Winter distribution of Eurasian lynx (*Lynx lynx*) in relation to prey distribution and anthropogenically altered landscape in south-eastern Norway

Jördis Damerau



MASTER OF SCIENCE THESIS IN APPLIED ECOLOGY

HØGSKOLEN I HEDMARK

June 2008

In collaboration with



WINTER DISTRIBUTION OF EURASIAN LYNX (*LYNX LYNX*) IN RELATION TO PREY DISTRIBUTION AND ANTHROPOGENICALLY ALTERED LANDSCAPE IN SOUTH-EASTERN NORWAY

VINTER DISTRIBUSJON AV EURASISK GAUPE (LYNX LYNX) I RELASJON TIL BYTTEDYRS DISTRIBUSJON OG ANTROPOGENISK ENDRET LANDSKAP I SØRØST NORGE

Jördis Damerau

M.Sc. thesis

Masteroppgave

Hedmark University College, Department of Forestry and Wildlife Management, Evenstad

Høgskolen i Hedmark, Avdeling for skog- og utmarksfag

Collaborators / samarbeitspartnere:

The Scandinavian Lynx Research Project - SCANDLYNX

Supervisors:

E. B. Nilsen Hedmark University College, Department of Forestry and Wildlife Management Evenstad, N-2480 Koppang

J.D.C. Linnell NINA – Norwegian Institute for Nature Research Tungasletta 2 N-7485 Trondheim

Contents

Abstract/ Sammendrag	4
Introduction	5
Methods	7
1. Study area 2. Field Method	7
3. GIS	9
4. Statistical analysis Results	10
Discussion/ Conclusion	15
References	18
Appendix	21

Tables

Table 1: Correlation matrix of environmental variables	9
Table 2a: PCA results/ Table 2b: PCA loadings	10
Table 3a: PCA results / Table 3b: PCA loadings	
Table 4: Lynx – prey relations for each prey type fitted alone in GLMMs (binomial distribution)	
Table 5: Explanation of prey distribution by environmental factors (poisson distribution)	12
Table 6: Final model	12
Table A7: Behaviour of prey and lynx respectively to residential houses	21
Table A8: Environmental factors that affect lynx	21
Table A9: Explanation of prey distribution by environmental factors (singular prey variables)	21

Figures

Figure 1: Interaction between the components Environment - Prey - Lynx	5
Figure 2: Map of Hedmark, with habitat classes & locations of transect lines and lynx observations	8
Figure 3: Properties of transect lines with or without lynx occurrence	11
Figure 4: Probability of lynx occurrence (diagram)	13
Figure 5: Probability of lynx occurrence in Hedmark County, Norway (map)	
Figure 6: Probability of lynx occurrence (comparison).	15
Figure A7: Percentage of transect lines on which lynx tracks were found during the study period	22

Abstract

Lynx is one of the large carnivores in Norway. Its movement might cause different levels of curiosity, admiration or concern and fright within the human society, which can lead to conflicts. Therefore it might be important to have better knowledge about lynx movement patterns and what causes them.

I compared presence and absence of lynx tracks on 611 transect lines in Hedmark, Norway, in order to investigate the habitat use of lynx.

The difference between transect lines with and without lynx occurrence was distinct. Lines on which lynx tracks were found held a bigger number of roe deer and hare tracks and were closer to fields. Lines with lynx tracks were closer to residential houses but further away from main roads than lines without lynx occurrence. My data showed that lynx stays down in the valley bottoms during winter; closer to human settlements, as this is where the prey occurs.

A principle component - consisting of roe deer and hare – as well as altitude and snow were of most influence on lynx distribution in Hedmark. Using this final model I created a map of probability of lynx occurrence in Hedmark during winter, to get a picture of lynx's spatial use in that certain period of time.

It seems that lynx is very much dependent on hare as well as on roe deer.

Sammendrag

Gaupe er en av de store rovdyrene i Norge. Gaupas forflyttning kan skape forskjellige nivå av nyskjerrighet, beundring, bekymring og frykt i våres samfunn, som kan føre til konflikter. Derfor kan det være viktig å ha bedre kunnskap om gaupas forflyttnings mønstre og hva som forærsaker det.

Jeg sammenlignet nærvær og fravær av gaupespor på 611 takseringslinjer i Hedemark, for å undersøke gaupas habitat bruk. Forskjellen mellom takseringslinjer med og uten gaupe var distinkt. Linjer hvor gaupas spor var funnet hadde flere hare og rådyr spor og var nærmere lanbruk areal. Linjer med gaupespor var nærmere bolighus men lengere fra store hovedveier enn linjer uten gaupespor. Mine data viser at gaupa bruker mye tid nede i dalbunner gjennom vinteren nærmere menneskelig bosettning, Noe som har sammenheng med hvor det er tettest med byttedyr.

En viktig bestanddel, bestående av hare og gaupe, i tilleg til høyde og snø var av mest innflytelse på gaupas utbredelse i Hedemark. Ved bruk av denne siste modellen laget jeg et kart over sannsynligheten for gaupesporp på kryssende linjer gjennom vinteren, for å gi ett slags bilde på gaupas arealbruk innen ett bestemt tidsperspektiv. Det virker som at gaupa er såvel avhengig av hare som rådyr.

Introduction

Habitat use is a central aspect of a species' ecology and distribution (MILLS et al. 1993), but also important for conservation and management (e.g. CARVELL 2002, PETIT 2002, LAW & DICKMAN 2004). With knowledge about the habitat a focal species uses, it is possible to improve e.g. conservation planning, reintroduction programs or prevention planning as e.g. in the case of lynx (*Lynx lynx*) and domestic sheep (*Ovis aries*) (ODDEN et al. 2002, ASHEIM & MYSTERUD 2004, LINNELL et al. 1996). Prey distribution and abundance have important influence on spatial distribution of carnivores (SUNQUIST & SUNQUIST 1989) - and random, even or clumped prey distribution may strongly affect a carnivore's space use patterns (DAVIES & HOUSTON 1984). The main prey of lynx is roe deer (*Capreolus capreolus*) (ODDEN et al. 2006), but it is not always available. In areas where medium-sized ungulates are lacking lynx survive on small game (JEDRZEJEWSKI et al. 1993).

HALL et al. (1997) defined habitat use as the way an animal uses a suite of abiotic and biotic resources to meet life-cycle needs of survival and reproduction. It is therefore also a result of trade-offs between finding food and avoiding predators. Earlier research in Scandinavia revealed that the most common cause of death among radio-collared Eurasian lynx is of anthropogenic origin (legal harvest, poaching, vehicle collisions; ANDERSEN et al. 2003; ANDRÉN et al. 2006) and studies from central Norway indicate that this mortality is closely linked to lynx appearing in areas of human activity (SUNDE et al. 1998a).

