Predator Management

Space Use and Monitoring of Lynx in the Reindeer Husbandry Area

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Abstract

Successful legislation during the 20th century has led to recovering populations of large carnivores in Europe and we are now facing the challenges of managing the populations to fulfil both national and international conservation goals as well as minimizing the conflicts resulting from depredation on domestic animals on a national level. I investigated the space use by Eurasian lynx (*Lynx lynx*) in relation to their migrating main prey, the semi-domesticated reindeer (*Rangifer t. tarandus*). Based on data from radio-collared lynx individuals seasonal activity range use did not seem to be affected by the seasonal migrations of the reindeer. For example, the mean distance from the centre of a lynx's activity rang to the centre point immediately following did not differ significantly between seasons, and were about one order of magnitude shorter than the distance of the reindeer migration. Hence, lynx in northern Sweden do not appear to move with the migrating reindeer and likely sustain on stray reindeer and alternative prey during part of the year. Successful management of wildlife populations also requires appropriate monitoring of population size to make new management decisions and evaluate the consequences of previous decisions and management actions. I evaluated the effect of varying accuracy and interval of population estimates on management success, and found that when funding is limited managers better focus on surveys with higher precision even if that means that the interval between surveys are longer.

Keywords: Lynx lynx, migration, monitoring *Rangifer tarandus,* space use, Scandinavia.

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Dedication

To my mother. This one is for you! Thank you for always letting me believe all things are possible.

Ingenting är omöjligt. Det omöjliga tar bara litet längre tid.

Winston Churchill

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 Danell, A. C., Andrén, H., Franzén, R and Segerström, P. (2006). Space use by lynx in relation to reindeer migration. *Canadian journal of Zoology* 84(4), 546-555.

II Danell, A. C. and Andrén, H. (2010). Precision beats interval. *Wildlife Biology* 16:409-418.

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1 Introduction

The challenges of management of wildlife increases as we fine-tune its goals. When a population is very small, the decision to protect the species is neither controversial, nor difficult to make. Likewise, when a population has grown very large, reducing its numbers or distribution through harvest is usually a non-controversial decision. The difficulty comes in that different stakeholders sometimes have opposing management goals and then to balance the population between goals of conservation and conflict minimizing. The narrower the goal statement is, the more difficult the balancing acts.

Successful legislation during the 20th century has led to recovering populations of large carnivores in Europe (www.IUCN.org), and we are now facing the challenges of managing the populations to fulfil both national and international conservation goals as well as minimizing the conflicts resulting from depredation on domestic animals on a national level.

For sustainable management of predators, we need knowledge not only of their population size, distribution and development, but also other ecological information such as spatial requirements and patterns, predation pattern and prey availability. Without reliable data, predator management will become qualified guesses at its best.

This licentiate thesis focuses on management issues concerning Eurasian lynx (*Lynx lynx*; hereafter called “lynx”) management in the reindeer husbandry area in Sweden. The two scientific studies included in this thesis investigate lynx spatial use in relation to movements (i.e. migration) of its main prey and the effect of varying accuracy and interval of population estimates on management precision.

1.1 Wildlife management.

In order to be successful, wildlife management needs to incorporate knowledge from several different disciplines. Managing species involves human interests from many different aspects to formulate management goals and funding. Besides ecological knowledge, which is of fundamental importance, successful management also requires knowledge of human attitudes toward natural values, issues concerning legal and economic consequences, and aspects pertaining to acceptance and confidence about the management actions.

Wildlife management is always performed under some level of uncertainty because of demographic and environmental variation in addition to varying quality and precision of population surveys. Changes in the resource system, such as changing prey availability or changing habitat availability as a result of human exploitation are other uncertainties to consider in wildlife management. Wildlife managers often need to make decisions for the management of certain species without fully knowing the consequences for the system they belong to.

New scientific knowledge from outside the management system will continuously add to the scientific bases of the ecology and the management of the species and its resources. During the implementation of a management programme, it also generates by itself new insights and knowledge about the managed system. This leads to adaptive management regimes (Figure 1), where models and actions are recursively adjusted, due to detected changes and improved understanding (Folke et al. 2004, Walters 1986, Walters & Hilborn 1978). It is important not only to know what to monitor, but also knowing how precise and how often monitoring need to be conducted in order to effectively evaluate the management programme.

The sequence of recurrent actions in adaptive management include: i) gathering knowledge about the system and identifying uncertainties, which need to be clarified, and sharing the knowledge for better insight about the system; ii) conceptualize and create measurable goals in order to be able to evaluate the management and ensure that the management is linked to appropriate temporal and spatial scales; iii) carefully plan what actions to implement into the system, and determine what to monitor and how monitoring should be done in order to evaluate the management; iv) implement actions and monitoring; v) analyze and evaluate the system response(s) to current management, vi) incorporate new information and adapt the management action to a refined management plan.

