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Arctic fox diet in Yamal peninsula

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BIO-3950 Master thesis in Biology, Northern populations and Ecosystems
May 2015

Abstract

Arctic fox in inland areas has been typically described as a species dependent on rodent populations, but being able to use alternative prey, therefore named an opportunistic specialist. Rodent populations in the low shrub tundra of southern Yamal peninsula exhibit at present low amplitude cycles. The hypothesis for this thesis is that the low abundance of small rodents is not enough to sustain arctic fox population numbers, and there is a need for alternative prey resources. This study uses four methods to assess the diet of the arctic fox in the low shrub tundra of southern Yamal peninsula: picture identification, identification of prey remains, scat analysis and stable isotope analysis. Results of the scat analysis showed that there was no differences between the presence of rodents in the diet in 2013 and 2014, a year with relatively higher and lower small rodent abundance respectively. The presence of birds was higher in the diet during 2013 than 2014. PCA showed a more varied diet in 2014 than in 2013, likely due to the presence of reindeer carcasses in the tundra. Stable isotope analysis supported the importance of *Microtus* species, previously found in the scat analysis. Correlation between numerical responses of the arctic foxes, quantified as the number of active dens, and the rodent abundance was not found. It seems that arctic foxes in the low shrub tundra of southern Yamal peninsula are following a generalist strategy.

Key words: Vulpes lagopus; Yamal peninsula; rodent cycles; diet; scat analysis; stable isotope analysis; numerical response.

Table of Contents

1. Introduction

Food chains in tundra communities may seem simple (Ims & Fuglei 2005) at first sight and they have been typically described by three basic trophic levels: plants, herbivores, and carnivores. However, when we take a closer look at the different guilds, their biological interactions, population dynamics and the interplay with other systems, then, these tundra communities become more complex.

Trophic dynamics in the Arctic are characterized by fluctuating populations of key stone species, lemmings and voles, which hold a whole predator guild. Rodent populations fluctuate with peaks every 3 to 5 years (Erlinge et al. 1999) simultaneously over large spatial scales (Christiansen 1983). The most accepted hypothesis to explain rodent cyclicity states that trophic interactions driven by a set of predators are responsible for this pattern. These predators are responsible for the fluctuations in amplitude and period of the cycles (Gilg et al. 2003; Berryman 2002).

Typical arctic predators interacting with rodent populations are stoats, arctic foxes, skuas and snowy owls. Arctic foxes, skuas and snowy owls stabilize lemming populations by preying on rodents after the snow melts, meanwhile, stoats induce multiannual fluctuations by preying on rodents throughout the year (Gilg et al. 2003). All these species have species specific numerical and functional responses (Gilg et al. 2006) and are to a greater or lesser extent specialized on lemming populations.

Climate change has been characterized as the most serious threat to Arctic biodiversity (Reid et al. 2013). Rodent populations, in particular lemming populations, are hypothesized to be dependent on winter snow conditions to be able to breed. Therefore climate change is predicted to affect their cycles by affecting winter conditions and snowmelts (Kausrud et al. 2008; Ims et al. 2011). This new scenario would initiate cascading effects on the ecosystem with serious consequences for the predator guild dependent on these species (Kausrud et al. 2008; Ims et al. 2011; Schmidt et al. 2012). However, since rodent species and their cycles are different across the Arctic, these changes will not have the same consequences at every location. Examples of different population dynamics are found across arctic locations. In Varanger, Norway, Norwegian lemming (*Lemmus lemmus*) populations show a cyclic

pattern with peak years in 2007 and 2011 and abundances going up to 15 animals per hundred trap nights. On Bylot Island, Canada, collared and brown lemmings (*Dicrostonyx groenlandicus* and *L. trimucronatus*) also show this cyclicity with abundances going up to 5 animals per hundred trap nights during the peak year in 2000-2001 (Gruyer et al. 2008). All along coastal Siberia the cyclic populations of Siberian lemming (*L. sibiricus*) varied from 6 to 30 animals per hundred trap nights during 1994 (Erlinge et al. 1999).

Arctic fox, *Vulpes lagopus* (Table 1), is the smallest species of the family *Canidae* and is the only mammalian predator endemic to the Arctic with a circumpolar distribution. It has developed morphological adaptations to cope with the extremely harsh environmental conditions of the high Arctic (Blix 2005). They live in couples (Goltsman et al. 2011) or small groups dominated by a single male and one or two females. Adults can be territorial and aggressive towards strangers (Korhonen & Alasuutari 1995).

Spatiotemporal distribution, predictability and availability of food resources determine different habitat use, life strategies and different use of prey communities (Fuglei & Ims 2008; Goltsman et al. 2011; Meijer et al. 2013). The availability of food has a direct impact on breeding, litter size and offspring survival. Consequently, two tundra arctic fox ecotypes can be considered: inland or lemming foxes, and coastal or island foxes.

Lemming foxes inhabit inland territories and are specialized on cyclic small rodents (Fuglei & Ims 2008; Meijer et al. 2013). The population respond numerically to lemming and vole cycles and their peak years coincide with the peak of rodents, every 3 to 5 (Dalerum & Angerbjörn 2000). Their principal food resources are small rodents, as well as for some of their competitors such as the red fox (Angerbjörn et al. 1995). During rodent peak years, foxes feed extensively on lemmings and voles, and this is when the average litter size is large, with the maximum number of pups being 22 (Meijer et al. 2013). Contrary to this, during the low phase of rodent's cycles, foxes will not breed (Fuglei & Ims 2008; Meijer et al. 2013) and will shift towards alternative prey resources such as hare, reindeer carcasses, geese and ptarmigan (Eide et al. 2005; Fuglei & Ims 2008). Depending on the phase of the rodent cycle, arctic foxes will adapt and adjust their reproductive effort to these fairly predictable changes in resources. This is an example of a species well adapted to respond numerically to ameliorating conditions.

Coastal foxes are typically found on islands, such as Svalbard, Medyi Island, and Iceland, and in coastal areas, like West Greenland (Fuglei & Ims 2008). These areas are characterized by non-fluctuating rodent populations (i.e. Iceland) or an absence of them (i.e. Svalbard), and high seasonal variation in food abundance (Meijer et al. 2013). Spatiotemporal distribution of resources in these territories are more stable and predictable than in inland tundra areas (Fuglei & Ims 2008; Meijer et al. 2013). Coastal areas offer high abundance of alternative resources such as migrant and nesting seabirds and eggs (Eide et al. 2005), seal carcasses, and other potential prey. Due to these conditions, foxes are able to breed constantly through the years with a stable litter size of 4 to 6 pups, and sometimes up to 11 (Fuglei & Ims 2008; Meijer et al. 2013). The reproductive strategy is directly linked to the abundance of food resources with predictable and stable distribution in space and time, but this response is stronger in lemming foxes. Depending on the islands different feeding strategies can be described. On Svalbard (Eide et al. 2005) foxes are truly opportunistic. Meanwhile, the isolated population on Mednyi island experienced a bottleneck that leaded to a specialized strategy (Goltsman et al. 2011). In areas where arctic foxes depend on lemming populations, a decrease in these will drastically reduce arctic fox populations due to starvation of the juveniles.

Relative to feeding strategies, the arctic fox has traditionally been considered an opportunistic predator (Goltsman et al. 2011), though studies such as Dalerum and Angerbjörn (2000) placed it as semi-generalist feeder or as opportunistic specialist (Elmhagen et al. 2000). Specialist predators are well adapted to hunt and kill certain prey on which they base their reproductive response (Kausrud et al. 2008; Hamel et al. 2013). The abundance of specialist species is related to the abundance of their main prey (Andersson & Erlinge 1977). Generalist species use a wide variety of resources and do not base their reproductive success in any concrete prey abundances (Andersson & Erlinge 1977). Thus, an opportunistic specialist will be a specialized predator that is able to switch to alternative prey resources when the availability of the prey on which it specializes fluctuates.

Predators respond numerically and functionally to changes in prey abundances. Numerical responses imply an increase in numbers of predators when prey densities are

abundant. Arctic foxes respond numerically to the abundance of rodents (Gilg et al. 2006). Functional responses are due to prey densities and cause changes in the diet of the predator. Accordingly, three types of responses can be described (Smith, 1978). Type I: number of captures increase with the abundance of the prey. Type II: number of captures also increase with the number of prey but the predator expends some time in searching, hunting and handling the prey so that capture rate at high prey densities approaches an asymptote. Specialist predators show this type II response. Type III or generalist: the predator exploits a prey resource until its abundance drops down. Then the hunting efficiency is low and the predator switches to some other prey resource. Different responses have been described for arctic foxes. According to Gilg et al. (2006) arctic foxes have a functional response type III. Contrary to this, a type II functional response was described by Angerbjörn and Erlinge (1999). Since arctic fox diet varies at different locations, to establish a specific type of functional response is not useful. Besides this, the threshold to discern between type II and type III responses is not so clear.

