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Does Supplementary Feeding of Arctic Fox (*Vulpes lagopus*) in Norway Boost Reproductive Success?

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Preface

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

I would like to give my sincere gratitude to Researcher Richard Bischof, 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 conducted under the arctic fox projects lead by the Norwegian Institute of Nature Research (NINA): “The Arctic fox captive breeding program” and “The National monitoring program on 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 Arild Landa for making this thesis happen. I would also like to thank my supervisor Senior Researcher Nina E. Eide for fast replies and remarks on my drafts. I would like to thank Kristine Ulvund, Anne-Mathilde Thierry and Lars Rød-Eriksen at NINA for help extracting data, and Jiska van Dijk, at NINA for guidance and help in analysing the faeces.

At last, I will thank my family and friends for being supportive and helping me through this process.

Ås 13.05.2016

Aina-Elise Bolstad Stokkenes

Abstract

Supplementary feeding is a popular conservation measure, used to help wildlife population gain viability. Supplementary feeding programs can have variable outcomes, due to differences in its implementation and behaviour of the target species. The Arctic fox on mainland Norway is designated as critically endangered on the national red list; with a population of less than 150 reproductive individuals. Major conservation actions are used to help the arctic fox population gain viability: supplementary feeding with dog food, captive breeding and release of pups, and red fox control in some parts of its Scandinavian range. Since the start of active management of the species in 2006, the Norwegian arctic fox population has increased. Important questions regarding arctic fox management and conservation in Norway concerns the impact of supplementary feeding. In this thesis I tested a series of hypotheses related to the use of supplementary food by arctic foxes and the potential effect supplementary feeding may have on reproduction and litter size.

Using arctic fox faeces collected at known active den sites, I quantified diet composition, and assessed the contribution of supplementary food (dog food) in the diet. I then explored the role of annual rodent abundance, climatic conditions, and the availability of feeding stations in the vicinity of a given den on the proportion of supplementary food in the diet. Finally, I tested for relationships between fecundity (probability of reproducing and litter size) and diet composition, environmental covariates. The study period spanned through portion of the rodent cycle and included years with both low and high rodent abundances. The diet analysis revealed that rodent was the main prey in all years. The result revealed that both the probability of reproduction and litter size are positively affected by rodent index. However, I detected no evidence of any effect of supplementary feeding on reproduction or litter size. Based on findings in this thesis I cannot conclude that supplementary feeding had an effect on arctic fox reproduction or litter size, and I will recommend future research on this topic.

Samandrag

Ekstra fôring er eitt av fleire bevaringstiltak som har blitt brukt for å auke dyrs levedyktigheit. Supplerande fôring har hatt ulikt resultat basert på dyrs åtferd, intensitet og tilpassing av tiltak. Fjellrev er i Noreg ført opp som kritisk truga i den nasjonale raudlista, og har ein bestand med færre enn 150 vaksne individ. Det er sett i gang ulike tiltak for hjelpe bestanden av fjellrev; supplerande fôring med hundefôrpellets, avl og utsetjing av kvalpar, samt raudrevkontroll i einskilde deler av Skandinavia. I løpet av åra som tiltak er gjennomført (2006-d. d) har ein lukkast med å auke fjellrevbestanden. For å tilpasse adaptive tiltak, er det viktig å finne ut om, og eventuelt i kor stor mengde supplerande fôring har påverka fjellrevbestanden. I denne avhandlinga testar eg ei rekkje hypotesar knytt til bruk av fôringsstasjonar av fjellrev og den moglege effekten supplerande fôring kan ha på reproduksjon og kullstorleik. Metoden eg har nytta i oppgåva er analyser av ekskrement frå fjellrev for å kvantifisere samansetjinga av- og bidraget av hundemat i dietten. Ekskrement vart samla inn på kjente hilokalitetar. Eg undersøkte vidare rolla av førekomsten av smågnagarar, klima og tilgjengelegheita av fòringsstasjonar i relasjon til nærleik for eitt gitt i hi i høve hundemat i dietten. Til slutt testa eg samanhengen mellom fekunditet (sannsynet for å reprodusere og kullstorleik) og diettsamansetjinga og klima variablar. Studieperioden inneheldt både år med låg og høg tettleik av smågnagarar. Diettanalysen viste at smågnagarar var hovudbyttet i alle år. Analysane viste at sannsynet for reproduksjon og kullstorleik var positivt påverka av smågnagartettleik. Derimot fant eg ingen bevis for noko effekt av ekstra fôring på reproduksjon, eller kullstorleik. Basert på mine funn i denne oppgåva kan eg ikkje konkludere med at ekstra fôring har ein effekt på reproduksjon, eller kullstorleik hjå fjellrev i Sør-Noreg. Eg tilrår vidare undersøkingar i høve dette emnet.

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Introduction

Anthropogenic impacts, such as habitat destruction and overhunting has led to widespread extinctions of species. To prevent extant, yet endangered or threatened species from becoming extinct, managers, and scientists have developed and implemented different management and conservation techniques. One action that has been applied in many conservation programs is supplementary feeding (Ewen et al. 2015).

Supplementary feeding has typically been used when natural foods are hypothesized to limit population growth (Armstrong & Perrott 2000; López-Bao et al. 2010), or in order to compensate for other sources of mortality, such as hunting (Delibes-Mateos et al. 2009; Putman & Staines 2004). Supplementary feeding has also been used as a safe food source that is free of contaminants, for example in situations where illegal poisoning is a problem (Oro et al. 2008; Oro et al. 2013). Effects of supplemental feeding vary, based on animal behaviour, intensity and specifics of application (Ewen et al. 2015). Studies evaluating the impact of supplementary feeding have shown mixed results. Some researchers has found that supplementary feeding has a positive effect on populations (Meijer et al. 2013). Supplementary feeding could cause harm, with increased mortality, lower productivity due to increased inter specific competition and intra-guild predation, to the populations it was intended to help. The negative effects could spread on to a wider recipient ecosystem (Blanco et al. 2011; Carrete et al. 2006; Cortés-Avizanda et al. 2010; Orros & Fellowes 2012).

Most carnivore populations are naturally food-limited (*Carnivore Conservation* 2001). Lack of food can in the worst case threaten the survival of a carnivore population. An alternative food resource could in some extant be food from supplementary feeding stations. Supplementary feeding has been shown to have a positive effect on some carnivore populations. For example have López-Bao et al. (2008) found that supplementary feeding can be applied to reverse the decline of food limited populations of Iberian lynx (*Lynx pardinus*), positive effect has also been showed on reproduction and pup survival of arctic fox (*Vulpes lagopus*) in Sweden (Meijer et al. 2013).

