

## Preface

This thesis is written as the final paper of the master program in Natural Resource Management at the Norwegian University of Life Sciences. The writing of this thesis has been an instructive process, rewarding me with experience of scientific work and in-depth knowledge of the arctic fox.

I would like to give my sincere gratitude to Professor Vidar Selås, my supervisor at NMBU, for good guidance, proofreading and tips during the whole process in addition to fast replies to all my questions. This thesis is part of NINA projects on arctic fox: Arctic fox captive breeding program, the National monitoring program on arctic fox and the Interreg project "Our Common arctic fox". These projects are all funded by The Norwegian Environmental Agency (Miljødirektoratet). I would like to give a special thanks to my supervisor Senior Researcher Nina E. Eide for making this thesis happen, for motivation and for constructive feedbacks during the whole process. I would also like to thank my supervisor Senior Researcher Arild Landa for fast replies and remarks on my drafts, my supervisor Lars Rød-Eriksen thank you also for good counselling on camera trap methodology and feedback on the drafts, and Aniko Hildebrand for guidance and help in analyzing the pictures.

I am also sincerely grateful to Nina and Arild for giving me access to the datasets used in this study and the opportunity to join the fieldwork at the arctic fox breeding program this summer.

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## Abstract

Despite being protected since 1930 in Norway, the arctic fox has not recovered. The small population size, lack of food availability and competition by the red fox are suggested to be the main reason inhibiting the recovery. Feeding dispensers exclusively made for the arctic fox have been constructed to increase food availability and to reduce intra-guild competition. This thesis investigates the arctic fox use of feeding dispensers and bait stations in relation to intra-guild competition and rodent abundance.

From 2011-2013, 51 cameras were placed at 32 feeding dispensers and 19 bait stations to investigate visits by, arctic foxes, red foxes and wolverines in central Norway. General linear mixed models were used to test the effect of bait stations and feeding dispensers, elevation above sea level, presence of competitors as well as the effect of rodent abundance on arctic fox visits. The effect of elevation above sea level and rodent abundance were also tested on red fox and wolverine visits. I found that arctic foxes visited feeding dispensers more frequently than bait stations and that red foxes visited bait stations more frequently than feeding dispensers. There was no effect of the visits of red fox and wolverine on arctic fox visits. Arctic foxes were more restricted to higher elevations whereas the red foxes were found at all elevations. Red foxes and arctic foxes visited bait stations at most during the rodent crash year and red foxes were also more frequently observed at feeding dispensers in the rodent crash year.

My results showed that the feeding dispensers worked exclusively for the arctic fox and thus reduced the intra-guild competition with potential predators, and in particular the superior red fox. The arctic fox showed no direct avoidance of red foxes, which indicates that feeding dispensers reduce the importance of red fox control. However, the arctic foxes were restricted to the highest elevations, which may indicate avoidance of areas with higher densities of red foxes. For both arctic and red foxes, the use at bait stations was more frequent when the rodent abundance was low, indicating a stronger competition at carcasses when rodent supply is scarce. Supplemental feeding should continue until the arctic fox population is at a sustainable level.



## Sammendrag

Selv om fjellreven ble beskyttet i Norge i 1930 har bestanden ikke tatt seg opp. En liten populasjonsstørrelse, dårlig mattilgang og konkurranse med rødreven er foreslått å være de viktigste grunnene til at bestanden ikke tar seg opp igjen. For å øke mattilgangen og redusere intraguild konkurranse ble det laget foringsautomater designet spesielt for fjellrev. Denne oppgaven undersøker fjellrevens bruk av foringsautomater og åteblokker i forhold til intraguild konkurranse og smågnager forekomst.

I årene 2011-2013 ble 51 kameraer plassert på 32 forings automater og 19 åteblokker for å undersøke besøk av fjellrev, rødrev og jerv i Midt-Norge. Generelle lineære mix-modeller ble brukt til å teste effekten av åteblokk og foringsautomater, høyde over havet, konkurrenter og gnagertilgang på fjellrevens besøk, og effekten av høyde over havet og gnagertilgang på besøk av rødrev og jerv. Jeg fant at fjellrev besøkte foringsautomatene oftere enn åteblokkene og at rødreven besøkte åteblokkene oftere enn foringsautomatene. Det var ingen effekt av besøk av rødrev og jerv på fjellrevens besøk. Fjellreven var mer begrenset til høyereliggende områder, mens rødrevene ble funnet på alle høyder. Rødrev og fjellrev besøkte åteblokkene mest i gnager bunnåret og rødreven ble også mer observert på foringsstasjonene i dette året.

Mine resultater viste at foringsautomatene ble kun brukt av fjellrev som kan tyde på at konkurransen med andre rovdyr og da spesielt den overlegne rødreven ble redusert. Fjellreven viste ingen direkte unngåelse av rødrev noe som indikerer at foringsautomatene reduserer viktigheten av rødrev kontroll. Fjellreven ble begrenset til de høyeste områdene, noe som kan tyde på unngåelse av områder med høyere rødrev tetthet. Både fjellrev og rødrev besøkte åteblokkene mer i gnager bunnår noe som kan antyde at konkurransen på kadaver er høyere i gnager bunnår. Støtteforingen bør fortsette frem til fjellrevbestanden har nådd et bærekraftig nivå.



## Table of contents

Preface .....	I
<b>Abstract .....</b>	<b>III</b>
<b>Sammendrag .....</b>	<b>V</b>
<b>Introduction .....</b>	<b>2</b>
<b>Materials and methods.....</b>	<b>5</b>
Study sites.....	5
Field method .....	6
Data processing .....	7
Variables .....	8
Statistical analysis.....	8
<b>Results .....</b>	<b>10</b>
Species visits at feeding dispensers and bait stations.....	10
Spatial and temporal use.....	12
Use of feeding dispensers and bait stations in relation to rodent cycle and season .....	14
<b>Discussion .....</b>	<b>16</b>
Species visits at feeding dispensers and bait stations.....	16
Species coexistence .....	17
Use of feeding dispensers and bait stations in relation to rodent years and seasons.....	19
<b>Conclusion and management implications .....</b>	<b>21</b>
<b>Cititations .....</b>	<b>22</b>





## Introduction

Climate change and anthropogenic disturbances is considered to be the biggest threats to biodiversity today (CAFF 2013). Species adapted to live in the arctic and alpine areas are the ones which will be most affected by a warmer climate (Parmesan & Yohe 2003; Post et al. 2009). A warmer climate will make the environment more suitable for species living at lower elevations and an expansion to higher elevations is expected. These species may outcompete endemic species in arctic and alpine areas (CAFF 2013).

The Arctic fox *Vulpes lagopus* is critically endangered in Fennoscandia (Kålås et al. 2010) and is classified by IUCN as one of the 10 flagship species (IUCN 2009). Present low population numbers is mainly due to historical fur harvest during the early 20th century but see Selås and Vik (2007) for another explanation. The arctic fox in Scandinavia did not recover despite being protected since 1928 in Sweden, 1930 in Norway and 1940 in Finland (Hersteinsson et al. 1989). Small population sizes (Herfindal et al. 2010), lack of food availability, in particular the lack of, or declining lemming *Lemmus lemmus* peaks during the last decades (Loison et al. 2001; Tannerfeldt et al. 2002; Henden et al. 2008) as well as competition with the superior red fox *Vulpes vulpes* is suggested to be the main reasons inhibiting the recovery (Frafjord et al. 1989; Hersteinsson et al. 1989; Hersteinsson & Macdonald 1992; Tannerfeldt et al. 2002). However, due to conservation actions including captive breeding and release, red fox control and supplemental feeding, there has been signs of recovery in some areas during recent years (Angerbjörn et al. 2013; Eide et al. 2013)

The Fennoscandian arctic fox is strongly dependent on microtines and especially lemming (Hersteinsson et al. 1989; Elmhagen et al. 2000). Lemming abundance normally has a cycle with a strong peak every 3-5 year and the arctic fox population fluctuates in relation to the abundance of the prey (Angerbjörn et al. 1999). The arctic fox population can differ widely between the different phases. In increase and peak years of the rodent cycle, the arctic fox has been recorded to have litters numbering up to 16-18 whelps, whereas in years with few rodents there are almost no reproduction (Tannerfeldt & Angerbjörn 1998). During low rodent years the arctic fox relies on other food sources (Elmhagen et al. 2000) Reindeer *Rangifer tarandus*, hare *Lepus timidus* and birds *Aves sp.* are also part of the arctic fox diet, and studies have showed that the proportion of these resources is higher in the arctic fox diet in low rodent years (Strand et al. 1999). The

arctic fox is also more depended on other food sources during winter, when microtines are less abundant and reindeer carcasses are an important food source (Kaikusalo & Angerbjoern 1995; Strand et al. 1999).

