Factors affecting presence and diet of red foxes and birds of prey

A large scale study in Finnmark

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Abstract

In absence of top predators, the red fox population reaches a higher number of individuals. The increased presence of red fox, as it invades alpine and tundra ecosystems, might have severe and negative consequences on the ecosystem as a whole. In Finnmark, Northern Norway, immense levels of large herbivores due to reindeer herding roam the tundra. The high numbers of reindeer provide resources (as carcasses) for scavenging species, a subsidy essential for the survival of the non-endemic predatory species during the low phase of the small rodent population cycle. This large-scale study in 2011, during a small rodent peak year, covers the three peninsulas located in the middle and eastern regions in Finnmark; Porsager, Sværholt and Nordkinn. In this study I map the diet of red fox and birds of prey, and investigate the importance the different factors have on distribution and diet. Expectedly, I discovered that red fox and raptor diets consisted largely of small rodents. Furthermore, it seems that reindeer are not a very important food resource for red fox, and even less important for raptors. This agrees with the fact that no relationship was found abundance of reindeer and abundance of red fox and raptors. Further studies of mesopredator diet should also be conducted during the low phase of the small rodent cycle.

Key words: Mesopredator release; red fox; birds of prey; diet; subsidies; scavenging; scat analyses; Finnmark

Content

Introduction

In the absence of apex predators (predators at the top of the food chains) in a community, mesopredators (medium sized carnivores) suffer less pressure from predation, and experience enhanced survival and population growth (Paine 1969, Pacala and Roughgarden 1984). This phenomenon was referred to as "mesopredator release" by (Soule et al. 1988) to describe the process of mesopredators growing in numbers when an apex predator is absent. Growing mesopredator populations may have negative cascading effects on the biodiversity (Lecomte et al. 2009, Prugh et al. 2009, Ritchie and Johnson 2009). It is also suggested that mesopredators are important drivers in ecosystems and that their impacts are even larger when the community structure is relatively simple (Roemer et al. 2009).

The trophic structure of an ecosystem may both result from bottom-up control and top-down control. Bottom-up control is based on nutrient limitations and energy inputs to the system, while top-down control refer to how predation by higher trophic levels affects the accumulation of biomass in lower trophic levels (Preisser 2008). Both bottom- up control and top-down control can occur at the same time (Gauthier et al. 2004). It is expected that the magnitude of a mesopredator release effect will reach towards a maximum when both the bottom-up and the top-down controls favours of the mesopredator outbreak (i.e. more available resources and relaxed predation pressure) (Prugh et al. 2009).

In northern Fennoscandia predation pressure from apex predators (such as wolf (*Canis lupus*), lynx (*Lynx lynx*) and wolverine (*Gulo gulo*)) is relaxed, as their population levels are low (Tveraa et al. 2014). The main reasons for this decline are arguably consequences of human interventions and anthropogenic stressors in the environment (Prugh et al. 2009, Ritchie and Johnson 2009). Among mesopredators, the red fox (*Vulpes vulpes*) is an adaptive species and it is often referred to as the ultimate generalist. Furthermore it is the most widespread mesopredator in the world (Hersteinsson and MacDonald 1992, Jędrzejewski and Jędrzejewska 1992, Post et al. 2009). Over the past 50 years red fox populations have expanded into the northern hemisphere (Hersteinsson and MacDonald 1992). With an expanding geographical range into Arctic tundra ecosystems, the red fox forces the native arctic fox (*Vulpes lagopus*) to retreat as a result of intraspecific competition (Hersteinsson and MacDonald 1992, Kaikusalo and Angerbjörn 1995, Tannerfeldt et al. 2002, Killengreen et al. 2007).

The expanding distribution of red fox was first proposed by Hersteinsson and MacDonald (1992) mainly as a response to increased ecosystem productivity through climate change. This theory was later reconsidered by Elmhagen and Rushton (2007), and the main mesopredator release mechanism of red fox in high-latitude and alpine ecosystems in northern Fennoscandia now reaches towards the idea of relaxed top-down control of absent apex predators. Relaxed predation pressure and a less extreme environment contribute to the prevalence of red fox populations in tundra ecosystems. Additionally, the red fox seem to be favoured by the increased amounts of anthropogenic subsidies (Selås and Vik 2006, Selås and Vik 2007, Killengreen et al. 2011).

Finnmark in northern Norway holds some of the most dens reindeer (*Rangifer tarandus*) herds in the World (Bråthen et al. 2007). The absence of apex predators has contributed to the increase of reindeer abundance (Næss and Bårdsen 2013). Originally, reindeer migrate from their costal summer pastures and calving grounds to inland habitats during winter (Gunn and Miller 1986, Fauchald et al. 2007). However, over the years changes in reindeer migration patterns in Norway have lead to parts of the herd to become all-year residents at the summer pastures (Henden et al. 2014). Since the mid-1970s the abundance of reindeer in Finnmark has dramatically increased (Riseth and Vatn 2009) and as a consequence, the amount of reindeer carcasses may have increased also.

Even though tundra ecosystems have a simple structure, the ecosystem functioning is quite complex due to fluctuations with both seasonal and multi-annual components (Ims and Fuglei 2005). There is migratory species like reindeer migrating between summer and winter pastures. Also, voles and lemmings typically produce a 3-5-year population cycle (Elton 1942, Korpimäki and Krebs 1996, Ims and Fuglei 2005) that is synchronous between species in the same community (Stenseth and Ims 1993). Finally, snow cover decreases availability of small rodents, and the greatest challenge for tundra predators is surviving through the low phase of a small rodent cycle during winter. While the arctic fox is adapted to such an environment the red fox may not survive without any subsidies (Hersteinsson and MacDonald 1992). It is suggested that the reindeer carcasses is an essential subsidy for the red fox during winter in the low phase of the small rodent population cycle (Killengreen et al. 2011).

Recently, Henden et al. (2014) discovered that area occupancy of carnivores increased notably in areas with increasing densities of non-migrating reindeer. This suggests that the altered reindeer migration patterns, leading to all-year residents, provide a bottom-up boost

for the mesopredators in Finnmark. These findings, therefore, lay the foundation for my study. I will, by collecting and analyse fox droppings and raptor pellets, map presence and diet of mesopredators in Finnmark in Norway. Red fox is considered to be stationary, raptors are migratory. Some raptors such as skuas (the long-tailed skua (*Stercorarius longicaudus*), the parasitic skua (*Stercorarius parasiticus*), and the pomarine skua (*Stercorarius pomarinus*)), owls (the snowy owl (*Bubo scandiaca*) and the short-eared owl (*Asio flammeus*)), and the one hawk species: rough-legged buzzard (*Buteo lagopus*), are only present during years with high abundance of small rodents (Killengreen et al. 2007). Other species are expected to be present more permanently (golden eagle (*Aquila chrysaetos*), white-tailed eagle (*Haliaeetus albicilla*) and gyrfalcon (*Falco rusticolus*)). Systematic surveys of droppings and pellets may both give information about the frequency of occurrence of species in an area (i.e. the density of pellets and droppings reflect abundance) as well as diet (i.e. composition of prey remains). Information about diet is essential when assessing the role of mesopredators in the ecosystem, to identify potential competition that may occur among predators and its impact on prey populations.

In this study I will investigate how geographical factors relating to carnivore resource availability in tundra, specifically altitude and distance from coast, affect the diet. I also want to investigate the relationship between frequency of occurrence (as reflected by pellet and dropping density) as affected by the presence of reindeer in my study sites as to suggest to what extent reindeer are an important subsidy for the mesopredators or not.

Material and methods

Study area

The study took place during August 2011 at peninsulas along the coast of middle to eastern Finnmark County in northern Norway. The three peninsulas used in the study were the peninsulas of Porsanger (69-70 °N and 25 °E), Sværholt (70 °N and 25-26 °E) and Nordkinn (70-71 °N and 27-28 °E). The coastal strip of northern Finnmark is classified as low arctic tundra, and the mean temperature in July lies between 8-12 °C (Walker et al. 2005). In general, the peninsulas range of altitude is relatively low. The southern part of the study area is, however, connected to areas with higher altitude.