Habitat selection on the other hand is a hierarchical process involving a series of innate and learned behavioural decisions made by an animal at different geographic scales to determine a location in which to acquire resources in a habitat (HALL et al. 1997). Mortality risk as well as prey abundance and distribution are likely to influence habitat selection. All animals have to face trade-offs in their habitat selection and use (BERGER 1991, ABRAMS 1994). They need to satisfy the basic requirements like food, i.e. trying to avoid starvation, finding mates and fight off competitors or avoid predators. Movement can be seen as a survival strategy for prey especially when considering a large landscape scale at which prev and predator respectively have many options for feeding or hunting sites (MITCHELL et al. 2002). Why, how and where prey moves influences the predator's reaction - and reversed (Figure 1). For this study I operate on county level, which could referring to JOHNSON (1980) be characterised as the second level of his system of habitat selection; which he saw as a hierarchical process. Firstly, species have a range/ distribution, second home ranges/ individuals are distributed within this distribution. Third, within each home range the individuals utilise the habitat at different rates. And finally, within each habitat patch feeding is not random.

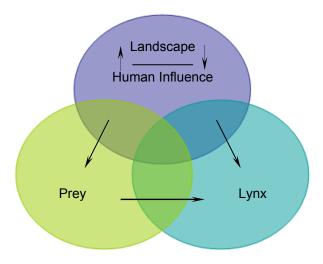


Figure 1: Interaction between the components Environment - Prey - Lynx

Large predators trigger emotions among humans (KALTENBORN & BJERKE 2002) – and the lynx is no exception. Since humans claim a major part of the land, problems with these large cats can arise (ANDERSEN 2003, BUNNEFELD et al. 2006). Thus it is important to understand its habitat use. During the last 30 years there has been an alteration in the society's view towards big predators, which has led to a change of management goals for lynx in Norway. Since 1980 the aim has been to incorporate the lynx into the cultural landscape. The change of management strategies led to a significant increase in lynx population size (www.nina.no). But still in Scandinavia the density of 0.3 - 1 lynx per 100 km² is quite low (ODDEN et al. 2002).

Lynx have very large home ranges in southern Norway (500 to 1500 km²) (LINNELL et al, 2001; HERFINDAL et al. 2005) probably because their main prey, roe deer (ODDEN et al. 2006), occur at exceptionally low densities in Østerdalen with an average of 0.02 (0.004 – 0.114) roe deer shot per km² during the last 5 years (NILSEN et al. submitted ms). Roe deer is confined to valley bottoms and artificial feeding sites during winter (LINNELL et al. 2007). Due to less snow at low elevations and the presence of artificial feeding sites, roe deer are more concentrated around human settlements during winter and therefore easy to locate for predators (ODDEN et al. 2006, BUNNEFELD 2006).

From the point of view of large carnivores in the modern world, humans represent by far the most dangerous intraguild predators. Both inside and outside protected areas people are generally the most common cause of death among large carnivores (WOODROFFE & GINSBERG 1998). From the large carnivore's point of view of reducing mortality risk, areas of high human activity should be avoided.

This study focuses on lynx distribution in Hedmark during winter and the factors influencing the predator's occurrence. Focusing on the issue of selecting roe deer as a main prey and avoiding people and their houses/ cabins or roads I investigate the hypotheses that (1) in winter high roe deer densities are related to areas of human activity. In Europe and North America some cervid species, which are the main prey of large carnivores, may occur at higher density in areas where humans have modified the habitat, or provide supplementary food (MCSHEA et al. 1997). In such cases there may be a clear trade-off between mortality risk and foraging efficiency. Roe deer represents the main prey of lynx in southern Norway (BIRKELAND & MYRBERGET 1980, ANDERSEN et al. 1998) and are closely associated with human-modified landscapes and the presence of agricultural land (MYSTERUD et al. 1997, MYSTERUD 1999, SUNDE et al. 2000). The lower threshold of wild ungulate density below which lynx switch to a diet dominated by small prey it is not clear (ODDEN et al. 2006). But as roe deer density in Hedmark is so low, I include hare (*Lepus europaeus*), forest game birds (*Tetraoidae*) and small rodents as a possible prey.

(2) Lynx occurrence is closely related to areas of high roe deer activity – thus, lynx occur close to humans as well during winter as this is where their prey occurs (BUNNEFELD 2006) even if they risk been shot.

Methods

1. Study area

Hedmark, a county in the south east of Norway, consists of several parallel river valleys (e.g. Østerdalen, Rendalen) running in north-south direction with low hillsides in between and with patches of agricultural land dispersed along the valley bottoms. The valleys have an altitude between 200 and 500 m above sea level. The area is dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which in most areas have been harvested during the last 100 years. The study area has a continental climate with stable warm summers and cold winters. The snow conditions vary between years, but the snow usually lasts from November to April with depths of between 20 cm and 120 cm (http://scandlynx.nina.no/).

Population density in the study area lies between 1.8 people/km² in the northern part of Hedmark and 18.3 people/km² in the southern part (border Elverum/ Hamar; Statistics Norway, 1. Jan. 2007).

2. Field Method

This study is based on data collected by the Large Carnivore Monitoring Program (overvåkningsprogram for store rovdyr) - administrated by NJFF (Hedmark Angler and Hunter Association) in the period 2003-2007 (see ODDEN et al. 2002). These data contain information about lynx tracks observations on a fixed set of transect lines (Figure 2) monitored during January/ February, as well as recordings of their main prey (roe deer) along the same set of transect lines (see also LINNELL et al. 2007). Apart from those, also tracks of hare, forest game birds, small rodents and other species as well as snow depths are recorded for further use in different projects. During 2003 - 2006 a total of 621 transect lines, each 3 km long, was monitored on foot within the study area. Of these, 611 lines were checked for lynx tracks between 1999 – 2006 by mainly local hunters, but all findings were reported to SNO (Statens naturoppsyn) for confirmation.