The arctic fox diet has been studied at different locations documenting the specializations previously described. Conventional methods such as direct observation, stomach sampling (Fay 1994) and scats analysis (Angerbjorn & Erlinge 1999) are the most common methods for diet analysis. Currently, stable isotopes analysis is gaining influence (Ben-David & Flaherty 2012; Tarroux et al. 2012; Ehrich et al. 2015).

Isotopes are different forms of an element which vary in the number of neutrons and their atomic mass (Ben-David & Flaherty 2012). They provide information about the average diet of each individual during a certain period. (Angerbjorn et al. 1994). This period depends on the growth rate of the tissue used for the analysis. For example, fur will reflect the diet during the last moult. Nutrient flow through the different trophic levels is a consequence of predation and herbivory. Therefore, consumers will reflect the isotopic signature of the prey consumed with an enrichment factor. This means that the proportion of heavy isotopes at one trophic level will be a bit higher than the amount at the level below. The isotopic composition of a consumer is then a reflection of the isotopic composition of their prey (Kelly 2000).

Thanks to these nutrients used by organisms within the lowest trophic level, we can follow the pathway that stable isotopes show through the different trophic levels until the one where the species of our interest belong (Ben-David & Flaherty 2012). This method lead to the observation that carbon, C, isotope composition in birds and mammals reflects their dependence on terrestrial or marine food webs (Angerbjorn et al. 1994; Kelly 2000; Tarroux et al. 2012).

This master thesis was undertaken to determine the diet of the arctic fox in the low shrub tundra of southern Yamal peninsula, and to assess which prey resources they are using in order to sustain their population in a setting where the rodent abundance is low and relatively stable. Specifically I want to describe and compare the diet of 2013 and 2014, years with contrasting small rodent abundance and determine the preferred prey item; and compare the different methods used. Moreover, I will assess whether is evidence for a numerical response of the arctic foxes to the rodent abundance at this study site where rodent dynamics appear to less fluctuating many other tundra areas.

Table 1. Biology of arctic fox.

Scientific name	*Vulpes lagopus* (Linnaeus 1758)
Distribution	Circumpolar: arctic and alpine tundra regions of Fennoscandia, Eurasia, North America and Arctic Islands.
Adaptations	Winter fur, small and round nose ears and legs, insulative fat layer.
Diet	Rodents, birds and eggs, medium size mammals, reindeer and seal carcasses, fishes, crabs, mollusks.
Social system	Couples or small groups dominated by alpha couple.
Migration	Long journeys into the pack ice and taiga, when food resources are limited.
Status	Only mammalian predator endemic to the Arctic. Fennoscandia and islands in the Bering sea the population is vulnerable. In Russia, Canada, coastal Alaska and Iceland the population is stable.

2. Material and methods

A. Study area

Yamal peninsula, Russia, is located in the Arctic zone of the west Siberian plain and it is surrounded by the Kara Sea. The total surface, 122.000 square kilometers (Pika and Bogoyavlensky 1995), is a geologically young area covered by permafrost with vast reserves of natural gas. The nomad tribes inhabiting there, Nenets and Khantys, base their subsistence on reindeer herding. The number of semi domestic reindeer in 2013 was almost 400.000 heads. With a mean temperature of -25.7ºC in January and 8.6ºC in July and precipitations values around 350 mm per year, Yamal is covered with snow from early October until early June (Sokolov et al. 2012).

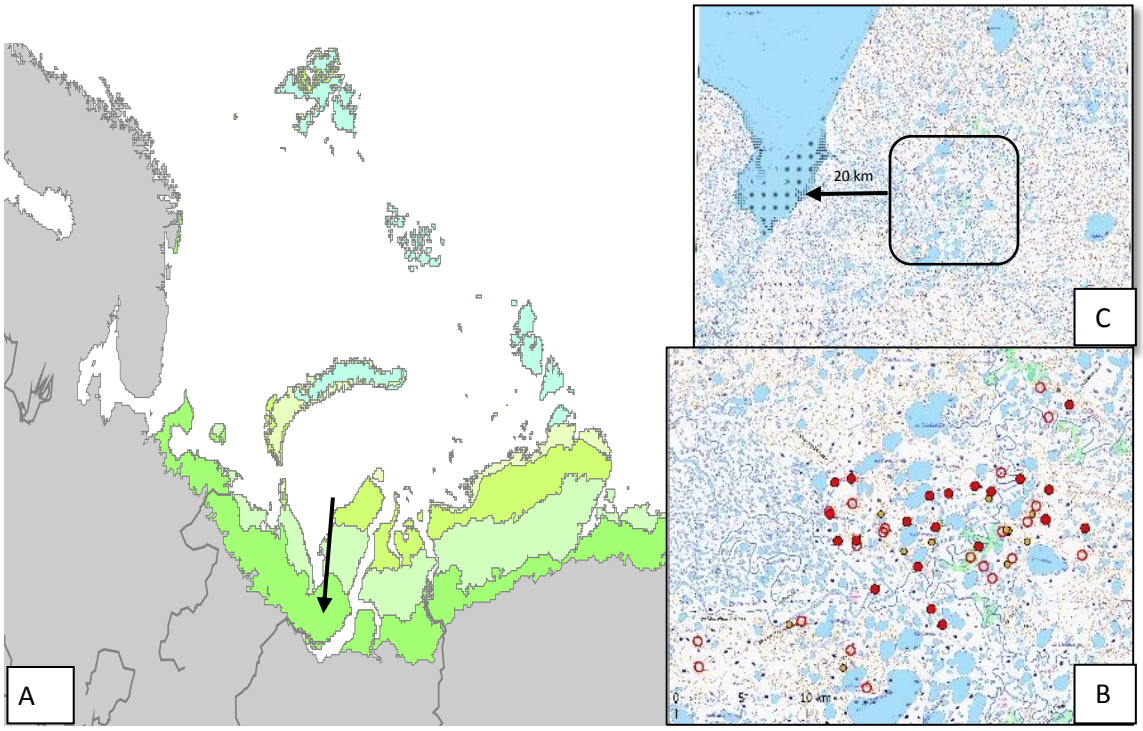

Fig. 1. A. Study area: southern Yamal peninsula in the bioclimatic subzone E, indicated by the arrow. B. Red dots show dens where reproduction has been recorded since 2007. Yellow dots: secondary dens with no reproduction observed. C. Study area, located 20 km inland from the sea.

According to the Circumpolar Arctic Vegetation Map, our study area (Fig. 1) located in southern Yamal, 68^0 16' 33'' N, 69^0 13' 33'' E, is considered within the bioclimatic

subzone E. This subzone is characterized by 80 to 100% cover of vascular plants and closed canopy, a moss layer of 5 to 10 cm deep, and a dwarf-shrub layer of 20 to 50 cm tall (Walker et al. 2005). The flat landscape is dominated by several freshwater lakes and ponds, and the main river, Erkuta, is surrounded by sandy cliffs where peregrine falcons nest. Aggregates of *Salix* sp. up to 2 m high are common the slopes. The ground dominating species are *Betula sp*, *Empetrum sp,* and mosses, resulting in a combination of wet and dry terrain, where the highest elevation is 52 meters.

Southern Yamal is an important breeding ground for migrating birds, such as geese, swans, waders, raptors and passerines. As resident predators, ravens (*Corvus corax*), artic foxes (*Vulpex lagopus*), wolverine (*Gulo gulo*) and stoats (*Mustela erminea*) are present in the area; and as herbivores, hare (*Lepus timidus*), ptarmigan (*Lagopus lagopus*) and rodents are some of the most representative species. Over the last 8 years the rodent populations have been fluctuating at low amplitude and low numbers, with abundances going up to 2 animals per 24 trap nights (Fig. 2) with small population changes during winter-spring (Sokolova et al. 2014). In this location, the last high amplitude peak was during 1999 (Sokolov 2003).

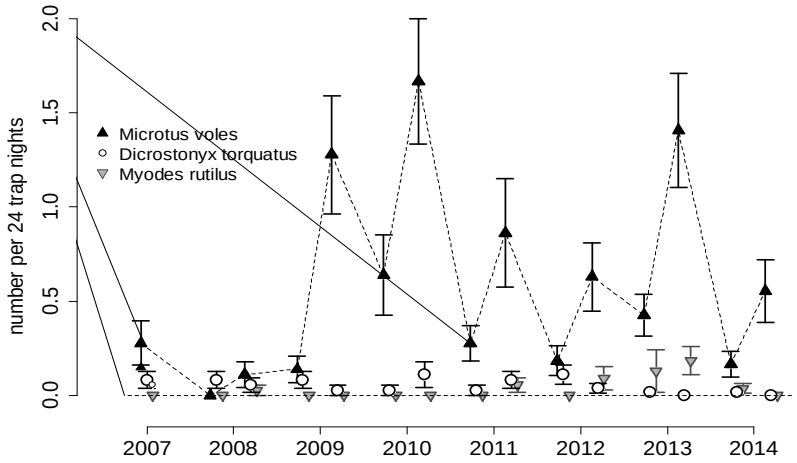

Fig. 2. Trapping data from the study area, Yamal. Rodents trapped since 2007 expressed in animals per 24 trap nights. Source: Sokolova et al. 2014.