The arctic fox is a small canid with a circumpolar distribution (Tannerfeldt 2014) including the alpine tundra environment in Scandinavia. The arctic fox can live in breeding groups of three to five or more adults (Angerbjörn et al. 1995; Tannerfeldt & Angerbjörn 1996), and can give birth to 16 pups (Angerbjörn et al. 1995). In the late 1800s there were probably more than 20 000 arctic foxes in Fennoscandia (Hersteinsson et al. 1989). The arctic fox became protected by law in 1928 in Sweden, 1930 in Norway and 1940 in Finland (Hersteinsson et al. 1989) as the population was characterized as critically small (Johnson 1980), due to hunting (Lönnberg 1927). Despite more than 80 years of protection, the arctic fox in Norway is still classified as critically endangered (Tannerfeldt 2014) with a minimum population estimate of less than 300 reproductive individuals in Norway, Sweden and Finland combined (Angerbjörn et al. 2013; Eide et al. 2016).

There are many different hypotheses as to why the Scandinavian arctic fox population has not recovered following protection. These hypotheses can be divided into those related to (1) changed food resource availability (Angerbjörn et al. 1991; Angerbjörn et al. 1995; Kaikusalo & Angerbjörn 1995); (2) increased interspecific competition and intraguild predation (Elmhagen et al. 2002; Frafjord et al. 1989; Hersteinsson & MacDonald 1992; Killengreen et al. 2007); and (3) loss of viability due to small population size (Henden et al. 2008; Herfindal et al. 2010; Loison et al. 2001).

Food limitation hypothesis

Small rodents such as voles (*Arvicola amphibious*) and lemmings (*Lemmus lemmus*) are the key prey for the arctic fox in Scandinavia, which is a sequential prey specialist (Elmhagen et al. 2002; Tannerfeldt & Angerbjörn 1998). The rodent cycles have peak years with high rodent abundance and low years with low rodent abundance, the cyclicity varies between regions (Angerbjörn et al. 2001; Henden et al. 2008; Herfindal et al. 2010; Ims & Fuglei 2005; Kaikusalo & Angerbjörn 1995; Strand et al. 1999; Sundell et al. 2004). In increase and peak phases of the rodent cycle, the arctic fox produces frequent and large litters, whereas in years with few rodents there are almost no reproductions (Meijer et al. 2013; Tannerfeldt & Angerbjörn 1998). During low phase of the rodent cycle, the arctic fox diet composition shifts towards other food resources (Angerbjörn et al. 1995; Elmhagen et al. 2000; Strand et al. 1999) using more often hares (*Lepus timidus*), reindeer carcasses (*Rangifer tarandus*) and various birds (Elmhagen et al. 2002; Frafjord 2000; Jepsen et al. 2002; Strand et al. 1999).

Predation hypothesis

Red fox (*Vulpes vulpes*), wolverine (*Gulo gulo*) and golden eagle (*Aquila chrysaetos*) are all potential predators on arctic fox (Elmhagen et al. 2002; Frafjord et al. 1989; Hersteinsson et al. 1989; Johnson 1980; Rudzinski et al. 1982). Negative impacts on smaller, less dominant carnivores are not limited to direct predation. Habitat use can be influenced by interspecific competition, and a superior species can exclude an inferior species from its fundamental niche (Elmhagen et al. 2002; Hamel et al. 2013), which might even make it go extinct. During the last century the larger red fox has increased its range above the forest line, were it competes with the arctic fox for food resources and through direct interspecific interactions, including intra guild predation. The red fox may have contributed to the continued decline of the arctic fox (Elmhagen et al. 2002; Frafjord 2000; Frafjord 2003; Herfindal et al. 2010; Hersteinsson et al. 1989; Killengreen et al. 2007; Linnell et al. 1999a; Selås & Vik 2007).

Low population size

In small populations demographic stochasticity is strong (May 1973). Inbreeding depression, social dysfunction and problem finding a mate, can reduce growth rates in small populations (Lewis & Kareiva 1993). In a small population, genetic variation is more likely to decrease. The genetic variation in the arctic fox population in Fennoscandia have decreased, due to isolation, height above sea level, problem finding a mate, and productivities of dens (Linnell et al. 1999b). Abundance of prey might affect a predators' population dynamics. An example of this is the Arctic fox which has a higher reproduction success in years with high rodent abundance, while in years with low abundance of rodent reproduction is low (Meijer et al. 2013). The arctic fox population size need to be large enough to survive until the next increase in rodent abundance (Linnell et al. 1999b).

The combination of several negative factors depressing populations that are already at critically low levels can severely increase the risk of extinction (Caughley 1994; Singer et al. 2001). Norway, Sweden, and Finland have been working together to recover the Fennoscandia arctic fox population. Enormous effort has been extended running large-scale conservation measures during the past 10 years (Eide et al. 2016). Due to conservations actions, such as release of captive-born foxes, supplemental feeding and red fox control, there are now signs of increased population size in some areas (Angerbjörn et al. 2013; Eide et al. 2016; Landa et al. 2015). Studies have revealed that supplementary feeding during both summer and winter may have led to increased litter size, and survival of pups (Angerbjörn et al. 1991; Angerbjörn et al. 1995; Meijer et al. 2013)

Angerbjörn et al. (1995) found that supplementary feeding during winter had a positive effect on the probability of reproducing during summer and litter size increased, while supplementary feeding over the summer reduced pup mortality (Tannerfeldt et al. 1994). However, the effect of supplementary feeding varies with the rodent phase (Meijer et al. 2013). The high cost of many conservation measures and the high stakes – survival vs. extinction of populations or even species - demand that the magnitude and mechanisms of their impact are assessed and understood. Although previous studies point towards positive effects of supplementary feeding on arctic foxes in Norway, many questions remain. In this thesis I investigated the relationship between food utilization (diet) and breeding success of feed arctic fox pairs, and test hypothesis relating to the "food limitation hypothesis", using the ongoing supplementary feeding program by the Norwegian Institute for Nature Research as an experimental platform for my study. I test the following hypothesis:

