Park (Kvikkjokk: 67°00'N, 17°40'E) as a part of an ongoing long-term individual-based study on lynx and wolverines (Fig. 1). The area is characterized by deep valleys, glaciers and high plateaus with peaks up to 2 000 m. Main vegetation is alpine tundra at higher elevations, sparse mountain birch forest (*Betula pubescens*) in higher valleys and hillsides and mixed conifer forest (*Pinus sylvestris*, *Picea abies*) at lower elevation. Mountain birch form the tree line at 600 m to 700 m and elevation ranges from 300 m to 2 000 m. Infrastructure in the area is limited to two dead end roads in the outskirts, some minor permanent settlements, a few cabins, and a hydropower plant. Paper I and IV include data from lynx radio-collared in cooperation with the County Administrations of Norrbotten, Västerbotten and Jämtland (61°80' – 66°80'N, 12°50 – '23°80'E; Fig 1). These areas are dominated by mixed conifer forest interspersed with wetlands and some alpine tundra. In paper IV, data was also collected in Troms and Finnmark (69°00 – 70°10´N, 19°90 – 25°00´E) in Northern Norway (Norwegian Institute for Nature Research), an area characterized by coastal alpine climate. Alpine tundra dominates the area followed by birch forest. Semi-domestic reindeer, managed exclusively and extensively by indigenous Sámi people, dominate the ungulate population in all study areas. The distribution of reindeer is widespread but patchy, and due to long distance migration densities vary both temporally and spatially, from extremely low to very high densities.
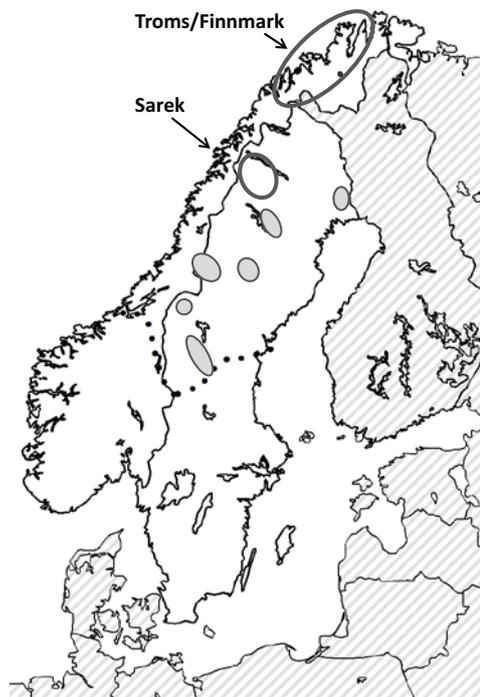
Figure 1. Map of Scandinavia showing the areas of data collection. Data from Sarek in Sweden is included in all papers. In paper IV, data was also collected in Troms and Finnmark in Northern Norway (Norwegian Institute of Nature Research). Filled circles represent areas of lynx, radio-collared in collaboration with the County administrations of Norrbotten, Västerbotten and Jämtland, included in Paper I and IV. The dotted line indicates the southern border of the reindeer husbandry area in Norway and Sweden.

2.2   Animal Location Data

All papers in this thesis are based on individual Global Positioning System (GPS) location data from collars fitted on lynx and wolverines. The use of GPS-collars provides a large amount of location data with high accuracy and precision. To equip lynx and wolverines with GPS-collars, we darted the animals from a helicopter or from the ground and immobilized them with a mixture of medetomidine and ketamine. The handling of the animals followed pre-established protocols (Arnemo et al. 2011). Individuals in Sarek were additionally equipped with intraperitoneally implanted VHF-transmitters (IMP/400/L, Telonics Inc., Mesa, AZ, USA). The handling protocol was approved by the Swedish Animal Ethics Committee and the Norwegian Experimental Animal Ethics Committee and fulfils their ethical

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requirements for research on wild animals. Between 2002 and 2007 we used store onboard GPS-collars (Televilt PosrecTM C300, TVP positioning AB, Lindesberg, Sweden), where the data was stored in the collar and received after retrieval of the collar (Paper I, III and partly in II and IV). We equipped 15 wolverines and 28 lynx with these collars. The collars were programmed to take 8 locations/day but when scanning the data we realised that the fix rate (i.e. the proportion of acquired locations of all programmed attempts) varied considerably among collar periods (i.e. battery life of a collar). Collars fitted on lynx had higher fix rate (80%) than collars fitted on wolverines (46%). Variation in fix rate due to e.g. environmental variables (Di Orio et al. 2003, Frair et al. 2004, Hebblewhite et al. 2007) or animal behaviour (Bowman et al. 2000, Graves and Waller 2006, Heard et al. 2008) may lead to misinterpretation of data analyses and our concern for this lead to paper I. To reveal the causes of this variation, we calculate three types of fix rates: (1) a total fix rate for the period the collar worked, (2) a monthly fix rate, and (3) a circadian fix rate for each programmed hour. We then tested the effects on collar fix rate of: species (using fix rate 1, 2, and 3 above), proportion of forest habitat in home range (fix rate 1), season (fix rate 2), denning behaviour (fix rate 2), circadian use of forest habitat (fix rate 3), and movement rate (fix rate 3; m/h travelled by the animal) primarily using general linear models (ANOVA and ANCOVA).

In 2008, new collars small enough to use for wolverines and lynx were available with GSM communication or UHF communication with VHF download (GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany). These collars were much improved compared to the store onboard collars, both considering battery life and fix rate. Fix rate for lynx was still higher (94%) than for wolverines (80%), but here the lowest fix rate matched the highest for the older collars and were therefore of less concern. In addition we received considerably more locations per individual, which decreased the risk of misinterpretation in the analyses. In this thesis, we have used data from 29 lynx and 8 wolverines equipped with these collars, that were programmed to take 3 or 8 locations/day as base schedule and re-programmed to ≤ 48 locations a day during periods with intensive studies of specific research questions (Paper II, IV and V).

2.3 Spatial and Temporal Interactions

To examine if there was any spatial segregation between lynx and wolverines, we calculated the overlap between each individual home range of species 1 with the complete range of locations of species 2 and vice versa.

Home ranges were estimated as Concave Polygons with restricted edge set to 0.2 using Ranges 8 (Anatrack Ltd., Wareham, UK). Home range overlap was also calculated for each individual dyad (i.e. a pair of individuals) with temporal overlap in GPS-locations. To investigate temporal interactions, we used Jacobs' index (Jacobs 1974) to compare distances between simultaneous locations (≤ 5 min) with all possible distances between one location of individual 1 to all locations of individual 2. All analyses were made for both inter- and intraspecific dyads. In addition, we used a repeated ANOVA to test if wolverines may express a delayed attraction towards lynx because of scavenging opportunities. The data was further split into late winter, summer and early winter to test for seasonal variation in both spatial and temporal interaction.