The arctic fox has few enemies on the mountain tundra. However, during the recent years, red foxes has expanded its range into mountainous habitat. The red fox is almost 60% heavier than the arctic fox (Hersteinsson & Macdonald 1982). The asymmetric-size hypothesis claims that bigger animals will be superior to the smaller by interference competition (Persson 1985). This has been proven in Canids (Palomares & Caro 1999) and we can expect the same between arctic and red foxes. However, competition occurs only when there is niche overlap. Elmhagen et al. (2002) showed that the red fox and arctic fox have a similar virtual niche. Experiments on the two fox diets carried out in captivity showed that there was no difference in preference between the two foxes (Barth et al. 2000). Encounters between the two species can lead to aggressive behavior and in some cases predation by the red fox (Frafjord et al. 1989; Pamperin et al. 2006). Arctic fox avoids red fox breeding sites (Tannerfeldt et al. 2002; Hamel et al. 2013) and studies has shown that red foxes have taken over old arctic fox dens (Linnell et al. 1999; Frafjord 2003).

Wolverine *Gulo gulo* is a mountain dwelling predator which also is a potential predator on both arctic and red foxes (Frislid & Semb-Johansson 1980). Other potential predators on arctic and red foxes in mountain areas is golden eagle *Aquila chrysaetos* and white-tailed eagle *Haliaeetus Albicilla* (Wille & Kampp 1983; Tannerfeldt et al. 1994; Elmhagen et al. 2002). The eagles, wolverine and foxes utilize carcasses during winter, and are within the same guild (Killengreen et al. 2012). A guild is defined “*as a group of species that exploit the same class of environmental resources in a similar way*” (Root 1967).

The conservation measure on supplemental feeding during both summer and winter has proven to increase litter sizes in arctic fox (Angerbjörn et al. 1995). Early supplemental feeding trials during winter time showed an unforeseen positive effect on red fox and resulted in red fox establishment at higher elevations (Angerbjörn et al. 1995; Kaikusalo & Angerbjoern 1995) To avoid unintended positive effects on the red fox and to reduce intraguild competition, feeding dispensers designed to exclusively feed the arctic fox were developed within the arctic fox captive breeding program (Landa 2006).

In this thesis I explore how the carnivore guild use these feeding dispensers compared to use of open bait stations, to test if the feeding dispensers feeds the arctic fox exclusively as they are intended to. In addition, I explore the use of feeding dispensers throughout the year and between years in relation to rodent cycles.

#### Predictions:

1. If feeding dispenser works exclusively for the arctic foxes, I predict that red fox and wolverine visits will be lower at feeding dispensers than at bait stations, and that arctic fox visits will be more frequent at feeding dispensers due to reduced intra-guild competition.
2. Co-existence between competing species can occur if they are spatially or temporally separated. I predict that arctic and red foxes will be separated spatially through elevation, and temporally by a difference in occurrence throughout the day.
3. Lemming is an important prey for arctic fox, red fox and wolverine, and hence I predict that the use of bait stations and feeding dispensers will be more frequent in low rodent years and during winter when food is scarce.

## Materials and methods

### Study sites

This study was conducted in one arctic fox core area and two stepping-stones areas in central Norway (Figure 1). The arctic fox area Snøhetta consists of Dovrefjell-Sundalsfjella national park (1.693 km<sup>2</sup> total area, 62° 21' 00" N 9° 6' 00" E) and some parts of Knutsø and Dalsida. Kjølifjellet/Sylane (64°09'00"N 13°14'00"E) is a stepping stone area for the southern distribution of the arctic fox. Skjærkerfjella/Blåfjella/Lierne consisting of Blåfjella-Skjærkerfjella National park (1 924 km<sup>2</sup> total area, 64° 15' 00" N 13° 11' 00" E) and Lierne National park (333 km<sup>2</sup> total area, 64° 20' 00" N 13° 58' 00" E) is classified as a stepping stone area between the northern and southern distribution of the Scandinavian arctic fox (Herfindal et al. 2010).

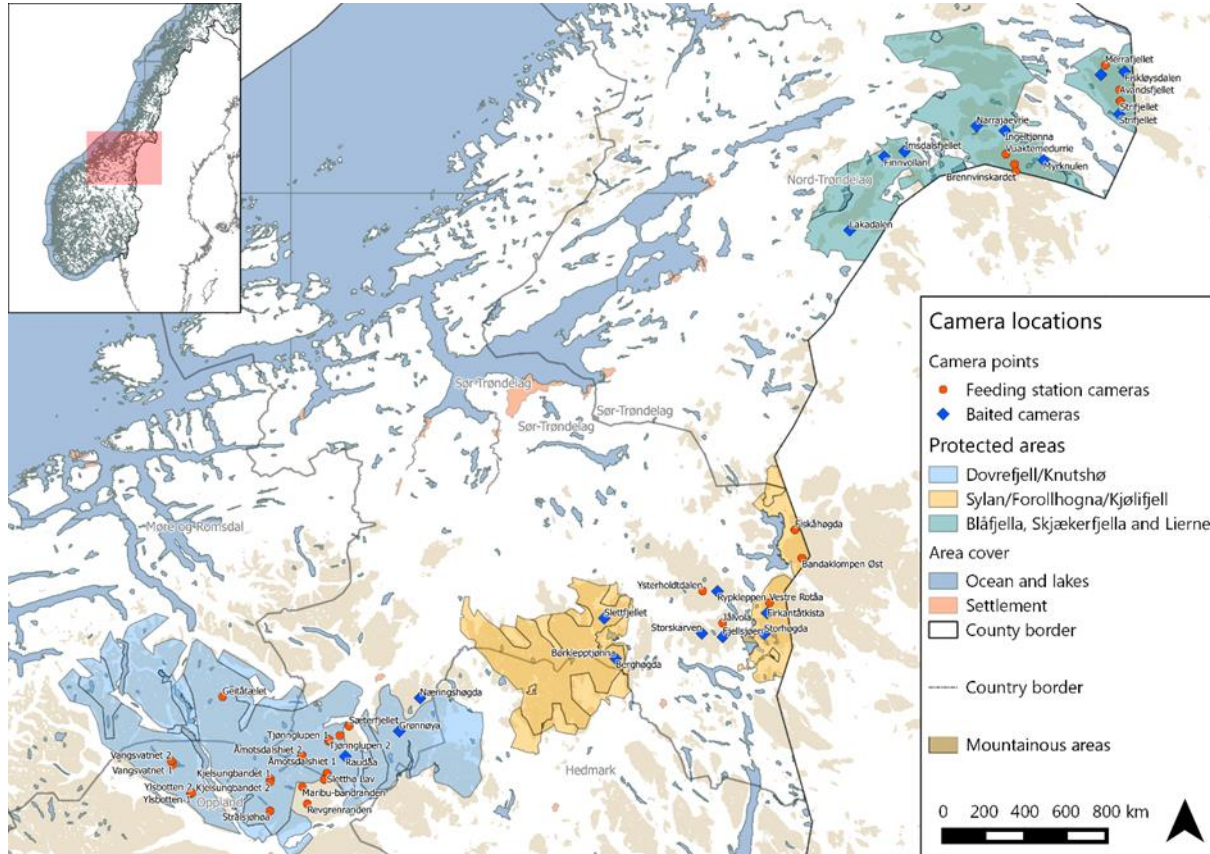


Figure 1 Map of study areas with points marking the locations of bait stations (blue) and feeding dispensers (red) (Map composed of data from Skog & Landskap, Statens Kartverk and Miljødirektoratet, 2014).