B. Fieldwork

The study area is located 20 km from the sea, and it covers approximately 200 km^2 where 56 fox dens were already described from previous years (Fig. 1). Of those 56 dens, 21 of them were active (reproduction took place) since 2007, first year of fieldwork. It started with the study of eight active dens out of 15, during 2007, and a study area of 100 km^2, and was gradually enlarged during the following years, adding new dens and expanding the study area until the present date. Fieldwork was performed during 2013 by the Russian fieldwork team, from to 5th of June to 10th July; and from 25th of July to 10th of August. During 2014 fieldwork was performed from 15th June until 8th August. During the first ten days, all known dens were visited and inspected. During the first visit to each den, number of entrances, prey remains, scats, winter fur samples and signs of activity such as barking, fresh digging, strong smell and presence of beetles, were recorded. Old prey remains and old scats were removed to avoid mixing with the new ones. During the consecutive days, camera traps PC9000 Reconyx Professional were placed on the dens during the whelping season (June, July and August) of 2013 and 2014. Pictures were taken every 3 seconds when movement was perceived. The total number of pictures obtained was 70561. Reconyx MapView Professional was the software used to analyze the pictures. The following variables based on the pictures were recorded: Prey item, Nº of pups, Nº of adults, and Comments. The prey categories used were "Small prey", "Bird", "Medium prey", "Goose" and "Undefined". The aim was to recognize possible prey items the foxes caught for the pups and brought to the dens.

After setting the cameras, active dens were visited every ten days in order to look for new prey remains and fresh scat samples for diet analysis in the laboratory. Prey remains were noted and removed and fresh scats samples were stored in paper bags with the number of the den and the date. Each paper bag was considered as a batch. Hair samples and muscle samples from foxes' prey were collected for stable isotopes analysis. All the samples were dried under the sun.

C. Laboratory work

Scat analysis

Scat samples were taken during the fieldwork in 2013 and 2014. 21 samples were analyzed from each batch and considered as a representative number for the prey consumption of the habitants in a given den and per period. The scats were placed in water with soap during 24 hours and then placed for 15 minutes in a sonicator, which uses sound waves to disrupt the material so they became softer and easier to handle. After this, they were washed with running water in a small sieve. With the material obtained, a percentage of the volume was established for the following categories that were sorted out: small mammal hair (including hare and muskrat), mammal bones, feathers, bird bones, vegetation, fish remains, reindeer hair, insects and soil. Then I picked up the material used for the identification of prey items such as jaws, teeth, feathers, bones and elytron; and tried to identify them at the species level in the case of small mammals. I also marked the presence/absence of other items such as seeds, eggshells and hare hair. In the case of small mammals, I counted as one individual each time I found a hemi mandible, or one hemi mandible from the left and another from the right side. So, 3 hemi mandibles from the same species were counted as 2 different individuals if they belonged to the left and right sides, or 3 individuals if they were all from the same side. In the case of birds the reference for an individual was the beak or a foot with fingers. In the case of insects the reference for an individual was the elytron. All the data were noted down in the lab sheets.

Stable isotopes analysis

We worked with arctic fox fur, and with muscle or egg samples from some of their main prey and carcasses they scavenge on. These samples were required to be carefully cleaned, thus fat and hair was removed to avoid any contamination.

Stable isotope of winter fur samples are good indicators of the diet during the late summer/fall before the samples are collected on dens, as this is the time when the fur has been growing. To carry out the isotopes analysis I followed the protocol provided by Sinlab, Stable Isotopes in Nature laboratory, at the Canadian Rivers Institute.

Fur samples were checked under the microscope to determine their origin and sort out hare samples. The fur samples were washed with distilled water, then introduced into the sonicator in order to remove dirt, and dried at 55ºC. The fat was removed by washing the samples again with a mixture of chloroform and methanol 2:1 under the extractor hood, and then dried again for at least 24 hours. Finally, the fur samples were clipped as small as possible in order to homogenize the sample, weighed to 1,1 mg., packed in small tin cups and sent to the laboratory. A number of *77* samples of arctic foxes and prey were processed. They were taken during fieldwork in 2013 and 2014. The rest of the samples used were already analyzed and belonged to different fieldwork seasons since 2007 (Ehrich et al. 2015).

The muscle samples were previously preserved in ethanol. I proceed to remove the fat and fur from the original samples, clip the material in small pieces and wash it with ethanol. Then they were frozen at -80ºC in order to break the cell membranes and dried at 60ºC for 48 hours. The next step was to grind the samples to homogenize them. To do so, I added carbide beads into the Eppendorf tubes and placed them into a Wretch Mixer Mill for 4 minutes. This machine shakes the samples at high speed and as a result, the carbide beans mashes them. The result is completely powdered sample. Then I weighed 1,1 mg (milligrams) of it and packed it into tin cups, as I did with the fur samples.

To determine the proportion of stable isotopes of ^{13}C and ^{15}N the mass spectrometer was used. The samples were homogenized and small amounts of material were burned in the mass spectrometer in order to separate the ions of the elements of interest. The isotopic ratios were expressed as $\delta^{13}C$ and $\delta^{15}N$ as ‰ of the deviation from standard isotopic ratios: Pee Dee Belemnite carbonate for C and air for N (Kelly 2000).

D. Statistical analysis

Software R (R core team 2013) was used for the statistical analysis. Percentage of volume for each prey category (*percentage volume*) was estimated by calculating the mean abundance of each prey category per den, (*Den ID*) for each year. Relative abundance of

rodents in the diet was estimated by plotting the number of different rodent species found during the teeth identification.

Whole faeces equivalent (WFE) was calculated from the percentage volume of the prey categories rodents and birds. WFE provides a frequency equivalent to the number of fecal units that contain 100% of the prey category per each of the batches I had (Dalerum & Angerbjörn 2000). The result shows the total number of scats per batch equivalent to certain prey category.

$$WFE = (Average\ mean\ of\ Prey * N°\ samples)\%$$

Generalize linear mixed models (GLMM) with a logit link function and binomial distribution, together with R package lme4 (Bates D., et all. 2014) were used to estimate the differences in consumption of rodents and birds between years 2013 and 2014. To do so, the effect of the predictor variable *Year* on the response variables *Presence of rodents* (0/1), *Presence of birds*, *Whole Faeces Equivalent* (WFE) *of rodents* and *WFE of birds* was analyzed. *Batch* and *Den ID* were considered random effects, and the predictor variable *Year* and *Week* as explanatory variables. *Week* was included to test for differences in the season. In case of *WFE*, only *Batch* was taken into account as random factor.

In order to find out which variables explain the differences or similarities between the two years of study 2013 and 2014, Principal Component analysis, PCA, were used. Before the PCA, the data were transformed using the function clr (R package composition) to account for their compositional nature. The variables were: Small mammals, Birds, Reindeer, Insects, Vegetation and Unidentified. PCA transforms the observed data into linearly uncorrelated variables and tries to find linear combinations of the different variables in order to maximize the variation contained within them (Crawley 2007). The result is a new set of principal components or factors independent from each other, resulting from the combination of the original variables (Salinas P et al. 2006).

Levels of $\delta^{13}C$ and $\delta^{15}N$ of the consumer (arctic foxes) and prey of interest were analyzed graphically. Discrimination factors used for the isotopic signature of the foxes were taken from Lecomte et al. (2011). Differences between $\delta^{13}C$ and $\delta^{15}N$ between years

were tested with linear model analysis (LM). The response variables were $\delta^{13}C$ and $\delta^{15}N$, and the variable *Year* was considered as explanatory factor.

Numerical responses of arctic foxes to rodent abundance both in the same and previous year (i.e. a delayed response) were analyzed with a simple Pearson correlation analysis with *Number of active dens per 100 km*^{2} against *Rodent abundance in the trapping data*. The entire 8-year time series since 2007 were used.

3. Results

A. Photo identification of prey

Camera traps were set at entrances of active dens during 2013 and 2014. (Table 2 and Appendix 1). Photo identification was difficult due to the quality of the pictures. Most of the time, the arctic foxes were too far away or in motion. Also the prey they carried were unclear or too small to be distinguished. Geese were identifiable but rodents, passerines and other small prey were not.

Table 2. Active dens where camera traps where set during 2013 and 2014. Total number of pictures taken per den and number of pictures with presence of prey. The number below the prey types indicate the number of pictures where that prey was present. Most of the times it was the same item carried by the foxes back and forth.