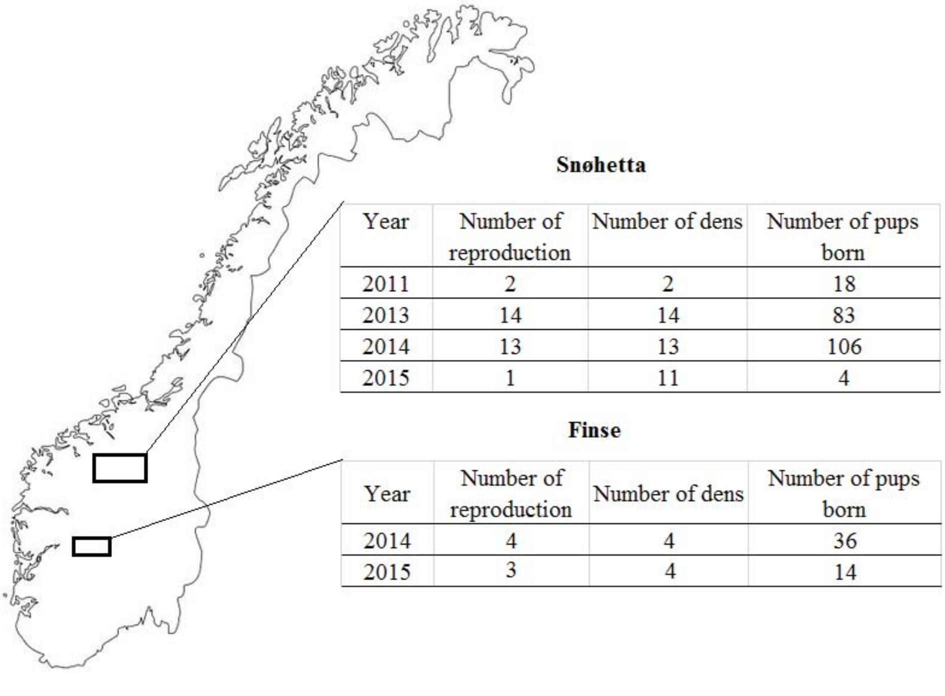
- H1: Arctic fox utilize supplementary food provided at feeding stations. Utilization is higher during years with unfavourable environmental conditions and low natural prey availability.
    - P1.1: The proportion of supplementary food in arctic fox faeces reflects the availability of active feeding stations in the den area. I expect that the proportion of supplementary food in faeces declines with increasing rodent abundance.
    - P1.2: The proportion of supplementary food in faeces declines with more environmental conditions for energetics and prey availability (increasing temperature, declining snow cover and snow duration)
- H2: Arctic fox reproduction is food limited and is greater during times with higher prey abundance.
    - P2.1: The rodent index (TOV) and/or the proportion of rodents has a positive effect on both the probability of producing a litter and litter size.
- H3: Use of supplementary food has a positive effect on Arctic fox reproduction and compensates for food limitation caused by low natural food abundance

- P3.1: Both the probability of producing a litter and litter size increase with an increased in the proportion of supplementary food in the diet or, alternatively, with the availability of supplementary food in vicinity of the den.
- P3.2: I predict that supplementary feeding will have the highest effect on reproduction in years with low rodent availability.

Material and methods

Study sites

This study was conducted in two arctic fox populations in central Norway (Figure 1). The mountain area Snøhetta consists of Dovrefjell-Sunndalsfjella national park (1.693 km² total area, 62° 21' 00 " N, 9° 6' 00" E) and some parts of Knutshø (23° 09' 33" N, 169° 36' 705" E). The Finse area consists of Hallingskarvet national park (67° 41' 465" N, 90° 24' 4" E) and an area between Hallingskarvet national park and Hardangervidda national park. The climate in these areas are long winters with short summers, snow cover from November until May and a short growing season from June until August (Sandvik et al. 2004; Strand et al. 2013).



Snøhetta

Year	Number of reproduction	Number of dens	Number of pups born
2011	2	2	18
2013	14	14	83
2014	13	13	106
2015	1	11	4

Finse

Year	Number of reproduction	Number of dens	Number of pups born
2014	4	4	36
2015	3	4	14

Figure 1. Number of dens, reproductions and number of pups born in different year, and regions.

Snøhetta region is a mountain plateau in the southern part of Norway, which lies in the alpine zone. It stretches from low alpine zone with shrubs and diverse vegetation to high alpine zone, with glaciers and mostly moss and lichen. The elevation of the mountain area ranges from approximately 1000-2286 meters above sea level (Bakkestuen et al. 2010). A minimum estimated of the arctic fox population size in Snøhetta was 23 individuals in 2015 (Eide et al. 2016).

Finse lies on the watershed between the western and eastern part of southern Norway, with Hardangerjøkulen in the south and Hallingskarvet in the north. Most of the region lies in the high alpine zone with many large and small glaciers ranging from approximately 1100-1900 meters above sea level. The vegetation cover is patchy and dominated by mosses and lichens (Klanderud & Totland 2007). An minimum estimated of the arctic fox population size in Finse was 17 individuals in 2015 (Eide et al. 2016)

Dominant animal species in both areas include small rodent species such as Norwegian lemming (*Lemmus lemmus*), field vole (*Microtus agrestis*), tundra vole (*Microtus oeconomus*) and grey-sided vole (*Myodes* rufocanus), wild reindeer (*Rangifer tarandus*), hare (*Lepus timidus)* and ptarmigan (*Lagopus*). The largest mammal species available as food for arctic fox in both regions are wild reindeer, carcasses of which are scavenged on by arctic foxes. The Snøhetta region there have been approximately 2700 wild reindeer in 2013-2015 (*Snøhetta villreinområde* 2016). The Finse area is part of the region Norefjella, which had approximately 2000 wild reindeer in 2014 and 2015 (*Nordfjella villreinområde*). Most reindeer carrion are a result of starvation, accidents and slaughter remains from hunter-killed animals (Landa et al. 1997). On Svalbard arctic fox has in some incidences killed reindeer calves (Prestrud 1992), but such kills have not been documented in any literature of my study areas.

Supplementary feeding

The Captive breeding programme has developed feeding dispensers exclusive for the arctic fox (Landa et al. 2016). Release areas and sites are prepared with a network of feeding stations that are placed close to locations with old arctic fox dens as well as at geographically selected locations to connect release areas when there are long distances in between release sites in Snøhetta and Finse. Feeding stations are built of plastic barrows (120 litres) with a plastic tube wide enough for the arctic fox, but to narrow for the larger red fox or wolverine to enter (Landa et al. 2016) (Figure 2).