Among the three peninsulas in this large scale study, I have 9 study sites (hereafter termed blocks). There are three study blocks on each of the peninsulas: One in the south, one to the north, and one in between (Figure 1). The study blocks are selected to cover a spatial variation in the number of resident reindeer during winter. The study blocks are also based on different herding districts with different management practices (Ims et al. 2007, Henden et al. 2014). For further mentioning in this thesis, block names will be abbreviated (see Table 1 for all abbreviations).
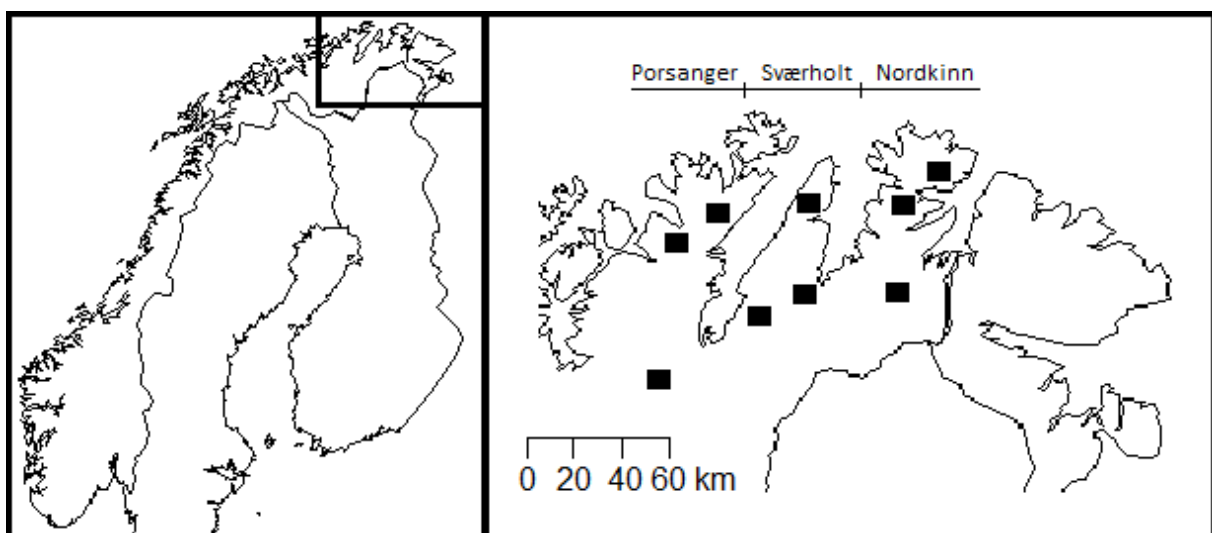
Figure 1: Map showing the three peninsulas in eastern Finnmark, northern Norway (Porsanger, Sværholt and Nordkinn) and the nine study blocks used in this study, indicated as black squares. Each of the peninsulas holds three study blocks; one southern, one in the middle, and one to the north.

Resource availability for mesopredators

The terrestrial fauna is typical for the low arctic tundra (Callaghan et al. 2004). Most of the birds are migratory. Resident terrestrial birds are either scavenging or predatory corvids or eagles. There are also two resident herbivorous ptarmigan species (*Lagopus muta*, *Lagopus lagopus*). Small rodents are represented by tundra voles (*Microtus oeconomus*), field voles (*Microtus agrestis*), grey-sided voles (*Myodes rufocanus*) and Norwegian lemming (*Lemmus lemmus*). Avian small rodent specialists are usually only present during peak years of the small rodent population cycle. There was a small rodent outbreak in 2011, and the population cycles reached a high peak during the autumn (Killengreen et al. 2013).

In middle and eastern Finnmark there are around 80000 individuals of reindeer according to official statistics in 2012 (Anonymous 2012). Most of the reindeer are herded to their winter pastures in late August, and they return to the summer pastures in April. A significant amount of the herds remain on the peninsulas during winter (Henden et al. 2014). A high mortality of the resident reindeer is expected due to the severe winter conditions at the coastal areas, providing carcasses as potential subsidies to scavengers (Tveraa et al. 2007).

Sampling design

As I intend to map the diet of red fox and birds of prey, I will identify the remains of a meal and undigested food. Concerning red fox this means finding fox droppings. As for birds of prey, I will be looking for regurgitation (expulsion) of eaten material. To avoid confusion in further reading, I will now settle the definition of my data: All data collected representing red fox is will be referred to as "faeces". All data collected representing birds of prey (raptors) will be referred to as "pellets".

Faeces from red foxes and arctic foxes are very similar. One can only distinguish the two via DNA extraction from fresh specimens (Dalén et al. 2004). It is, however, most likely that all faeces collected originate from red foxes (Frafjord 2000). Previous studies show that the foxes (arctic fox and red fox) have a very similar diet, and differences are only caused by variation in habitats (Frafjord 2000, Elmhagen et al. 2002). I therefore assume that all faeces origin from red foxes.

Pellets in the study area have most likely originated from three species that are to be considered as small rodent specialists (rough-legged buzzards, long tailed-skuas, snowy owls and short-eared owls) (Killengreen et al. 2007), as well as generalist such as golden eagle, white-tailed eagle and the ptarmigan specialist gyrfalcon.

Transects were purposely established for collection of faeces and pellets (Table 1), and were built up by GPS-positions. The intention was to walk in a straight line from one GPS-mark to the next. All transects were looped and shaped like an eight (8). The total length of the loop varied between 30 and 37 km. There were in total 9 transects, i.e. one per study block (Figure 1). Since mammalian and avian predators tend to prefer leaving their faeces and pellets on elevated areas such as small hills, large rocks or other viewpoints, all the data were collected at such locations. Each elevated area within a range of 100 meters from the straight line of the GPS-route was visited. Faeces and pellets were collected in different paper bags. These bags were marked with the transect number and the current GPS-position, which allowed us to register altitude and distance from the coast. Distance from the coast was measured in kilometres as a straight line between the GPS-position of the found faeces/pellet and the nearest coast line. Data were collected by two teams of field assistants.

Table 1: The number of faeces and pellets found in each study block on the different peninsulas.

Peninsula	Block	Transect length (km)	Faeces	Pellets
Porsanger	North (PN)	33.5	2	11
	Middle (PM)	33.8	20	10
	South (PS)	32.7	18	45
Sværholt	North (SN)	30.1	15	2
	Middle (SM)	29.7	21	88
	South (SS)	30.1	0	5
Nordkinn	North (NN)	37.1	8	87
	Middle (NM)	31.8	7	41
	South (NS)	34	27	45
Sum		292.8	118	334

Reindeer data

To perform analyses for my final objective in this study, the relationship between presence of scavenging mesopredators and presence of reindeer, I used reindeer counts obtained from Henden et al. (2014) (Table 2). The numbers of resident reindeer were counted annually during February and March, before the migratory reindeer return to the summer pastures. The count was done by aerial surveys in each study block in the time period 2009-2011. An experienced observer counted reindeer on both sides of an air plane. This was done according to a strip transect design (see Henden et al. (2014)).

Table 2: Reindeer counts done by Henden et al. (2014). Note that Henden et al. (2014) did not perform any counts for Nordkinn Middle.

Peninsula	Block	Survey area (km^2)	Count 09	Count 10	Count 11
Porsanger	North	252	32	0	0
	Middle	290	2	0	0
	South	614	27	0	180
Sværholt	North	266	128	93	0
	Middle	358	44	88	0
	South	555	1585	1356	88
Nordkinn	North	283	289	0	0
	South	253	0	52	141

Diet analysis

All samples have been dry stored since collected in 2011. Before I handled any of the samples, all the samples had to undergo a 24 hour freeze at -80° C to exterminate the potential contamination hazard of the tapeworm *Echinococcus multilocularis* (presence of this species in foxes is not yet recorded in Norway). After the freeze, in preparation to analyse the samples, unfrozen samples were soaked in water: Making them more manageable and easier to rinse without harming or breaking the content. I washed the samples and rinsed them in water using sieves. Fragmenting the faeces and pellets by hand, washed out content were sorted and identified. To determine prey species I investigated hairs, bones and teeth through either a loupe or a microscope. Identified items were listed in one of six major categories; (1) lemming, (2) grey-sided vole, (3) *Microtus* vole (field voles and tundra voles), (4) bird, (5) hare and (6) reindeer. Three additional minor categories were also used; (1) unidentified small rodent, (2) vegetation and (3) other (unidentified and uncategorised items). By sorting the content on a Petri dish, I would approximate the volume each prey item present in the sample (e.g. if there were only found remains of lemming in a sample: "lemmings: 100 %". If I found an equal amount of lemmings and grey-sided voles, and nothing else: they were both given a value of 50 %.). I also measured the proportion of these nine categories relative to each other in faeces and pellets found in each of the nine study blocks.