			Pictures		
Year	Dens ID	Number of pictures	Rodents	Geese	Unidentified
2013	8	880	-	-	-
2013	22	490	-	-	14
2013	42	3221	11	57	62
2013	45	150	-	-	-
2014	2A	230	-	-	-
2014	21	10977	-	-	6
2014	23	28033	-	-	3
2014	39	240	-	-	-
2014	42	1054	-	-	-
2014	45	402	-	-	-
2014	47	1087	-	-	-

During 2013 only pictures from the dens 22 (July/August) and 42 (July/August) show arctic foxes carrying prey. In case of den 42, geese were taken to the den. This den is located next to a lake where geese are known to nest. During 2014, only dens 21 and 23 show foxes with prey. All of them were classified as “Undefined”.

B. Scat analysis

Figures 3 and 4 show the food content expressed as the percentage of volume of each prey category per den. The main prey category identified in 2013 and 2014 was rodent fur, with abundances ranging from 40% to 80%. During 2013 the prey category "Vegetation" (berries, grass, and small leaves) was the second in percentage of the volume. Seeds of *Rubus sp.*, were found when analyzing the batches, and we considered the rest of vegetation remains as "accidentally ingested" when eating something else. "Bird" category was important also, being present in most of the dens with abundances ranging from 10% to 30% of the total diet (feathers and bones). Egg remains (shells and inner membranes) and insects were found at one location, and reindeer fur was present at only two dens. Unidentified remains constituted an important percentage of the volume. Remains in this category were totally fragmented and the identification by sight was impossible.

Food content plot for 2014 shows that birds in the diet were the second preferred prey, with abundances going from 5% to 20%. Insects were found in small percentage at two dens with abundances of 2-3%, much lower than during 2013. The vegetation category was present in every den but never exceeded 10% volume. Reindeer fur was present in only one den and hare fur in two dens.

The only prey category that was not found at any den in 2013 and in 2014 was fish.

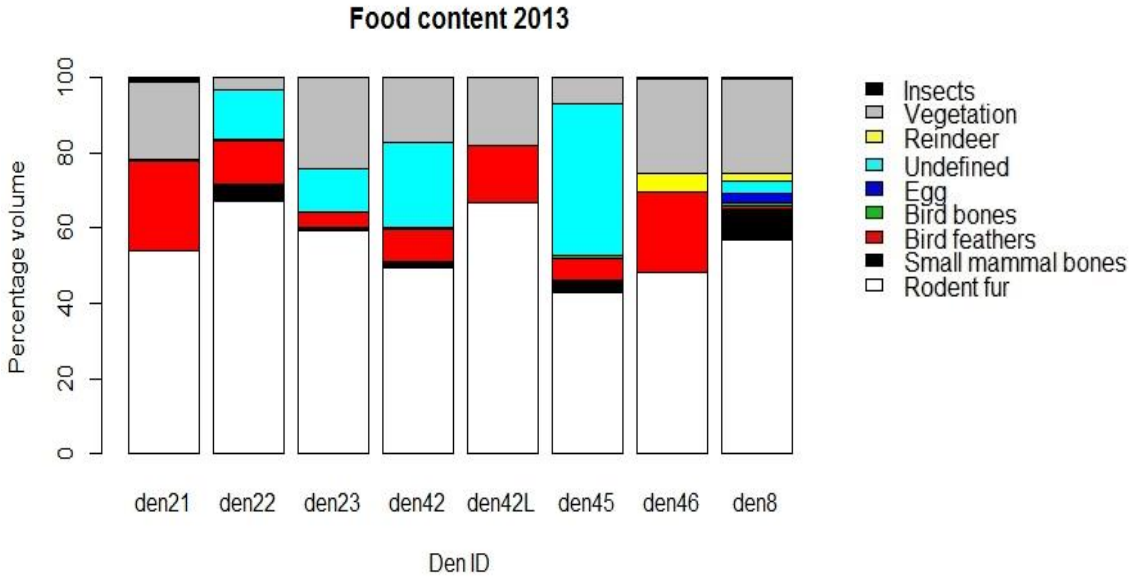

Fig. 3. Percentage in volume of food content during 2013 of the prey categories consumed at the different active dens.

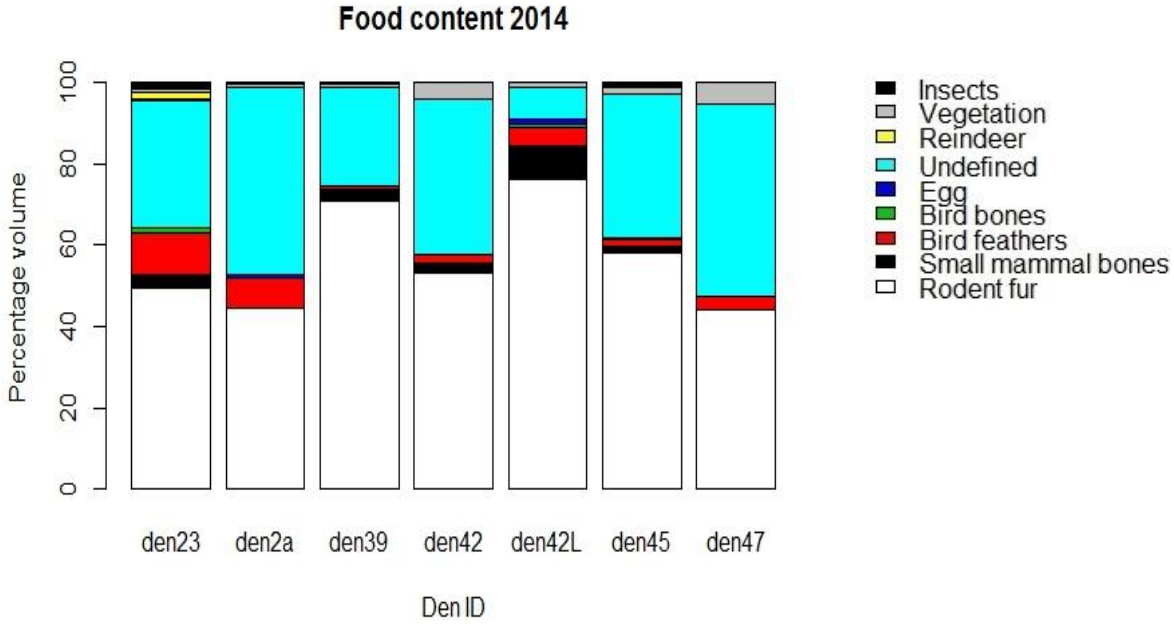

Fig. 4. Percentage in volume of food content during 2014 of the prey categories consumed at the different active dens.

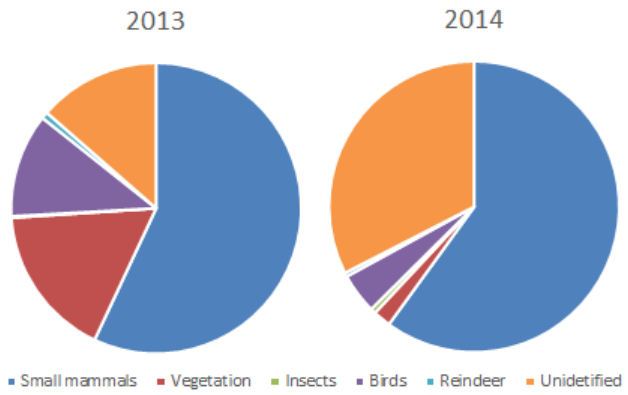

Fig. 5. Overview of the arctic fox diet during 2013 and 2013.

The most common rodent species in the dietary analysis were *Microtus* species*: M. gregalis*, *M. middendorffi*, and *M. sp.*; and *Dicrostonyx torquatus*, which are the three most common rodent species present in the area (Table 3 and Fig. 6). Only one single individual of *Lemmus sibiricus* was identified in the scats during 2013 and none during 2014. Hare was found also during 2013 but not during 2014. The "Small mammal" group is composed of unidentified rodents.

Table 2 shows the percentage of different rodent species found in the trapping data and scat analysis during the spring season (June) of 2013 and 2014. Total number of rodents trapped and present in the scat analysis was higher during 2013 than in 2014 (Appendix 2).

Table 3. Percentage of rodents in the trapping quadrats and scat analysis per year. Small rodents were trapped according to the method described by Sokolova et al. 2014 in three different habitats.