The study was conducted at altitudes from 574 to 1493 meters above the sea level (m.a.s.l), except for some bait stations located in the upper boreal zones. The study was located in the low and middle alpine zones and in the continental section. Characteristics for the climate in these

areas are long winters with short summers, snow cover for 150-225 days normally from November-May and a short growing season of 110-120 days (Moen et al. 1999). Small rodent species, such as Norwegian lemming, tundra vole *Microtus oeconomus*, field vole *Microtus agrestis*, grey-sided vole *Myodes rufocanus* and bank vole *Myodes glareolus* are found in the areas, with population cycles of 3-5 year period (Frafjord 1995). Wild reindeer are found in the Snøhetta area, while the two stepping-stones areas hold populations of domestic reindeer. In addition, wolverine, red fox, hare, least weasel *Mustela nivalis*, stoats *Mustela ermine*, golden eagle and white tailed eagle are also found in the mountain tundra (Frafjord 1995; Framstad 2014).

#### Field method

This study is based on open baited camera traps available for all species, and feeding dispensers exclusively made for the arctic fox. A total of 51 cameras were placed at 32 feeding dispensers and 19 bait stations during 2011-2013. Different sampling design were used at bait stations and feeding dispensers. At feeding dispensers, triggered Cuddeback cameras of models “Attack and Capture” were used to detect species during the whole year. The cameras were for the most placed on the feeding dispenser and pointed downwards to capture animals (Figure 2). At the bait stations, non-triggered Reconyx HyperFire PC800 cameras were used to detect animals. The cameras were set up to take a picture every fifth minute and only active during March-May, with some variation in deployment between study sites and years. The cameras were attached to a wooden pole 1.5 meters above the snow approximately six meters from the bait.



Figure 2: Feeding dispenser with two arctic fox whelps, one inside (left). Red fox outside feeding dispenser (right).

The camera/bait setups were located at altitudes from 538 to 1392 m.a.s.l., both above and below the tree line. The bait consisted of frozen reindeer offal/fat in a block measuring 60x40x10 cm and weighing 15 kg. The same size, shape and consistent was used at every location and refilled every 3 weeks. The feeding dispensers were located close to arctic fox dens and in altitudes from 792 to 1493 m.a.s.l, all above the tree line. The feeding dispensers consist of one or two entrances, a food chamber and a food depot/dispenser in the last standing barrel. The entrance is made by a tube with a diameter of 130-or 150 mm to hinder other competitors to enter (Landa et al., 2012), see figure 3. The feeding dispensers contain dog pellets of type Elite food designed for adult dogs (Landa et al. 2012).

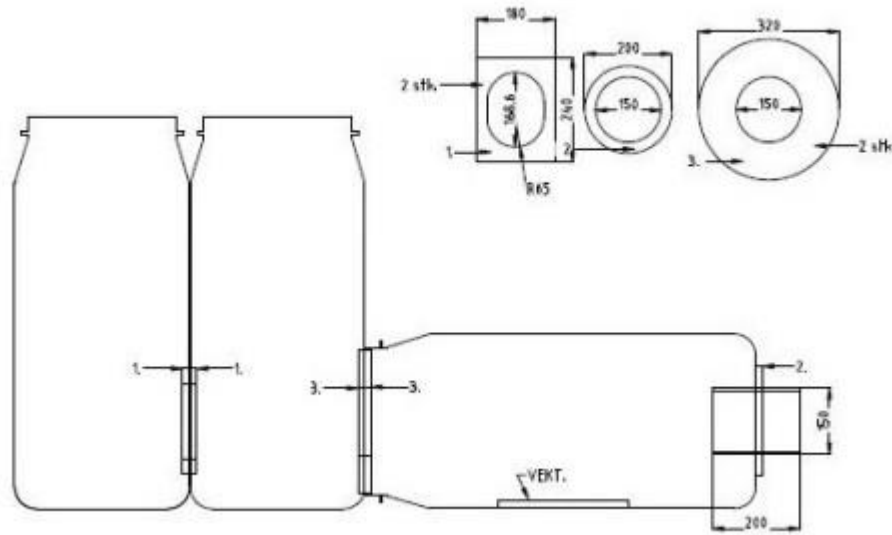


Figure 3: Construction of feeding dispenser (Landa et al.,2012).

### Data processing

Data from three locations that did not have active cameras all three years were discharged from the analysis. The data from the remaining 48 cameras were extracted into an excel sheet by an ad-hoc software (Rød-Eriksen 2013). The program created an excel workbook with metadata (time, date, month, mountain, location and light for feeding dispenser cameras and the approximate moon phase and temperature for cameras at bait stations). From the images and pre-defined custom variables, 29 variables were recorded for bait stations and 35 for feeding dispensers into a

desired standard format for the Norwegian Institute of Nature Research. The pictures were analyzed manually and species observations were recorded into an excel dataset.

### Variables

The aim of this study is to test the effect of other species on arctic fox visits at bait stations and feeding dispensers. I used the number of days with observations of the species from March-May of 2011-2013 for each bait stations and feeding dispensers as an index of visits for each of the three species; arctic fox, red fox and wolverine. This was in order to compensate for the different approaches used at bait stations and feeding dispensers. The arctic fox population increased through the study, and to account for this the minimum number of arctic foxes registered for the three areas was included as an explanatory variable. The annual minimum number of arctic foxes was collected from reports from the National monitoring program for arctic fox (Flagstad et al. 2011; Ulvund et al. 2012; Eide et al. 2013). Rodents and especially lemmings is an important food resource for all three carnivores in the mountain tundra (Myhre & Myrberget 1975; Landa et al. 1997; Elmhagen et al. 2002). Annual lemming abundance was set to poor in 2012 and good in 2011 and 2013. Data on rodent abundance was collected from the NINA report on terrestrial ecosystem monitoring (Framstad 2014).

Seasonal activity for the three species at feeding dispensers throughout the year was investigated by plotting the mean out of the number of days with registrations, for each month and year per feeding dispenser. Because the cameras at feeding dispensers were not active throughout the whole month, the number of days with registrations was divided by the number of active camera days. Months with less than 10 active camera days were excluded. To investigate the daily activity at the open bait stations for the different species, I registered the number of observations of each species per hour at each bait station.

### Statistical analysis

All statistical analyses were done in R 3.1.1 or JMP 10.0.0. Figures were made in JMP or Excel.

The General linear mixed model (GLMM) package MASS with negative binomial distribution was used to test the effect of other species visits, elevation, rodents and bait stations/feeding



dispenser on arctic fox visits. Study area was set as a random effect to control for unknown effects. Negative binomial distribution was used to compensate for overdispersion (Crawley 2012). The *theta* was found by a general linear model without study area as a random factor. The same procedure was also used to test for effects of elevation, bait stations/feeding dispenser and rodents on red fox and wolverine visits. “Fit least squares” in JMP was used to test for relationship between elevation and bait/feeding dispensers.

## Results

A total of 12 889 trap nights at feeding dispensers yielded 157 569 pictures of arctic foxes, 5292 of red foxes and 967 of wolverines, whereas 3164 trap nights at bait stations yielded 1314 pictures of arctic foxes, 5041 of red foxes and 1579 of wolverines. Other species observed are given in Table 1.

Table 1: Species (ranked after pictures taken) observed by use of cameras at bait stations and feeding dispensers aimed for arctic foxes in central Norway.

SPECIES	BAIT STATIONS	FEEDING DISPENSERS
ARCTIC FOX	X	X
COMMON RAVEN <i>CORVUS CORAX</i>	X	X
RED FOX	X	X
WOLVERINE	X	X
HOODED CROW <i>CORVUS CORNIX</i>	X	X
REINDEER	X	X
GOLDEN EAGLE	X	
PTARMIGAN <i>LAGOPUS MUTA</i>	X	X
SMALL MUSTELIDS <i>MUSTELA SPP.</i>	X	X
LEMMING	X	X
WHITE-TAILED EAGLE	X	
GULLS <i>LARUS SP.</i>	X	
ROUGH-LEGGED BUZZARD <i>BUTEO LAGOPUS</i>	X	
PEREGRINE FALCON <i>FALCO PEREGRINUS</i>	X	
HARE		X

### Species visits at feeding dispensers and bait stations

There was a significant difference between visits at bait stations and feeding dispensers for both arctic fox and red fox (DF = 130, t-value = -6.30,  $p < 0.001$ ). Red fox and wolverine visits had no significant effect on arctic fox visits at bait stations and feeding dispensers (Table 2). Red foxes visited bait stations more often than feeding dispensers, and arctic foxes visited feeding dispensers more often than bait stations (Figure 4). There was a non-significant difference between wolverines visits at bait stations and feeding dispensers (DF = 130, t-value = -1.74,  $p = 0.084$ ; Figure 4).