Concerning the pellets, their length was measured before being rinsed and their content identified. I did not determine which species each pellet originated from due to the fact that species identification through pellets would result in uncertainties. Pellets were instead categorized as either small (<7 cm) or large (>7 cm) to get an idea of whether the raptor was small or large. A majority of all the pellets were relatively small; by categorizing with a 7 cm

separation mark I got enough data to investigate whether there was a trend or not (size wise). Unfortunately not all pellets were measured. Some pellets were not "pellet shaped" (e.g. whole lemming), and some measures were neglected (after the rinse it is too late to measure length). I measured a total of 200 small and 58 large pellets. Further, in pellet size analyses, I assumed that small pellets originated from the small rodent specialists, and the large pellets represented diet of the larger generalists (i.e. eagles).

Field voles and tundra voles are similar, both morphologically and ecologically; they were therefore treated as one category (*Microtus* voles). Birds and hares were later excluded from further analyses due to too few findings/observations in faeces and pellets.

Statistical analysis

Due to the binary nature of the response variable, I used logistic regression to produce the results. Logistic regression is a tool used when the response variable is categorical (e.g. yes/no, dead/alive, absence/presence). My binary response variable is the absence/presence (0/1) of prey items in faeces and pellets as a response. The analyses were performed using the open-source statistical software R, version 3.0.1 (R-Development-CoreTeam-2013).

For presence of small mammals in the faeces/pellet, the predictor variables/explanatory variables used includes distance from the coast and altitude. I also looked at regional differences between the three peninsulas.

Furthermore there is a need to address another issue of using both distance from the coast and altitude as variables in my statistical analyses. A typical trend is that inland areas are (by nature) higher elevated than coast-near areas. I did a Pearson correlation analysis of the two variables, and found the variables to not be correlated (Pearson correlation =0.66). However, the Pearson correlation coefficient ranges on a scale from -1 to 1. I would assume a correlation of the variables if the correlation coefficient was at 0.7 or higher. This indicates that my predictor variables are very close to be positively correlated. However, the best model of my candidate models never consisted of both distance from the coast and altitude (Appendix Table 1 - 8).

For presence of reindeer in diet, I used predictor variables including distance to the coast, altitude, and reindeer counts as a mean of the years 2009, 2010 and 2011 divided on the survey area (see table 2 for reindeer counts). I do not know how old the faeces and pellets are and they could be older than one year. Comparing faeces and pellets from a different set of

years to just one specific year of reindeer counts could potentially result in wrong estimates. I did not include regional differences as a predictor variable because it would provide more or less the same information as the reindeer mean count variable.

Prior to any analyses, I normalised the distance from the coast, altitude, and reindeer counts. Since the variables are scaled differently (distance from the coast range from 1.7 to 31.1 km, altitude range from 140 to 740 m, and reindeer counts were preformed in areas ranging between 252 and 614 square km), this normalisation was necessary in terms of having the variables on a common scale.

Model selection was based on three to six candidate models (whereas one was a full model). All models showed different properties. The more parameters present in a model, the better is the fit of the model. However, a model with too many parameters would not have any explanatory power. One should always try to keep a model as simple as possible, and not use unnecessary predictor variables to explain an observation. There will always be a trade-off between the goodness of fit and the number of parameters needed. I used the Akaike information criterion (AIC) in the process of model selection. AIC is a useful tool because it penalizes redundant parameters by adding to the deviance. The more deviance, the higher is the uncertainty of my predictions.

$$AIC = -2 * (\ln(\text{likelihood})) + 2K,$$

where likelihood is the probability of the data given a model, and K is the number of estimating parameters in my models. Estimating parameters are also called free parameters, parameters that can be adjusted to make the model fit the data.

I will be using AIC with bias-correction (AICc). AICc takes sample size into the equation by increasing the penalty of complex models (models with many predictor variables) with small data sets:

$$AICc = AIC + \frac{2K(K+1)}{n-K-1},$$

where n is the sample size.

AICc should almost always be used as, when the sample size (n) gets larger, AICc converges to AIC (Tveraa et al. 2014). The model with the lowest AICc value was chosen (Burnham and Anderson 2002). If the differences in AICc (ΔAICc) between the models were less than two

(2), I went with the simplest model. Note that model selection through AICc provides the relative quality of my models by comparing them to each other, but will not provide any information of how good the models actually are. Additionally, in Appendix Table 1 – 8, I show number of parameters that may vary independently (K) and weight (a measure of model selection uncertainty) for each model.

After model selection I also found the goodness of fit for the best models using Pearson's chi-squared test (χ^2). A Pearson's chi-squared test evaluates how likely differences in observations happened by chance.

Furthermore, I investigated differences between avian small rodent specialists and avian generalists (by assuming that small pellets originate from the specialists and large pellets represent diet of the generalists). Presence of reindeer in diet was in this analyses my response variable, and pellet size (small/large) was my predictor variable. In addition to dietary analyses, I examined whether or not the presence of reindeer affects the presence of red fox and raptors. In the analyses, I used the number of faeces/pellets dived on the survey area as measurer of abundance was my response variable, and reindeer abundance (reindeer counts as a mean of the years 2009, 2010 and 2011 divided on the survey area) functioned as my predictor variable. These analyses did forgo model selection and was not initiated, as I wanted to analyse specific models.

The following three tables (Table 3, 4, and 5) summarises my model selection for the dietary analyses. A complete and more detailed model selection is listed in the appendix (Appendix Table 1 - 8).

Table 3: Model selection summary of small rodents in diet of red fox. Model structure is explained by 'x', showing which parameters are present in each model. Colour coded 'x' (red, blue, and green) represent which model was best suited for explaining the different small rodent categories in diet of red fox. Lemming = red (model 1), grey-sided vole = blue (model 2), and *Microtus* vole = green (model 4). Additionally, K and ΔAICc are represented to show support for the selected model.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Distance from coast	x		x		x	x
Altitude		x	x			x
Region				x	x	x
K	2	2	3	4	3	5
ΔAICc (lemming)	0.00	4.34	1.87	1.62	0.35	2.37
ΔAICc (grey-sided vole)	0.14	0.00	1.61	1.22	3.06	4.23
ΔAICc (*Microtus* vole)	13.17	11.27	13.11	0.00	1.47	1.18

Table 4: Model selection summary of small rodents in diet of raptors. Model structure is explained by 'x', showing which parameters are present in each model. Colour coded 'x' (red, blue, and green) represents which model was best suited for explaining the different small rodent categories in diet of red fox. Lemming =red, grey-sided vole = blue, and *Microtus* vole = green. Model 4 was chosen in all three cases. Additionally, K and ΔAICc are represented to show support for the selected model.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Distance from coast	x		x		x	x
Altitude		x	x			x
Region				x x x	x	x
K	2	2	3	3	4	5
ΔAICc (lemming)	29.52	29.03	25.52	1.40	2.97	0.00
ΔAICc (grey-sided vole)	6.31	9.58	6.26	0.31	0.00	0.17
ΔAICc (*Microtus* vole)	19.32	21.87	20.66	0.00	1.20	1.73

Table 5: Model selection summary of reindeer in diet of red fox and raptors. Model structure is explained by 'x', showing which parameters are present in each model. Colour coded 'x' (red and blue) represents which model was best suited explaining reindeer in diet of red fox and raptors. Red fox = red, and raptors = blue. Model 1 was chosen in both cases. Additionally, K and ΔAICc are represented to show support for the selected model.