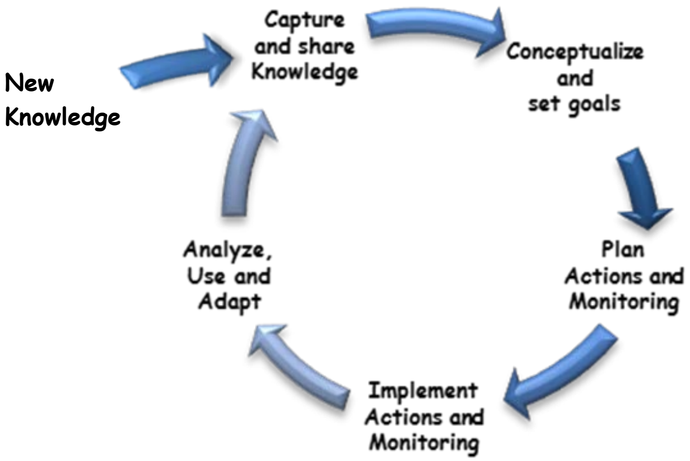

Figure 1. Schematic figure of the different phases in the iterative adaptive management process.

1.2 Monitoring

Successful adaptive management of wildlife populations requires appropriate monitoring of population size to make new management decisions and evaluate the consequences of previous decisions and management actions (Walters & Hilborn 1978, Shea et al. 2002, McCarthy & Possingham 2007, Hauser & Possingham 2008).

In addition to performance, a monitoring program also has to consider costs. The sought objective is generally to find a monitoring programme at lowest cost possible, which still fulfils the ability to make sound management decisions (Pople 2008). While the most accurate monitoring method is desirable, it may not be economically possible to achieve. Hence, managers often have to compromise between reliability and costs. This has led to the optimizations of cost and monitoring reliability, which has applications in a wide range of wildlife management problems such as invasive species (Bogich & Shea 2008), conservation (Gerber et al. 2005, McCarthy & Possingham 2007), and harvest under uncertainty (Hauser et al. 2006, Månsson et al. 2011). Like many other large predators, the lynx population is geographically spread over very large areas and at low density which in turn make monitoring very resource demanding. Knowing how to best utilize the funding is imperative in order to make management successful.

1.3 Space use

The importance of a species use of space for successful conservation or management has been long known (Burt 1943, Woodroffe & Ginsberg 2000). Variation in seasonal space use is possibly one of the most important parameters needed in determining the carrying capacity of a species in order to achieve effective management of a species (Herfindal et al. 2005). Understanding space use and its determinants can be important for management success.

In an ecosystem with territorial predators and migratory prey, the predators experience large variations in prey availability between seasons. Their response to such changes however varies both between and within species. As an example, in north-western Alaska and the Northwest territories of Canada, the primary prey for gray wolves (*Canis lupus*) is migratory caribou (*Rangifer tarandus* ssp.) (Kuyt 1972; Dale et al. 1995; Ballard et al. 1997). In some areas and populations, wolves shift to resident moose (*Alces alces*) as an alternative prey, when the caribou migrate out of the territory (Ballard et al. 1997; Dale et al. 1995). In other areas wolves display seasonal movements and follow their main prey (Forbes & Therberge 1996; Ballard et al. 1997; Pierce et al. 1999; Walton et al. 2001).

1.4 The target species - the Eurasian lynx

The lynx is the largest wild cat in Europe, with a shoulder height of 60-70 cm and body mass of 15-30 kg (females: 17 kg, males: 22 kg). Lynx is a solitary felid and an efficient predator largely specialized on medium-sized ungulates when available (Pedersen et al. 1999; Odden et al. 2006; Molinary-Jobin et al. 2007). The main prey for lynx in Scandinavia within the reindeer husbandry area is semi-domesticated reindeer (*Rangifer t. tarandus,* Haglund 1966; Pedersen et al. 1999; Mattisson et al. 2011b) and roe deer (*Capreolus capreolus*) outside the reindeer husbandry area (Odden et al. 2006; Gervasi et al. 2013).

The lynx has a very broad distribution from Western Europe through the boreal forests of Russia, and down into central Asia and the Tibetan plateau (Nowell & Jackson 1996; Sunquist & Sunquist 2002). The populations found in the southwestern parts (Western Europe and south-west Asia) are generally small and fragmented, whereas the majority of its historic range from Scandinavia through Russia and Central Asia is largely intact (Breitenmoser et al. 2008)

The abundance and distribution of lynx in Scandinavia has varied greatly during the latest two centuries. During the latter half of the 1800's the population declined in numbers and was close to extinction in the early to mid-1900's. After the introduction of new management regulations (bounty in Sweden was stopped in 1927 and in Norway in 1980), lynx increased throughout Scandinavia both in number and in distribution (Liberg 1997). Today, lynx are present throughout large parts of Scandinavia with an estimated population of 1000-1500 in Sweden (winter 2012/2013; Zetterberg 2014) and 320-350 in Norway (winter 2012/2013; Brøseth & Tovmo 2013). Their number and distribution is partly regulated by hunter harvest and lethal control in response to conflicts with livestock owners and ungulate hunters (Linnell et al. 2009).