Table 2: Model 1: The effect of bait stations/feeding dispensers, red fox visits, wolverine visits, rodents, elevation and minimum number of arctic foxes in the study area on arctic fox visits. Model 2: The best model with the effect of bait stations/feeding dispenser and elevation on arctic fox visits. Area was included as a random factor in the models.

	<b>ARCTIC FOX</b>	<b>VALUE</b>	<b>STD. ERROR</b>	<b>DF</b>	<b>T-VALUE</b>	<b>P-VALUE</b>
<b>MODEL 1</b>	<b>BAIT STATIONS/FEEDING DISPENSER</b>	1.8941	0.3051	130	6.21	<b>&lt;0.001</b>
	<b>RED FOX</b>	0.0253	0.0165	130	1.53	0.127
	<b>WOLVERINE</b>	-0.0039	0.0173	130	-0.22	0.824
	<b>RODENTS</b>	0.0321	0.1661	130	0.19	0.447
	<b>ELEVATION</b>	0.0037	0.0012	130	3.16	<b>0.002</b>
	<b>MINIMUM ARCTIC FOX</b>	0.1454	0.0235	130	6.18	<b>&lt;0.001</b>
<b>MODEL 2</b>	<b>BAIT STATIONS/FEEDING DISPENSER</b>	1.7589	0.0284	133	6.19	<b>&lt;0.001</b>
	<b>ELEVATION</b>	0,0032	0.0011	133	2.75	<b>&lt;0.0068</b>
	<b>MINIMUM ARCTIC FOX</b>	0.1428	0.0023	133	6.33	<b>&lt;0.001</b>

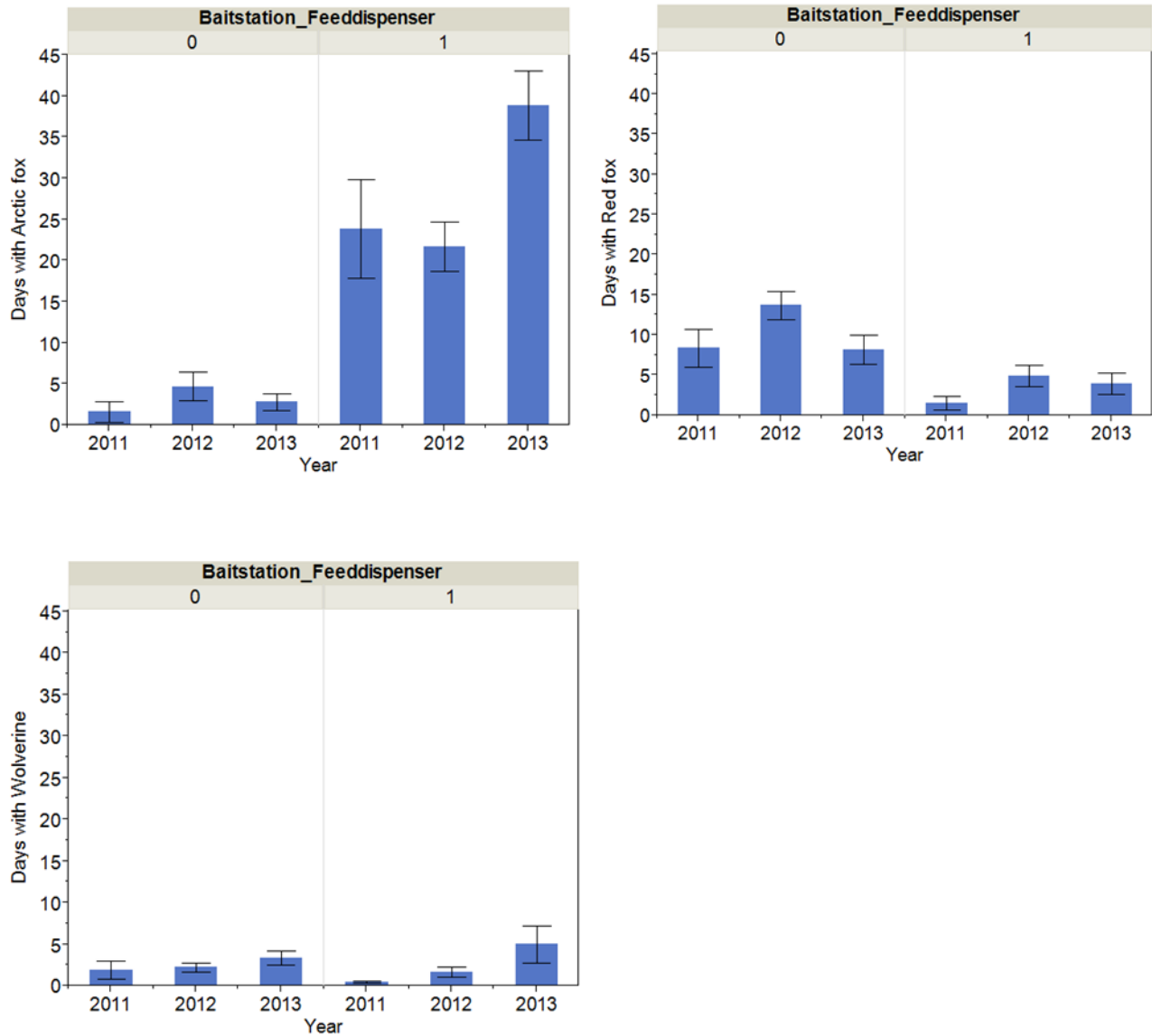


Figure 4: Mean (with SE) number of days with observations of arctic fox, red fox and wolverine at feeding dispensers (1; n=29) and bait stations (0; n=19) during March-May 2011-2013.

### Spatial and temporal use

Elevation had a significant effect on occurrence of arctic fox (Table 2), and wolverine visits (DF = 133, t-value = 2.512, p = 0.013), but not on red fox visits (DF = 133, t-value = -0.31, p = 0.756; Figure 5). Arctic foxes were mainly observed at higher elevations, and there were almost no observations at the lowest locations. Bait stations were in general located at lower elevations than feeding dispensers (SE = 88.1172, t-ratio = -4.17, p < 0.001), influencing results.

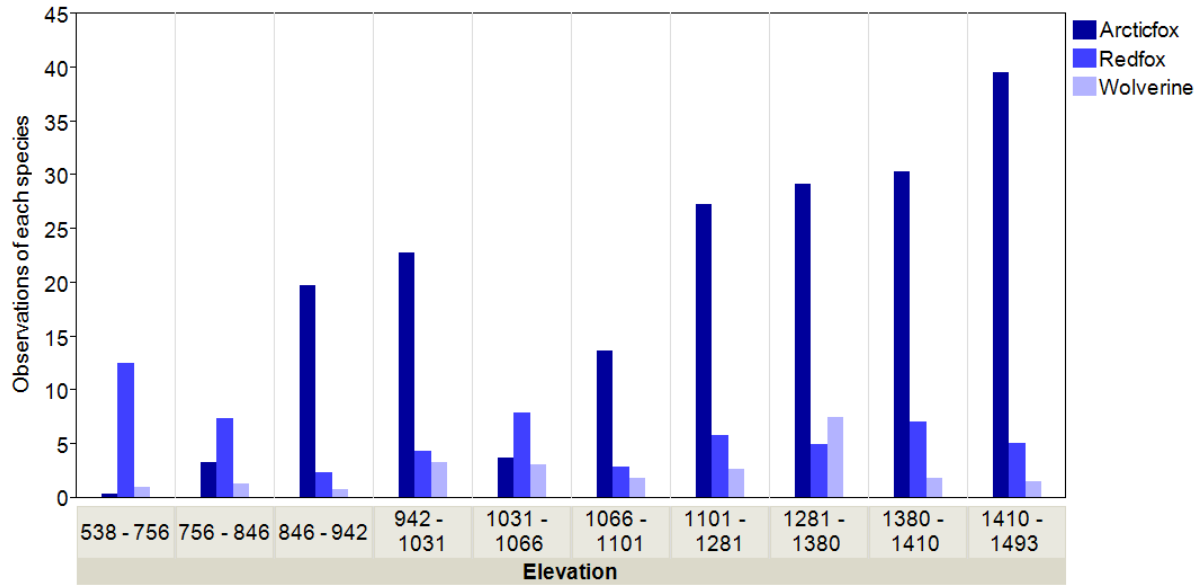


Figure 5: Mean number of observations of red fox, arctic fox and wolverine at different elevations during Mars-Mai 2011-2013.