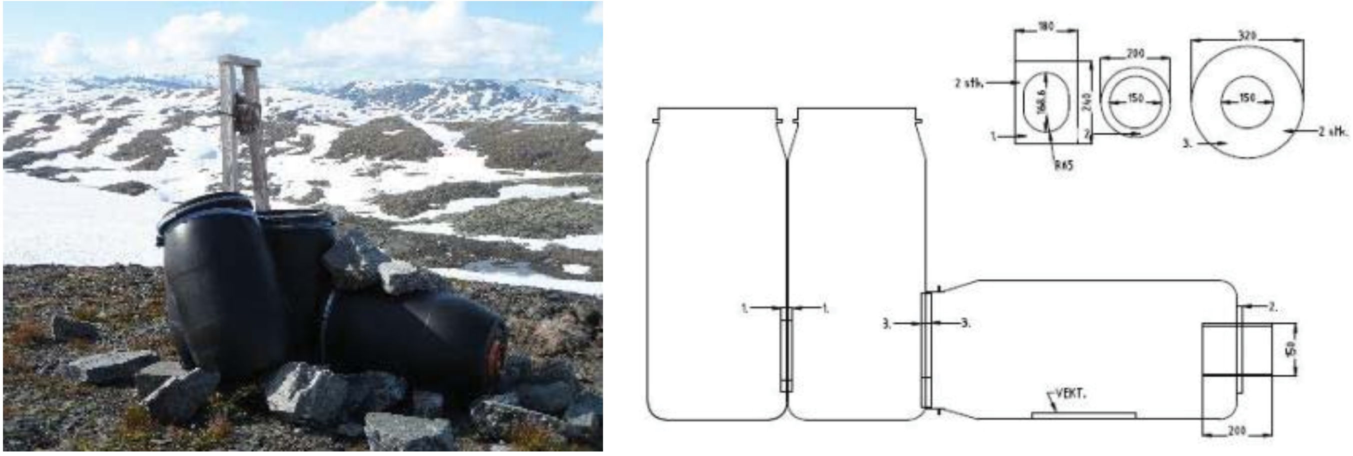


Figure 2. Illustration of a design of a feeding station (Roger Meås, NINA) and a picture of a feeding station. Foto: Aina-Elise Stokkenes.

Den site monitoring

All 24 active natal den sites in the two study areas (Snøhetta: N=19; Finse: N=5) were visited during summers annually between 2011-2015. Reproduction was first confirmed by the national monitoring program, subsequently visited by the captive breeding program to estimate litter size and mark pups. Litter size was estimated by one visual observation attempt at distance (250 - 500 meters) in at least 30 minutes, from the start of July until beginning of August. There are a possibility that not all pups were observed (Eide et al. 2016). In total there had been six reproductions with a total of 36 pups in the Finse region in 2014 and 2015. In the Snøhetta region there have been 30 reproductions with 247 pups born during the years 2011 and 2013-2015. Arctic fox can use more than one den when raising a litter, and do often move between two dens (Prestrud 1992). In my study 14 litters were moved between dens. When a litter used more than one den, the scats from these dens were lumped as belonging to one den (or one litter) in the analysis.

Scat collection and diet analysis

Fresh scats for the diet analysis were collected at the end of the breeding season from 2 dens in 2011, 14 in 2013, 17 in 2014 and 15 in 2015 from the Snøhetta region. Fresh scats from Finse were collected from 4 dens in 2014 and 2015. In total there were analysed 413 faeces.

Scats analysed from the study were collected during June-September 2011, 2013-2015. Old scats were discharged. Scats from adult and juvenile foxes were not separated. After collection, the scats were stored in a super freezer for five days, at - 80°C, to kill potential eggs from the parasite *Echinococcus multilocularis*, which pose a serious risk to human health. Between 8-15 scats were analysed per breeding den, summing up to 16 faeces from 2011, 116 from 2013, 151 from 2014, 130 from 2015, 413 scats in total.

Before analyses, each scat was dried at 50 ˚C for 15-48 hours. Then each scat was washed in a sieve with a diameter of 0.5 mm until the water was clear, and then dried again for 12-48 hours. Remains were separated into categories: reindeer, moose, red deer, roe deer, rodents, domestic sheep, passerine birds, ptarmigan, hare, arctic fox, unidentified bones, plant material, and dog food.

To assist identification of dog food in scats, 3 gram of dogfood was soaked in water for 24 hours. The resulting mass was exposed to the laboratory protocol for processing faecal samples described above yielding reference material for comparison with faecal contents (Figure 3a, 3b).

Figure 3a. Washed dogfood for reference. **3b.** Dry dogfood before washing

Hairs and feathers were identified to species level, using microscopic characteristics following published identification keys (Day 1966; Williamson 1951) and reference collections. I visually estimated the contribution of each species in the hair and feather category to the nearest 5 %.

Rodent phase and abundance index

Small rodents were systematically snap-trapped each summer in September, in both regions under the Terrestrial Monitoring program (TOV), and an index was calculated using numbers for how many rodents trapped per 100 nights (Framstad 2016). For the Snøhetta region the snap-trapping was conducted in the valley Åmotsdalen, while in the Finse region it was conducted in the area around Finse (Figure 4).