2.4 Habitat Selection

We explored habitat selection of lynx and wolverines in Sarek at different scales using a K-select analysis (Calenge et al. 2005) where differences between individual use (GPS-locations) and available habitats (both at study area level and within individual home ranges) were expressed as marginality. The length of the marginality vector reflects habitat selection strength and its direction indicates which habitat variables that are selected. We used three continuous topographical layers of elevation, terrain ruggedness and slope and one categorical vegetation layer with seven vegetation classes in the analyses. To analyze behaviour specific habitat selection we introduced ranging models based on animal trajectories (Calenge 2009), i.e. the distance travelled between successive observations: a long distance ranging mode, an intermediate distance ranging mode, and a stationary mode. We included behaviour specific habitat selection partly to deal with the behavioural induced loss of successful GPS locations observed in Paper I. All analyses were performed in program R (R Development Core Team 2009), using package "adehabitat" (Calenge 2006).

2.5 Predation and Foraging Behaviour

To examine lynx predation and wolverine foraging behaviour, we visually identified clusters of GPS-locations using GIS-software (ArcView 3.3 and ArcMap 9.3, ESRI). The number of locations required to define a cluster was based on 2 locations ≤ 100 m apart. The first clusters on lynx were visited already in 2002 and on wolverines in 2006. We have since then increased our knowledge of the animals' behaviour helping to identifying

clusters indicating a kill or a scavenging event. In total, we visited over 3 700 lynx clusters (Sweden and Norway) and 461 wolverine clusters (in Sarek only). A cluster indicating a typical kill site for lynx is shown in figure 2a; where the lynx alternate feeding sessions at the carcass (central locations) with rest sites. Rest sites can be as far away as 7.5 km from the kill (Falk 2009) and the lynx stay on average 2.2 days (± 2.4 SD) on a killed reindeer (Odden et al. 2010). A wolverine kill or scavenging site looks similar to a lynx kill site but in addition they run back and forth between the carcass and cache sites and do so more irregular and over a longer time span than lynx (Fig. 2b; Odden et al. 2010). Cache sites are often located among boulders or as cavities in deep snow but could also be under a rock, or in bogs. We often found prey items of different age at cache sites indicating that they were reused. At several clusters, we found only bed sites, often with hair from the lynx or wolverine. These clusters were usually associated with a series of daytime locations within a very limited area, with no revisits, and located in steep and inaccessible places. This type of cluster was given lower priority in favour for sites that were revisited by the lynx or the wolverine (≥ 2 locations) or where they stayed ≥ 1 night. Fieldwork mostly took place in remote areas and clusters could be > 40 km from nearest roads and although we tried to visit as many clusters as possible, we sometimes had to prioritise between clusters.
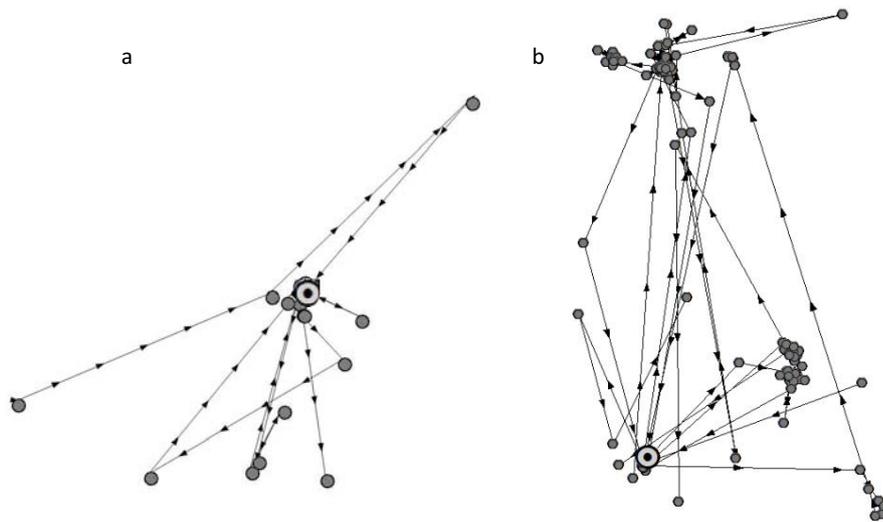
Figure 2. Movement pattern around a reindeer carcasses for (a) lynx (8 locations/day) and (b) wolverines (38 locations/day). Filled circles are animal locations and the large circle with dot indicates the location of the carcass. The large clustering of locations in (b) are food caches.

Lynx kill rate, i.e. number of reindeer killed per lynx during a given time interval, was estimated for 35 lynx in Sweden and Norway, during 128 periods including 3 667 monitoring days (Paper IV). To model the variation in lynx kill rate, we used zero-inflated negative binominal models (ZINB; Zuur et al., 2009). All models were run in program R (R Development Core Team 2009) with the add on libary pscl (Zeilies et al. 2008). Lynx social status (male, solitary female or family group) and an indicator of ecological conditions representing season (winter or summer) and reindeer density (low or high) was included in the models.

To assess if wolverine scavenging influenced lynx predation on reindeer (Paper V) we modelled lynx time to next kill using general mixed models in SPSS (GLMM; IBM®SPSS® Statistics, 19.0.0, Chicago). Time to next kill was calculated as the number of days between the first GPS-location at a lynx-killed reindeer and the first location at the next prey killed by the lynx. Possible variation among lynx individuals was included in the model by allowing the intercept to be random. We introduced three variables in the model: wolverine scavenging while the lynx was still handling the reindeer (yes or no), vegetation at kill site (tundra or forest) and age of reindeer (calf or adult). Model performance was evaluated using Akaike's information criteria (Burnham and Anderson 2002) in both paper IV and V.

We categorised wolverine foraging behaviour (Paper V) into predation and scavenging and the relative importance of lynx-killed reindeer in wolverine diet was estimated as both proportion of carcasses visited and time spent at carcasses where number of GPS-locations was used as an index of time. Biomass (kg/km^2/month) from lynx-killed reindeer in the wolverines' area was estimated based on reindeer slaughter weight and average lynx consumption.