The lynx population in Finland, which is to a lesser extent connected with the Swedish-Norwegian population, is protected since the 1970's. It has since then recovered and is found throughout the country with the highest density in south-eastern Finland. The current population size is estimated to be at least 2500 animals (Harri Norberg, Finnish Wildlife Agency, personal comm.).

1.5 The main prey species – the semi-domesticated reindeer

Reindeer husbandry is based on herding of domesticated reindeer, and is performed throughout the northern part of the Eurasian continent. In Sweden, all reindeer are semi-domesticated. In Norway, however, there are also wild/feral reindeer of the same subspecies, south of the reindeer husbandry area, all with varying degrees of domestication. There is also a small population (around 900 animals) of wild reindeer (*Rangifer t. fennicus*) south of the reindeer husbandry area in Finland (Kojola et al. 2009, Ministry of Agriculture and Forestry 2007).

The reindeer husbandry area in Sweden covers 52 % (213 000 km^2) of the Swedish land area (SOU 2006:14) and includes the three northernmost counties in Sweden (Norrbotten, Västerbotten, Jämtland), as well as parts of Dalarna and Västernorrland counties (Figure 2). Semi-domesticated reindeer in Sweden are part of a pastoral production system, where reindeer are herded by indigenous Sámi. The reindeer are migrating, herded or transported on trucks between seasonal grazing ranges as a part of the herding practices. There are 51 reindeer herding districts in Sweden, all utilizing the grazing resources on a common property basis based on immemorial rights. The number of reindeer in winter stock in Sweden has varied from 200 000 to 250 000 since the early 1900's and is currently close to 250 000 animals. (Richard Doj, Sami parliament, personal comm.).

The reindeer husbandry areas in Norway and Finland cover 43 and 34 % of the land areas, respectively (Danell et al. 1999). The numbers of reindeer are currently just above 250 000 in Norway (Reindriftsforvaltningen 2013) and 200 000 in Finland (Mauri Nieminen, Finnish Game and Fisheries, personal comm.).

Large carnivores cause substantial losses of reindeer, where lynx and wolverine (*Gulo* gulo) are the most important predators (Swenson and Andrén 2005, Hobbs et al. 2012), but also brown bear (*Ursus arctos*), gray wolf and golden eagle (*Aquila chrysaetos*) prey on reindeer. To large extent, the predator populations are overlapping in Sweden and Norway and to different degrees connected with populations in Finland. The predator management policies are however separate in all three countries.

1.6 Objectives

The aim of the studies included in this thesis was to investigate different aspects pertaining to long-term management of the lynx population in Scandinavia. The main questions asked for the articles were:

Paper I. What happens when the food moves on? Do lynx change their activity range as their main prey migrates between summer and winter ranges?

Paper II. How should we balance monitoring precision and frequency against cost? Should population census be performed more often or more carefully when money matters?

2 Material and Methods

2.1 Study area

This thesis is a part of an ongoing long-term study on lynx (http://scandlynx.nina.no/). The core study area in northernmost Sweden covers 10 000 km^2 in the county of Norrbotten, mainly between the two large river systems Lilla and Stora Luleälv (Figure 2). The area encompasses Sarek, Padjelanta and Stora Sjöfallet national parks, which form the core parts of the Laponia world heritage area (Swedish Environmental Protection Agency 1998).

The climate of the study area has a largely oceanic influence from the northwest Atlantic and the Gulf Stream, with average temperatures of -10˚C in January and in 13˚C in July. Snow depths during winter exceed 1 meter. The area is characterized by deep valleys, mountain plateaus and high peaks with glaciers. The altitudinal gradient ranges from 200 m a.s.l. to 2000 m a.s.l., with tree-line occurring at 850 m. The south-eastern part of the study area consists mainly of coniferous forest, with a mixture of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), comprising 30 % of the total area. Twelve percent of the study area is covered by deciduous forest, mainly sub-alpine birch (*Betula pubescens*), 28 % are heath and meadows, and 10 % boulders and bedrock outcrops. Nine percent of the total study area consists of water (lakes and rivers), 8 % of wetlands, 2 % of permanent snowfields and glaciers, and less than 1 % of the study area is classified as cultivated land.

Human settlements and infrastructural developments are minimal in the area. Moose, are found throughout the valleys and in the forested parts of the area. Brown bears and wolverines are abundant in the study area, whereas wolves are restricted to occasional dispersers.

Figure 2. Map over Sweden with the study area and the reindeer husbandry area with the extensions of individual Sami herding districts.

The study area overlaps with the reindeer husbandry area. The reindeer in the area are seasonally migratory and highly mobile within seasons, resulting in large spatial and temporal variations in densities. There are however always stray reindeer remaining in the mountain region while the vast majority of them migrate to the forested regions during winter. Mountain hare (*Lepus timidus*), willow grouse (*Lagopus lagopus*), ptarmigan (*Lagopus muta*), Capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), red fox (*Vulpes vulpes*), and small rodents (*Clethrionomys spp.*, *Microtus spp*. and *Lemmus lemmus*) are potential alternative prey species for lynx in the study area.