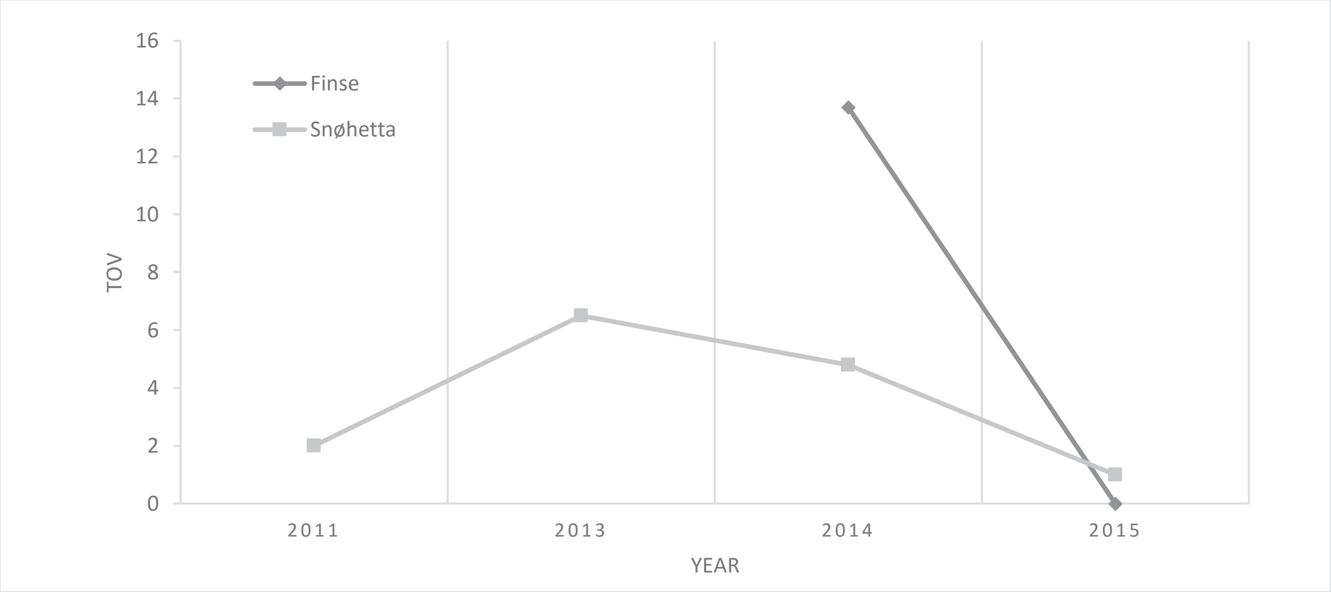


Figure 4. The summer index of rodents in Finse (dark grey) and Snøhetta (light grey) based upon the number of lemmings and voles caught during 100 trap days in September each year faces from the regions were selected and used in the analysis. The rodent population had a peak in Finse in 2014, and a declining phase in 2015. The rodent population had a declining phase in 2011 and 2014, an increase phase in 2013 and a low phase in 2015 in Snøhetta

Environmental covariates

Information about temperature, snow cover duration and snow depth were obtained from www.senorge.no and are provided by the Norwegian Water Resources and Energy Directorate and the Norwegian Mapping Authority. Average temperature and snow duration were extracted for each den for each year. Snow cover duration was based on continuous snow cover above 10 cm depth (Bartoń & Zalewski 2007), calculated for each winter season for each den.

Data analyses

Statistical analyses were performed using the software R, version 2.15.1 (R Core Team 2014). The proportion of diet items in a given scat summed to 1, thus changes in the contribution of diet item affected that of all other items. I used principal component analysis (PCA) to investigate patterns in diet composition and to derive predictors (principal components, PC) for subsequent analysis that took into account the relationship between multiple diet items. Further in the analysis I used PC axis one and axis two, to keep the most variance with the fewest number of variables possible. A principal component analysis is a multivariate technique for the analysis and visualization of data where observations are composed of several correlated dependent variables (Abdi & Williams 2010). The main goal conducting a PCA is to reduce the dimensionality of datasets, which have a large number of related variables, but at the same time retain much of the variation present in the original data (Jolliffe 2002).

Supplementary food utilization (H1)

To test if supplementary availability, rodent abundance and environment had an effect on the supplementary food in the faeces, I conducted a Linear Mixed Effects Model using the function lmer (Bates 2015). I conducted an arcsine square root transformation on the proportion of supplementary food to deal with parameters which were unable to evaluate a scaled gradient and uniquely determined. The explanatory variable; winter season duration was scaled. Explanatory variables were tested as additive effects, and den id was set as a random effect. The most complex model had these explanatory variables; Rodent index, number of feeding stations closer than 200 metres from den, year, region, average temperature and average snow cover in a year, and winter season duration. Backwards selection was used to find the best model.

Reproduction (H2 and H3)

I conducted a separate Generalized Linear mixed effects model (GLMM) with R function glmer (Bates 2015) to test the effects of diet composition, rodent abundance and environment on the arctic fox reproduction with den id as random effects. Family was set to “binomial” and link function to “logit” (logistic regression), all explanatory variables were tested as additive effects.

Predictor variables were tested as multiple additive effects based on biological background. Winter season was scaled and used in the analysis.

To test the different covariate effects on the litter size, I needed to accommodate for an over-abundance of zero values in the data. To do this I used a Zero-Inflated count data regression with R function zeroinfl in the R Package Political Science Computational Laboratory (Jackman 2015) to test additive and multiple additive effects of rodent abundance, diet composition (PC values) and environment; Average snow cover, and temperature, and number of days in winter season, on the arctic fox litter size. Multiples additive variables was chosen based on biological meaningful combinations.

Model selection was conducted using Akaikes Information Criterion (AIC). AIC is a measurement which shows how well the data is fitting the model against the explanatory variables, and therefore do AIC give a foundation for choosing the best model after the parsimony- principal. The best model was found using a difference in 2 AIC units between the candidate model and the top model (Arnold 2010). If models had less than 2AIC units in difference, the model with the fewest explanatory variables was picked as the best model.

Results

Diet composition

Rodents were the most common diet item in faecal samples of arctic fox (73 %), then vegetation (9 %), and dogfood (6%). Ptarmigan constituted only 1.7 % and wild reindeer only 1.9 % (see Figure 5). Arctic fox fur comprised on average 3.3 %, and never more than 11.25 %. The “other” category contributed 6.7 % in total of both regions. The composition of the diet was very similar in 2011, 2013, 2014 and 2015 (Figure 5). Rodent absent in faeces varied between 67-81 % in Snøhetta, with 81 % in 2011, 67 % in 2013 and 2015 and 72 % in 2014. Finse had a larger proportion of rodent in their faeces; 74 % in 2014 and 83 % in 2015. The proportion of dogfood in faeces varied between 2.7-3.9, with 11 % in 2015, 5% in 2014, 10% in 2013 and 4 % in 2011, while in Finse there were 7 % in 2014 and 1 % in 2015. Vegetation in Snøhetta varied between from 2.5 % in 2013 to 12.54 % in in 2015, and in Finse the proportion of vegetation varied between 9.0 % in 2015, and 5.6 in 2014.