3 Results and Discussion

3.1 Behaviour Induced Variation in GPS Fix Rate (Paper I)

In this paper, we showed a species-specific influence on fix rate. Although the same individual GPS-collars were used on both wolverines and lynx, collars fitted on lynx had much higher fix rate (80%) than collars fitted on wolverines (46%). In all performed analyses, species had a significant effect on fix rate ($p < 0.001$). We observed species-specific circadian pattern in fix rate that corresponded well with the movement patterns of both lynx and wolverines (Fig. 3) revealing a decrease in fix rate when the animals were inactive, similar to previous studies (Bowman et al. 2000, Graves and Waller 2006, Heard et al. 2008). This was further supported by a decreased fix rate for females during the denning period, especially for lynx. Bedded animals may obstruct the collars from finding satellites (Bowman et al. 2000) and thereby decrease fix rate. The proportion of forest within home ranges, or daily use of forest did not influence fix rate. As lynx and wolverines occupy similar habitat (Paper III), the differences in fix rate between lynx and wolverines cannot be explained by general habitat use. The lower fix rate in wolverines compared to lynx is rather explained by wolverines' tendency to take cover, or cache food, below ground (in cavities under large boulders, cliffs or snow) where the collar is obstructed from making contact with the satellites. This was later supported in paper III, where we revealed that wolverines preferred low alpine tundra above the tree line when resting, a habitat were little cover is available above ground. Altogether, this suggests that fix rate is more influenced by animal behaviour than by measurable habitat characteristics.

The observed variation in fix rate was accounted for in paper III by including behaviour in the habitat selection analyses. In paper II, the analyses

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were less dependent on fix rate and a comparison with the included data from later years with much higher fix rate did not reveal any differences in the results. Kill rate estimations (Paper IV) are quite robust to collar fix rate (Knopff et al. 2009) and as only lynx data, that average 80% successful fixes, was used, no adjustments were taken.
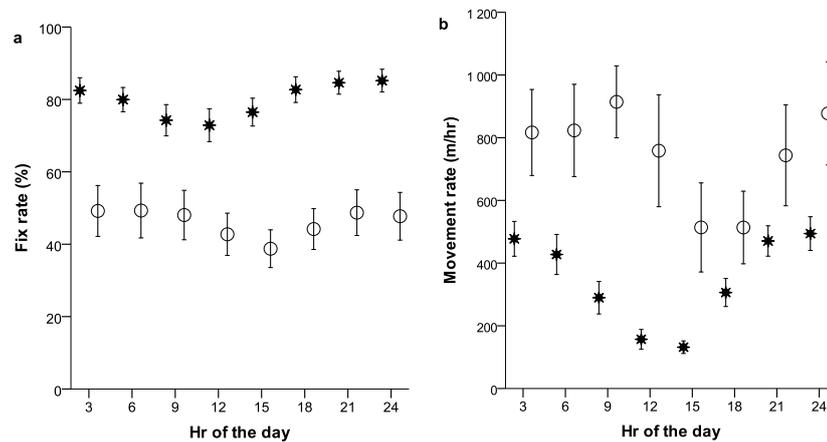
Figure 3. Circadian pattern of (a) fix rate (proportion of successful fix attempts), and (b) movement rate (mean straight distance travelled between GPS fixes 3 hours apart) for lynx (stars) and wolverines (open circle). Mean values were calculated for each programmed hour (n = 8) of each GPS-period (lynx: n = 46, wolverines: n = 35) and are presented with 95% confidence intervals.

3.2 Lynx and Wolverines in Time and Space (Paper II)

Home range size was smaller for wolverines: F = 195 km^2 ($\pm$ 26 SE), M = 733 km^2 ($\pm$ 167 SE) than for lynx: F = 777 km^2 ($\pm$ 102 SE), M = 1 776 km^2 ($\pm$ 263 SE). An individual wolverine home range overlapped completely with the pooled lynx range (96 – 100%) and a male lynx home range included completely or partly 6 to 13 wolverines. Wolverines and lynx with overlapping home ranges showed neither attraction to, nor avoidance of each other. They were often visiting the same sites (Fig. 4) but seldom at the same time (0.1% of locations) and were on average 16 km apart from each other. Spatial and temporal interactions did not change over the year. As expected, this study shows no evidence of spatial or temporal segregation between lynx and wolverines and suggests that the level of general interference competition is low, as observed among other carnivore species (Hass 2009, Schmidt et al. 2009, Wikenros et al. 2010). We expected that wolverines would be attracted (directly or delayed) to lynx as they scavenge

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lynx-killed reindeer (Paper V) but this was not observed (c.f. Ruth et al. 2003) except for a few dyads. One male wolverine showed attraction to one male and two female lynx. Wolverines likely avoid direct confrontation with lynx even though they scavenge on their kills. In contrast to the interspecific relationships we found a strong spatial avoidance in consexual wolverines; with only 7-9 % overlap of home ranges, suggesting strict territoriality (Persson et al. 2010). We observed a small attraction between males and females of both species, which increased with increasing home range overlap for lynx. Altogether, this suggests that individual space use is more influenced by conspecific interactions than by the other species, facilitating a stable interspecific co-existence (Futuyma 1986).
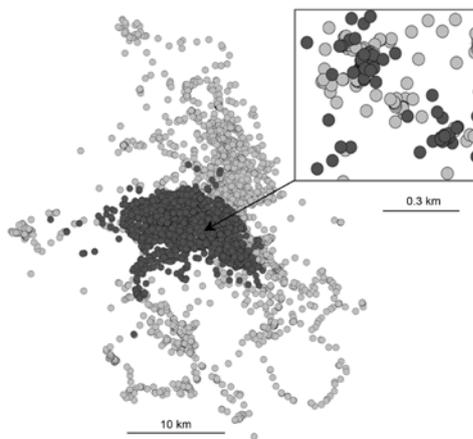
Figure 4. Locations of a female lynx (light grey) and a female wolverine (dark grey) in Sarek, Northern Sweden, showing a complete spatial overlap.

3.3 Habitat Selection in Lynx and Wolverines (Paper III)

In a mountainous region with limited infrastructure, both wolverines and lynx selected for steep and rugged terrain independent of scale, behaviour or home range habitat composition. Except for inactive wolverines, deciduous forest and heath were the vegetation classes selected for. Poaching is the main cause of adult mortality in both species (Andrén et al. 2006, Persson et al. 2009) and the selected habitats correspond to areas providing safety from human disturbance because of restricted accessibility for snowmobiles. The selected habitats also encompass areas where most lynx-killed reindeer are found (Paper V) and areas which are rich on several smaller prey species (May et al. 2010, and references therein).