	Year	Dicrostonyx torquatus	Lemmus sibiricus	Microtus gregalis	Microtus middendorffi	Myodes rutilus	Microtus sp.	Small mammals	Hare
Trapping data	**2014**	8,3	0,0	58,3	16,6	16,6	-	-	-
	2013	3,2	0,0	61,2	12,9	22,5	-	-	-
Scat analysis	**2014**	9,8	0,0	49,1	34,4	0,0	0,0	6,5	0,0
	2013	21,2	1,2	31,2	21,2	0,0	10,0	13,7	1,2

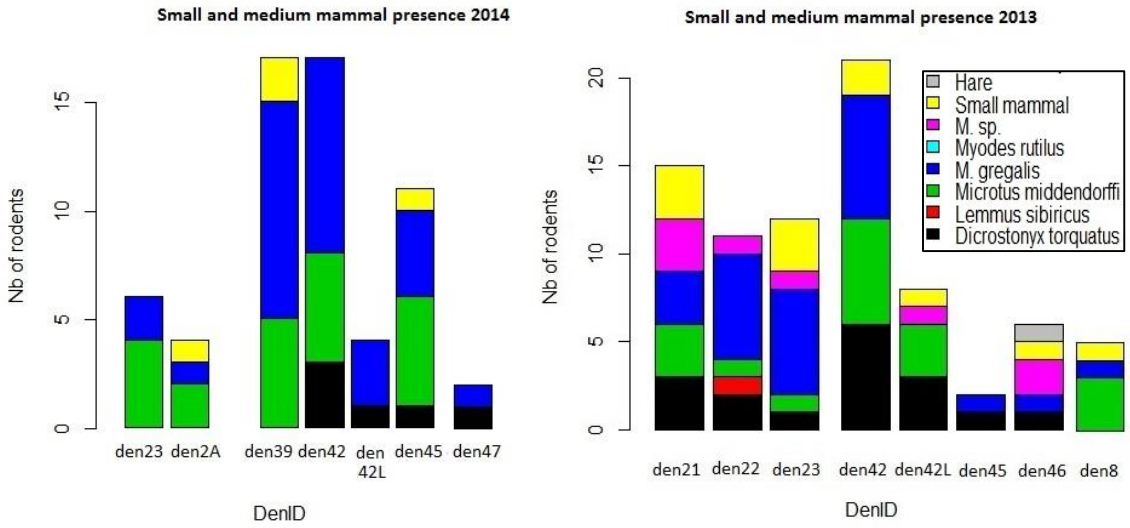

Fig. 6. Consumed rodent species during 2013 and 2014.

Statistical analysis showed no difference in diet for the years 2013 and 2014 for the variables *Presence of rodents* and *WFE* for rodents (p= 0.638, p= 0.551), though we could see a minor effect of *Week* (p=0.051) for *Presence of rodents*, and a significant effect in case of *WFE* (p=0.042). The estimate value for *Presence of rodents* (estimate in logit scale, -0.013 ±0.06) indicated a slight decrease in the consumption as the season moved forward. The estimate for *WFE* (-0.102±0.05) indicated a stronger decrease in the consumption of rodents during 2014.

The same analysis was done for *Presence of birds* and *WEF* referred to this prey category to test for the effect of *Year* and *Week*. The glmer show a difference in the consumption of birds between 2013 and 2014, where p=0.011, for the variable *Presence of birds*; and p=0.042 for the variable *WFE* for birds. The estimate values for *Presence of birds* and *WFE* were -1.233±0.48, and -1.035±0.51, indicating a decrease in bird consumption in 2014. *Presence of birds* was not significantly different through 2014 (p=0.868) with estimate value of -0.018. In case of *WFE* there were no differences in the consumption of birds during the field season of 2014 (p=0.274), and the value for the estimate was -0.127±0.11 (Appendix 4).

Principal Component Analysis was used to look for similarities on diet between the different years and to test a correlation between the different prey categories. Figure 7 shows an almost total overlap in diet for both years, though diet in 2014 varied more and a possible shift from birds to reindeer carcasses could be reported. The first and second axes of the scatter plot explain 39.7% and 24.7% of variation respectively (Table 4).

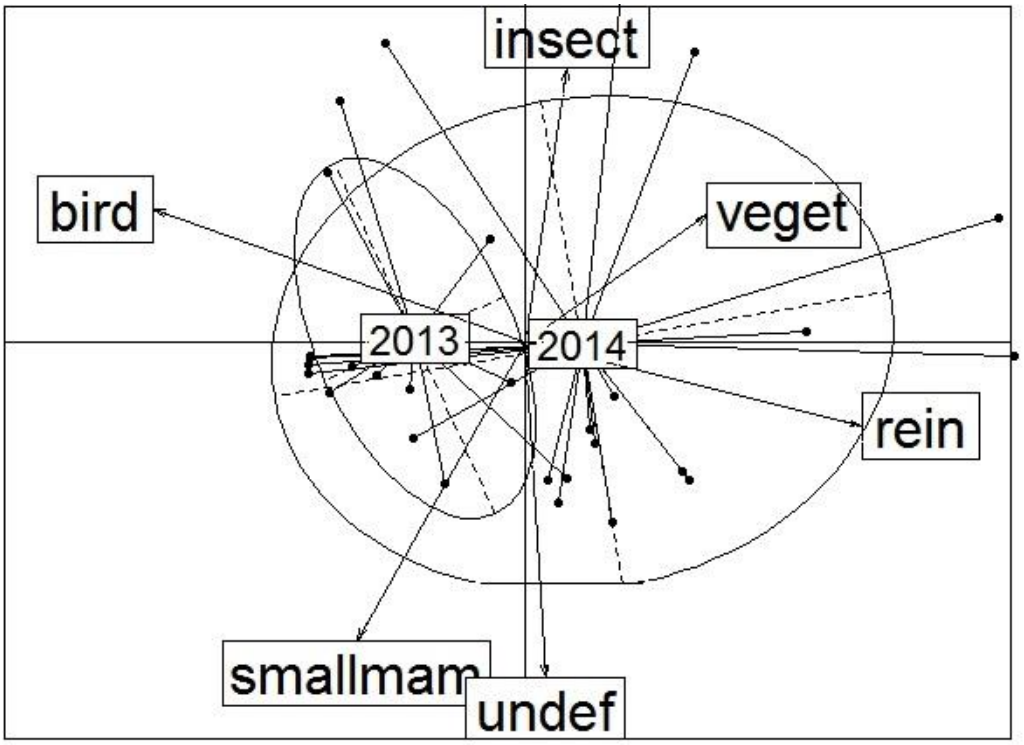

Fig. 7. PCA plot. Ellipses describe the variability between 2013 and 2014. Prey categories explain the shape of the ellipses. Bird category includes bird bones, feathers and eggs; small mammal category includes rodent fur and rodent bones. "Veget" is for vegetation, "rein" for reindeer, "undef" for undefined, and "insect" for insects.

Table 4. Variability explained by the different axis obtained from the eigenvalues of the PCA model.

PCA					
First axis	Second axis	Third axis	Forth axis	Fifth axis	Sixth axis
0,397	0,247	0,194	0,1436	0,117	0,04

C. Prey remains

Prey remains were found at the entrance of every den. The most common prey were passerines, small mammals and waterfowl. We found fish remains at the entrances of the different dens but it was not represented in the scat analysis. The same occurred for muskrat and reindeer, which are not present or are present in low abundance in the scat analysis, but several remains such as carcasses, bones and fur were present at the dens. Appendix 3 shows the presence/absence of different prey remains found at the entrance of the active dens during both years.

D. Stable isotopes analysis

Isotopic signatures for arctic foxes for the different years and mean isotopic signature with standard deviation for the different prey categories are graphed in Figure 8 to show which prey groups are most influential to fox diets. The category waterfowls includes seven different species of ducks and geese (*Clangula hyemalis*, *Melanita nigra*, *Anser albifrons*, *Anser* sp., *Anas acuta*, *Anas crecca*, *Anas penelope*). The terrestrial bird category includes nine species (*Anthus cervinus*, *Calcarius lapponicus*, *Anthus pratensis*, *Carduelis flamea*, *Lagopus lagopus*, *Luscinia svecica*, *Phylloscopus collibita*, *Riparia riparia*, *Tordus iliacus*), and wader category includes three species (*Phalaropus lobatus*, *Calidris temminkii*, *Pluvialis apricaria*). *Lemmus sibiricus* has only one individual and that is the reason why it does not have standard error bars. The closer the consumer is to a certain prey category, the more common is the presence of such prey in the consumer's diet. Signatures for *Microtus gregalis*, *Microtus middendorffi* and *Myodes rutilus* are closely placed. *Dicrostonyx torquatus* is further away, although the proportion in diet was the same as *Microtus middendorffi*. Passerines is the bird category closely related with the overall fox signature. Most of the isotopic signatures for the foxes are grouped in a certain area. This area is comprised among the prey categories *M. gregalis*, *M. middendorffi*, *Myodes rutilus* and Passerines, which explain the overall diet. Isotopic signatures of foxes during 2014 and 2013 are between the values of this four prey categories, although two values of 2014 are

distant from the "tendency cloud". Signatures in 2012 are still close to the mentioned prey, but the tendency moves towards *M. gregalis*. During 2011, 2010 and 2009 the isotopic values tend to stay within the tendency group. Isotopic signatures of foxes during 2007 and 2008 are more disperse. It is necessary to keep in mind that isotopic values reflect only the diet of arctic foxes during the time frame where the fur grew. The graph resulting from plotting values of $\delta^{15}N$ and $\delta^{13}C$ of the consumers and the different prey is shown at Figure 8.