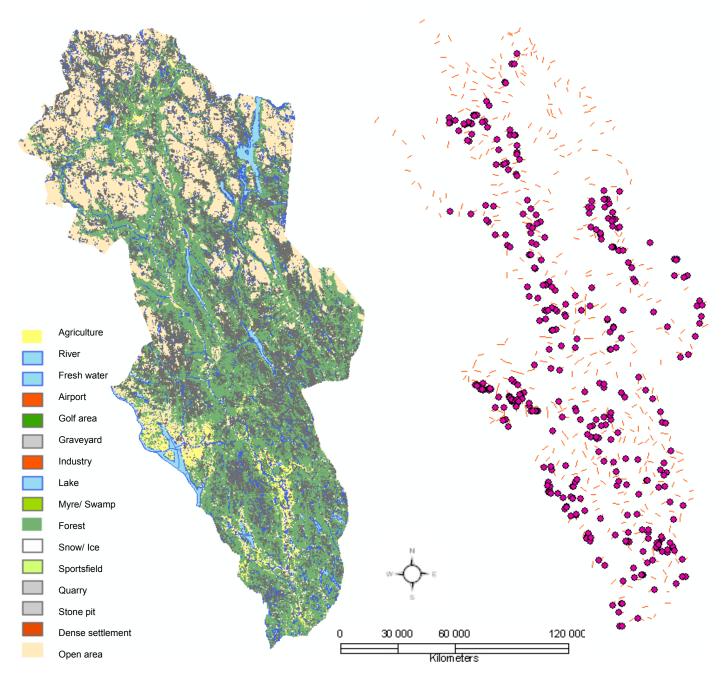


Figure 2: A map of Hedmark County showing habitat classes (left) and locations of transect lines and lynx observations (right)

3. GIS analyses

To acquire additional habitat information about the transect lines they were imported into ArcGIS 9.2 (ArcMap). In order to meet the slight inaccuracy of transect-line-positions (only start and end points were available), they were defined as 500m wide, i.e. each line were surrounded by a 250 m buffer on each side of the centreline. For each line the program ArcMap, with extension Hawth Tools, was used to create ten random points within the buffers around the transect lines. The additional values were obtained by measuring distances to the variable in question from each point. I used the average value as a descriptor of the line:

I calculated the distance from lynx locations (where lynx tracks crossed the transect line) to houses by creating a raster map of houses for the county of Hedmark with the extension Hawths Tools, splitting them into residential houses and cabins. The lynx and random points were each intersected with the house-density-grid, which resulted in a raster value, i.e. number of houses per grid cell, where I used 1km² grid cells. Roads were classified into two categories, 1 = public main roads and, 2 = gravel forestry roads. Euclidean straight line distances from lynx locations to roads were calculated using ESRI ArcGIS 9.2, extension Spatial Analyst: The road lines were converted into raster data and the distance-value for each location point was than calculated. The distances from lynx locations to cultivated field were calculated with the ArcGIS function join, to check for edge habitats (cover and food), where roe deer often gather (RATIKAINEN et al. 2007). For the altitude calculations the lines were also converted into a rasta grid using Spatial Analyst and each lynx and random point was connected to the underlying raster value.

Finally to compile a probability map of lynx occurrence I uploaded the backtransformed data from the final model equation into ArcGIS and created a raster map using inverse distance weighting with the Geostatistical Analyst (see Figure 6 in the results chapter), were the 15 closest neighbours were included.

4. Statistical analysis

Based on the data described above, I constructed Generalised Linear Mixed Models (GLMM) in SAS (SCHABENBERGER 2005) to evaluate the habitat use of the lynx. The data material consisted of a total of 2557 observations of data points (i.e. transects lines with lynx presence/ absence), on which 1874 lynx tracks were observed, excluding 44 data points due to missing or unrealistic values. A total of 603 lines were transected, but as most of the lines were investigated several years, this was controlled for by using line ID as a random factor. One could expect several environmental variables to be correlated. However, the correlation matrix (Table1) indicates that only the variables distance to road and distance to field are strongly correlated (r>0.5). This could be problematic when both variables enter the same model. Thus I did a Principal Component Analysis (PCA), extracted the scores for each line, and used that as a new variable in the modelling, hereafter called PC1 (Table 2). PC1 is related to roads and fields as given in Table 2b.

	cabins	field	forest	forest roads	roads
houses	-0.355	0.016	-0.383	0.022	-0.196
cabins	1.000	-0.088	-0.043	-0.092	-0.071
field		1.000	0.130	0.230	0.667
forest			1.000	0.363	0.180
forest roads				1.000	0.225
roads					1.000

 Table 1: Correlation matrix of environmental variables (high correlation shaded)

Table 2a: PCA results, impo showing how much is explai		Table 2b: PCA loa relation of PC1 to	dings – the variables field and roads
	PC1		PC1
Standard deviation	2257.9593276	field	0.465
Proportion of Variance	0.8682208	roads	0.885

Among the main prey species, one could also expect some covariation in their distribution. Indeed, hare density was significantly positively related to roe deer density. (Table A9). During winter time all areas suitable for roe deer are also hare habitats (HULBERT & ANDERSEN 2001). So I created a PC for the two prey types, which is hereafter called PC2. The relations concerning PC2 are described in Tables 3a & b.

Table 3a: PCA results, importance of components, showing how much is explained by PC2		Table 3b: PCA loadings – relation of PC2 to the variables field and roads		
-	PC2		PC2	
Standard deviation	1.0473459	roe deer	0.707	
Proportion of Variance	0.5484667	hare	0.707	

Using a GLMM (Glimmix script) I set up a logistic regression of lynx presence/absence (as response), assuming a binomial error structure and a logit link function. First I did a series of prey models, then a series of environmental models to see the impact of each type of data set on lynx. Afterwards I combined environmental and prey data. I used line ID as a random effect. Starting with all explanatory variables in one model (no. of prey per line, average snow depth – collected during snow tracking; altitude, distance to field edge, distance to forest edge, residential houses and cabins – calculated as described in paragraph 3.) I used a backwards selection procedure (PEARCE & FERRIER 2000), after checking the importance for lynx of every variable on its own, to find the final model. The model selection was based on p-values (DALLAL 2007), where p<0.05 is assumed to be significant.

Results

Figure 3 shows the differences between transect lines with and without lynx occurrence. Overall, transect lines on which lynx tracks were found were situated closer to fields and main roads, but further away from forest roads. Also, they are found at lower altitudes (Figure 3a). They were much closer to residential houses than lines were no lynx tracks were found (Figure 3b). Furthermore on lines with lynx occurrence also more roe deer and hare tracks were monitored, but less bird signs (Figure 3c).