Although lynx and wolverines in general selected for the same habitat categories, we observed different patterns in habitat selection between the species. Wolverines displayed a high variation when selecting home ranges whereas lynx selected stronger for the preferred habitats (Fig. 5). Habitat composition of wolverine home ranges ranged from low elevations with large portions of conifer forest to high elevation with large portions of bare rock and glaciers. The differences between lynx and wolverines may be explained by species-specific behaviour. Wolverines have a tendency to seek shelter below ground, in deep snow or in boulder fields, a behaviour seldom observed in lynx, and may thus be less dependent on steep hillsides for safety. Wolverines have smaller home ranges than lynx (Paper II) which allows for a greater diversity in home range composition in a heterogeneous landscape. Finally, the high variation in wolverines may reflect a relatively high density of wolverines in our area, thus the selection for home range placement may be restricted by a lack of available territories to occupy.
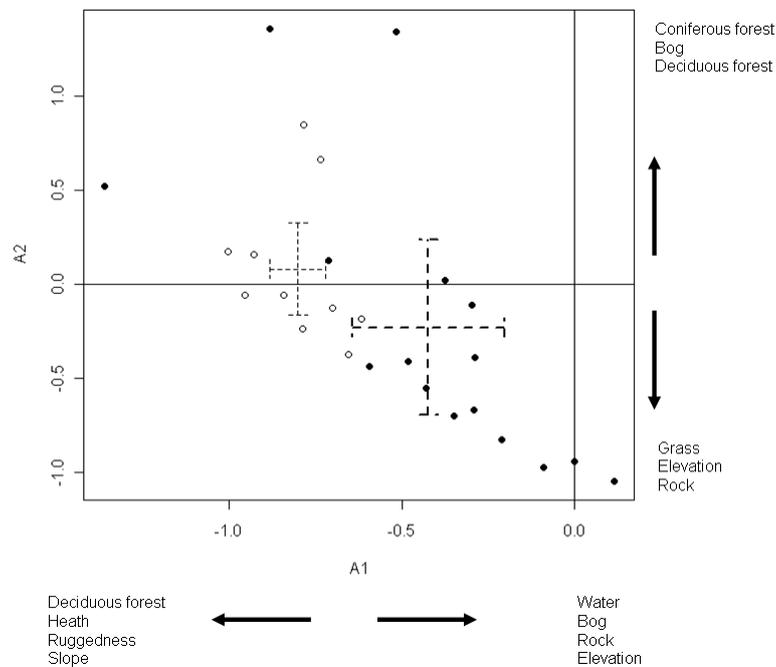
Figure 5. Result of the K-select analysis of selection for home ranges (second order selection) in lynx and wolverines in northern Sweden. The first axis A1 represents 49 % of marginality, whereas A2 represents 24 %. Dots represent the end point of the marginality vector for each individual projected on the first factorial plane. As all individuals have the same available habitats, the origin of space is the same for all individuals, i.e. (0,0). Open dots represent lynx individuals, and filled dots represent wolverine individuals. Bars represent 95% CI of mean marginality for the two species.

Lynx selected stronger for habitats within their home range than wolverines, but selection strength decreased with increasing home range size. This decrease in selection is probably a result of males having larger home ranges than females and lynx males do not raise offspring and are thus expected to have a weaker association to preferred habitat. Lynx habitat selection was only slightly related to home range composition while wolverines displayed a functional response to habitat availability.

Habitat selection for the three ranging modes was not different in lynx but in wolverines. Wolverines selected stronger for the preferred habitat when inactive compared to when they were active. When inactive they selected for rugged terrain in grass vegetation while avoiding deciduous forest, which was selected for in the active modes. Selection during the inactive mode reflects a strong habitat selection for both den sites and for favourite daybed sites that are often located above tree line in rugged terrain.

When two species live in sympatry, the subordinate species is expected to be constrained from using the most suitable resources (Belant et al. 2010). Despite the differences in habitat selection strength and selection mechanisms at the scales of the study, the overall picture display a high degree of overlap in habitat selection between lynx and wolverines, in contrast to a previous study (May et al. 2008). We observed no interference competition between the species, resulting in an exclusion of preferred habitat or spatial segregation (Paper II), but rather a selection for habitats rich on several prey species (May et al. 2010, and references therein) and against habitat that increased the risk of human encounters.

3.4   Lynx Predation on Reindeer (Paper IV)

The most important prey for lynx in this study was semi-domestic reindeer (70%). All monitored lynx individuals killed reindeer although there was a high variation in kill rate. Even during winter in areas where reindeer density was extremely low (due to migration) 15% of lynx kills were reindeer. These reindeer were mostly killed by females with dependent young, with high energy requirements (Laundré 2005). Solitary females and males survived on hares, birds and other carnivores, like red fox and domestic cats (*Felis catus*). Even at high reindeer density, several lynx (29% of the individuals) periodically switched completely to small prey. This behaviour was only observed in solitary females or family groups during summer when the females are restricted in their movements by their young kittens (sensu Laurenson 1995, Schmidt 1998).
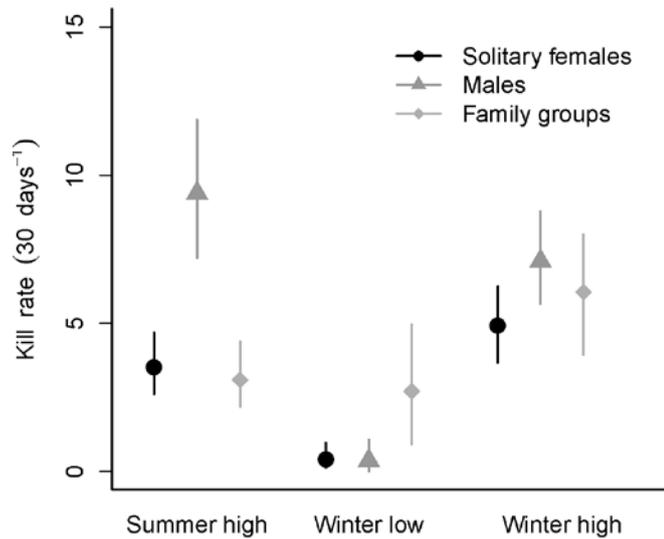
Figure 6. Predicted lynx kill rate on reindeer with 95% bootstrap confidence interval based on 128 kill rate periods from 35 lynx in northern Sweden and Norway, separated by lynx social status. High-low indicates presence-absence of reindeer pasture within the lynx home range at the time of the kill rate period.

Lynx are known to be efficient predators and kill rates on ungulates remain high even at very low prey densities (Nilsen et al. 2009), a finding also confirmed by our study. Our best performing model suggested that kill rates were dependent on ecological conditions (season and reindeer density), but also that lynx of different social status responded differently to these conditions. Kill rates were generally higher in winter than in summer, and males killed more reindeer than females (Fig. 6). But the highest kill rates were observed for males in summer when the proportion of reindeer calves among the killed reindeer was high (65%).