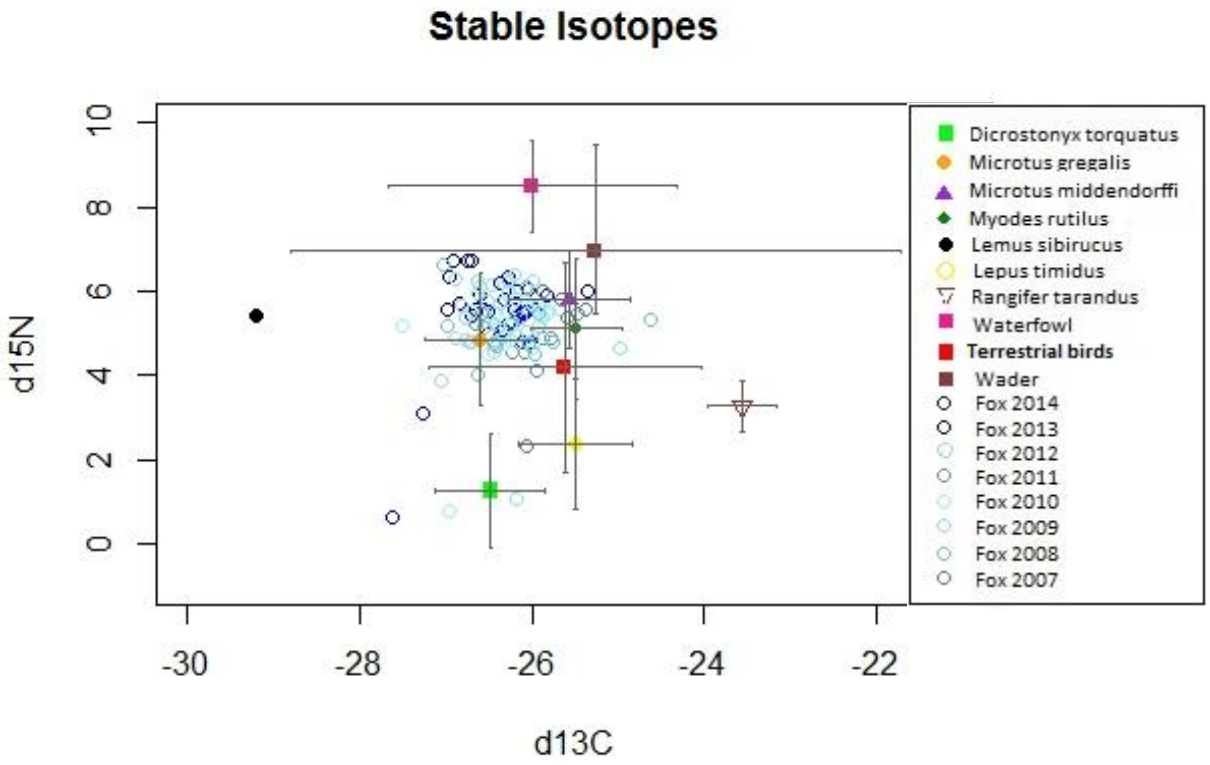

Fig. 8. Stable isotope analysis plot for the mean and SD of different prey species and arctic foxes during the 8 years of study.

Differences in $\delta^{13}C$ and $\delta^{15}N$ between years show that for the variable $\delta^{13}C$, mean isotopic values of all the estimates for the different years were statistically different from the intercept 2007. Differences were higher in case of years 2012 and 2013. In case of $\delta^{15}N$, the estimates did not show significant differences (Appendix 5). The ANOVA tests for the

same variables show a significant difference among the years in case of $\delta^{13}C$ (p=001), and no differences for $\delta^{15}N$ (p=0.08). Post Hoc test comparisons indicated a significant difference between the groups of years 2007-2012 and 2007-2013 of $\delta^{13}C$, and no differences in case of $\delta^{15}N$.

Isotopic signatures for some of the foxes with a $\delta^{15}N$ value below 2 could be due to errors during the identification of the fur under the microscope. Although all fur samples were checked for correct identification under a microscope, these values might belong to hare with a similar winter fur coloration.

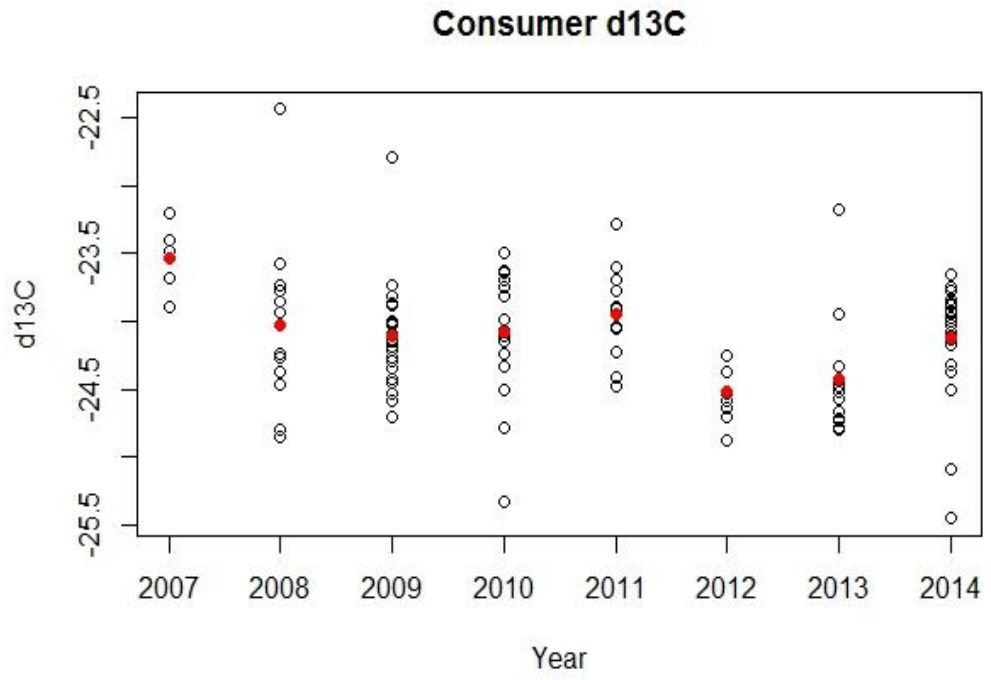

Fig. 9. Stable isotope signature ^{13}C for individual foxes during different years. Mean values indicated by red dots. Post Hoc comparisons showed statistical differences for the group years 2007-2012, and 2007-2013.

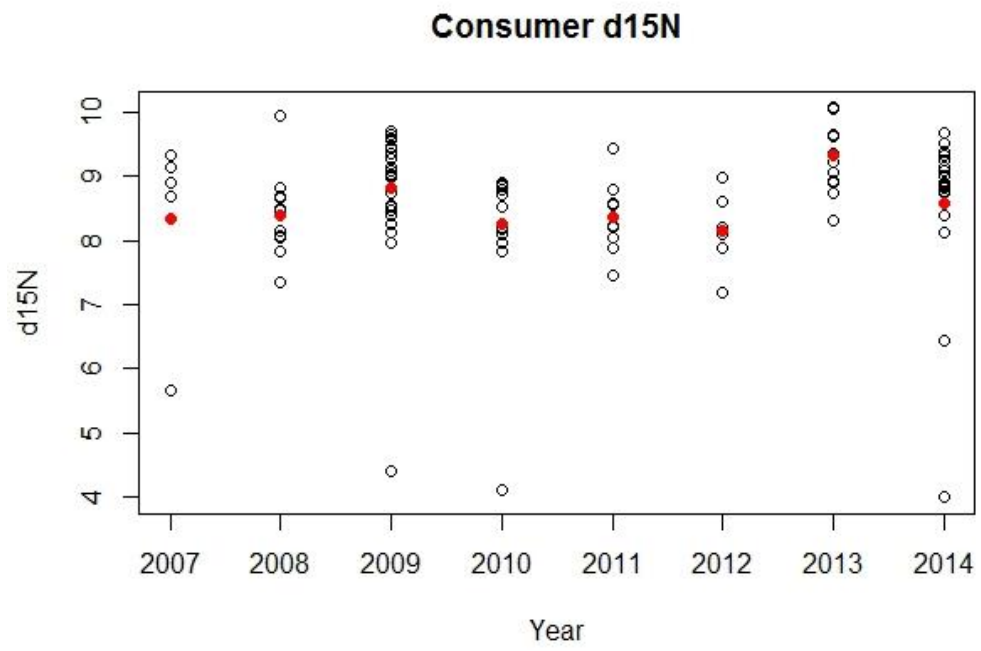

Fig. 10 Stable isotope signature 15N for individual foxes during different years. Mean values indicated by red dots. Post hoc comparisons did not show significant differences between the years.