2.2 Paper I. Space use by lynx in relation to migrating prey

2.2.1 Lynx data

The lynx data in the analyses are based on information from radio-collared lynx during 1994-1998. Lynx were live-captured by darting from a helicopter and immobilised with a mixture of ketamine (5 mg per kg) and medetomidine (0.2 mg per kilo; Kreeger et al. 1999) and equipped with a VHF radio-collar (Telonics Mod 335, Mod 400, or Televilt TXH-3). The handling protocol for lynx has been examined by the Swedish Animal Welfare Agency and fulfils the ethical requirements for research on wild animals (Arnemo et al. 2012). Lynx were radio-tracked at least 2-4 times per month, mostly by airplane.

2.2.2 Lynx activity ranges

We estimated activity ranges using 100% minimum convex polygons (MCP) for 3 seasons (see below). The numbers of positions per individual per season were sometimes too few (a minimum of 6 positions for each season) to formally estimate home ranges, but the activity ranges provide an index for seasonal space use. These activity ranges were calculated using the animal movement extension in ArcView® version 3.3 (Environmental Systems Research Institute, Inc. 2002). We measured size of each activity range for each season, distances between centre points between seasons and the direction of movement between centre points between seasons.

Two measures (mean and largest) of activity range overlap between periods were calculated. The largest overlap will range somewhere between mean overlap and 100%, where 100% indicates that one activity range is completely overlapping with the other.

2.2.3 Reindeer movements

The year was divided into 3 seasons; winter (December-April), summer (May-July) and autumn (August-November), based on management practices and the movement of radio-tracked reindeer during 1984-1986 (Bjärvall et al. 1990). Assumed reindeer movements were then analyzed based on reindeer husbandry land-use plans in each of the reindeer husbandry districts.

2.2.4 Alternative prey density

Abundance of alternative prey (ptarmigan and willow grouse pooled together, and mountain hare) was estimated through fecal pellet counts (Lindström et al. 1994; Newey et al. 2003). The study area was divided into a grid of 10 x 10 km squares. The starting point of one 3 km equilateral triangle was randomly positioned within each square. Thirty-two of the triangles were located in the south-eastern coniferous forest part of the study area and 37 of the triangles were located in the north-western mountainous part.

We surveyed 56 triangles in 1999 and 28 triangles in 2000, of which 15 triangles were surveyed in both years. Sixty equidistantly spaced plots of 10 m^2 were surveyed along the sides of the triangle, i.e. the distances between plots were 150 m. The level of degradation and the presence of leaf litter covering the droppings were used to discriminate between old and new droppings, and only droppings judged to be from the preceding winter were counted. For each triangle a prey species index was calculated as the proportion of 10 m^2 plots with faecal pellets of the particular species present.

2.3 Paper II. Precision beats interval

2.3.1 Data

Data on survival (Andrén et al. 2006) and reproduction (Andrén et al. 2002, and updated) for different sex and age classes were obtained from the Scandinavian lynx project in the reindeer husbandry area. Harvest numbers in the reindeer husbandry area were based on a fitted regression of actual harvest decisions made by the Swedish Environmental Protection Agency in 1998 to 2006 and the estimated population size at each corresponding year.

2.3.2 Population modelling

We used a stochastic stage-structured population model with 4 age-classes (kittens [0-1 yr.], 1 year old, 2 year old, and 3 year old and older) and sex-specific survival and harvest rates.

The model was based on the life history events during a “lynx year”. The kittens were born in June, the survey was done in February and the harvest was done immediately after the survey. All these events were treated as pulses with no extension in time.

All modeling was done in Microsoft Excel® software with PopTools add-in (Hood 2004). Initial population size in June year one was set to the equivalent of 100 family groups. Fifty-eight percent were females and 42 % males. The initial age-distribution was based on stable age distribution given the parameters we have used. The analyses were based on simulated years 6 to 55. Deterministic population growth (λ), given the mean reproduction and survival, and without harvest, was 1.06.

2.3.3 Analyses

The model was evaluated based on frequency of different outcomes after 1000 simulation replicates. We recorded the proportions of time that the population was below 80, above 120 and above 140 family groups, respectively. We also recorded the number of years that there was no harvest, and when we modelled the state-dependent monitoring scheme, we recorded the total number of surveys performed during a 50 year period.