The three species were nocturnal, with most visits from 19:00 to 05:00. The red fox was active through the whole day but had a peak from 20:00 until 04:00. The wolverine was also active throughout the day. The arctic fox was active only during evening and night, and there was only one registration between 08:00 and 17:00 (Figure 6).

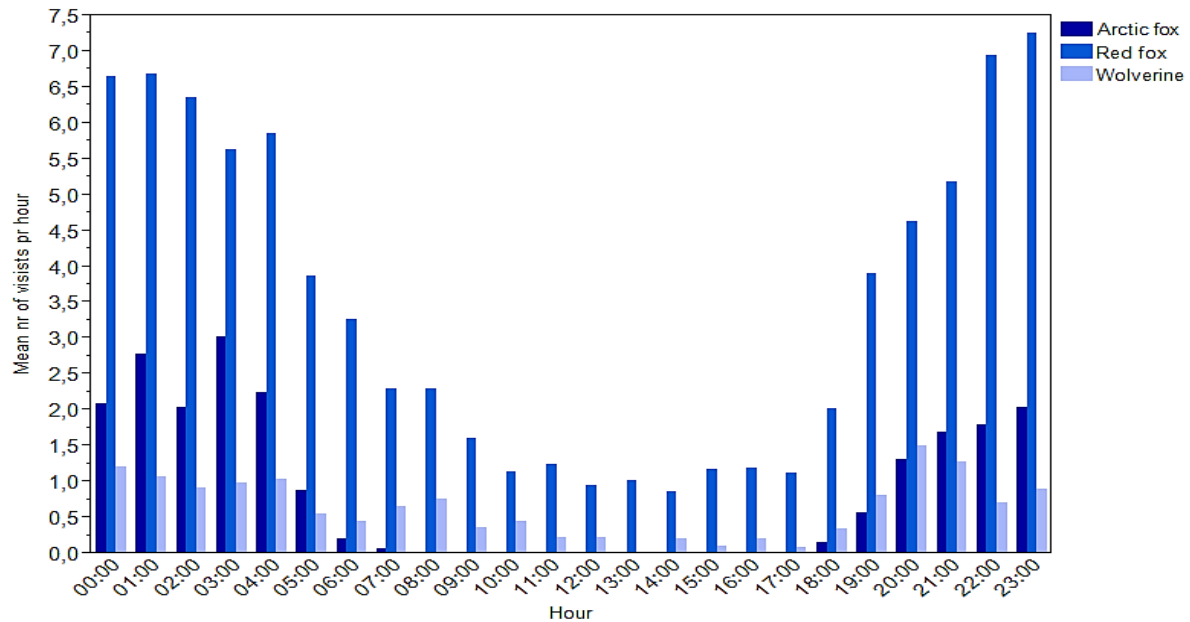


Figure 6: Mean number of visits pr. hour of wolverine, arctic fox and red fox at bait stations..

## Use of feeding dispensers and bait stations in relation to rodent cycle and season

There was no effect of rodents on the frequency of visits by arctic foxes (Table 2) or wolverines (DF = 122, t-value = 1.31,  $p = 0.192$ ), but rodents had a negative effect on red fox visits (DF=130, t-value=-2.58,  $p < 0.01$ ), also when the effect of bait stations and feeding dispensers was included in the model. When solely including data from bait stations, rodents had an effect also on arctic fox visits (DF = 49, t-value=-2.91,  $p = 0.005$ ). Red foxes visited both bait stations and feeding dispensers more frequently in the rodent crash year 2012. Arctic foxes visited bait stations most frequently in 2012 and feeding dispensers in the rodent increase year 2013. Wolverine was recorded with the highest number of visits in 2013 at both bait stations and feeding dispensers (Figure 4).

Snøhetta was the only area with sufficient data to analyze for monthly visits each year of the study period (2011-2013). The arctic fox was the most active species at feeding dispensers in all three years, whereas the wolverine was the least active species (Figure 7).

The activity of the arctic fox was evenly distributed over the whole year of 2011, with the exception of a decrease in December. The smaller amount of data from this month could be the reason for this deviation. In 2011, the red fox was at the most active during the winter months, whereas wolverine activity was nearly absent at feeding dispensers this year.

There was a general high amount of arctic fox visits during all of 2012, and the most frequent visits occurred during spring and summer. The red fox showed a similar pattern, with most visits during spring and early summer. Wolverine activity was nearly absent at feeding dispensers this year.

In 2013, the arctic fox activity was generally high throughout the year, with a peak during March and late summer/early autumn. The red fox and wolverine activity was nearly absent, except for an increase in red fox activity during November and December (Figure 7).

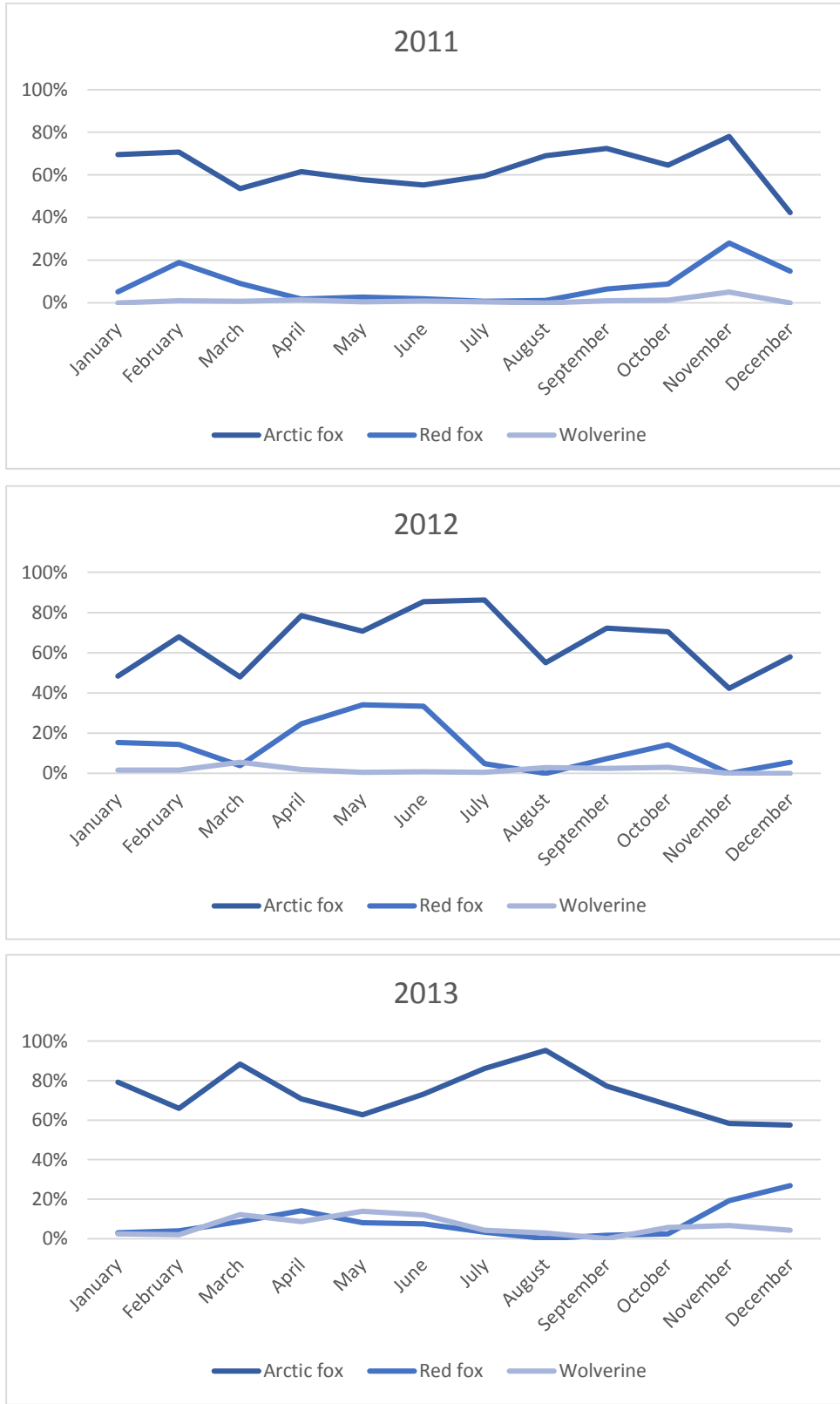


Figure 7: Mean activity at Snøhetta for arctic fox, red fox, and wolverine at feeding dispensers for each month during 2011, 2012, and 2013. 100% = active all days in the month

## Discussion

The most striking observation of this study was the difference in number of visits at bait stations and feeding dispensers for both red foxes and arctic foxes. This indicates that the feeding dispensers worked exclusively for the arctic fox and thus, probably reduces the interspecific competition between these species. There were no direct effects of visits of the other carnivores on the frequency of arctic fox visits, but the arctic fox was more restricted to the higher elevations and had a narrower temporal use. The rodent cycle seemed to influence both arctic and red foxes use of both feeding dispensers and bait stations.