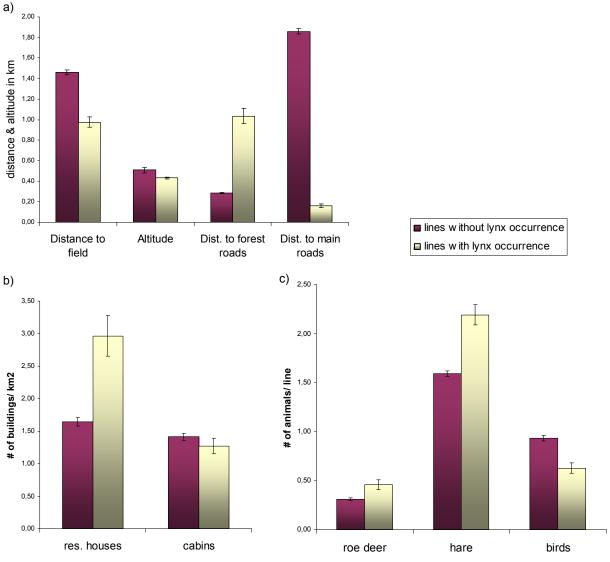


Figure 3: Properties of transect lines in Hedmark with lynx occurrence in comparison to transect lines without any lynx occurrence, according to a) environmental variables b) number of buildings and c) prey distribution

To increase understanding of lynx distribution, I checked what kinds of variables were of main influence on the prey. After all variables entered the model, Table 4 only shows those that remained after the backward selection.

Table 4: Explanation of prey distr	ibution by envi	ronmental factors	s (poisson di	stribution), s	ample size =
1898 observation points					_

Model	Estimate	SE	F	P-value
Roe Deer = f(
Altitude	-0.00183	0.000406	20.18	<0.0001
Residual houses	0.1951	0.02225	76.90	<0.0001
PC1 ~ distance to fields	-0.00011	0.000040	7.95	0.0049
& main roads)				
Hare = f(
Altitude	0.000663	0.000167	15.80	<0.0001
Residential houses	0.04558	0.009941	21.03	<0.0001
Average_Snow)	0.003422	0.001043	9.32	0.0011

The observation of roe deer, hare and small rodent tracks on the lines show significant positive relationships to lynx occurrence (Table 5).

 Table 5: Lynx – prey relations for each prey type fitted alone in GLMMs (binomial distribution), sample size = 1898 observation points

Model	Estimate	SE	F	P-value
Lynx = f(roe deer)	0.06627	0.02356	7.91	0.0050
Lynx = f(hare)	0.03833	0.008622	19.76	<0.0001
Lynx = f(PC2	0.2973	0.05889	25.49	<0.0001
~ roe deer + hare)				
Lynx = f(birds)	-0.00632	0.01568	0.16	0.6869
(capercailie, grouse)				
Lynx = f(small rodents)	0.02686	0.01330	4.08	0.0437

However, if all prey types enter the same model, only roe deer (estimate = 0.0435; SE = 0.0201; x^2 = 4.6888; p = 0.0304) and hare (estimate = 0.0316; SE = 0.0079; x^2 = 15.8754; p < 0.0001) are significant.

When houses were categorised into residential houses and cabins, residential houses had a significantly positive effect on lynx occurrence (estimate = 0.08080; SE = 0.02939; $F_{(1,1304)}$ = 7.56; p = 0.0061). Cabins also had a positive estimate but were not significant (estimate = 0,03437; SE = 0.03481; $F_{1,1304}$ = 0.97; p = 0.3237).

Lynx had a negative estimate for main roads (estimate = -0.00031; SE = 0.000068; $F_{1,1304}$ = 21.47; p <0.001). The small forest roads were likewise significantly negative (estimate = -0.00069; SE = 0.000294; $F_{1,1304}$ = 5.50; p = 0.0192).

If only environmental variables enter the model process, the only significant factors are altitude (estimate = -0.00189; SE = 0.000519; F_{1,1302} = 13.29; p = 0.0003) and snow (estimate = -0.01261; SE = 0.003275; F_{1,1302} = 14.81; p = 0.0001) likewise in the full model. Table 6 shows the most parsimonious model how lynx is explained by prey and landscape together. Lynx avoid high altitude and snow (Table 6/ detail Table A8), but seek areas with high prey abundance.

Model	Estimate	SE	F	P-value
Lynx = f(
PC2 ~ roe deer & hare	0.2790	0.05901	22.36	<0.0001
Altitude	-0.00176	0.000522	11.33	0.0008
Average Snow)	-0.01238	0.003319	13.91	0.0002

Table 6: Final model = best explanation for lynx occurrence, sample size = 1898 observation points

Figure 4 shows the rough predictions calculated with the final model from Table 6. The less snow and the more prey occurrence, the higher is the probability of finding a lynx. I choose a constant altitude of 300 m a.s.l., which is approximately in accordance to the average altitude of a valley bottom in Hedmark. The highest score for snow depth was 125 cm and for PC2 10.8 units, so I restricted the model to those estimates.

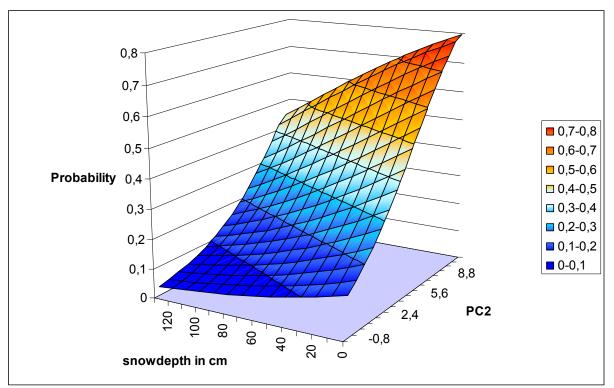


Figure 4: The probability of finding a lynx on a transect line in Hedmark, south-eastern Norway in the period 2003-2007, in relation to snow depth and prey density (see methods for PC2). The full model is given as Lynx = -1.0866 + (0.2790*PC2) - (0.00176*Altitude) - (0.01238*Snow), the altitude is fixed at 300 m a.s.l.

With the same predictions from the final model it was possible to create a map in ArcGIS, where I printed the probability of lynx occurrence for Hedmark (Figure 5, Methods described in chapter 3. GIS). According to the model the probability of finding a lynx on a transect line varies between 3 - 46%.