3 Results

3.1 Paper I. Space use by lynx in relation to migrating prey

3.1.1 Size of Activity Range

The seasonal activity range sizes for males and single female lynx were not significantly different among the three periods of the year (December-April, May-July and August-November; males: Friedman, $\chi^2 = 0.1$, $n = 5$, $p = 0.95$, females: Kruskal-Wallis, $H = 0.933$, $n_1 = 7$, $n_2 = 4$, $n_3 = 6$, $p = 0.62$). The grand mean for males and single females were 274 km^2 and 209 km^2, respectively. The mean activity range size for family groups (i.e. female with kittens) was significantly smaller (68 km^2) during the summer period than during autumn (127 km^2) and winter (320 km^2; Kruskal-Wallis, $H = 10.151$, $n_1 = 6$, $n_2 = 9$, $n_3 = 8$, $p = 0.0062$).

3.1.2 Distance between activity range centre points

The mean distance between the centre of the individual lynx activity range one season to the centre of the activity range the immediately following season did not differ significantly for any of the three categories of animals: males (Friedman $\chi^2 = 1.200$, $n = 5$, $p = 0.54$), single females (Kruskal-Wallis, $H = 2.279$, $n_1 = 7$, $n_2 = 4$, $n_3 = 6$, $p = 0.31$, and family groups (Kruskal-Wallis, $H = 2.704$, $n_1 = 6$, $n_2 = 9$, $n_3 = 8$, $p = 0.25$). The distances were on average 6.6 km for males, 7.3 km for single females, and 8.4 km for family groups between seasons. This is about one order of magnitude shorter than the distances between summer and winter ranges for the reindeer in this area (100-150 km).

3.1.3 Range overlaps between seasons

There were no significant differences among the three periods in overlap of the activity range of an individual on that individual's activity range the former season, for males (Friedman, $\chi^2 = 2.800$, $n = 5$, $p = 0.24$), for single females (Kruskal-Wallis, $H = 1.707$, $n_1 = 6$, $n_2 = 9$, $n_3 = 8$, $p = 0.42$), and for family groups (Kruskal-Wallis, $H = 278$, $n_1 = 6$, $n_2 = 9$, $n_3 = 8$, $p = 0.87$). The grand mean in overlap was 53 % for males, 50 % for females and 44 % for family groups. The grand mean in largest overlap found was 72% for males, 64% for females and 57% for family groups.

3.1.4 Direction of movements

The direction of movements between the summer-autumn and autumn-winter were not significantly different from the uniform circular distribution (Rayleigh's test $p > 0.2$ in all cases). The direction of movements between winter and summer was significantly different from a uniform circular distribution for both single females (Rayleigh's test, $z = 3.309$, $n = 7$, $p < 0.05$) and family groups (Rayleigh's test, $z = 5.976$, $n = 6$, $p < 0.001$). The direction of movements between winter and summer was 111 degrees for the single females and 147 degrees for family groups, i.e. similar direction as the reindeer movements between southeast and northwest. The distance moved, however, was one order of magnitude shorter than the average reindeer movement between the seasons (see above). For males, the movements between winter and summer were not different from a uniform circular distribution (Rayleigh's test, $p > 0.1$).

3.1.5 Alternative prey densities

The index of hare density was significantly higher in the mountain habitat (0.073 ± 0.012 SE) than in the coniferous forest habitat (0.045 ± 0.009 SE) (Mann-Whitney U test, $U = 212.5$, $n_1 = 37$, $n_2 = 32$, $p = 0.03$). This would correspond to actual mean hare densities of about 0.6/km^2 (range 0-2.3/km^2) in the mountains and 0.3/km^2 (range 0-1.6/km^2) in the forest (Åke Pehrson, Grimsö Wildlife Research Station, personal comm. [based on fecal pellet production estimates from captive hares on natural diet observed for 1000 days]). Likewise, the index of ptarmigan/willow grouse density was higher in the mountain habitat (0.107 ± 0.091) than in the forest habitat (0.042 ± 0.066) (Mann-Whitney U-test, $U = 257.0$, $n_1 = 37$, $n_2 = 32$, $p < 0.0001$). Concurrent population censuses of ptarmigan/willow grouse densities in the same region have shown winter populations of 6-10 individuals/km^2 (Hörnell-Willebrand 2005).

3.2 *Paper II. How often and how carefully should we monitor to optimize costs and goal attainment?*

3.2.1 Increasing precision

In general, monitoring strategies with higher accuracy improved the management performance, i.e. the lynx population remained within the preferred population interval for a larger proportion of the time. With more effort put into monitoring, i.e. increasing the proportion of family groups found and concurrently decreasing the error of this estimate from 0.7 (± 0.2 SD) to 0.9 (± 0.05 SD), the probability that the population drops below 80 family groups was halved (from 0.14 to 0.07).

The probability that the population exceeded the upper management level of 120 family groups increased with higher accuracy in the survey and varied between 0.27 and 0.37. The number of years with no harvest was higher for the less reliable surveys, ranging between 21.4 years out of 50 years (42.9 %) for accuracy 0.7 (± 0.2) performed every fourth year and 8.7 years out of 50 years (17.4 %) for accuracy 0.9 (± 0.05) performed every year. With complete knowledge (accuracy 1.0 ± 0) and survey performed every year, the number of years with no harvest was 8.2 years out of 50 years (16.5 %).