|	Model 1	Model 2	Model 3
Reindeer count	x x	x	x
Distance from coast		x	
Altitude			x
K	2	3	3
ΔAICc (red fox)	0	1.76	2.02
ΔAICc (raptor)	0	0.24	0.55

Results

Diet composition of red fox and raptors consist mainly of small rodents (Figure 2). I can also see that the proportion of reindeer as part of the diet is much higher in red fox than in raptors diets. A full overview of diet compositions of red fox and raptors in every study block is found in the appendix (Appendix Figure 2 and 3). An overview of dietary differences between small and large pellets is also found in the appendix (Appendix Figure 4)
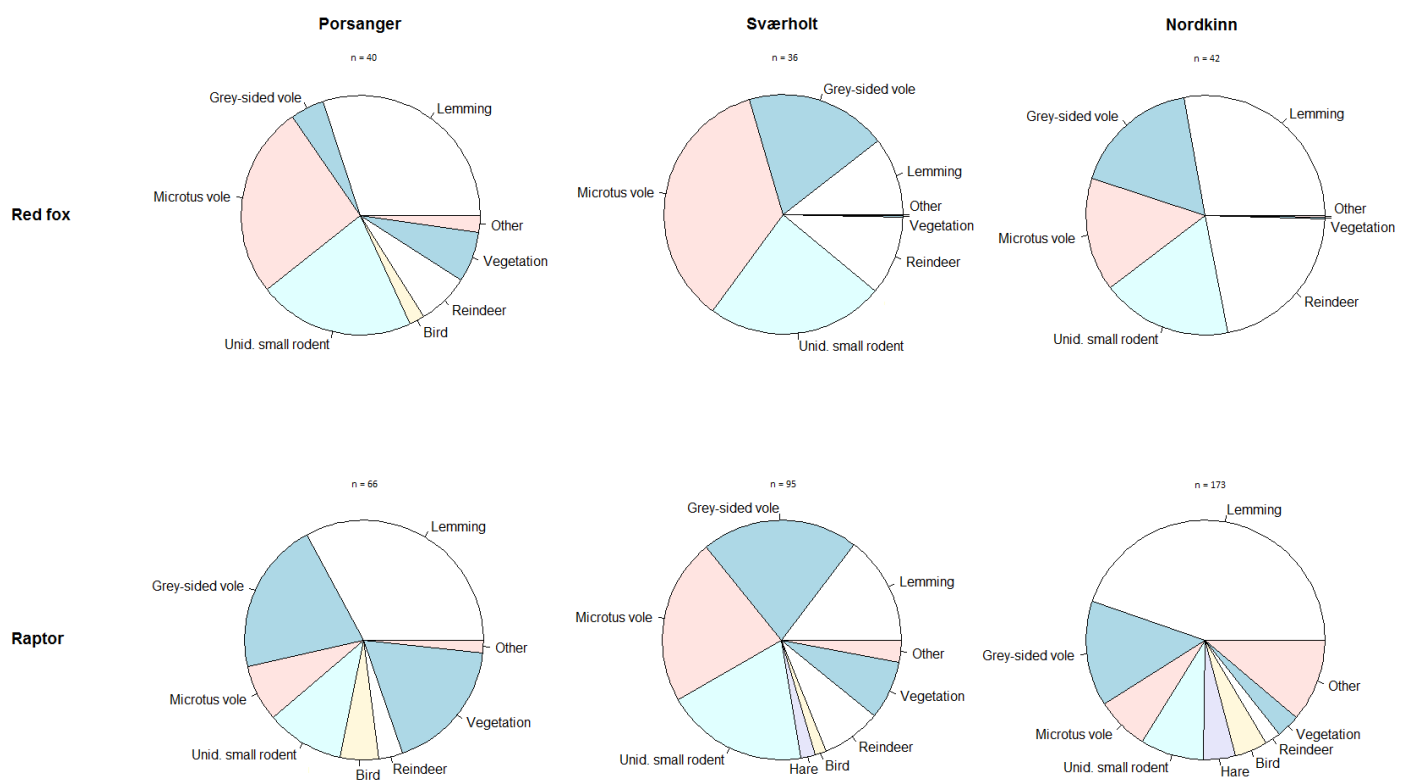
Figure 2: Diet composition of red fox and raptors among the three peninsulas (Porsanger, Sværholt, and Nordkinn). Pie charts are showing the proportion of prey items (lemming, grey-sided vole, *Microtus* vole, unidentified vole (Unid. small rodent), hare, bird, reindeer, vegetation and unclassified remains (other)) found in faeces (upper row) and pellets (lower row). 'n' shows the number of faeces/pellets.

Presence of prey in diet of red fox

Through model selection, I found that presence of lemming in faeces was best explained with use of one predictor variable: the distance from the coast (Table 3). A positive relation between presence of lemmings and distance from the coast was found. This indicates that the probability of detecting lemming in faeces increases the further away from the coastline the faeces was sampled (Table 6).

Table 6: Estimates from the selected generalized model (Appendix Table 1) relating presence of lemming in diet of red fox in East Finnmark, Norway. Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	-0.8224	0.2059		
Distance from coast	**0.4898**	**0.2037**	**2.405**	**0.0162**
Null deviance	146.77	117 df		
Residual deviance	140.74	116 df		

Model selection suggests that altitude is the best predictor for explaining presence of grey-sided voles in faeces (Table 3). The slope of the altitude predictor was negative, but mot statistically significant (Table 7a). The presence of *Microtus* voles in faeces was best explained by the regional differences (Table 3). It was significantly more likely to observe remains of *Microtus* voles in faeces samples gathered from Porsanger and Sværholt than in samples gathered from Nordkinn (Table 7b).

Table 7: Estimates from the selected generalized model (Appendix Table 2 and 3) relating presence of (a) grey-sided vole and (b) *Microtus* vole in diet of red fox in East Finnmark, Norway. Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
(a) Grey-sided vole				
Intercept	-1.7792	0.2709		
Altitude	-0.4445	0.2857	-1.556	0.12
Null deviance	100.794	117 df		
Residual deviance	98.185	116 df		
(b) *Microtus* vole				
Intercept	-2.0015	0.4765		
Porsanger	**1.9014**	**0.5721**	**3.324**	**0.000888**
Sværholt	**1.7783**	**0.5827**	**3.052**	**0.002273**
Null deviance	151.12	117 df		
Residual deviance	135.47	115 df		

The model for best explaining presence of reindeer in faeces consisted of the mean reindeer count as the only predictor variable (Table 5). Surprisingly the coefficient of the reindeer predictors was negative, however, not statistically significant (Table 8).

Table 8: Estimates from the selected generalized model (Appendix Table 7) relating presence of reindeer in diet of red fox in East Finnmark, Norway. Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	-1.3416	0.2414		
Mean reindeer count	-0.4400	0.2394	-1.838	0.066
Null deviance	115.90	110 df		
Residual deviance	112.39	109 df		

Presence of prey in diet of raptors

Presence of small rodents in diet of raptors was in all categories best explained by regional differences (Table 4). The best model for explaining lemmings found in pellets was model 4 (Table 4). It is significantly less lemming observed in pellets found on Sværholt than in pellets found on Nordkinn (Table 9).

Table 9: Estimates from the selected generalized model (Appendix Table 4) relating presence lemming in diet of raptors in East Finnmark, Norway. Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	0.2205	0.1530		
Porsanger	-0.5259	0.2923	-1.799	0.072
Sværholt	**-1.5423**	**0.2945**	**-5.23**	**1.63e-07**
Null deviance	456.67	333 df		
Residual deviance	425.50	331 df		

The model best explaining presence of grey-sided voles in pellets was model 4 (Table 4). I found that the probability of observing grey-sided voles in pellets found on Nordkinn was less than in pellets found on Sværholt (Table 10a). Explaining presence of *Microtus* voles found in pellets, regional differences again is the better model (Table 4). It was found that *Microtus* voles are more present in pellets on Sværholt than on Nordkinn (Table 10b).