PC1 and PC2 obtained during the PCA explain approximately 47 % (PC1: 31.02%; PC2: 17.63%) of the variation in correlation between the variables (Figure 6). Higher values of PC1correspond to an increasing proportion of rodents and unidentified bones, and the PCA suggest that perhaps most unidentified bones belong to rodent. With lower values of PC1 there are a decrease in the proportion of dogfood and vegetation. With an increasing value on axis two (PC2) the proportion of ptarmigan, passerine, arctic fox and reindeer increases in the faeces. (Figure 6).

Supplementary food utilization (H1)

Following backwards selection based on AIC, the GLMM with supplementary food availability emerged as the top model predicting the proportion of dog food in arctic fox faeces. According to this model, availability of an active feeding station within 200 meters had a positive effect on the proportion of dogfood in the diet of arctic foxes ($\beta = 0.16$, $t=2.83$, $p<0.01$).

Reproduction (H2 and H3)

The GLMM with rodent index, PC1 and PC2 from diet analysis as covariates emerged as the top model (based on AIC) predicting the probability of reproduction of arctic fox at monitored dens

(Appendix 1). Rodent index exhibited a positive effect on the probability of reproductions (β=25.89, SE=4.06, z=6.37, p<0.01), whereas PC1 (β=0.79, SE=3.55, z=0.23, p=0.82) and PC2 (β=0.56, SE=4.98, z=0.11, p=00.91) were positively, but not statistically significant. I detected no effect of proportion of dogfood in faeces (β=-2.44, z=-1.27, p=0.20), or the availability of supplementary food closer than 200 meters (β=-1.46, z=-1.31, p=0.18), on arctic fox reproduction.

Model selection based on AIC identified as the top zero-inflated Poisson model, the model with rodent index as a predictor on both the count component and the binomial component (Appendix 1). Higher rodent index had a significant negative effect on the probability of producing an extra 0 (β=-1.03, SE=0.38, z=-2.69, p=0.007). The coefficient associated with the effect of rodent index on litter size (count component) was positive but not statistically significant (β=0.02, SE=0.02, z=1.5, p=0.13).

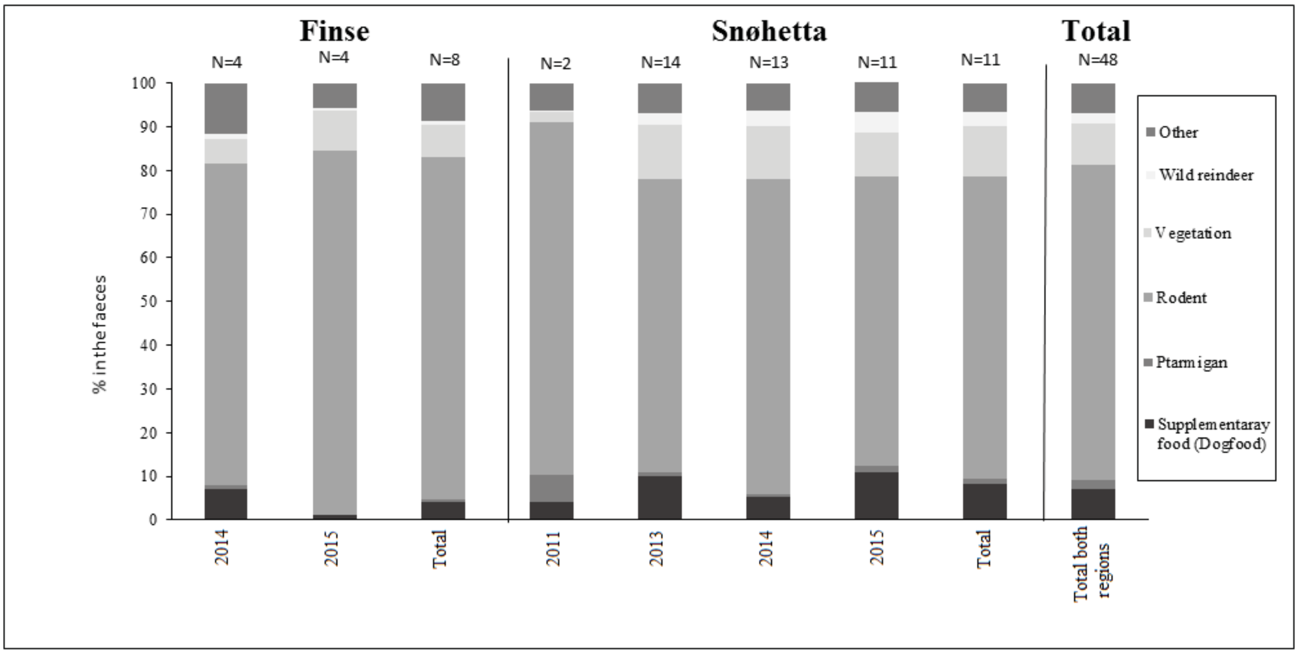


Figure 5. Diet composition in arctic fox faeces at den sites during 2011, 2013-2015 at Snøhetta and 2014 and 2015 at Finse. The term "Other" refers to moose, sheep, deer, passerine, hare, muskox, arctic fox and unidentified bones.