Individual differences (Linnell et al. 1999, Nilsen et al. 2009), density and condition of reindeer (Tveraa et al. 2003), alternative prey densities, area (Bjärvall et al. 1990), scavengers (Paper V) or human disturbance (Zimmerman et al. 2007) could all play a significant role when explaining variation in kill rates, but we were not able to test for them. Lynx predation on reindeer differs from predation on both domestic sheep and roe deer in several aspects. Lynx predation on sheep is dominated by males (Odden et

al. 2002), much more so than predation on reindeer. Multiple or surplus killing of sheep is common (Odden et al. 2002) while only 5.5 % of the killing events on reindeer involved more than one kill. Sheep are mainly killed by lynx incidentally when encountered during other activities, while lynx actively search for reindeer and roe deer as their main prey (Odden et al. 2008). Kill rates on reindeer also seem to fluctuate more than for roe deer, although the mean kill rate is similar (Okarma et al. 1997, Nilsen et al. 2009, Andrén and Liberg unpublished). Reindeer occur more clumped than roe deer and their presence is less predictable and can vary from none to very high densities in a single day.

3.5 Wolverine Use of Lynx-killed Reindeer (Paper V)

Reindeer was the most important food source for wolverines (85%), mainly as carrion but partly as prey (Fig. 7). Wolverines spent three times as much time scavenging than feeding on wolverine-killed reindeer. Thirteen percent of the reindeer carcasses utilised by wolverines were killed by wolverines, while 61% were killed by lynx and scavenged by the wolverines. Most of the remaining reindeer scavenged by wolverines was killed in accidents (Fig. 7). Of all wolverine locations at any carcass, 28% were on lynx-killed reindeer, less than expected from availability, but still slightly more than on wolverine-killed reindeer (24%). The less time spent at each lynx-killed reindeer compared to each wolverine-killed can partly be explained by the lesser amount of available biomass after lynx consumption and partly by a possible enhanced intensity of caching when the reindeer was killed by lynx compared to when killed by themselves. This behaviour by the wolverine may minimize the risk of an encounter with the lynx. Still, lynx predation provided monthly 0.8 kg biomass of reindeer per km^2 for the wolverines, more than twice wolverine food requirements, emphasizing the importance of the lynx as a top-predator in this ecosystem.

Lynx is an efficient predator on reindeer (Paper IV) providing a reliable year round food source for wolverines even when reindeer density fluctuates. Wolverines scavenged 68% of all available lynx-killed reindeer, which did not change seasonally, suggesting that wolverines take advantage of these opportunities to scavenge even during summers when other food resources are more abundant. In the study area (Sarek), wolverines were responsible for only 7–10% of the combined lynx and wolverine predation.
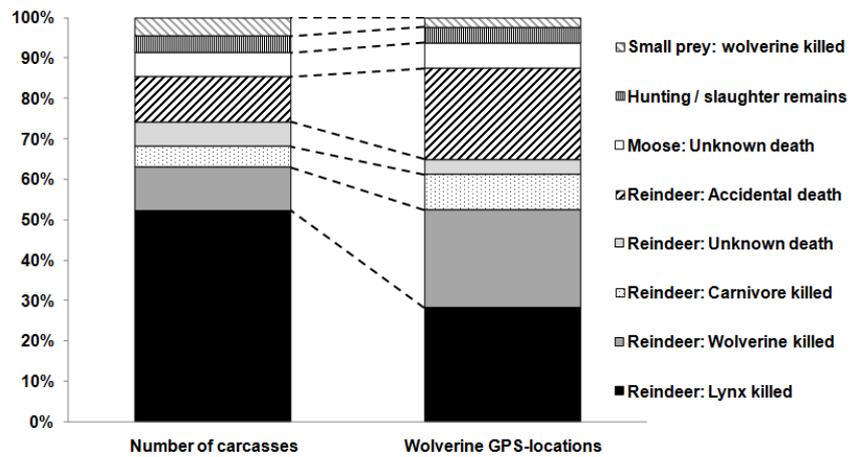
Figure 7. Relative importance of different carcass categories (species and cause of death), illustrated by both the number of carcasses visited (n = 151) and the associated number of GPS-locations (n = 2 034) from eight wolverines, monitored for 868 days in northern Sweden, 2008-2009.
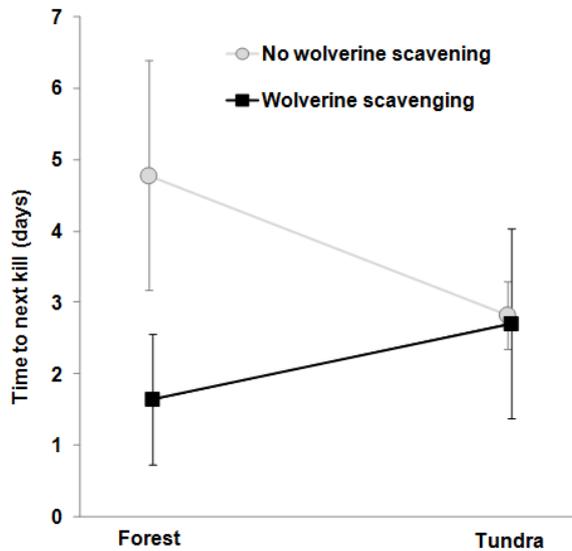
Figure 8. Lynx time to next kill (predicted mean with 95% confidence intervals) in relation to vegetation (forest and tundra) at kill site and separated by presence or absence of wolverine scavenging while the lynx still utilize the kill (≤ 24 hours between lynx and wolverine GPS-locations at the kill site).

28

At 20% of all lynx-killed reindeer that was available for the wolverines, the wolverine arrived at the kill site while it was still being utilised by the lynx. If wolverine scavenging forces lynx to abandon their kill, or the amount of available meat for the lynx decreases, the lynx needs to kill a new prey sooner to sustain energy balance, i.e. lynx kill rate will increase (Gorman et al. 1998, Murphy et al. 1998). The best performing models revealed that lynx time to next kill was effected by wolverine scavenging, but only when the kill was an adult reindeer and the kill site was located in the forest. Here, time to next kill was decreased by 3.1 days (Fig. 8). On the tundra, where the majority of the lynx-killed reindeer were located (71%), wolverine scavenging had no effect but time to next kill was still shorter than after non-scavenged kills in the forest (Fig 8). Lynx only spend 30% of their total handling time near the carcass, and even less on tundra than in forest, and they can move several kilometres away to find bed sites more sheltered than the kill sites (Falk 2009). Together this suggests that lynx are more vulnerable to the influence of other scavengers at kill sites in open habitat, primarily raven (*Corvus corax)* and golden eagles that can quickly remove large part of the carcass (Selva et al. 2005, Kacensky et al. 2005). This is further supported by the lack of influence of the age of the killed reindeer on the time to next kill in the tundra, while in the forest, time decreased by 2.8 days after the lynx prey upon a summer calf (< 5 months) compared to an adult reindeer.