Table 10: Estimates from the selected generalized model (Appendix Table 5 and 6) relating presence of (a) grey-sided vole and (b) *Microtus* vole in diet of raptors in East Finnmark, Norway. Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
(a) Grey-sided vole				
Intercept	-1.4451	0.1935		
Porsanger	0.2214	0.3517	0.629	0.529134
Sværholt	**0.9511**	**0.2867**	**3.318**	**0.000907**
Null deviance	376.73	333 df		
Residual deviance	365.43	331 df		
(b) *Microtus* vole				
Intercept	-1.9794	0.2328		
Porsanger	-0.1523	0.4626	-0.329	0.742
Sværholt	**1.5298**	**0.3138**	**4.875**	**1.09e-06**
Null deviance	329.22	333 df		
Residual deviance	299.57	331 df		

Model selection suggests that the mean reindeer count is the best way of explaining presence of reindeer in pellets (Table 5). The reindeer coefficient was positive, however statistically non-significant (Table 11).

Table 11: Estimates from the selected generalized model (Appendix Table 8) relating presence of reindeer in diet of raptors in East Finnmark, Norway. Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	-3.6338	0.3729		
Mean reindeer count	0.2850	0.1856	1.540	0.124
Null deviance	73.391	292 df		
Residual deviance	71.739	291 df		

Analyses were preformed to investigate whether or not pellet size can explain presence of reindeer in diet of raptors. The pellets size coefficient of large pellets was positive, however statistically non-significant (Table 12).

Table 12: Estimates from the generalized model relating presence of reindeer in diet of raptors based on pellet size (small/large). Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
Intercept	-3.6636	0.4529		
Large pellet	0.7548	0.7461	1.012	0.312
Null deviance	71.326	257 df		
Residual deviance	70.376	256 df		

Presence of reindeer affecting mesopredator and raptor abundance

The abundance of red fox and raptors was not explained by the presence of reindeer but there were surprisingly a negative trend in the coefficients, both for red fox (Table 13a) and raptors (Table 13b). This effect did not, however, prove to be statistically significant (Table 13).

Table 13: Estimates from the generalized models relating (a) red fox abundance and (b) raptor abundance to the presence of reindeer. Significant coefficients are highlighted in bold.

	Estimate	Std. Error	z-value	p-value
(a) Red fox				
Intercept	0.5318	0.1129		
Reindeer abundance	-0.2819	0.1684	-1.674	0.1452
Null deviance	0.6226	7 df		
Residual deviance	0.4244	6 df		
(b) Raptor				
Intercept	1.3021	0.4794		
Reindeer abundance	-0.5226	0.715	-0.731	0.4924
Null deviance	8.3288	7 df		
Residual deviance	7.6479	6 df		

Discussion

Overall results

In light of obtaining more knowledge about terrestrial ecosystem in northern Fennoscandia, I addressed factors affecting diet and presence of red fox and birds of prey. I conducted a large scale study in middle and eastern Finnmark, covering the three northernmost peninsulas; Porsanger, Sværholdt and Nordkinn. Faeces and pellets were collected on each of the peninsulas. My goals were to map the diet of the mesopredators, and follow the continuous expanding red fox in Finnmark. Throughout the study blocks I found that the diet of red fox consists largely of lemmings and *Microtus* voles and the diet of raptors consist largely of lemmings and grey-sided voles. Small rodents are in all cases heavily represented in faeces and pellets. Remains of reindeer were in a much larger portion found in faeces than in pellets. Among the nine study blocks reindeer constitute, on average, 13.3% of red fox diet and 4.5% of raptor diet. Presence of reindeer in each study block did not, however, affect the abundance of red fox nor raptors.

Presence of small rodent species in faeces (diet of red fox) were all explained best by different models. While distance from the coast was selected as the parameter with the most explanatory power for lemmings as part of red fox diet, altitude was chosen to explain the occurrence of grey-sided voles. I found that the probability of observing remains of lemming in faeces increased as the distance to the coast increased, and that altitude did not affect presence of grey-sided voles. This corresponds somewhat with the results of (Ims et al. 2011) who found that lemmings were most abundant in high altitude areas far from the coast. Regarding *Microtus* voles (field voles and tundra voles) the results show that *Microtus* voles are more observed in faeces gathered on Porsanger and Sværholt than in faeces gathered on Nordkinn. As for presence of reindeer in the diet, I found that the mean reindeer count over a three year period was the best explanatory variable. Surprisingly, the effect was measured to be negative, meaning the probability of observing reindeer in faeces decreases as the mean reindeer abundance increase. These findings were, however, not statistically significant.

Concerning the diet of birds of prey (raptors), all small rodent categories were explained by the regional differences (distribution among Porsanger, Sværholt and Nordkinn). While remains of lemmings were most frequent in pellets on Nordkinn, observations of both grey-sided voles and *Microtus* voles were most frequent in pellets on Sværholt. The probability of finding remains of reindeer in pellets was not explained by any of the predictor variables. I

was not able to detect any effects indicating avian generalists preying more on reindeer than avian specialists.

Red fox

In my study, I found that red fox eat more lemmings in in-land areas compared to coastal areas. I did expect this outcome based on two things: First, previous studies show that lemmings are more common in unproductive mountain tundra habitats and at higher altitudes, which might represent the in-land areas of the study area (except - for instance - valleys) (Saether 1999). Killengreen et al. (2011) found the same trend, showing that the proportion of lemming in diet of red fox increase further away from the coast. Second, small rodents is the most important food resource for red foxes (Elmhagen et al. 2002), and lemmings is the favourable prey species (Killengreen et al. 2011). One possibility that might make lemmings the favourable small rodent prey is their colourful fur. Norwegian lemmings with their bright yellow and contrasting black-white features might make them easier detected than the grey and brown grey-sided voles and *Microtus* voles (Hellström et al. 2014, Andersson 2015). In addition to colouration, the behaviour might come to importance. The Norwegian lemming has an aggressive defence style that seems to work well against smaller predators. However, the effect of this mechanism against mesopredators has yet to be studied (Andersson 2015).

Concerning grey-sided voles, there was no relation between presence in diet of red fox and altitude. One factor affecting my results may have been the relatively small sample size. I had only 18 faeces containing remains of grey-sided voles. Grey-sided voles are considered to be key-species in mountain birch forest (Ecke et al. 2013, Hellström et al. 2014). Compared to the mountain tundra habitats where lemmings prevail, studies show that grey-sided voles are to be found in all habitats where small rodents in Finnmark are present (Hellström et al. 2014). Furthermore, my results is in coherence with another study finding that grey-sided voles in Finnmark show no effects of altitude dynamics (Ims et al. 2011). The general pattern of the distribution of grey-sided voles seems to be oriented around habitats with cover, either in form of shrubs or boulders (Hellström et al. 2014). Risk of predation is supposedly lower in such habitats, as the small rodents have better hiding places than in the more open landscapes.

The last category of small rodents in red fox diet, the *Microtus* voles, was best explained by the regional differences of the three peninsulas. I found that red fox eat more *Microtus* vole on Porsanger and Sværholt than on Nordkinn. As the grey-sided vole, *Microtus* voles prefer habitats with cover and protection from predators (Henden et al. 2011, Hellström et al. 2014).

In contrast to the grey-sided vole, *Microtus* voles are often the dominant small rodent species in habitats with willow thickets (Lambin et al. 1992). In the low arctic tundra, habitats with willow thickets are often along creeks or rivers providing nutrition rich sediments (Henden et al. 2011). These habitats provide food plants such as herbs, and the willow thicket function as cover. When comparing the peninsulas based on landscape characteristics, Porsanger and Sværholt are relatively similar. They are different to Nordkinn in the sense of altitude and productivity. Porsanger and Sværholt typically consist of lower altitudes and more productive habitats (see Appendix Figure 1). Nordkinn on the other hand is more tundra like, consisting of higher altitudes and less vegetation.

In my final analyses of diet of red fox, I investigated how the mean number of reindeer in winter would affect the presence of reindeer in faeces. I did not find any significant relationship between the reindeer counts and presence of reindeer in red fox diet. 2011 was a peak year in the small rodent cycles, and lemmings together with *Microtus*- and grey-sided voles were extremely abundant (Killengreen et al. 2011, Killengreen et al. 2013). I also assumed that a large part of the faeces found most likely originated from 2011. This sum up to an expectation of the content to be dominated by remains of rodent. Interestingly, even while the tundra is overwhelmed with small rodents, it is still observed that reindeer count for a significant proportion of the red fox's diet. This strengthens the theory about reindeer being an important subsidy to the red fox in Finnmark (Killengreen et al. 2011, Henden et al. 2014).