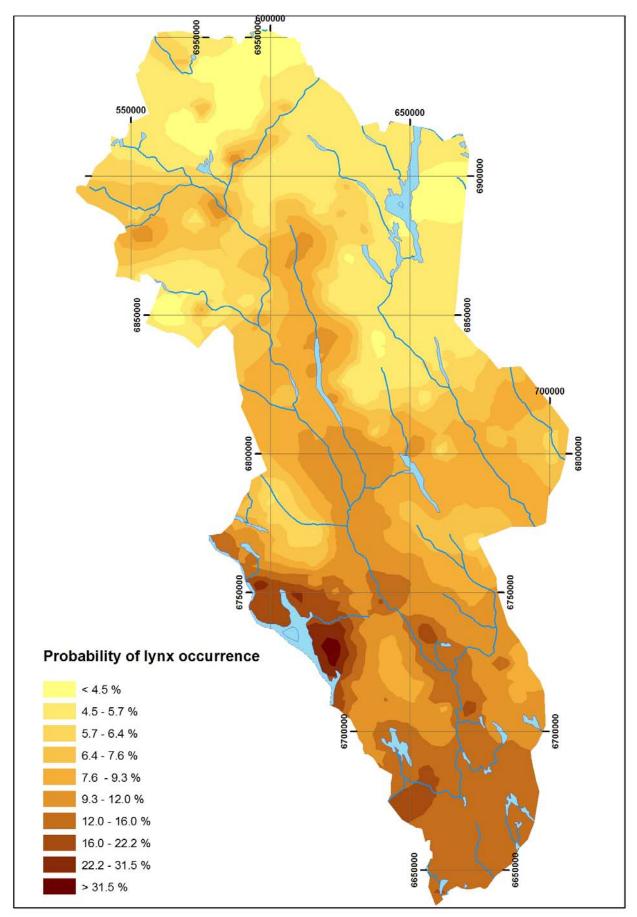


Figure 5: Probability of lynx occurrence in Hedmark County, Norway

Discussion/ Conclusion

For the lynx as one of the large carnivores in Europe people would like to know its whereabouts. Therefore we have to know what influences its distribution to be able to make predictions. I investigated these influences for the county of Hedmark, south-eastern Norway, using snow track data on a set of fixed transect lines.

The difference between transect lines with and without lynx occurrence was distinct (Figure 3): lines on which lynx tracks were found held a much higher number of roe deer and hare tracks. Lines with lynx tracks have more resident houses but fewer cabins, and they are closer to fields. Further, lines with lynx occurrence are generally much further away from main roads than lines without lynx occurrence, whereas the pattern is clearly opposite for small roads. ANDERSEN & ONSAGER (1997) also observed that wolves were often found close to human settlements, as patchiness and edge effects are likely to affect prey distribution.

The prediction that lynx occur close to roe deer and therefore close to human settlement during the winter was supported by my analysis: where the prey is, there is also the predator (Table 4 & 6) and roe deer and hare seek human vicinity (Table 5, also Table A7). According to the diet data presented by ODDEN et al. (2006) roe deer is the most important prey for lynx in south-eastern Norway, with hare second. For the southwestern Northwest Territories e.g. POOLE (1997) clarified the lynx' dependence on the snowshoe hare cycle.

The calculations with each prey type singularly suggested first that lynx occurrence is much more dependent on hare than on roe deer tracks (Table A10). That was inconsistent with ODDEN et al. (2006). But the strange inference between the two prey types (Table A9, Figure 3) also suggested a correlation. For comparison I present a hare-model to hare-roe deer-model in Figure 6. The highest probability of finding lynx tracks in Hedmark depending only on hare is 35%, whereas the probability increases to 46% when roe deer and hare are combined. But otherwise regarding to density distribution the maps differ only in local patches. For management decisions it could be advantageous to use both maps and the local hunter's experience in addition.

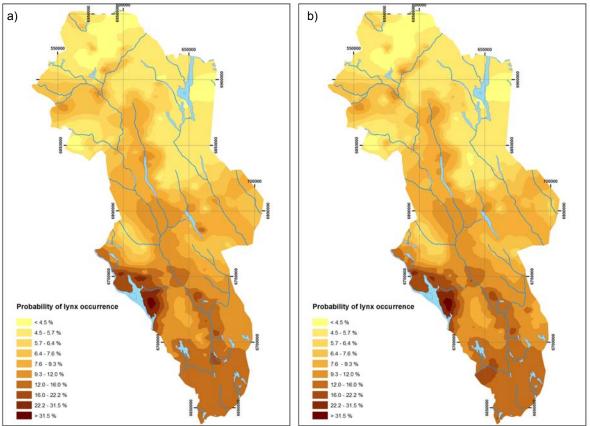


Figure 6: Probability of lynx occurrence in Hedmark County, Norway.

a) Simulation with only hare in the model: Lynx =-1.1433+(0.04271*Hare)-(0.00207*Altitude)-(0.01267*Snow) b) Simulation with PC2 (~roe deer + hare): Lynx =-1.0866+(0.2790*PC2)-(0.00176*Altitude)-(0.01238*Snow)

As shown in Figure 3 there is a very large difference between lynx/no-lynx lines for hare, but not so for roe deer. I got the same results when using ln(hare) and ln(roe deer). This could be due to density - hare density in Hedmark is much higher than the density of roe deer (ODDEN et al. 2006). The data revealed an average of 5.40 hare tracks per line, but an average of 1.06 roe deer tracks per line. Hare move quite unpredictable in contrast to roe deer, which have a more straight forward movement pattern (ARONSON & ERIKSSON 1998). It might be easier for a predator to catch prey which he encounters two or three times a day than only once. Even if roe deer is the main prey, lynx may switch prey type when necessary depending on what is accessible. In the north-eastern part of Hedmark the model simulation does not overlap with the track findings (compare also Figure 5): That area is very continental, with low precipitation and very dry so that hare and roe deer densities are low. However, there are recordings of lynx tracks.

Very many animals seek cover and food at the valley bottoms, because of richer vegetation (JACKS et al. 1995). In my study area, valley bottoms also have more residential houses and agricultural activity, which affects landscape structures that are favourable to roe deer (HANSSON 1979, LINNELL et al. 1998). People also tend to live in the valley bottoms (thus more houses) with lower snow depths, where it is with increasing prey density more likely to encounter lynx. These findings support similar results from ODDEN et al. (2006), BUNNEFELD et al. (2006) and SUNDE et al. (1998a) amongst others. Also HELLDIN (2004) found that red fox as well as lynx established themselves close to human settlements. Lynx have to face trade-offs by selecting areas with high prey density but at the same time avoiding humans. BUNNEFELD et al. (2006) showed that this is to some extent possible: distances from lynx locations to human activity were significantly greater for females with newborn kittens than for males, but this decreased with kitten age. Nevertheless, females with kittens are able to maintain higher kill rates on roe deer than do solitary males and females throughout the year (NILSEN et al. submitted ms). SUNDE et al. (1998a) found that lynx avoid closeness to humans when resting, but in general are able to tolerate high human activity as long as sufficient stands of undisturbed, mature forest with dense horizontal cover are present. My data and results are from lynx on the move (hence the tracks), which suggests that while travelling or hunting lynx are not discouraged to pass close by humans.