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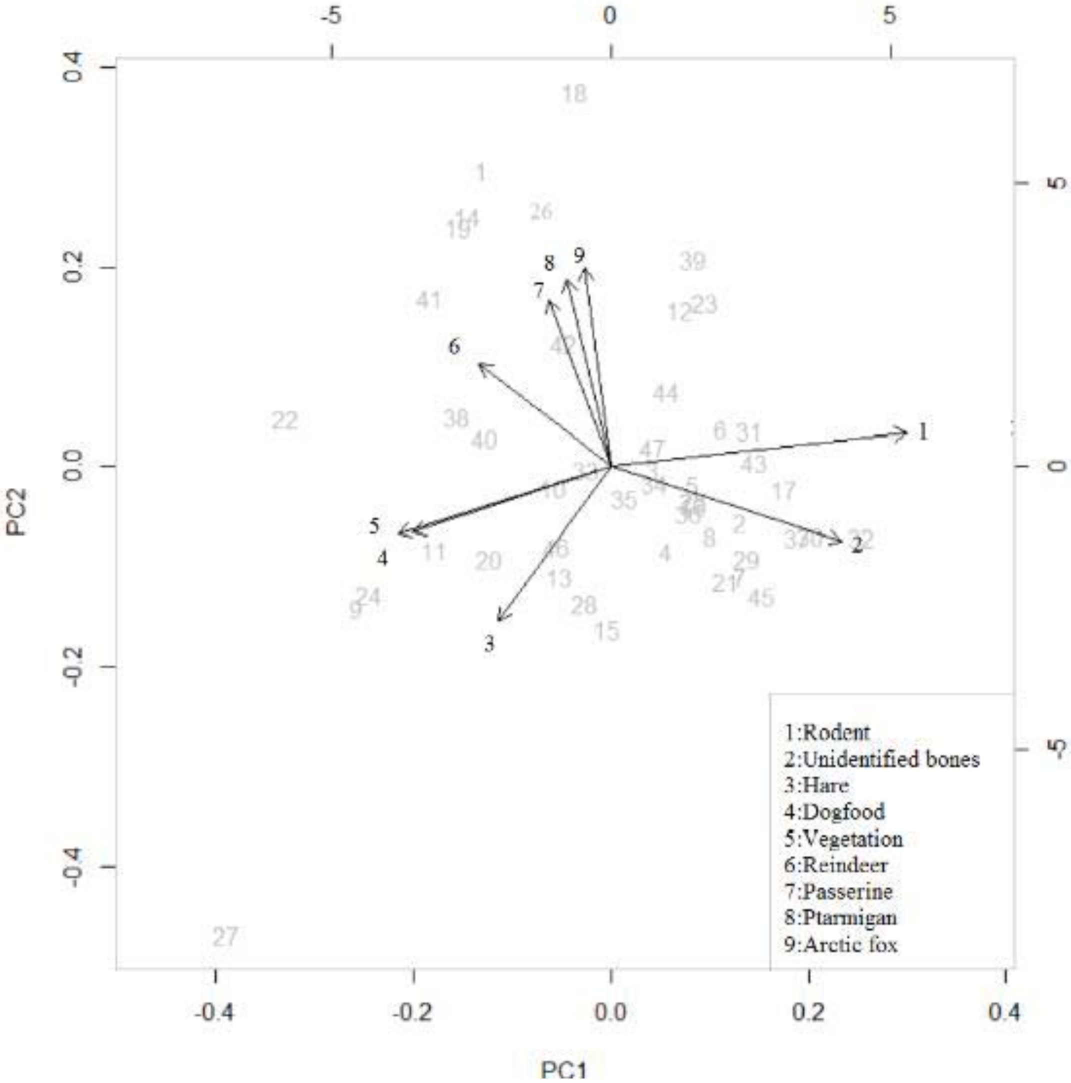

Figure 6. Principal Component Analysis (PCA) of faeces content. Den numerations: grey numeric symbols, black arrow symbolizes different diet content

Discussion

My study revealed that artic fox utilize supplementary food when available and that proportion of dog food consumed increased with declining proportion of rodent prey in the diet. The results did not clarify the relationship between supplementary feeding and reproduction in the context of environmental conditions and natural prey availability. However, findings should be informative for arctic fox management in Scandinavia.

Diet composition and use of supplementary food

The diet analysis show that rodents are the main prey in all years and in both regions with little between-year variation. These findings are consistent with earlier studies from Snøhetta (Strand et al. 1999). Arctic fox diet at Finse generally contained a higher proportion of rodents and lower proportion of reindeer, compared to Snøhetta, that had more vegetation and reindeer in their faeces.

The proportion of supplementary food found in the faeces varied between years and regions, in accordance with rodents: with an increasing proportion of dogfood in the faeces the proportion of rodents decreased. The proportion of dogfood in the faeces could be effected by variation in snow cover. When feeding stations are under snow, food might be out of reach for arctic fox. Temperature variation between years and seasonal variation might affect amount of snow cover, snow composition and arctic fox behaviour. However, I found no effect of temperature, snow cover and duration of winter season.

Other prey species were also detected in faeces, but represents only a small proportion of total diet contents. The assumption of diet analysis is that faecal composition reflects dietary habits in arctic fox. If this is the case, the results suggest that alternative prey species are consumed, but, generally, do not constitute a significant part of diet. This implies that arctic fox shifts towards dogfood, resulting in a smaller prey niche, using more supplementary food and lower the number of different species in the diet. when it is energy efficient. When comparing feed and non-feed arctic fox dens, supplementary feeding had a positive effect on reproduction success when rodent abundance decreased (Meijer et al. 2013).

A higher proportion of ptarmigan and reindeer in faeces was found in the Snøhetta region than in the Finse region. The proportion of birds are low and foxes likely catch ptarmigan and passerines whenever available rather than actively selecting them. Other studies indicate that the ptarmigan is difficult to catch for the arctic fox during summer (Birks & Penford 1990; Larson 1960). Elmhagen et al. (2000) indicated that inconsistent pattern of bird remains in the faeces could be due to individual differences in the ability of catching birds, as well as regional differences in availability between home ranges. The difference in proportion of reindeer in different regions could be due to regional and local differences in the abundance of reindeer. In years with low abundance of rodents reindeer might make up a larger proportion of the arctic fox diet (Elmhagen et al. 2000), which is also the case for red foxes living in alpine environments (Killengreen et al. 2011).

Higher variance in the composition of diet was expected. The low variation in proportion of rodent could be due to a lack of data material from years with very low rodent abundance. Both Strand et al. (1999) and Elmhagen et al. (2000) found a high variation of rodent in diet with different rodent abundances. Strand et al. (1999) found that rodents always were the main prey with the highest percentage volume in scats inn all years, and suggest that a change in foraging dynamic, and especially in searching time might explain the relatively small change in the occurrence of rodents in faeces.

The reindeer populations in these areas are in good condition, and the amount of reindeer carcasses to scavenge might be low. Faecal diet contents variation could also have been low because arctic fox uses supplementary food instead of natural alternative prey. However, Fine (1980) and Angerbjörn et al. (1997) (as cited in Elmhagen et al, 2000) found indications that the arctic fox prefer natural prey and continues to hunt, even when they are using “artificial” food resources.

The lack of variation in diet composition could also be a result of sampling design weakness. With a small sample size, extreme or un-normal faeces, and imperfect detection of categories might have affected the analysis. The foundation of detecting dogfood in the diet has constraints, regarding how the experiment was done on dogfood. Non-random placement of supplementary feeding stations, and an unbalanced selection of dens could have impacted the study. There could also be a time lag from when a feeding station was set up and when arctic foxes started using the feeding station. Sample size of dens and faeces in different years varies and one have to look at these results with an uncertainty, especially 2011 in Snøhetta.