Birds of prey

I also looked at how the small rodent composition in the diet of raptors changed over the different peninsulas. Lemmings were more abundant on Nordkinn than on Sværholt. Both grey-sided voles and *Microtus* voles were more abundant on Sværholt than on Nordkinn. These results are consistent with what I earlier discussed; that lemmings find more of their preferred habitat on Nordkinn, and that Sværholt has more preferable habitats for grey-sided voles and *Microtus* voles (Lambin et al. 1992, Hellström et al. 2014). Interestingly enough, results regarding Porsanger were never in any case significant. Given my assumptions that Porsanger and Sværholt have similar landscape characteristics, it is expected that distribution of small rodents on Porsanger would be similar to the distribution on Sværholt. As 2011 was a peak year small rodents was expected to be very abundant and present in most territories regardless of their habitat preferences (Killengreen et al. 2013). Since many raptors are only present during peak years of small rodent cycles (Killengreen et al. 2007), their distribution might be random. Studies of raptor diet choice have shown that selection and preference of

prey species can be explained by coincidence in habitat choice in time and space of the raptor and its prey (Dickman 1992, Rohner and Krebs 1996). Consequently, this might end up in a scenario where predation on Porsanger is fully explained by coincidence. This coincidence is based on which small rodent species is present at a certain time, and whether the raptor is present or not during the same time frame.

The probability of observing remains of reindeer in pellets was not explained by reindeer counts. Because most of the raptors are present only during peak years (Killengreen et al. 2007) and 2011 was a peak year (Killengreen et al. 2013) I did suspect small rodents to be the highest priority and favourable prey item. I did also assume that all pellets origin from 2011. I already addressed the issue of the reindeer counts and that the reindeer counts get over-shadowed by the abundance of small rodents, which reflects the content found in pellets. As a conclusion I can state that reindeer is never important as part of raptor diet during the peak years in small rodent cycles. Since reindeer as a subsidy is important to red foxes during the low phases of the small rodent cycles; this would not be an issue concerning the migratory raptors/small rodent specialists, as they are only present during the peak years (Killengreen et al. 2007, Killengreen et al. 2011).

No significant results were found when investigating the relationship between reindeer abundance, the abundance of raptors and foxes. The lack of relationship may be explained by the rodent peak year, as there is no need for subsidies due to an overflow of resources. Therefore, the distribution of red fox and raptors can be assumed not to be oriented around reindeer densities in years of high rodent abundance.

Red fox and raptors in Norwegian tundra ecosystems
Considering the four main prey items; lemming, grey-sided vole, *Microtus* vole, and reindeer, raptors prey almost exclusively on small rodents. The red fox does more frequently utilize reindeer carcasses. My study was carried out during a small rodent peak year. I would therefore assume that diet of mesopredators consists mainly of small rodents, and that subsidies such as reindeer carcasses may not be very important. However, reindeer as a food source should not be neglected. While the raptors follow the pattern of being present during years with high abundance of small rodents, the red fox is a resident species. Even though small rodents are the favourable prey item, I have observed that reindeer counts for an appreciable part of the diet despite the high numbers of small rodents. This indicates that the red fox, being a generalist, do utilize other resources even in years with high abundance of

small rodents in the Arctic tundra ecosystems. Global warming is one of the greatest threats to Arctic ecosystems (Callaghan et al. 2004). As all of the Arctic is suffering a change, the low Arctic tundra zone is especially exposed because these ecosystems balance against non-Arctic communities (Epstein et al. 2004). Upper trophic levels are particularly vulnerable, as these species (e.g. arctic fox) are sensitive to fundamental changes in the ecosystem (Schmitz et al. 2003). While the greening of the Arctic indicates increased primary production (Myneni et al. 1997, Olthof et al. 2008), key species such as voles and lemmings seem to be declining in parts of the tundra biome (Ims et al. 2008, Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011). Generalists have dampening effects on population dynamics. With dampened and less distinct peak years in small rodent population cycles, one might expect a future decline of raptors that are specialists on rodents. As a consequence to the exclusion of arctic fox, the structure of the ecosystem is moving towards a top-down control lead by generalist rather than by specialists. Tundra ecosystems are relatively simple and susceptible to change (Epstein et al. 2004). Endemic species in these systems are adapted to low temperatures and scarce resource availability. These traits often come in expense of competitive abilities against invasive species (Callaghan et al. 2004). Scandinavian predator communities are now dominated by the red fox, supposedly because of mesopredator release (Saether 1999).

As a final note to the distribution of red fox and raptors in middle and eastern Finnmark, the expanding red fox population is indeed affecting the ecosystem, and raptors might not continue to follow the distinct distribution patterns of being active only when small rodents are present. Since the small rodent population cycle peak year provided data saturated with lemmings, grey-sided voles and *Microtus* voles, studies should be conducted also during the low and intermediate phases.