4 Lynx and Wolverines: Friends or Foes?

The results of this thesis suggest that there is no major competition between lynx and wolverines although they share the same main prey, and sometimes even the same carcasses (Paper V). Lynx and wolverines have similar daily activity pattern, i.e. they are both mostly active from dusk till dawn (Fig 3a), but wolverines are much more active than the lynx even though they have smaller home ranges (Fig. 9). There is no spatial avoidance between lynx and wolverines as shown by a complete overlap of their home ranges (Paper II). Moreover, individuals with overlapping home ranges do not avoid nor attract each other but seem to move independent of each other. Lynx and wolverines both select for steep and rugged terrain and neither of the species seems to constrain the other from using the most suitable resources. This study was conducted in an area with high densities of both predators and prey and the outcomes may look different under other ecological conditions. Especially, low prey densities are likely to enhance the potential for competition (Linnell and Strand 2000).

The presence of lynx greatly increases scavenging opportunities for the wolverine, which may enhance reproductive success of female wolverines (Persson 2005). Although the lynx is larger than the wolverine and still may constitute a threat to the wolverine in direct encounters, intraguild predation has not been observed (Persson et al. 2009). Still, wolverines and lynx are seldom at the same site at the same time even when using the same carcass. Wolverines often approach carcasses when the lynx are temporarily away (Falk 2009) and thereby minimize a possible risk associated with an encounter. We have observed one occasion when a male lynx returned to its kill and chased off a wolverine female. Wolverines have been observed to track other carnivores, sometimes for long distances, but not directly to carcasses (Haglund 1966, van Dijk et al. 2008a). If this is an avoidance strategy, or just a result of wolverines saving energy by travelling in previous

tracks is unknown. However, wolverines' high movement rate allows them to cover most of their home range in short time (Inman et al. 2007) and will therefore be much more efficient in finding carcasses by their highly developed smell (Pasitschniak-Arts and Lariviére 1995) than by tracking other predators.

It is obvious that wolverines benefit from the presence of lynx, but how is the outcome of the interactions affecting the lynx? Is it neutral, indicating mutualism, or negative, indicating a parasitic interaction? Lynx do not benefit from being sympatric with the wolverines but still seem to tolerate the wolverine. This indicates that the cost for the lynx to co-exist with the wolverine is not greater than the cost of repelling it (Minta et al. 1992). Lynx in our area were, at least in the forest, slightly affected by wolverine scavenging, which forced them to kill a new prey sooner than without wolverines. If the effects are sufficient to have any significant impact on the lynx is still unknown. So far we have no indications that wolverines have chased lynx away from carcasses. This suggests that the observed negative effect on lynx is rather a result of a decreased amount of food at a kill than direct interference from the wolverine. The caching behaviour of the wolverine has the potential to quickly remove large part of a carcass. However, the lynx may still choose not to go back to a carcass if a wolverine is present. Altogether, it seems like it is most beneficial for both species to avoid direct confrontation and associated risks of injury.
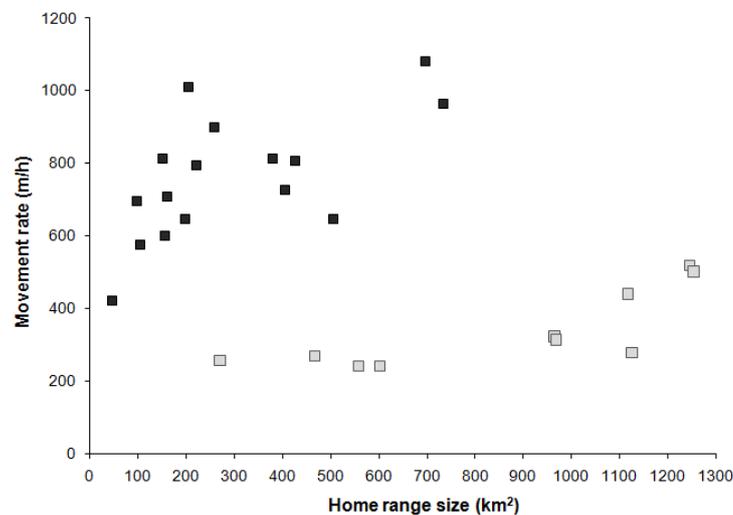
Figure 9. Movement rate in relation to home range size for wolverines (black) and lynx (light grey). Movement is calculated as the mean of straight line distances between two consecutive GPS locations.

The results in this thesis emphasize the importance of knowledge about interactions between coexisting carnivore populations. This knowledge will increase our understanding of what is limiting populations and be useful for conservation and management in multi-predator systems. Historically, lynx only occurred at low densities in the mountain region of Scandinavia (Bjärvall and Lindström, 1991). It was not until the 1990's that the lynx population started to increase and expand into this area. Wolverines, on the other hand, used to be common in the Scandinavian mountains, but were hunted down to low numbers in the 1960's. After protection in 1969 the wolverine population slowly started to recover (Bjärvall and Lindström, 1991) but it was not until the beginning of the 1990's that the population really started to increase. I can only speculate that the increase in lynx numbers was a contributing factor in the recovery of the wolverine population. The opportunistic wolverine takes advantage of any opportunity to get a free meal and when the lynx became sympatric with the wolverine, a new predictable food resource also became available.

5 Future Perspectives on Management and Research

The largest threat to wolverines and lynx in the reindeer husbandry area is neither interspecific competition nor prey depletion, but the conflict with the reindeer husbandry. Ironically, the prey that has made them thrive in the area, the semi-domestic reindeer, is also what will indirectly restrict their distribution and population size. This human–wildlife conflict is unique in the sense that livestock is the main prey for the carnivores. Reindeer occur at relatively high densities and can sustain a large number of lynx and wolverines but consequently depredation from lynx and wolverines causes great losses for the reindeer herders. The magnitude of the depredation is uncertain and discussions about the problem are largely influenced by disagreement regarding actual depredation levels. However, there is no doubt that primarily lynx (Paper IV), but also wolverines (Paper V), can have a considerable impact on the reindeer management (Bjärvall et al. 1990, Swenson and Andrén 2005). Reindeer herders have expressed a certain acceptance level of depredation by carnivores (5% of winter herd; the National Association of Swedish Sami, SSR), if economically compensated. However, this tolerance level is believed by many herders to be far exceeded today and they argue that compensation payments do not cover their losses. Reindeer husbandry covers large parts of the Scandinavian countries and to maintain the lynx and wolverine populations at the level set by national management goals, lynx and wolverines cannot be excluded from this area. As reindeer is the main prey for both species it is not possible to completely stop depredation, but rather limit depredation to levels that are considered acceptable and ensure that fair compensation is paid.