3.2.2 Decreasing frequency

When the interval between surveys was increased, the probability of the lynx population dropping below 80 family groups increased. However, a more accurate survey usually performed better than a less accurate survey even if performed less frequently. The probability that the population drops below 80 family groups decreased from 0.14 at accuracy 0.7 (± 0.2) performed every year, to 0.10 at accuracy 0.9 (± 0.05) performed every fourth year. The probability that the population exceeds 140 family groups increased with survey frequency, but not with survey accuracy. For all monitoring strategies, the probability that the population would exceed 120 family groups was higher than the probability that the population would drop below 80 family groups.

3.2.3 State-dependent monitoring scheme

When the state-dependent monitoring scheme was used, a survey was performed every year if population was less than 90 family groups, and at an alternative 2-4 year interval otherwise, the total number of surveys during a 50-year period varied between 18 (± 4.1) and 29 (± 2.8) at survey accuracy 0.9 (± 0.05). The number of surveys performed at a less reliable survey 0.7 (± 0.2) varied between 26 (± 2.9) surveys when alternative survey interval was 4 years, and 33 (± 5.3) when the alternative survey interval was 2 years. The proportion of years with no harvest was highest (0.43) at the least reliable survey (0.7 ± 0.2) with alternative survey interval of 2 years. With state dependent monitoring, complete knowledge, and alternative survey interval of 4 years, the proportion of years with no harvest decreased to 0.175.

3.2.4 Harvest stability

When running the simulations with lower survey accuracy, the proportion of years with no harvest increased. The number of years with no harvest ranged from 21.4 years out of 50 (42.9 %) at accuracy 0.7 (± 0.2) performed every fourth year to 8.7 years out of 50 (17.4 %) at accuracy 0.9 (± 0.05) performed every year.

3.2.5 How good can we get?

With complete knowledge of the population (i.e. accuracy 1.0 ± 0), the probability of the population decreasing below 80 family groups varied between 0.08 if survey was performed every year, to 0.10 if survey was performed every fourth year. This is probably due to stochastic variation in vital rates and reproduction.

4 Discussion

This thesis deals with two important issues for the development of lynx management in the reindeer husbandry area. In **Paper I**, I show that lynx do not follow their main prey as they migrate. Nor do they expand their activity range to incorporate all the seasonal ranges of their prey. In **Paper II**, I show that when trying to balance population size, it is better to focus efforts on monitoring the lynx population more precisely even if that means longer intervals between monitoring occasions rather than monitoring more often but with lower precision.

4.1 Do lynx change their activity range as their main prey migrates between summer and winter ranges?

Lynx in northern Sweden do not appear to move with their migrating main prey, the semi-domesticated reindeer. This is in similarity with other populations of large predators feeding on migratory prey, who remain in place. For example, some populations of lions in Africa switch to an alternative prey as their primary prey, the wildebeest (*Connochaetes taurinus*), migrates (Schaller 1972). Some populations of wolves (Ballard et al. 1997; Dale et al. 1995) and mountain lions (*Felis concolor*; Elbroch et al. 2013) in North America also remain in place as their primary prey migrates. In other studies, populations of lions in Africa (Schaller 1972), wolves (Forbes & Theberge 1996, Ballard et al. 1997) and mountain lions in North America (Pierce et al. 1999) have shown a different behavior and actually migrate with their primary prey. Other species may remain in place but travel great distances to hunt their primary prey (Hofer & East 1993). What drives some predator populations to follow their main prey while others stay behind is unclear, but the availability of alternative prey is likely an important factor. Some species are also limited in their movements while attending their young.

Despite having a migrating prey source, the lynx in our study showed a behavior similar to that of predators with a more constant access to their main prey. In our study area, lynx remaining in the area as reindeer migrate, likely sustained on a small number of stray reindeer remaining in the area together with alternative prey such as mountain hare and tetranoids (Mattisson et al. 2011b). Lynx in other parts of the reindeer husbandry area however, where the distance between summer and winter ranges of reindeer is much shorter such as in the easternmost Sámi districts in Sweden or some of the districts where reindeer remain in the forest year round, or where the availability of the alternative prey is lower, may follow the reindeer as they migrate.

4.2 Costs of migrating prey

Besides affecting the spatial behaviour over the seasons, large-scale seasonal variations in prey availability can also depress the predator population size by delaying time of first reproduction or decreasing the reproductive rate among adults in the predator population (Holdo et al. 2011). Andrén et al. (2002) documented a higher reproductive success among lynx in south-central Sweden as compared to lynx in northern Sweden. The lower reproductive rate in our study area as compared to south-central Sweden is possibly an indication of the cost of having migrating prey or large seasonal variation in prey availability. This is similar to the findings of Ballard et al. (1997), who pointed out that wolves living within the migratory range of the Western Arctic Caribou Herd existed at a lower density than predicted by average prey densities.