E. Numerical responses

Analyses of the numerical responses of the arctic foxes to rodent abundance show no correlation between them. The variables used were *Number of active dens per 100 km^2* and *Rodent abundance in spring* obtained from the trapping data (Pearson correlation test= 0.415, p= 0.305); and *Number of active dens per 100 km^2* against *Rodent abundance in fall of the year before* (Pearson correlation test= 0.228, p= 0.663). Figure 11 shows the correlation of these variables since 2007. The abundance of rodents eaten will determine the breeding decision of female arctic foxes for next season.

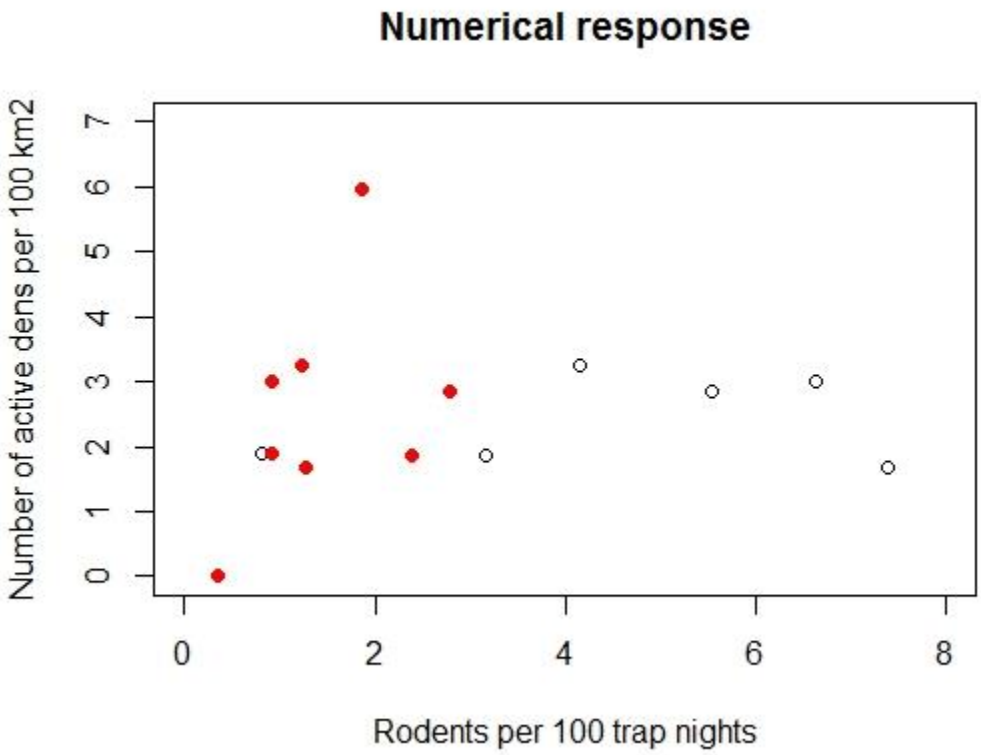

Fig. 11. Numerical response of the arctic fox to rodent abundance. Red dots: relationship between rodents trapped during spring (June) and number of active dens per 100 km^2. Black dots: relationship between rodents trapped during fall season the year before (August) and the number of active dens per 100 km^2. Number of occupied dens in the total study area were: 8 in 2007, 0 in 2008, 4 in 2009, 6 in 2010, 3 in 2011, 6 in 2012, 4 in 2013, and 7 in 2014.

4. Discussion

Arctic fox diet relative to prey abundance

The main prey category for arctic foxes during 2013 and 2014 were rodents, mostly *Microtus gregalis*, *M. middendorffi* and *Dicrostonyx torquatus*, which matches with the species sampled with the trap lines. The trapping data showed, in general, a higher abundance of rodents in 2013 than 2014 with *M. gregalis* as the most important species. The same low number of *D. torquatus* was trapped in both years.

Common prey categories found at the entrance of the dens were reindeer, hare and ptarmigan, all of which had high abundances within the study area. Reindeer carcasses were common in the tundra due to bad winter conditions and posterior starvation in 2014. Hares and ptarmigans were abundant in 2014, as determined by faeces counts (Ehrich et al. 2015). The faeces count values were almost constant over the years for hares, but varied more in case of ptarmigan, which abundances were higher after 2011 (Sokolov et al., unpublished).

Presence of *M. gregralis* in the scats was higher than the other rodent species for both years and number of *D. torquatus* and *M. middendorffi* consumed was the same during 2013 (Table 2). Despite the low abundance of *D. torquatus* trapped during both years, their presence in the diet is higher compared with other rodent species. A preference for lemmings could be stated. Supporting this hypothesis, it is known that arctic foxes in Sweden prefer lemmings to voles

(Angerbjorn & Erlinge 1999; Elmhagen et al. 2000; Elmhagen et al. 2002). Another possible explanation for the low abundance of lemmings is bias during the trapping.

The statistical analysis showed no differences in rodent consumption during 2013 and 2014 though we could see a minor decrease in rodent abundance during the season of 2014. Contrary to this, consumption of birds was statistically different between 2013 and 2014, and did not change through the season.

PCA analysis showed almost a complete overlap in diet for both years. Diet for 2013 is explained by Small mammals and Bird categories. Those two categories were the most abundant prey items consumed during 2013. The diet for 2014 is wider and its variation is explained by Reindeer and Small mammals categories. Arctic foxes used more diverse prey resources than in 2013, and small mammals were the most abundant items consumed. It seems there was a shift from Bird to Reindeer from 2013 to 2014 (Fig. 7). Both statistical models (GLMER and PCA) agreed on the similarity of diet for both years.

Stable isotope analysis supported the importance of rodent species especially *Microtus* species, and passerines among the different bird categories. Contrary to the proportion of rodents in the diet, *D. torquatus* signature is placed further away from the arctic foxes group. Arctic foxes were not feeding extensively on this prey probably due to their low abundance in the study area. A possible switch of prey categories could be over-shaded by the similarities on isotopic signatures of the prey. Post hoc comparisons of carbon and nitrogen, C and N, isotopes of foxes indicate that the most significant differences in diet are for the groups of years 2007-2012 and 2007-2013. There are no significant differences between the years 2013 and 2014, corroborating the previous analysis of scats (Fig. 6).

Studies regarding the diet of lemming foxes describe an overall rodent abundance higher than 75% of the total diet (Angerbjorn & Erlinge 1999; Dalerum & Angerbjörn 2000). In our case, despite rodent seems to be the most important prey category, their abundance in the diet do not exceed 60% (Fig. 5). Moreover, diet seems to be more diverse as it was stated for coastal foxes (Dalerum & Angerbjörn 2000). Many reindeer carcasses were observed during fieldwork in 2014. Since arctic foxes are opportunistic predators (Elmhagen et al. 2000) they took advantage of this resource, as PCA indicated. Isotopic

values of $\delta^{13}C$ are typically lower in species that use terrestrial system resources than in species that use marine resources (Killengreen et al. 2011). Values of $\delta^{13}C$ between -20 and -28 (Angerbjorn et al. 1994; Savory et al. 2014; Ehrich et al. 2015) have been described for arctic foxes in different studies. The values of $\delta^{13}C$ obtained in this analysis ranged between ca -24 to -28, commonly found in species that use terrestrial resources. According to all this, arctic foxes in the low shrub tundra of southern Yamal peninsula seem to base their diet on terrestrial resources. Moreover, their feeding strategy seems to be closer to a generalist predator, as stated for coastal foxes, opportunistically preying on more accessible food resources (i.e. reindeer carcasses).

Lack of numerical response to rodents

Despite the fact that rodent appear to be a dominant prey item, there was no evidence for numerical responses of the arctic foxes to the rodent abundance. When looking at the plot (Fig. 8, red dots) it may seem there is a correlation between the variables *Number of active dens per 100 km^2* and *Rodents trapped in spring* explained by the effect of no reproduction during 2008. If this point is ignored, there is no correlation and the number of dens occupied seems constant through the years. When considering *Number of active dens per 100 km^2* and *Rodents trapped in fall the year before* (Fig. 8, black dots) there is no correlation between them neither. Rodent abundance in spring (June) seems to not be related with reproduction; and rodent abundance in fall (August) seems to not be related with the arctic fox reproduction in next season. It is well known that lemming and coastal foxes respond numerically to rodent abundance (Angerbjorn & Erlinge 1999; Dalerum & Angerbjörn 2000; Gilg et al. 2006), but it does not seem the same in this case. Following this hypothesis, lack of numerical response to rodent abundance indicates that despite of being the preferred prey, rodents are not as important in the diet for foxes in this area as for foxes in other localities. Thus, rodents are not determinant of arctic fox population in the low shrub tundra of southern Yamal peninsula.