For road use in wolves HAMRE (2006) found they used gravel forestry roads for travelling. This was however a summer study. MURRAY & BOUTIN (1991) compared the influence of snow on lynx and coyote movements and found that because lynx feet are much larger (ratio of body mass to foot area), it resulted in greater mean sinking depths of coyote limbs. It is therefore more likely for lynx than for wolves to use off-road tracks during winter. NELLEMANN (2007) found that bears (*Ursus arctos*) generally avoid towns and resorts, i.e. areas of human activity, which includes main roads. Whereas DICKSON et al. (2005) found that travelling cougars (*Puma concolor*) avoided 2-lane paved roads, but dirt roads may have facilitated movement. Even though forest roads and paved roads display a big difference between lynx/ no lynx lines when tested singularly (Figure 3) they do not appear after the backward selection in the final model. My results reveal that lynx avoid main as well as small gravel roads (Table A8). But that is only true for my data set, which contains snow tracks during January/ February. It could well be that during summer the small unpaved roads are much more used for travelling.

When large carnivores, such as lynx, approach territory claimed by humans conflicts can arise. My results show close association between lynx and humans. Roe deer and hare seek human vicinity and lynx is thus also forced to stay close. This fits with the findings of MYSTERUD (1999) and BUNNEFELD et al. (2006), who found that lynx follow their prey into the valley bottom, where there is less snow and more food. So it is easier for lynx to actually catch prey.

The knowledge about lynx' spatial use during winter (Figure 5, see also Figure A7) could economise the management, e.g. by allocating transect lines or by directing hunters etc. It is a tool of prediction how high the density in different placed probably is. That is important for the hunt (developing methods, quotes) and prevention of damage on livestock.

In connection with a summer probability study (e.g. radio tracking) this should give managers a good instrument of prediction, e.g. an improved probability map.

This could also be interesting on a Scandinavian scale for a comprehensive Peninsulamanagement.

Acknowledgements

My thanks go to Scandlynx for providing the data for this study and Henrik Brøseth, NINA and DN for allowing me to use the lynx data.

I would like to thank Barbara Zimmermann for her patience and help with GIS; also Floris van Beest for his help with the ephemeral Spatial Analyst and very much Jos Milner and Oddgeir Andersen for their spontaneous proof-reading.

I also thank my supervisors John Linnell and Erlend Nilsen for their help.

References

http://scandlynx.nina.no/ http://www.lcie.org/ http://www.environment.no/templates/themepage____2251.aspx http://www.hedmark.org http://www.ssb.no/

ABRAMS P.A. 1994: Should Prey Overestimate the Risk of Predation? The American Naturalist, Vol. 144, No. 2 pp. 317-328

ANDERSEN O., ONSAGER C. 1997: Fordeling av klauvvilt i kulturlandskap og indre skogtrakter brukt av ulv. Bachelor. Hedmark College avd. Evenstad.

ANDERSEN R., LINNELL J. D. C., BRAINERD S., HUSTAD H. (red.). 2003: Large predators and human communities in Norway. A guide to coexistence for the 21st century – NINA. Temahefte 25.48 pp.

ANDERSEN R., LINNELL J. D.C., ODDEN J., ANDRÉN H., SÆTHER B.E., MOA P.F., HERFINDAL I., KVAM T., BRØSETH H. 2003: Lynx - population dynamics, development, and harvest [Gaupe - bestandsdynamikk, bestandsutvikling og høstingsstrategier]. - Norwegian Institute for Nature Research Fagrapport 059.

ANDERSEN R., LINNELL J.C.D., ODDEN J., GANGÅS L., NESS E., KARLSEN J., WANNAG A., RENÅ J.T. 1998: Sosial organisering, spredning, reproduksjon og predasjonsatferd hos gaupe i Hedmark. Framdriftsrapport 1995-97: (Social organisation, dispersal, reproduction and predation behaviour in Lynx in Hedmark). - NINA Oppdragsmelding 519: 1-25.

ANDRÉN H., LINNELL J.D.C., LIBERG O., AHLQVIST P., ANDERSEN R., DANELL A., FRANZÉN R., KVAM T., ODDEN J., SEGERSTRÖM P. 2002: Estimating total lynx (Lynx lynx) population size from censuses of family groups. - Wildlife Biology 8: (4) 299-306.

ANDRÉN H., LINNELL J. D. C., LIBERG O., ANDERSEN R., DANELL A., KARLSSON J., ODDEN J., MOA P. F., AHLQVIST P., KVAM T., FRANZÉN R., SEGERSTRÖM P. 2006: Survival rates and causes of mortality in Eurasian lynx (Lynx lynx) in multi-use landscapes. Biological Conservation 131:23-32.

ARONSON Å., ERIKSSON P. 1992: Dyrespor og kunsten å spore. Cappelen.

ASHEIM L.J., MYSTERUD I. 2004: Economic Impact of Protected Large Carnivores on Sheep Farming in Norway. Sheep & Goat Research Journal, Vol. 19.

BERGER J. 1991: Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Anim. Behav. 41 pp. 61–77.

BIRKELAND K.H. & MYRBERGET S. 1980: The diet of the lynx (Lynx lynx) in Norway. Fauna. Norv. Ser. A 1. 24–28.

BRØSETH H., ODDEN J., LINNELL J.D.C. 2005: Minimum antall familiegrupper, bestandsestimat og bestandsutvikling for gaupe i Norge i 2005. – NINA Rapport 79.17pp.

BRØSETH H., ODDEN J., LINNELL J.D.C. 2007: Minimum antall familiegrupper, bestandsestimat og bestandsutvikling for gaupe i Norge i 2007. – NINA Rapport 271.19 s.

BUNNEFELD N., LINNELL J.D.C., ODDEN J., ANDERSEN R. 2006: Risk-taking by Eurasian lynx in a human-dominated landscape: effects of sex and reproductive status. - Journal of Zoology, London 270:31-39.

BURNHAM K. P., ANDERSON D. R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York, USA.

CARO T. 2005: Antipredator defenses in birds and mammals. University of Chicago Press. **CARVELL C.** 2002: Habitat use and conservation of bumblebees (*Bombus spp.*) under

different grassland management regimes. Biological conservation 103 (1) 33-49.

DALLAL G.E. 2007: Historical background to the origins of p-values and the choice of 0.05 as the cut-off for significance.