### Species visits at feeding dispensers and bait stations

There was a broader diversity of species at baited camera traps than at feeding dispensers in all study years. The arctic fox was the dominant species at the feeding dispensers, but visits from red fox, wolverine, raven, hooded crow and small mustelids were also detected. From the observations at the pictures, these other species were never inside of the feeding dispensers (Rød-Eriksen pers. com.), which is concurrent with its design for the size of the arctic fox. As predicted, the arctic fox was more active at feeding dispensers than at bait stations, whereas the red fox was the dominant carnivore at baited stations and less active at feeding dispensers. The higher occurrence of arctic foxes at feeding dispensers is probably explained by the reduced presence of red foxes and other carnivores. The exclusion from the food at feeding dispensers makes the area less attractive for the competitors hence reduces their presence there. The reduced occurrence of arctic foxes at bait stations is so explained by the presence of competitors. In contrast to the prediction, there was no significant difference between wolverine visits at bait stations and feeding dispensers. This may be due to the low number of observations of wolverines, which is not an abundant species in the study areas and where the individuals utilize vast home-ranges compared to arctic foxes (Landa et al. 1998). Visits by wolverines may thus be more random. Red foxes also have larger home ranges than arctic foxes, but still much smaller than wolverines (Hersteinsson & Macdonald 1982). In addition, the red fox is abundant, which may explain why it was the most frequent guest at bait stations. Mattisson et al. (2013) found that wolverines visited bait stations less frequently than other food sources (Mattisson et al. 2013), a



behavior that may explain the low frequency of observations of wolverines at bait stations in my study.

The spatial positioning of the feeding dispensers might affect how much they are used by the different species. In a supplemental feeding experiment on scavengers in Spain they found that bearded vultures *Gypaetus barbatus* and red kites *Milvus milvus* used feeding stations located close to favorable habitats and close to their breeding territories (Cortés-Avizanda et al. 2010). The arctic fox also use dens during winter (Kålås 1997) and the preferred use of the feeding dispensers over bait stations may hence also be due to their location close to arctic foxes home range and breeding dens. The red fox preference for bait stations might also be influenced by the fact that these are generally located at lower elevations. However, the arctic fox preference for feeding dispensers is most likely due to reduced intra-guild competition.

#### Species coexistence

My results showed no significant negative influence of red fox or wolverine on arctic fox visits at bait stations and feeding dispensers. This differs from studies conducted during the breeding season, where arctic foxes have avoided areas where they can encounter red foxes (Linnell et al. 1999; Smith & Hellmann 2002; Tannerfeldt et al. 2002; Killengreen et al. 2007; Hamel et al. 2013). My results are, however, in compliance with Dalén et al. (2004), and indicates that arctic and red foxes may be sympatric in the winter season. The winter is a bottleneck for many carnivores, because the food access is limited due to snow cover (Prestrud 1991; Lindström & Hörnfeldt 1994). The arctic fox may have to enlarge its home-range to find enough food, even if it means encounters with the superior red fox. However, a camera trap study in Finnmark County during winter showed reduced activity of arctic foxes at sites where red foxes were observed (Hamel et al. 2013). There has been observed more winter activity by red foxes at dens in Finnmark compared to the other arctic fox areas (Flagstad et al. 2011; Ulvund et al. 2012; Eide et al. 2013). The difference from Hamel et al. (2013) and my study may therefore be explained by the observed differences of red foxes density. According to Durant (1998), the avoidance behavior of the lesser competitor may be facultative, meaning that the density of the superior competitors has to reach a certain level before the lesser competitor show avoidance behavior (Cortés-Avizanda et al., 2010) and abandon an area. With lower densities of red foxes, the arctic

fox may just hide and avoid direct contact with the red fox, as has been observed in earlier studies at carcasses (Haglund and Nilsson, 1977) and from picture analysis (Rød-Eriksen pers. com.).

Arctic foxes used bait stations and feeding dispensers constantly more frequent at the highest elevations. The arctic fox appears to seek higher altitudes in Fennoscandia (Landa et al. 1998; Dalerum et al. 2002; Elmhagen et al. 2002; Tannerfeldt et al. 2002), possibly due to an expansion of the superior red fox to the alpine areas (Hersteinsson & Macdonald 1992; Linnell et al. 1999; Frafjord 2003; Fuglei & Ims 2008). The red fox is less adapted to the cold climate, and it is suggested that the distribution of the red fox is limited by the productivity of the habitat (Hersteinsson & Macdonald 1992). However, my study shows that the red fox is not limited to the lower tundra; the species was observed at all elevations. This is in accordance with observations from recent studies on the same species in Finnmark (Killengreen et al. 2012). The expansion of the red fox to alpine areas has been explained by a warming climate, making productivity higher and thus the alpine areas a more suitable habitat for the red fox (Hersteinsson & Macdonald 1992). Gallant et al. (2012) challenges the climate hypotheses, and showed that the red fox had not increased in abundance in north Yukon during 40 years in spite of documented warmer temperatures and increase in primary productivity. However, the expansion of the red fox to the highest elevations during wintertime probably come by increased access of food from carcasses and organic waste from humans (Henden et al. 2014; Savory et al. 2014). Killengreen et al. (2011) found that red foxes had a higher amount of carrion in their winter diet in rodent low years, implying the importance of supplemental food when rodents are scarce. This is in accordance with my study, showing that the red fox visited bait stations and feeding dispensers more often in low rodent years. Even though my study shows that the two fox species are not spatially segregated, the arctic fox seems to use the uppermost mountain areas, which can indicate avoidance behavior.

The red fox and wolverine showed a wider temporal use at bait stations than the arctic fox, which was only active at evening and night. This is in compliance with camera studies done at bait stations in East-Finnmark (Killengreen et al. 2013). A study was conducted with the same methods in Nenetsky and Yamal in Russia. Here, the arctic fox showed activity at bait stations during both day and night (Rodnikova et al. unpublished). The arctic fox was the most frequent guest at the tundra in Russia, and there were almost no pictures of red foxes (Rodnikova pers.

com.), which probably indicates that the red fox was less abundant at her study site. Diurnal predators such as eagles were also absent in this study (Killengreen et al., 2013). The narrow temporal use in my study may be explained by the presence of red foxes, but it could also be due to the presence of diurnal raptors. Temporal segregation is a strategy to avoid predators and competitors, and is commonly explain by coexistence between sympatric competing species (Blázquez et al. 2009; Lucherini et al. 2009; Di Bitetti et al. 2010).