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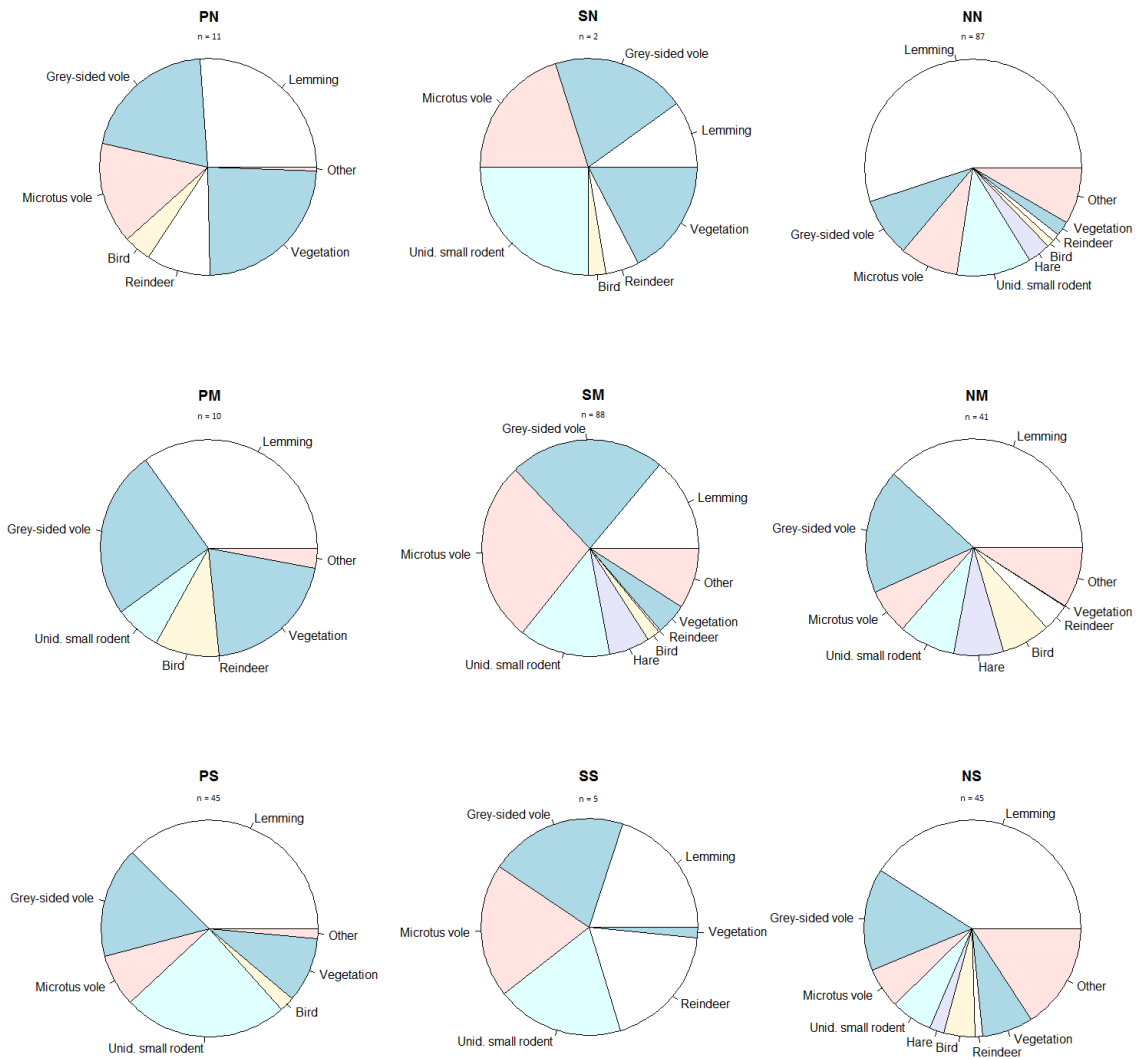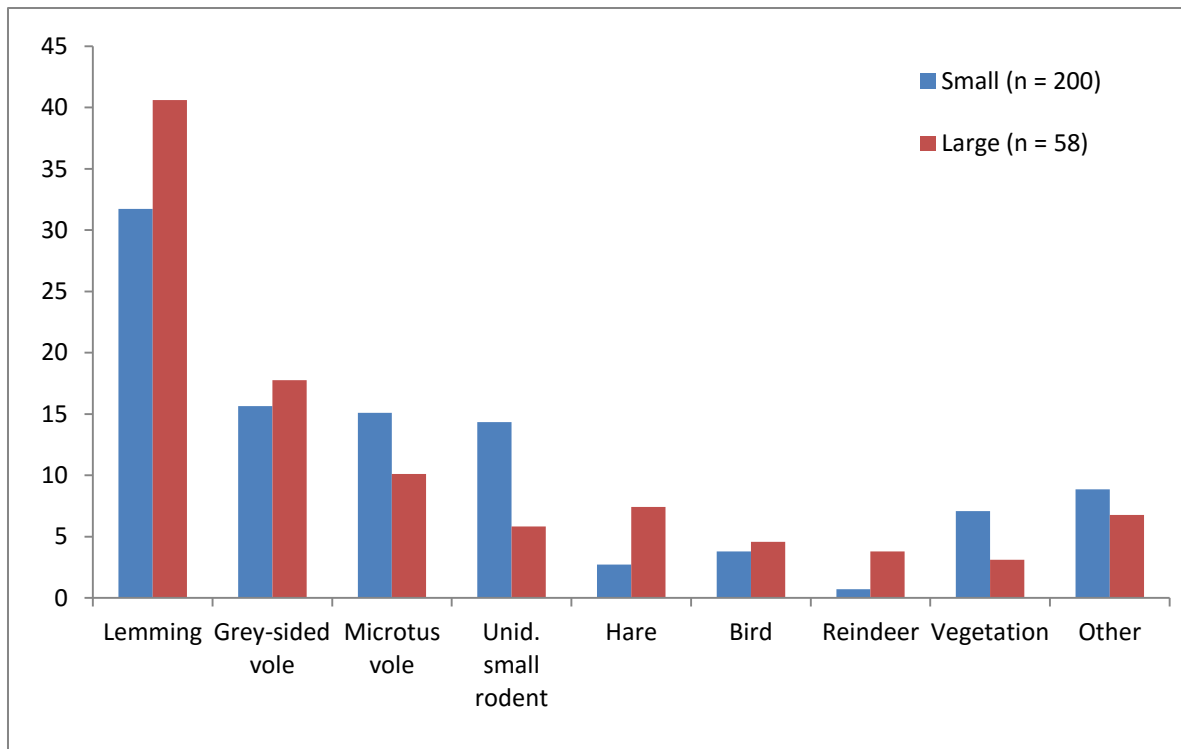
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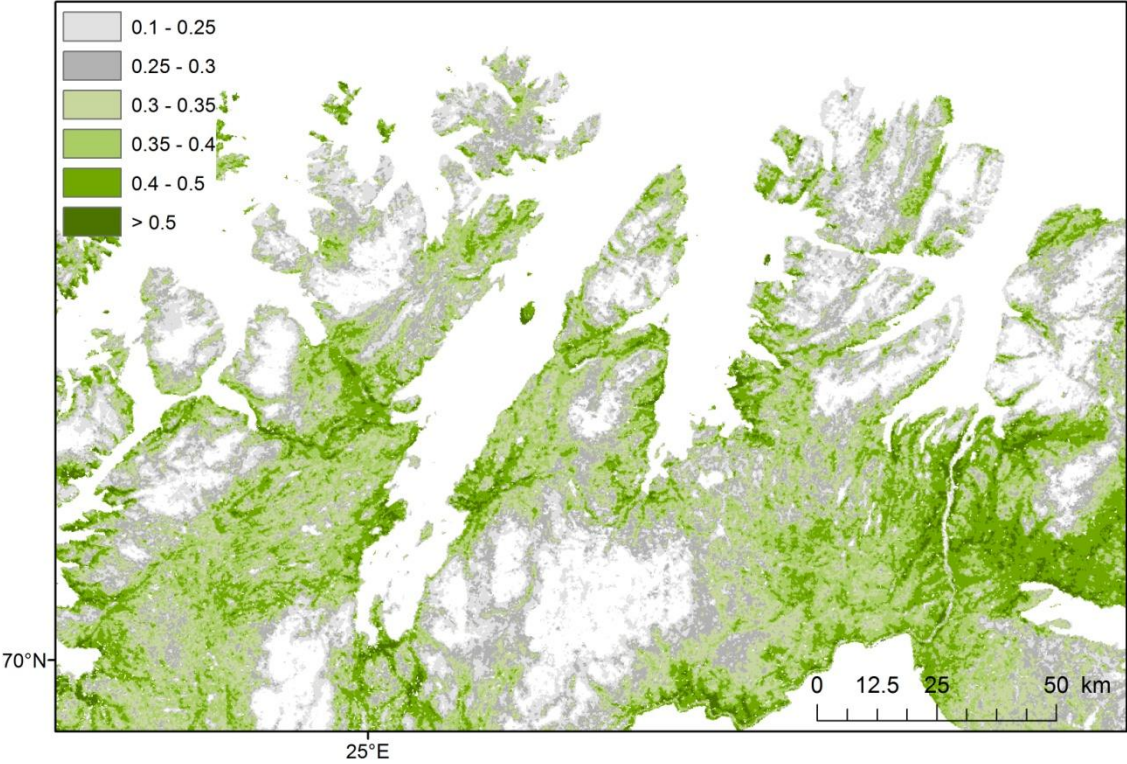
Appendix Figure 1: Enhanced vegetation index (EVI) of Porsanger, Sværholt, and Nordkinn in East Finnmark, Norway. This map shows the mean maximum EVI of the years 2000 – 2014.
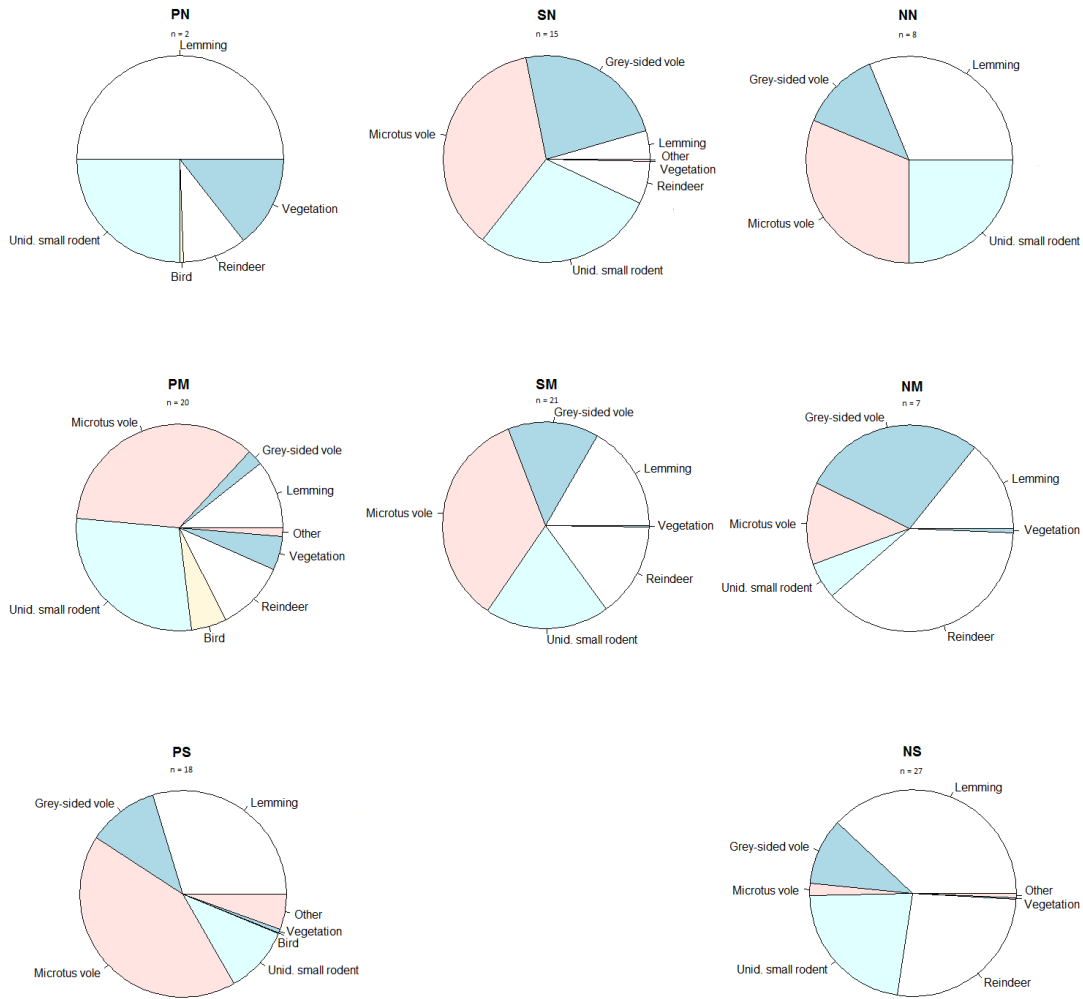
Appendix Figure 2: Diet composition of red fox among the nine study blocks. Pie charts are showing the proportion of prey items (lemming, grey-sided vole, *Microtus* vole, unidentified vole (Unid. small rodent), bird, reindeer, vegetation and unclassified remains (other)). The first column represents the Porsanger peninsula, the second column represents the Sværholt peninsula, and the third column represents the Nordkinn peninsula. The upper row represents the northen study blocks, the middle row represents the middle study block, and the lower row represents the southern study blocks. 'n' shows the number of faeces/pellets. In the materials and methods section, see Figure 1 for comparisons and Table 1 for abbreviations.