DAVIES N.B. & HOUSTON A.I. 1984: Territory economics. In Behavioural ecology: an evolutionary approach. 2nd edn. 148–169. KREBS J.R. & DAVIES N.B. (Eds). Sinauer: Sunderland, MA.

DELIBES M., GOANA P. & FERRERAS P. 2001: Effects of an attractive sink leading into maladaptive habitat selection. Am. Nat. 158, 277–285.

DICKSON B. G., JENNESS J. S., BEIER P. 2005: Influence of vegetation, topography, and roads on cougar movement in southern Carlifornia. Journal of Wildlife Management 69(1):264–276. **HALL L. S.**, KRAUSMAN P.R., MORRISON M.L. 1997: The habitat concept and a plea for the use of standard terminology. Wildlife Soc. B. 25: 173-182.

HAMRE Ø. 2006: Spatial and temporal use of forest roads by wolves in Skandinavia during summer. M. Sc. thesis. University of Tromsø.

HANSSON L. 1979: On the Importance of Landscape Heterogeneity in Northern Regions for the Breeding Population Densities of Homeotherms: A General Hypopthesis. Oikos, Vol. 33 (2), 182-189.

HELLDIN O.-J. 2004: Lodjurspredation på räv - och dess sekundära effekter på bytespopulationerna.

HERFINDAL I., LINNELL J.D.C., ODDEN J., NILSEN E.B., ANDERSEN R. 2005: Prey density, environmental productivity, and home range size in the Eurasian lynx (Lynx lynx). - Journal of Zoology, London 265: 63-71.

HULBERT I. A., ANDERSEN R. 2001: Food competition between a large ruminant and a small hindgut fermentor: the case of the roe deer and mountain hare. Oecologia Vol. 128 (4), 499-508.

JACKS G., SHARMA V. P. 1995: Geochemistry of calcic horizons in relation to hillslope processes, southern India. Geoderma 67, 203-214.

JĘDRZEJEWSKI W., NIEDZIAŁKOWSKA M., MYSŁAJEK R.W., NOWAK S., JĘDRZEJEWSKA B. 2005: Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. Acta Theriologica 50 (3): 417-428.

JĘDRZEJEWSKI W., SCHMIDT K., MILKOWSKI L., JĘDRZEJEWSKA B., OKARMA H. 1993: Foraging by lynx and its role in ungulate mortality: the local (Białowieźa Forest) and the Palaearctic viewpoint. Acta Theriol. 38: 385-403.

JONGMAN R.H.G., TER BRAAK C.J.T., VAN TONGEREN O.F.R. 1995: Data analysis in community and landscape ecology. Cambridge University Press.

JOHNSON D. H. 1980: The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, Vol. 61, No. 1 (Feb., 1980), pp. 65-71.

Kaltenborn B. P., Bjerke T. 2002: The relationship of general life values to attitudes toward large carnivores. I: Human Ecology Review, Vol. 9. Nr. 1, s. 55-61. ISSN: 1074-4827. LAW B. S., DICKMAN C. R. 2004: The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. Biodiversity and Conservation 7 (3) 323-333. LINNELL J.D.C., ANDERSEN R., KVAM T., ANDRÉN H., LIBERG O., ODDEN J., MOA P. 2001: Home range size and choice of management strategy for lynx in Scandinavia. -Environmental Management 27: (6) 869-879.

LINNELL J.D.C., DUNCAN P., ANDERSEN R.: The European roe deer: A portrait of a successful species. in ANDERSEN R., DUNCAN P., LINNELL J.D.C. 1998: European roe deer: The biology of success. Scandinavian University Press.

LINNELL J. D. C., FISKE P., HERFINDAL I., ODDEN J., BRØSETH H., ANDERSEN R. 2007: An evaluation of structured snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. Wildl. Biol. 39:456-466.

LINNELL J.D.C., ODDEN J., PEDERSEN V., ANDERSEN R. 1998: Records of intra-guild predation by Eurasian lynx, *Lynx lynx*. - Canadian Field Naturalist 112: (4) 707-708.

LINNELL J. D. C., ODDEN J., SMITH M. E., AANES R., SWENSON J. E. 1999: Large carnivores that kill livestock: do "problem individuals" really exist? - Wildlife Society Bulletin 27(3): 698-705.

LINNELL J. D. C., SMITH M. E., ODDEN J., KACZENSKY P., SWENSON, J. E. 1996: Carnivores and sheep farming in Norway. 4. Strategies for the reduction of carnivore livestock conflicts: a review. NINA Oppdragsmelding 443: 1-108.

LINNELL J.D.C., STRAND O. 2000: Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distribution 6, 169-176.

NELLEMANN C., STØEN O.-G., KINDBERG J., SWENSON J. E., VISTNES I., ERICSSON G., KATAJISTO J., KALTENBORN B. P., MARTIN J., ORDIZ A. 2007: Terrain use by an expanding

brown bear population in relation to age, recreational resorts and human settlements. Biological Conservation 138. 157-165.

NILSEN E.B., LINNELL J.D.C., ODDEN J., ANDERSEN R. submitted ms

McLoughlin P.D., Gaillard J.-M., BOYCE M.S., BONNEFANT C., MESSIER F., DUNCAN P., DELORME D., VAN MOORTER B., SAID S., KLEIN F. 2007: Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88(12), 3192-3201.

MCSHEA W.J., UNDERWOOD H.B. & RAPPOLE J.H. 1997: The science of overabundance: deer ecology and population management. London: Smithsonian Institution Press.

MILLS L.S., SOULÉ M.E., DOAK D.F. 1993: The Keystone-Species Concept in Ecology and Conservation. *BioScience*, Vol. 43, No. 4 pp. 219-224.

MITCHELL W. A., LIMA S. L. 2002: Predator-prey shell games: large-scale movement and its implications for decision-making by prey. OIKOS 99: 249-259.

MURRAY D. L., BOUTIN S. 1991: The influence of snow on lynx and coyote movements: does morphology affect behavior? Oecologia. Volume 88 (4) 463-469.

Mysterud A. 1999: Seasonal migration pattern and home range of roe deer (Capreolus capreolus) in an altitudinal gradient in southern Norway. J. Zool. (Lond.) 247, 479–486. **Mysterud A.,** Bjørnsen B.H., Østbye E. 1997: Effects of snow depth on food and habitat selection by roe deer Capreolus capreolus along an altitudinal gradient in southcentral Norway. Wildl. Biol. 3, 27–33.

MYSTERUD A., LIAN L.-B., HJERMANN D.Ø. 1999: Scale-dependent trade-offs in foraging by European roe deer (Capreolus capreolus) during winter. Canadian Journal of Zoology 77: 1486-1493.