#### Use of feeding dispensers and bait stations in relation to rodent years and seasons

In the lemming low year 2012, I found more frequent visits of red foxes and arctic foxes at bait stations, which is in accordance with my prediction. Wolverine visits however, were most frequent during the rodent increase year 2013, in contrast to my prediction. The arctic fox is considered a facultative specialist, meaning it is a specialist in lemming years but switches to other prey when the lemming abundance is low (Hersteinsson & Macdonald 1982; Elmhagen et al. 2000; Henden et al. 2010). Also red foxes living in the alpine areas may be characterized as facultative specialist (Henden et al. 2010). Diet studies on the red fox in Finnmark showed that lemmings were the dominant diet in lemming peak years, and that other nutrient sources, such as reindeer and birds, were the dominant food source in rodent low years (Killengreen et al. 2011; Killengreen et al. 2013). Red foxes also visited the feeding dispensers more frequently during the lemming low year, indicating their need for other food sources when rodents are scarce. However, there was no relation between rodents and feeding dispenser visits for the arctic fox. This could be due to the increase in the arctic fox population in all three areas during the study period, although there was a higher visit rate during 2011 than during 2012 (Eide et al. 2013). The higher visit rate during 2011 could also be influenced by the high number of breedings this year. At Snøhetta there were 11 litters, and since the feeding dispensers were located close to active arctic fox dens, the activity increase can simply be due to larger energetic needs. The non-relation between wolverine visits and lemming years might be due to the diet of the wolverine. The wolverine is mainly a scavenger and less dependent on rodents than the foxes; its main diet consists of cervids both summer and winter (Landa et al. 1997; Van Dijk et al. 2008). However Landa et al. (1997) found a relation between survival of wolverine pups and rodent abundance.

The seasonal activity at the feeding dispensers differed from my prediction. Except for the year 2011, which was a rodent peak year, the arctic fox activity was at lowest during winter. Reduced winter activity may be a strategy to save energy during the coldest months. In harsh weather, the arctic fox save energy by resting under snow cover or hide inside dens (Prestrud 1991). Such weather may last for many days, and thus reduce the visits at the feeding dispensers. The increase in activity during spring and summer for the arctic- and red fox in 2012 was probably related to the reduced abundance of rodents this year. Rodents are the most eaten prey during spring and summer for both fox species in alpine areas (Frafjord, 1995). Rodent populations increased in Snøhetta in 2013, which may explain the reduced activity at feeding dispensers during spring and summer. However, the activity peaked during March and autumn. The increase in activity during March might be due to the cold temperatures recorded this year, it was the coldest March month during all study years (*eKlima* 2014). The activity peak during the following autumn was most probably caused by the high number of breedings this year; 14 litters born in Snøhetta (Eide et al. 2013). The feeding dispensers were located close to active arctic fox dens. Hence, increased activity from kits using the feeding dispensers should be expected.

## Conclusion and management implications

My results showed that the feeding dispensers worked exclusively for the arctic fox and reduced the intra-guild competition with potential predators and especially the superior red fox. The arctic fox showed no direct avoidance to red foxes at the feeding stations. This indicates that exclusive feeding dispensers reduce the importance of red fox control. However, the arctic foxes were restricted to the highest elevations, which may indicate avoidance of areas with higher densities of red foxes at the lower altitudes. This indicates that red fox control should be concentrated to areas in the alpine zone where the red fox seems to be established permanently. I found no preference for season or year in the use of feeding dispensers, indicating that feeding is important all year through. For both arctic and red foxes, the use of bait stations was more frequent when the rodent abundance was low, indicating a potential for stronger competition when rodents are scarce. The use of feeding dispensers is a successful action and should be continued until the arctic fox population has reached a sustainable level. The results of this study can also be transferred to the management of other species. Building constructions to release competition pressure can be recommended to other conservation programs where competition is a challenge.

## Citations

- Angerbjörn, A., Tannerfeldt, M. & Erlinge, S. (1999). Predator–prey relationships: arctic foxes and lemming. *Journal of Animal Ecology*, 68 (1): 34-49.
- Angerbjörn, A., Tannerfeldt, M., Bjärvall, A., Ericson, M., From, J. & Norén, E. (1995). *Dynamics of the arctic fox population in Sweden*. Annales Zoologici Fennici: Helsinki: Suomen Biologian Seura Vanamo, 1964-. 55-68 pp.
- Angerbjörn, A., Eide, N. E., Dalén, L., Elmhagen, B., Hellström, P., Ims, R. A., Killengreen, S., Landa, A., Meijer, T. & Mela, M. (2013). Carnivore conservation in practice: replicated management actions on a large spatial scale. *Journal of Applied Ecology*, 50 (1): 59-67.
- Barth, L., Angerbjörn, A. & Tannerfeldt, M. (2000). Are Norwegian lemmings *Lemmus lemmus* avoided by arctic *Alopex lagopus* or red *Vulpes vulpes* foxes? A feeding experiment. *Wildlife Biology*, 6 (2): 101-109.
- Blázquez, M., Sánchez-Zapata, J. A., Botella, F., Carrete, M. & Eguía, S. (2009). Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. *Acta Oecologica*, 35 (5): 645-650.
- CAFF. (2013). *Arctic Biodiversity Assessment: Conservation of Arctic Flora and Fauna* (CAFF) International Secretariat, Akureyri, Iceland. <http://www.arcticbiodiversity.is>.
- Cortés-Avizanda, A., Carrete, M. & Donazar, J. A. (2010). Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. *Biological Conservation*, 143 (7): 1707-1715.
- Crawley, M. J. (2012). *The R book*, vol. 2: John Wiley & Sons.
- Dalén, L., Elmhagen, B. & Angerbjörn, A. (2004). DNA analysis on fox faeces and competition induced niche shifts. *Molecular Ecology*, 13 (8): 2389-2392.
- Dalerum, F., Tannerfeldt, M., Elmhagen, B., Becker, D. & Angerbjörn, A. (2002). Distribution, morphology and use of arctic fox *Alopex lagopus dens* in Sweden. *Wildlife Biology*, 8 (3): 185-192.
- Di Bitetti, M. S., De Angelo, C. D., Di Blanco, Y. E. & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, 36 (4): 403-412.
- Eide, N. E., Ulvund, K., Flagstad, Ø., Kleven, O. & Landa, A. (2013). *Fjellrev i Norge*. NINA Rapport, vol. 992. Trondheim: Norsk institutt for naturforskning. 43 pp.
- eKlima. (2014). Meteorologisk institutt. Available at: [www.eklima.no](http://www.eklima.no) (accessed: 26.11.2014).
- Elmhagen, B., Tannerfeldt, M., Verucci, P. & Angerbjörn, A. (2000). The arctic fox (*Alopex lagopus*): an opportunistic specialist. *Journal of Zoology*, 251 (2): 139-149.
- Elmhagen, B., Tannerfeldt, M. & Angerbjörn, A. (2002). Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology*, 80 (7): 1274-1285.
- Flagstad, Ø., Eide, N. E., Ulvund, K., Tovmo, M., Andersen, R. & Landa, A. (2011). *Fjellrev i Norge* NINA Rapport, vol. 767. Trondheim.
- Frafjord, K., Becker, D. & Angerbjörn, A. (1989). Interactions between arctic and red foxes in Scandinavia: predation and aggression. *Arctic*, 42 (4): 354-356.
- Frafjord, K. (1995). *Summer food habits of arctic foxes in the alpine region of southern Scandinavia, with a note on sympatric red foxes*. Annales Zoologici Fennici: Helsinki: Suomen Biologian Seura Vanamo, 1964-. 111-116 pp.
- Frafjord, K. (2003). Ecology and use of arctic fox *Alopex lagopus dens* in Norway: tradition overtaken by interspecific competition? *Biological Conservation*, 111 (3): 445-453.
- Framstad, E. (2014). Terrestrial Ecosystems Monitoring in 2013: Ground vegetation, epi-phytes, small mammals and birds. Summary of results. *NINA Report*. 158pp. pp.
- Frislid, R. & Semb-Johansson, A. (1980). *Norges dyr*. Oslo: Cappelen.