Semi-domestic reindeer are free ranging and migrate over large areas and few efficient damage prevention measures exist that could be applied to the modern day extensive herding system (Mattisson et al. 2007). The most

commonly used mitigation tool in Scandinavia is lethal control and quota hunting. Wolverines exist almost exclusively within the reindeer husbandry area, so an extensive removal of wolverines will affect wolverine population viability (Sæther et al. 2005). Lynx, on the other hand, is abundant also outside the reindeer husbandry area, and the present reduction of the lynx population within the area will not necessarily affect the viability of the lynx population. However, lynx removal or zoning (i.e. separate management zones for lynx and wolverines, currently applied in parts of Norway) is likely to have negative consequences for the wolverine population as lynx-killed reindeer is an important part of wolverines' food resources (Paper V). Reduced scavenging opportunities may result in (1) lower wolverine reproduction (Persson 2005) and (2) increased wolverine depredation on reindeer, as wolverines need to sustain their energy balance.

Reliable estimates on individual wolverine kill rate on reindeer is still lacking but we observed a much lower predation rate by wolverines than by lynx within the study area (1:9; Paper V). In Sweden, lynx and wolverines are treated similar when considering level for compensation payments i.e. the species are considered to cause an equal amount of damage. Contrary, our results and calculations based on energy requirements (Andrén et al. in press) suggest that wolverine predation is much lower than lynx predation, at least in the presence of lynx. Wolverines are most likely held responsible for killing more reindeer than they actually do, as their tracks are left behind when scavenging reindeer that were actually killed by lynx. However, wolverine predation may temporally increase during reindeer calving season when there is an abundance of vulnerable neonates or when snow-conditions are favourable.

If the political goal is to have a set number of lynx and wolverine reproductions in the husbandry area, letting them overlap will probably be most beneficial for both the conservation of wolverines and for reindeer herders if a carnivore presence compensation scheme is applied. Andrén et al. (in press) modelled the system and found that total predation decreased when lynx and wolverine occurred together compared to when they occurred separately. Reindeer districts will then benefit by having both lynx and wolverines because the compensation payments are added independent of species co-existence. However, this requires that lynx kill rate is not considerably increased by wolverine scavenging, which is in line with the findings in paper V. In addition, the level of disturbance or stress for the reindeer due to carnivores may also decrease if wolverine depredation is reduced. Wolverines are much less skilled predators than lynx (Haglund

1966) and they can follow reindeer for long distances and scatter the herds, causing extra work for the herders.

An increasing acceptance for carnivores in the reindeer husbandry area is dependent on a fair level of compensation, but the current level of compensation is based on uncertain and limited information on individual kill rates. Ideally, variation in kill rate should be small enough to allow for a simplification to base depredation on reindeer on a single mean estimate per carnivore species, but paper IV shows a wide range of values within which lynx kill rate are likely to occur. Our findings revealed a high variation in kill rate estimates for lynx depending on social status of the lynx, season and reindeer density which needs to be considered when trying to evaluate a fair compensation level for a carnivore presence scheme. Uncertainties in family group surveys (Linnell et al. 2007) and in lynx densities, i.e. the number of solitary females and males associated with each family group (Andrén et al. 2002), are other factors that would need to be included for a more accurate prediction of depredation. The density and body condition of reindeer varies dramatically across northern Scandinavia which may also influence lynx kill rates. In areas where reindeer co-exist with roe deer, lynx seem to prefer roe deer even when reindeer densities are ten times greater (Sunde et al. 2000, Moa et al. 2006), which will decrease lynx kill rate on reindeer. Our estimates on lynx kill rates were still obtained from a diversity of situations and will therefore provide kill rate estimates that are likely to occur and is thereby one of many steps towards reaching a fairer compensation scheme.

To fully understand the mechanisms influencing interactions between species one need to have general knowledge about the species and their behaviour when they interact but also how they behave when they are not sympatric. Future research is therefore needed on (1) wolverine kill rate on reindeer in areas with and without lynx, both to be able to state with confidence how wolverine predation is influenced by the presence of lynx and to use for evaluating compensation levels, and (2) lynx kill rates in areas without wolverines to more accurately estimate the effects on lynx kill rate and behaviour by wolverine presence. In addition, kill rate studies for both species should be complimented with studies of reindeer demographics (Tveraa et al. 2003) and individual kill rates should be studied in areas where reindeer and roe deer occur together.

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Svensk Sammanfattning

Inom förvaltning och bevarandebiologi studeras ofta olika arter av rovdjur var för sig, men eftersom flera arter som lever i samma område kan ha stor påverkan på varandras beteende, överlevnad, reproduktion, och utbredning är det viktigt att man känner till vilken inverkan de har på varandra. I denna avhandling har jag studerat samspelet mellan lodjur och järv som lever sida vid sida inom renskötselområdet i norra Sverige, där båda arterna till stor del livnär sig på ren. Lodjuret är ett utpräglat rovdjur medan järven är både en opportunistisk jägare och en asätare. Genom att i samma område följa individer av båda arterna med hjälp av GPS-sändare har vi kunnat studera deras rörelsemönster. Vi har besökt platser som lodjuret eller järven stannat upp vid eller återbesökt, s.k. kluster av GPS-positioner, och har på så vis ökat vår kunskap om deras födoval. Lodjurens födoval har även studerats i de nordligaste delarna av Norge.

Järv och lodjur i samma område

När två arter lever i samma område och utnyttjar samma resurser kan man förvänta sig att arterna konkurrerar med varandra. Hos rivaliserande arter förekommer det att den dominerande arten hindrar den underordnade arten från att utnyttja gemensamma resurser och i extrema fall dödar individer av den andra arten. Lodjuret är något större än järven och kan därmed förväntas vara dominant över järven. Vi har inte observerat något tillfälle där ett lodjur dödat en järv trots 55 kända dödsfall av järv i studieområdet, men det kan ändå vara möjligt att lodjuret tränger undan järven. I en av våra studier undersökte vi hur lodjuret och järven rör sig i förhållande till varandra i både tid och rum. Vi fann att lodjur och järvar har helt överlappande hemområden och eftersom lodjurens genomsnittliga hemområden (hona = 777 km^2, hane = 1 776 km^2) är större än järvens (hona = 195 km^2, hane =

773 km^2) kan en lodjurshane överlappa helt eller delvis med upp till 13 olika järvar. Även om två arter har hemområden som överlappar varandra kan det fortfarande vara så att de undviker att utnyttja samma område samtidigt. Eftersom järven utnyttjar lodjursdödade renar skulle man kunna förvänta sig det omvända, att järven till och med kan vara attraherad av lodjuret. Vår studie visar dock att lodjur och järvar varken undviker varandra eller är attraherade av varandra utan använder sina hemområden till synes oberoende av varandra.