ODDEN J., FISKE P., HERFINDAL I., LINNELL J.D.C., BRØSETH H., ANDERSEN R. 2002: Instruks for bruk av indekslinjer I overvåkning av gaupebestander. Nasjonalt overvåkningsprogram for store rovdyr.

ODDEN J., LINNELL J.D.C., ANDERSEN R. 2006: Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. Eur J Wildl Res. 52: 237-244.

ODDEN J., LINNELL J.D.C., MOA P.F., HERFINDAL I., KVAM T., ANDERSEN R. 2002: Lynx depredation on domestic sheep in Norway. - Journal of Wildlife Management 66: (1) 98-105. **PEARCE J.**, FERRIER S. 2000: An evaluation of alternative algorithms for fitting species distribution models using logistic regression. Ecological Modelling 128,127–147.

PETIT D. R. 2000: Habitat use by landbirds along nearctic-neotropical migration routes: Implications for conservation of stopover habitats. Stopover ecology of nearctic-neotropical landbird migrants 20. 15-33.

POOLE K. G. 1997: Dispersal Patterns of Lynx in the Northwest Territories. *The Journal of Wildlife Management*, Vol. 61, No. 2, pp. 497-505.

RATIKAINEN I.I., PANZACCHI M., MYSTERUD A., ODDEN J., LINNELL J.D.C., ANDERSEN, R. 2007: Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. Journal of Zoology 273: 192-199.

SCHABENBERGER O. 2005: Introducing the GLIMMIX Procedure for Generalized Linear Mixed Models. SAS Institute Inc., Cary, NC. Paper 196-30.

SIDOROVICH V.E. 2006: Relationship between prey availability and population dynamics of the Eursaian lynx and its diet in northern Belarus. Acta Theriologica 51: 265-274.

SCHMIDT K. 2008: Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. Acta Theriologica 53 (1): 1-16.

SUKUMAR R. 1991: The management of large mammals in relation to male strategies and conflict with people. Biol. Conserv. 55, 93–102.

SUNDE P., OVERSKAUG K., KVAM T. 1998: Culling of lynxes Lynx lynx related to livestock predation in a heterogeneous landscape. - Wildlife Biology 4: (3) 169-175.

SUNDE P., KVAM T., MOA P., NEGARD A., OVERSKAUG K. 2000: Space use by Eurasian lynx (Lynx lynx) in central Norway. - Acta Theriologica 45: (4) 507-524.

SUNDE P., STENER S., KVAM T. 1998a: Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. - Wildlife Biology 4: (3) 177-183.

SUNQUIST M.E. & SUNQUIST F.C. 1989: Ecological constraints on predation by large felids. In Carnivore behavior, ecology, and evolution: 355–378. GITTLEMAN J.L. (Ed.). New York: Cornell University Press.

WOODROFFE R. & GINSBERG J.R. 1998: Edge effects and the extinction of populations inside protected areas. Science 280, 2126–2128.

Appendix

Table A7: Behaviour of prey and lynx respectively to residential houses

Model	Estimate	SE	DF	F	Р
Roe deer	0.2423	0.02115	1/1303	131.16	<0.0001
Hare	0.02926	0.009760	1/1304	8.99	0.0028
Birds	-0.1350	0.02010	1/1303	45.16	<0.0001
Small rodents	0.04537	0.01577	1/1304	8.28	0.0041
Lynx	0.08056	0.02948	1/1303	7.47	0.0064

Table A8: Environmental factors that affect lynx

Model	Estimate	SE	DF	F	Р
Lynx = Altitude	-0.00233	0.000513	1302	20.66	<0.0001
Lynx =	-0.00027	0.000094	1304	7.92	0.0050
distance to field					
Lynx =	-0.00430	0.003396	1304	1.60	0.2058
distance to forest					
Lynx = residential	0.08056	0.02948	1303	7.47	0.0064
houses					
Lynx = cabins	0.03343	0.03503	1304	0.91	0.3402
Lynx = roads	-0.00031	0.000068	1304	21.47	<0.001
Lynx = forest roads	-0.00069	0.000294	1304	5.50	0.0192
Lynx = average snow	-0.00941	0.002124	1303	19.62	<0.0001

Table A9: Explanation of prey distribution by environmental factors

Model	Estimate	SE	DF	F	Р
Roe deer = f(
Altitude	-0.00183	0.000406	1/1303	20.18	<0.0001
Residual houses	0.1951	0.02225	1/1303	76.90	<0.0001
PC1 ~ distance to fields	-0.00011	0.000040	1/1303	7.95	0.0049
& main roads)					
Hare = f(
Roe deer	0.02241	0.007780	1/1300	8.30	0.0040
Birds	0.01996	0.002836	1/1300	49.53	<0.0001
Altitude	0.000702	0.000172	1/1300	16.74	<0.0001
Forest	-0.00365	0.001144	1/1300	10.15	0.0015
Residential houses	0.04428	0.01001	1/1300	19.56	<0.0001
Average_Snow)	0.002175	0.001066	1/1300	4.16	0.0416

Table A10: Final model, with prey singularly

Model	Estimate	SE	DF	F	P-value
Lynx = f(
Hare	0.04271	0.008787	1/1302	23.63	<0.0001
Altitude	-0.00207	0.000521	1/1302	15.84	<0.0001
Average_Snow)	-0.01267	0.003321	1/1302	14.57	0.0001

About 410-440 lynx were counted in 2007 (www.environment.no). During the snow tracking administered by NINA but locally arranged by NJFF, a decrease/ stagnation in population size was monitored till 2005; but since 2005/2006 the population is slightly increasing again (BRØSETH et al. 2003 - 2007). It is possible to convert the number of family groups counted on those occasions into total population size (ANDRÉN 2002). With increasing population the percentage of found lynx tracks is also increasing as is the percentage-line (triangle symbol) in Figure A7, which shows the increase of lynx tracks found on transect lines with varying number of transects monitored per year.

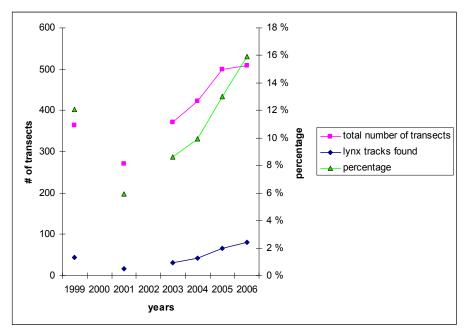


Figure A7: Percentage of transect lines on which lynx tracks were found during the study period, years 2000 and 2002 were not monitored