- Fuglei, E. & Ims, R. A. (2008). Global warming and effects on the arctic fox. *Science progress*, 91 (2): 175-191.
- Gallant, D., Slough, B. G., Reid, D. G. & Berteaux, D. (2012). Arctic fox versus red fox in the warming Arctic: four decades of den surveys in north Yukon. *Polar biology*, 35 (9): 1421-1431.
- Hamel, S., Killengreen, S., Henden, J.-A., Yoccoz, N. & Ims, R. (2013). Disentangling the importance of interspecific competition, food availability, and habitat in species occupancy: Recolonization of the endangered Fennoscandian arctic fox. *Biological Conservation*, 160: 114-120.
- Henden, J.-A., Ims, R. A., Yoccoz, N. G., Hellström, P. & Angerbjörn, A. (2010). Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. *Oikos*, 119 (1): 27-34.
- Henden, J. A., Bårdsen, B. J., Yoccoz, N. G. & Ims, R. A. (2008). Impacts of differential prey dynamics on the potential recovery of endangered arctic fox populations. *Journal of Applied Ecology*, 45 (4): 1086-1093.
- Henden, J. A., Stien, A., Bårdsen, B. J., Yoccoz, N. G. & Ims, R. A. (2014). Community-wide mesocarnivore response to partial ungulate migration. *Journal of Applied Ecology*, 51 (6): 1525-1533.
- Herfindal, I., Linnell, J. D. C., Elmhagen, B., Andersen, R., Eide, N. E., Frafjord, K., Henttonen, H., Kaikusalo, A., Mela, M., Tannerfeldt, M., et al. (2010). Population persistence in a landscape context: the case of endangered arctic fox populations in Fennoscandia. *Ecography*, 33 (5): 932-941.
- Hersteinsson, P. & Macdonald, D. (1982). *Some comparisons between red and arctic foxes, Vulpes vulpes and Alopex lagopus, as revealed by radio tracking*. Symposia of the Zoological Society of London: Published for the Zoological Society by Academic Press. 259-289 pp.
- Hersteinsson, P., Angerbjörn, A., Frafjord, K. & Kaikusalo, A. (1989). THE ARCTIC FOX IN FENNOSCANDIA AND ICELAND - MANAGEMENT PROBLEMS. *Biological Conservation*, 49 (1): 67-81.
- Hersteinsson, P. & Macdonald, D. W. (1992). Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*: 505-515.
- IUCN. (2009). *Species and climate change. More than just polar bears.*: Int. Union for Conservation of Nature and Natural Resources.
- Kaikusalo, A. & Angerbjörn, A. (1995). *The arctic fox population in Finnish Lapland during 30 years, 1964-93*. Annales Zoologici Fennici: Helsinki: Suomen Biologian Seura Vanamo, 1964-. 69-77 pp.
- Killengreen, S. T., Ims, R. A., Yoccoz, N. G., Bråthen, K. A., Henden, J.-A. & Schott, T. (2007). Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic fox. *Biological Conservation*, 135 (4): 459-472.
- Killengreen, S. T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N. G. & Ims, R. A. (2011). The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. *Journal of Animal Ecology*, 80 (5): 1049-1060.
- Killengreen, S. T., Strømseng, E., Yoccoz, N. G. & Ims, R. A. (2012). How ecological neighbourhoods influence the structure of the scavenger guild in low arctic tundra. *Diversity and Distributions*, 18 (6): 563-574.
- Killengreen, S. T., Ims, R. A., Henden, J.-A., Yoccoz, N. & Ehrich, D. (2013). Fjellrev i Finnmark - Rapport for perioden 2008-2012.
- Kålås, J., Viken, Å., Henriksen, S. & Skjelseth, S. (2010). The 2010 Norwegian red list for species. *Norwegian Biodiversity Information Centre, Trondheim*.
- Kålås, J. A. (1997). Terrestrisk naturovervåking. Fjellrev, hare, smågnagere og fugl i TOV-områdene, 1996. *NINA Oppdragsmelding*, 484: 1-37.
- Landa, A., Strand, O., Swenson, J. & Skogland, T. (1997). Wolverines and their prey in southern Norway. *Canadian Journal of Zoology*, 75 (8): 1292-1299.

- Landa, A., Strand, O., Linnell, J. D. & Skogland, T. (1998). Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology*, 76 (3): 448-457.
- Landa, A., Tovmo, M., Flagstad, Ø., Eide, N. E., Ulvund, K. R. & Andersen, R. (2012). *Avlsprogrammet for fjellrev. Årsrapport 2011*, vol. 796. Trondheim: Norsk institutt for naturforskning. 51 s. pp.
- Landa, A., Eide, N. E. Flagstad, Ø., Herfindal, I., Strand, O., Andersen, R., Dijk, van, I. Linnell, J. D. C. . (2006). Bevaringsbiologi – Fjellrev i NINA. *NINA Rapport* 39 pp.
- Lindström, E. R. & Hörnfeldt, B. (1994). Vole cycles, snow depth and fox predation. *Oikos*: 156-160.
- Linnell, J. D., Strand, O. & Landa, A. (1999). Use of dens by red *Vulpes vulpes* and arctic *Alopex lagopus* foxes in alpine environments: Can inter-specific competition explain the non-recovery of Norwegian arctic fox populations? *Wildlife Biology*, 5 (3): 167-176.
- Loison, A., Strand, O. & Linnell, J. D. (2001). Effect of temporal variation in reproduction on models of population viability: a case study for remnant arctic fox (*Alopex lagopus*) populations in Scandinavia. *Biological Conservation*, 97 (3): 347-359.
- Lucherini, M., Reppucci, J. I., Walker, R. S., Villalba, M. L., Wursten, A., Gallardo, G., Iriarte, A., Villalobos, R. & Perovic, P. (2009). Activity pattern segregation of carnivores in the high Andes. *Journal of Mammalogy*, 90 (6): 1404-1409.
- Mattisson, J., Odden, J., Gomo, G., Persson, J. & Stien, A. (2013). Jervens atferd ved kadaver – kunnskap relevant for åtejakt på jerv. *NINA Rapport*. 20 pp.
- Moen, A., Lillethun, A. & Odland, A. (1999). *Vegetation*. [Hønefoss]: Norges geografiske oppmåling. 200 pp.
- Myhre, R. & Myrberget, S. (1975). Diet of Wolverines (*Gulo gulo*) in Norway. *Journal of Mammalogy*, 56 (4): 752-757.
- Palomares, F. & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, 153 (5): 492-508.
- Pamperin, N. J., Follmann, E. H. & Petersen, B. (2006). Interspecific killing of an arctic fox by a red fox at Prudhoe Bay, Alaska. *Arctic*: 361-364.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421 (6918): 37-42.
- Persson, L. (1985). Asymmetrical competition: are larger animals competitively superior? *American Naturalist*: 261-266.
- Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S. & Høye, T. T. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, 325 (5946): 1355-1358.
- Prestrud, P. (1991). Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. *Arctic*: 132-138.
- Root, R. B. (1967). The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher. *Ecological Monographs*, 37 (4): 317-350.
- Rød-Eriksen, L. (2013). *Red fox expansion in alpine areas: relations to climate, productivity, humans and ungulates*. Evenstad: HEDMARK UNIVERSITY COLLEGE. 37 pp.
- Savory, G. A., Hunter, C. M., Wooller, M. & O'Brien, D. M. (2014). Anthropogenic food use and niche overlap between red and arctic foxes in Prudhoe Bay, Alaska. *Canadian Journal of Zoology* (ja).
- Selås, V. & Vik, J. O. (2007). The arctic fox *Alopex lagopus* in Fennoscandia: a victim of human-induced changes in interspecific competition and predation? *Biodiversity and conservation*, 16 (12): 3575-3583.
- Smith, J. N. & Hellmann, J. J. (2002). Population persistence in fragmented landscapes. *Trends in Ecology & Evolution*, 17 (9): 397-399.
- Strand, O., Linnell, J. D., Krogstad, S. & Landa, A. (1999). Dietary and reproductive responses of arctic foxes to changes in small rodent abundance. *Arctic*: 272-278.



- Tannerfeldt, M., Angerbjörn, A. & Arvidson, B. (1994). The effect of summer feeding on juvenile arctic fox survival - a field experiment. *Ecography*, 17 (1): 88-96.
- Tannerfeldt, M. & Angerbjörn, A. (1998). Fluctuating resources and the evolution of litter size in the arctic fox. *Oikos*: 545-559.
- Tannerfeldt, M., Elmhagen, B. & Angerbjörn, A. (2002). Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, 132 (2): 213-220.
- Ulvund, K. R., Flagstad, Ø., Eide, N. E., Landa, A. & (2012). *Fjellrev i Norge*. NINA Rapport, vol. 909. Trondheim.
- Van Dijk, J., Gustavsen, L., Myrnes, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H. & Landa, A. (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology*, 77 (6): 1183-1190.
- Wille, F. & Kampp, K. (1983). Food of the white-tailed eagle *Haliaeetus albicilla* in Greenland. *Ecography*, 6 (1): 81-88.



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