While reindeer distribution within the study area is clustered in time and space, the roe deer in south-central Sweden is much more evenly distributed. Assuming that an average of the approximately 25 000 reindeer in the 4 herding districts in our study area would have an even distribution in their year-round grazing area; then, it would equal a density of 1.4 reindeer per km^2. The average body mass of a reindeer in a net herd in early winter range between 30 and 80 kg, with an average weight of 60-65 kg (Danell, Ö. & Danell, A. unpublished data [results from a herd simulation program]). In central Sweden, the density of roe deer is 3-4 individuals per km^2 (Danell, A. unpublished data [pellet counts]). During winter, the body mass of adult roe deer in central Sweden vary between 20 and 30 kg (Aanes et al. 1998), with an average of 23.3 kg (Per Grängstedt, Grimsö Wildlife Research Station, personal comm. [live weights of 409 individuals]).

The total annual average available prey resource is roughly the same within the study area (87.5 kg/km^2) as in south-central Sweden (81.6 kg/km^2), but whereas lynx in south-central Sweden have a fairly regular access to its prey, lynx in our study area experience larger variation in the density of prey. Lynx density is higher in south-central Sweden (1.0 to 2.2 individuals per 100 km^2) as compared to northern Sweden (0.2 to 0.7 individuals per 100 km^2) (Liberg & Glöersen 2000, Liberg & Andrén 2005). Thus the total annual average available prey biomass per predator might actually be higher in northern Sweden than in south-central Sweden. The lower reproductive rate in the lynx population in the reindeer husbandry area shows may therefore be a consequence of the high seasonal variability in prey availability, i.e. extended periods of low prey availability.

4.3 High precision is better than high frequency when implementing cost-efficient surveys of lynx populations

In **Paper II** I showed that it was more beneficial to increase the accuracy of lynx population monitoring rather than increasing its frequency in terms of maintaining the population within the set management goals. Based on the simulations, the analyses suggest that managers should design their surveys in a manner which secures that the accuracy is at least 0.8. At accuracies lower than 0.8, the management performance clearly worsened. The analyses further suggest that when financial resources are limited, it is better to maintain high survey accuracy rather than decreasing the survey interval.

This involves a pedagogic problem. It is important in management applications to both understand and to communicate the limitations of the information we gather through monitoring to the different stakeholders. For example, no matter of the accuracy of our population monitoring, uncertainties caused by demographic and environmental variation may still cause the population to end up outside the management goal. The need to monitor depends also on the level of the previous population estimate, and also on the precision of the estimate. Hauser et al. (2006) showed that it is more important to have frequent surveys when the population level is close to population thresholds. This further increases the need for adaptive management regimes, where the management results are evaluated against the different goal statements and management decisions are revised if necessary.

4.4 Balancing the different management goals.

It is also important to clarify and determine the priority of different management goals and to analyze whether the management actions we make actually moves us in the right direction. In our analysis, the results of the harvest decisions, which were based on actual management decisions in the past, maintaining the population above a minimum level seemed to have a higher priority than avoiding increasing the population above the upper limit.

This was probably due to a very careful harvest regime in the simulations, in which harvest was not necessarily aimed at strongly limiting the lynx population. Should management decide that it is equally bad or worse to have a population size above the upper limit, it would be necessary to change to a more aggressive harvest regime at the upper level of the management goal.
This may be the case when high depredation has severe economic consequences (Danell et al. 2009) or jeopardize the prey population (Åhman 2013), thus in the long run also jeopardize the population of the predator, as is the case in parts of the reindeer husbandry area today.

5 Future perspectives on lynx management and research

5.1 Range use

In **Paper I** aspects of seasonality in the use of the activity range were analyzed but questions remain about the stability of range use outside of the reindeer husbandry area. While prey availability often is identified as an important factor in explaining intra-specific variation in home-range size, it does not offer a complete explanation. A better understanding of seasonal stability in lynx space use, including other factors than prey availability, will improve our understanding and capability to compose reasonable management plans for different regions.

As a result, the county administration boards within the reindeer husbandry area in collaboration with the Sámi herding districts are developing management plans for the large predators in the area. The aim is to continuously collect new knowledge about the large predators (wolf, bear, lynx, wolverine and golden eagle), reported damages and performed mitigation measures to evaluate the results of the predator management. Such plans will aim to create a more active adaptive management for the region where different stakeholders on a local level contribute to a successful predator management.

How lynx should be managed in the reindeer herding area is dependent on the population status in the country as a whole. The most recent national predator management policy in Sweden (Prop. 2012/13:191) states that lynx should be allowed in its natural range, i.e. it should be found in all counties. In order to succeed with this management goal for lynx in Sweden, we cannot eliminate lynx from the reindeer husbandry area despite the substantial losses for the reindeer husbandry. Removing or considerably lowering the lynx density further would require the population outside the reindeer husbandry area to increase significantly in order to fulfil the national numerical goal. It is however questionable how high density of lynx the roe deer population can sustain, or if it is spatially possible given the much higher density of roads, human settlements and infrastructural developments in the southern half of the country. With lynx showing seasonal stability in its range use, it is discussed whether there is a possibility to zonate the predator population such that especially important areas for the reindeer husbandry practices (such as calving grounds) are relieved from some of the predation. Such an alteration of habitat use may however affect other species that may rely on carcasses from lynx kills such as wolverines or arctic fox (*Alopex lagopus*; Mattisson et al. 2011a). I would argue that it is better to manage the system (predators/prey/grazing resources) rather than managing five different species of predators separately. This will require more holistic research on systems level than hitherto.