I en annan studie undersökte vi vilken typ av miljö som arterna föredrar att vara i och inte heller här finner vi någon större skillnad mellan lodjur och järvar. Båda arterna föredrar generellt att vara i brant, kuperad terräng i fjällbjörkskog, en typ av miljö som man finner längs dalsidorna runt trädgränsen mellan dalgångar och högfjäll. Denna terräng är svårtillgänglig för oss människor, både till fots och på skoter, och kan således vara ett bra val om lodjur och järvar önskar undvika sin största fiende, människan. Det är också en rik miljö där vi kan förvänta oss finna en större tillgång på mindre bytesdjur. Även om de båda arterna generellt väljer samma miljö, skiljer sig järvens val av miljö från lodjurens när de är inaktiva, d.v.s. när de vilar eller har lya. Då söker järven sig högre upp på fjällsidorna, till kalfjället ovan trädgränsen. Här föredrar de brant kuperad terräng med stenblock och klippkanter som de kryper under för att söka skydd, ett beteende som man sällan ser hos lodjur.

Lodjurets predation på ren

Lodjuret är en skicklig jägare och våra studier visar att renen är det klart viktigaste bytet för lodjuret men att deras predationstakt, d.v.s. hur många renar ett lodjur dödar under en given tidsperiod, varierar mycket mellan kön, årstider och med tillgången på ren. Under vintrar med god tillgång på ren är det ingen större skillnad i predationstakt mellan honor och hanar. Men under sommaren, då en stor andel av de rivna renarna är kalvar som fötts under våren, dödar hanar betydligt fler renar än honor. Lodjurshonor med ungar och ensamma honor dödar färre renar på sommaren än på vintern även om de har god tillgång på ren och en del av lodjurshonorna dödar under perioder inte en enda ren utan livnär sig istället på hare, skogsfågel, ripor och andra smådjur. Eftersom renen flyttas mellan vinter- och sommarbetesmarker kan tillgången på ren variera mycket inom ett lodjurs hemområde. För vissa lodjur kan det bli i princip helt tomt på ren under perioder eftersom lodjuren är stationära och inte följer renarna på deras vandringar. Under denna tid måste lodjuren livnära sig på småvilt och

dödar då även rödrävar och tamkatter, något som vi observerat framför allt i norra Norge. I detta område har lodjuren också, i några enstaka fall, utnyttjat kadaver vilket antyder att tillgången på föda varit tillfälligt begränsad. Honor med nästan fullvuxna ungar under vintern är de lodjur som är mest angelägna att hitta de enstaka renar som blir kvar efter att de flesta renar flyttat.

Järven - en jägare och asätare

Jämfört med lodjuret är järven inte en speciellt skicklig jägare även om den är fullt kapabel att döda fullvuxna renar. I vårt studieområde dödar lodjuren betydligt fler renar än vad järven gör. Trots det är renen det viktigaste bytet för järven, men till skillnad från lodjuret så dödar den bara ett fåtal av de renar som den utnyttjar. Vår studie visar att endast 13 % av de renar som järven utnyttjar är järvdödade medan 61 % är dödade av lodjur. Resterande 26 % var renar som dött i olyckor (t ex. rasat i stup) eller av okänd orsak. Järven utnyttjar även enstaka älgkadaver och tar en del småvilt. Även om järven utnyttjar en järvdödad ren under än längre tid än en lodjurdödad ren, spenderar den ändå totalt sett något mer tid vid lodjursdödade renar än vid järvdödade eftersom dessa är betydligt talrikare.

Påverkas lodjuret av järvens snyltande?

Vi har sett att järven besöker 68 % av alla tillgängliga lodjursdödade renar oberoende av årstid. Under 29 % av dessa besök har lodjuret ännu inte lämnat sitt byte. Men vi ser inget som tyder på att järven jagar bort lodjuret från sitt byte och det verkar som järven och lodjuret sällan är på kadavret samtidigt utan järven är där när lodjuret ligger i daglega en bit därifrån. Järven är en samlare som effektivt kan stycka upp kadaver och transportera bort stora delar till matgömmor under kort tid. Detta beteende kan minska matmängden för lodjuret och tvinga det till att döda ett nytt byte snabbare än den behövt om järven inte varit där. Vår studie visar att lodjuret påverkas till viss del av järven men bara då den dödat en vuxen ren i skogen, då kortas tiden till nästa slagna byte med några dagar. Men på kalfjället, där 71 % av lodjursdödade renarna hittas, har järven ingen påverkan på lodjuret, men däremot verkar det som andra asätare som t.ex. korp och kungsörn har lika stor påverkan på lodjurets beteende här som järven har i skogen.

Förvaltningsaspekter

Våra studier visar att det är viktigt att känna till hur olika arter påverkar varandra för att förstå deras ekologi bättre. Inom förvaltningen av lodjur och järv i Skandinavien används strategier där man försöker separera förekomsten av lodjur och järv i olika förvaltningszoner eller kraftigt minska lodjurstammen i vissa områden för att minska skador på ren från rovdjur. Denna förvaltning av lodjuret kan påverka järvstammen negativt. Vi har visat att lodjur bidrar till en ökad födotillgång för järven och har tidigare sett att en ökad tillgång på kadaver under vintern påverkar järvens reproduktionsframgång positivt. Om antalet lodjur minskar mycket eller försvinner helt kan det resultera i en lägre reproduktion hos järvhonor. Järvens predation på ren påverkas troligen också av tillgången på kadaver. I områden utan lodjur kan vi därför förvänta oss att järvens predation ökar då det finns mindre mat i form av lodjursdödade renar. Men tyvärr saknar vi ännu detaljerad kunskap om järvens predation i områden utan lodjur.

Sammanfattningsvis har jag visat att renen är det klart viktigaste bytet för både arterna. Trots det kan lodjur och järv samexistera utan större negativ påverkan på varandra. Järven drar till och med fördel av att samexistera med lodjuren, genom att den kan utnyttja lodjursdödade renar.

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