Appendix Figure 3: Diet composition of raptors among the nine study blocks. Pie charts are showing the proportion of prey items (lemming, grey-sided vole, *Microtus* vole, unidentified vole (Unid. small rodent), hare, bird, reindeer, vegetation and unclassified remains (other)). The first column represents the Porsanger peninsula, the second column represents the Sværholt peninsula, and the third column represents the Nordkinn peninsula. The upper row represents the northen study blocks, the middle row represents the middle study block, and the lower row represents the southern study blocks. 'n' shows the number of faeces/pellets. In the materials and methods section, see Figure 1 for comparisons and Table 1 for abbreviations.

Appendix Figure 4: Diet composition of small and large pellets among Porsanger, Sværholt and Nordkinn. The histogram is showing the percentage (y-axis) of each prey item of small pellets (blue) and large pellets (red). 'n' shows the number of pellets in each category.

Appendix Table 1: Model selection for presence of lemming in diet of red fox. Selected model marked in bold. The table shows the number of free parameters (K), weight, AICc and ΔAICc for the chosen models.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Distance from coast	**x**		x		x	x
Altitude		x	x			x
Region				x	x	x
K	**2**	2	3	4	3	5
Weight	**0.290**	0.033	0.114	0.129	0.243	0.089
AICc	**144.85**	149.19	146.72	146.46	145.20	147.22
ΔAICc	**0.00**	4.34	1.87	1.62	0.35	2.37

Appendix Table 2: Model selection for presence of grey-sided vole in diet of red fox. Selected model marked in bold. The table shows the number of free parameters (K), weight, AICc and ΔAICc for the chosen models.

	Model 1	**Model 2**	Model 3	Model 4	Model 5	Model 6
Distance from coast	x		x		x	x
Altitude		**x**	x			x
Region				x	x	x
K	2	**2**	3	3	4	5
Weight	0.212	**0.228**	0.102	0.124	0.050	0.028
AICc	102.43	**102.29**	103.90	103.51	105.35	106.52
ΔAICc	0.14	**0.00**	1.61	1.22	3.06	4.23

Appendix Table 3: Model selection for presence of *Microtus* vole in diet of red fox. Selected model marked in bold. The table shows the number of free parameters (K), weight, AICc and ΔAICc for the chosen models.

	Model 1	Model 2	Model 3	**Model 4**	Model 5	Model 6
Distance from coast	x		x		x	x
Altitude		x	x			x
Region				**x**	x	x
K	2	2	3	**3**	4	5
Weight	0.000	0.001	0.000	**0.287**	0.133	0.154
AICc	154.86	152.96	154.79	**141.69**	143.15	142.87
ΔAICc	13.17	11.27	13.11	**0.00**	1.47	1.18

Appendix Table 4: Model selection for presence of lemming in diet of raptors. Selected model marked in bold. The table shows the number of free parameters (K), weight, AICc and ΔAICc for the chosen models.

	Model 1	Model 2	Model 3	**Model 4**	Model 5	Model 6
Distance from coast	x		x		x	x
Altitude		x	x			x
Region				**x**	x	x
K	2	2	3	**3**	4	5
Weight	0.000	0.000	0.000	**0.207**	0.094	0.416
AICc	459.69	459.20	455.69	**431.57**	433.14	430.17
ΔAICc	29.52	29.03	25.52	**1.40**	2.97	0.00

Appendix Table 5: Model selection for presence of grey-sided vole in diet of raptors. Selected model marked in bold. The table shows the number of free parameters (K), weight, AICc and ΔAICc for the chosen models.

	Model 1	Model 2	Model 3	**Model 4**	Model 5	Model 6
Distance from coast	x		x		x	x
Altitude		x	x			x
Region				**x**	x	x
K	2	2	3	**3**	4	5
Weight	0.013	0.003	0.013	**0.265**	0.308	0.284
AICc	377.51	380.77	377.46	**371.50**	371.20	371.36
ΔAICc	6.31	9.58	6.26	**0.31**	0.00	0.17

Appendix Table 6: Model selection for presence of *Microtus* vole in diet of raptors. Selected model marked in bold. The table shows the number of free parameters (K), weight, AICc and ΔAICc for the chosen models.

	Model 1	Model 2	Model 3	**Model 4**	Model 5	Model 6
Distance from coast	x		x		x	x
Altitude		x	x			x
Region				**x**	x	x
K	2	2	3	**3**	4	5
Weight	0.000	0.000	0.000	**0.320**	0.175	0.135
AICc	324.96	327.51	326.30	**305.64**	306.85	307.37
ΔAICc	19.32	21.87	20.66	**0.00**	1.20	1.73

Appendix Table 7: Model selection for presence of reindeer in diet of red fox. Selected model marked in bold. The table shows the number of free parameters (K), AICc and ΔAICc for the chosen models. Note that 'weight' is not included.

	Model 1	Model 2	Model 3
Reindeer count	**x**	x	x
Distance from coast		x	
Altitude			x
K	**2**	3	3
AICc	**116.50**	118.26	118.52
ΔAICc	**0.00**	1.76	2.02

Appendix Table 8: Model selection for presence of reindeer in diet of raptors. Selected model marked in bold. The table shows the number of free parameters (K), AICc and ΔAICc for the chosen models. Note that 'weight' is not included.

	Model 1	Model 2	Model 3
Reindeer count	**x**	x	x
Distance from coast		x	
Altitude			x
K	**2**	3	3
AICc	**75.78**	76.02	76.33
ΔAICc	**0.00**	0.24	0.55