5.2 Prey resilience

In addition to understanding the effect of prey availability on range use, it would be of importance to evaluate the resilience of the prey populations to the current predation rate, and get further understanding of what drives the predator-prey dynamics between lynx and its prey before determining long term national goals for lynx management in Sweden.

Partly as a consequence of the current predation pressure within the reindeer husbandry area, prey population collapses have been predicted using population simulation models (Danell & Danell 2009, Danell et al. 2009) as well as been observed in some districts (Åhman 2013). Fulfilling the national management goal in such a situation will likely not be possible.

Outside the reindeer husbandry area, the recolonization of lynx caused a strong decline in roe deer densities. Monitoring data from outside the reindeer husbandry area show that the lynx population increase with high roe deer densities but decrease when prey availability dwindled (Andrén et al. 2010). The roe deer population is clearly affected by the lynx densities but also by other aspects such as winter severity and fox densities (Melis et al. 2010). There is a potential risk of lynx maintaining a high predation pressure on the roe deer and reindeer causing the two species to remain at low densities. This would clearly limit the possibility to fulfil our management goals.

5.3 Size of management unit matters

Decreasing the size of the management unit to include only one Sámi district, will consequently lead to a narrow range of acceptable levels of lynx, wolverines, golden eagle, and bears for each management unit although the national level is still the same. In accordance with Hauser (2006) such a decrease in acceptable levels of the species would require more frequent monitoring than it would be should we choose to manage on a larger scale. Succeeding in each management unit though can prove to be very difficult and consequences of management in smaller units while aiming to fulfil the national goal need to be further investigated.

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Svensk sammanfattning

Att förvalta naturresurser är alltid en balansgång, men utmaningen ökar om vi förfinar våra mål. När en population är väldigt liten är beslutet att skydda den varken svårt eller kontroversiellt. På samma sätt är inte ett beslut att minska populationens storlek eller utbredning särskilt svårt när den växt sig väldigt stor. Svårigheten ligger i att balansera populationen mellan olika mål, och ju snävare vårt förvaltningsmål är desto svårare blir balansgången.

Framgångsrik förvaltningsbeslut under 1900-talet har lett till växande populationer av stora rovdjur (björn, varg, lodjur, järv och kungsörn). Nu ligger svårigheten i att balansera dessa populationer mellan de förvaltningsmål som satts av Sverige och EU, samtidigt som vi ska minimera de skador som ökande rovdjursstammarna orsakar på tamdjur.

För att lyckas med sådan förvaltning behöver vi, utöver regelbunden inventering för populationsstorlek, utbredning och utveckling, även kunskap om deras ekologi, till exempel hur stora hemområden de har, hur de utnyttjar sina hemområden, vilka byten de föredrar och hur manga byten de tar. Utan sådan kunskap kommer rovdjursförvaltningen istället att bygga på gissningar. Den här avhandlingen handlar om olika aspekter rörande lodjursförvaltning inom renskötselområdet i Sverige.

Renen är det främsta bytet för lodjur i norra Sverige. Renarna rör sig långa sträckor (100-150 km) mellan betesområden olika årstider (december-april, maj-juli och augusti-november). Lodjuren i området upplever stora variationer i bytestillgång och det är därför angeläget för förvaltningen att se om det förändrar hur de använder sitt hemområde mellan årstiderna. Jag fann att lodjurshannar och ensamma honor inte förändrade storleken på sitt hemområde mellan årstiderna, medan familjegrupper (hona med ungar) hade ett mindre område på sommaren. Jag undersökte också om mittpunkten av hemområdet flyttade sig mellan olika årstider och fann att det inte var någon skillnad i det avstånd som mittpunkten flyttades mellan olika årstider. Medelförflyttningen mellan årstiderna var 6.6 km för hanar, 7.3 km för ensamma honor och 8.4 km för familjegrupper. Det är mindre än en tiondel av den sträcka som renarna vandrar eller flyttas mellan årstiderna. Det verkar därför som lodjuren inte följer med renarna när de flyttar. Det minskade hemområdet för honor med ungar är troligen ett resultat av att de inte kan röra sig över lika stora områden när de tar hand om små ungar. De lodjur som är kvar i området livnär sig på strövrenar som blir kvar i fjällen när majoriteten av renarna flyttas. Studie visade också att mängden hare, ripa och tjäder är högre i fjällen än det är i skogen, och dessa arter är nog också viktiga som alternativa byten för lodjuren när det är låg tillgång på renar.

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