Effects on reproduction

There was a positive effect of rodent availability on reproductive success, and a relationship between diet composition (PC1 and PC2) and reproductive response was detected. Other studies have confirmed arctic foxes reproduce when the availability of rodents is high (Angerbjörn et al. 1995; Tannerfeldt & Angerbjörn 1996). Meijer et al. (2013) compared feed dens and non-feed dens, and found that supplementary feeding increased reproduction success in a decrease in rodent abundance, and winter feeding increased litter size most in years with an increase in rodent abundance. In years with low rodent abundance it was reported a lack of response in arctic fox reproduction, despite supplemental feeding (Meijer et al. 2013). This implies that supplementary feeding did not diminish the strong impact of rodent abundance, but supported a trade-off in addition to food determining arctic fox reproduction.

Differences in reproduction success between regions might be due to differences in intra-guild predation or competition with other predators Shirley et al. (2009). It is documented that arctic fox might be killed by dominant species (Frafjord et al. 1989), if a dominant species is visiting an arctic fox den or a feeding station it could have had direct and/or indirect effects on reproduction.

Most arctic fox females mate every year (Macpherson 1969), the amount of stored fat explains the number of egg at ovulation or number of embryos implanted (Hall 1989). Resorption and abortion are known to be common in foxes (Englund 1970; Macpherson 1969) and linked with food availability (Englund 1970)(Englund1970). Reproduction and litter size are dependent on female condition, and when there is little natural food, supplementary food does not give females enough energy to breed successfully and she resorbs or aborts her litter. When natural food abundance reaches a certain level, supplementary food begins having an effect on breeding success (Angerbjörn et al. 1995)

Arctic fox litter size is depending on rodent abundance (Angerbjörn et al. 1995; Kaikusalo & Angerbjörn 1995; Meijer et al. 2013). During an increase in rodent phase, specialist predators on rodents have shown to invest a larger reproductive effort than during peak phase. This is likely because it is the best chance for the offspring to survive (Korpimäki & Hakkarainen 1991; Lindström 1988).

In accordance with other studies (Elmhagen et al. 2000; Herfindal et al. 2010; Strand et al. 1999), my findings confirm that arctic fox is dependent on rodents and are vulnerable to changes in the rodent cycle. The irregularities in the rodent cycle during the last decades, have led to prolong periods of food scarcity for the arctic fox (Angerbjörn et al. 2013; Henden et al. 2008; Ims & Fuglei 2005; Loison et al. 2001). Consistent results from different climate models suggest that the high amplitude peaks in the rodent dynamics will fade out and be replaced by low amplitude cycles and irregular dynamics or low abundance of rodents (Gilg et al. 2009; Ims et al. 2008). Changed lemming dynamics might have enormous knock- on effects on trophic linked species (Schmidt et al. 2012).

Implications - optimizing conservation efforts

The effects of supplemental feeding vary, based on animal behaviour, intensity and customization (Ewen et al. 2015). Body condition, growth rates, survival and reproductive success might be improved by supplementary feeding in general (Draycott et al. 2002; Elliott et al. 2001; Jonsson et al. 2002). My results from the diet composition showed that rodent was the main prey, while supplementary food was found in varying proportions between years and regions, this indicates that in some point the arctic fox do find supplementary food more beneficial than to hunt or scavenge on carcasses.

My results did not allow me to generate guidelines for optimizing the use of supplementary feeding as a conservation measure for arctic fox. Meijer et al. (2013) found that arctic fox reproduction and litter size were positively correlated with rodent abundance. Arctic fox had several reproductions and larger litter sizes when arctic fox had supplementary food in decrease and increase phases of rodent abundance compared to non-feed dens (Meijer et al. 2013). In years with low abundance of rodents do Henden et al. (2009) recommend direct actions towards increased survival, while in years with an increase and decrease in rodent phase the actions should be directed towards reproduction. I would suggest to continue with supplementary feeding according to Henden et al. (2009), and change design of the study according to recommendations put forward in this thesis and Meijer et al. (2013), and test the effect of supplementary feeding once more.

Recommendations for further studies

In further studies of this kind, feeding stations should be randomly designated to dens, to allow for treatment comparisons and establishment of causality. In addition, unless faeces from all dens are collected and processed for diet analysis, selection of dens to be sampled should be random. In addition, the proportional contribution of dog food to faecal contents vs. diet should be established under controlled conditions, e.g. through a feeding experiment.

Further research is needed to investigate possible predator effects on arctic fox reproduction and litter size at den sites and around feeding stations. There is also a need to investigate the role of supplementary food provision for attracting competitors and predators, and how this will affect the arctic fox population.

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Appendix 1:

Table 1. Response variable in the model are reproduction and litter size with different explanatory variables. Choice of best model (top model) is based on the lowest Akaike Information Criterion (AIC). Delta AIC (dAIC) is the difference between the candidate model and the best model.

Explanatory variables	*Reproduction*		*Litter size*	
	AIC	dAIC	AIC	dAIC
~1	49	24	245	21
PC1 from diet analysis	51	26	247	23
PC2 from diet analysis	49	24	246	22
Region	51	26	229	5
Number of feeding stations closer than 200 meters	49	24	244	20
Summer abundance of rodents (TOV)	29	4	**224**	**0**
Average temperature	51	26	247	23
Average snow cover	48	23	244	20
Length of winter season	50	25	246	22
Multiple explanatory variables				
Summer abundance of rodents (TOV) + Number of feeding stations closer than 200 meters	30	5	227	3
Summer abundance of rodents (TOV)+PC1 from diet analysis + Number of feeding stations closer than 200 meters	30	5	228	4
PC1 from diet analysis+PC2 from diet analysis + Summer abundance of rodents (TOV)	**25**	**0**	228	4
PC1 from diet analysis + PC2 from diet analysis + Number of feeding stations closer than 200 m	49	24	249	25
PC1 from diet analysis+ PC2 from diet analysis+ Number of feeding stations closer than 200 meters + Average temperature	51	26	249	25
PC1 from diet analysis+ PC2 from diet analysis+ Number of feeding stations closer than 200 meters + Length of winter season	51	26	249	25
PC1 from diet analysis + PC2 from diet analysis + Number of feeding stations closer than 200 meters + Summer abundance of rodents (TOV)	29	4	231	7

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