Methodological issues

The methods used in this thesis were not new. Scat analysis is one of the most common methods for diet identification (Angerbjorn et al. 1994). Many studies though, used the weight of each prey category per sample instead of the volume estimates. This can lead to overestimation of certain prey since material such as bones are heavier than feathers or fur. Both methods are subject to biases and measuring the weight does not increase the accuracy of the results. Frequency of occurrence is an example of a qualitative method, but it should be used with other analysis in order to assess the importance of different food categories in the diet. It will help to understand the role of the carnivore's feeding strategy (Klare et al. 2011). In this study, scat analysis was done with volume estimates in order to avoid overestimation of certain categories, such as bones. The scat analysis does not represent some of the important prey items that were at high abundances as remains at the entrances of the dens. For the frequency of rodents in the scats, identification was sometimes difficult due to the condition of the material, and lose teeth were more frequent than the whole hemi mandible.

Camera traps is a good method to estimate the pup abundance but here they were not found to be a good method for the identification of different prey items. It is very time consuming and the quality of the pictures is not good enough to distinguish among different prey.

Prey remains collected at the entrance of the dens are useful to determine the diet frame and describe the diet in a qualitatively way. In our case, some of the items found at the dens were not represented in the scat analysis.

Stable isotopes analysis is gaining weight in dietary analysis, not only for carnivores but also for many sorts of species. This method provides information on diet for each individual over a longer period (Angerbjörn et al. 1994) and reflects temporal and spatial variability in the use of prey (Ehrich et al. 2015). On the other hand, this method is not useful to distinguish prey with similar isotopic signatures, such as different rodent species (Klare et al. 2011).

Thus, a combination of different methods should be more useful to determine the diet and the relative importance of the different prey. In this case, scat analysis served to

describe the diet during the study period and in particular the frequency of occurrence of prey items in scats appeared to efficiently determine what the preferred prey was.

Conclusion

At the study site in the low arctic shrub tundra in Yamal peninsula the fox population is relatively stable and its number seems to not be related to rodent abundances, which exhibits multiannual fluctuations with low amplitude and abundance (Sokolova et al. 2014). Therefore, it is likely that foxes are able to use alternative prey resources make them able to cope with the low abundance of rodents and to be able to sustain their population number. Rodents and birds were the most important prey categories but rodents were not determinant of the breeding success of the arctic foxes, and reindeer carcasses may have been an important prey category when available. It seems that arctic foxes in the low shrub tundra in southern Yamal peninsula are closer to a terrestrial opportunistic generalist feeding strategy, and the absence of a numerical response to the abundance of rodents supports this hypothesis though they could be classified as coastal foxes.

Acknowledgments

I would first like to thank to my supervisors Dorothée Ehrich for infinite patience, great support and helpful and encouraging attitude, and Rolf Ims; the Erkuta field team 2014: Shasha, Natasha & Co., for making a two-month fieldwork in Yamal an unforgettable experience with amount of stories, songs and football matches, “spasibo”. I would also like to thank to my fellow students at the office for endless distractions, beer-evenings and “lunch at some point”; and a special thanks to all my friends for their support through this period.

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Appendix

Appendix 1

Table 1. Number of samples analyzed per batch, at the different active dens during 2013 and 2014.

Scat analysis			
Year	Den ID	Batch	Samples
2013	21	27/06/2013	22
2013	46	27/06/2013	22
2013	42l	25/06/2013	22
2013	22	04/08/2013	22
2013	42	26/07/2013	21
2013	23	23/06/2013	22
2013	8	28/07/2013	22
2013	42	05/08/2013	21
2013	42	25/06/2013	21
2013	45	29/07/2013	22
2014	23	01/07/2014	21
2014	23	13/07/2014	21
2014	23	21/07/2014	21
2014	23	31/07/2014	21
2014	42	28/06/2014	21
2014	42	07/07/2014	21
2014	42	17/07/2014	21
2014	42	28/07/2014	21
2014	42l	28/07/2014	21
2014	39	27/06/2014	21
2014	39	16/07/2014	21
2014	39	26/07/2014	21
2014	39	02/08/2014	21
2014	45	02/07/2014	21
2014	45	12/07/2014	21
2014	45	22/07/2014	21
2014	45	03/08/2014	21
2014	2a	21/07/2014	21
2014	47	28/07/2014	21

Appendix 2

Table 2. Total number of rodents and small mammals trapped during spring (Trapping data) and in the scat analysis.

	Year	Dicrostonyx torquatus	Lemmus sibiricus	Microtus gregalis	Microtus middendorffi	Myodes rutilus	Microtus sp.	Small mammals	Hare
Trapping data	**2014**	1	0	7	2	2	-	-	-
	2013	1	0	19	4	7	-	-	-
Scat analysis	**2014**	6	0	30	21	0	0	4	0
	2013	17	1	25	17	0	8	11	1

Appendix 3

Table 3. Presence/absence (1/-) of different prey remains found at the entrances of the dens during the sampling dates (batches).

			Prey remains recorded at the entrances of the dens									
Year	**Den**	**Date**	**Feathers (Passerines and unidentified)**	**Waterfowl**	**Small mammals**	**Wader**	**Eggs**	**Reindeer**	**Hare**	**Muskrat**	**Fish**	**Ptarmigan**
2013	5	17/06/2013		1								
2013	8	30/06/2013		1								
2013	8	07/07/2013	1		1				1			
2013	8	28/07/2013		1								
2013	8	08/08/2013		1		1						
2013	9	21/06/2013	1	1	1	1	1			1		
2013	9	24/06/2013	1									
2013	9	06/07/2013	1									
2013	21	27/06/2013	1	1		1	1					
2013	21	29/07/2013									1	
2013	22	27/06/2013	1		1							
2013	22	29/07/2013			1					1		
2013	26	02/07/2013	1		1							
2013	41	25/06/2013									1	
2013	42	25/06/2013		1								
2013	42	09/07/2013	1									
2013	45	01/07/2013	1									1
2013	45	06/07/2013	1		1							1
2013	45	29/07/2013		1							1	
2013	46	01/07/2013	1									
2013	47	25/06/2013	1	1	1							
2013	r2	19/06/2013	1		1					1		
2013	r6	26/06/2013			1							

2013	2a	26/06/2013	1			1									
2013	36	27/06/2013				1									
2013	51	02/07/2013	1			1							1	1	
2013	53	02/07/2013	1			1									
2014	5	17/06/2014	1												
2014	9	23/06/2014	1			1								1	
2014	21	24/06/2014	1	1		1	1			1					
2014	21	03/07/2014	1			1									
2014	21	10/07/2014		1				1							
2014	21	21/07/2014	1							1					
2014	21	05/08/2014	1							1					1
2014	23	21/06/2014	1												1
2014	23	01/07/2014	1												
2014	23	13/07/2014	1												
2014	23	21/07/2014	1	1		1			1	1					
2014	23	31/07/2014		1											
2014	25	19/06/2014	1										1		1
2014	41	28/06/2014	1											1	
2014	42	28/06/2014	1						1						
2014	42	07/07/2014	1	1				1							
2014	42	28/07/2014				1			1	1					
2014	42	17/07/2014	1			1				1					
2014	42	28/07/2014	1			1			1						
2014	43	28/06/2014	1												
2014	5A	28/06/2014	1						1					1	
2014	7H	28/06/2014	1												
2014	45	23/06/2014	1			1									
2014	45	02/07/2014	1			1									
2014	45	12/07/2014	1	1											
2014	45	22/07/2014	1												

2014	45	04/08/2014										1				
2014	46	23/06/2014			1											
2014	47	28/06/2014								1						
2014	47	28/07/2014	1			1				1						
2014	2A	25/06/2014	1			1		1								
2014	2A	06/07/2014	1													
2014	2a	15/07/2014	1													
2014	2a	02/08/2014	1			1										
2014	36	24/06/2014			1											1
2014	Vostrovka	10/07/2014	1													
2014	33	01/07/2014	1													
2014	50	25/06/2014	1													1
2014	61	21/06/2014				1				1		1		1	1	
2014	62	27/06/2017	1													
2014	39	27/06/2014				1									1	
2014	39	06/07/2014	1												1	
2014	39	16/07/2014	1			1										
2014	39	26/07/2014	1												1	
2014	39	02/08/2014	1			1				1						

Appendix 4

Table 4. Values for the estimate, standard deviation, Z, p, and odd ratio for the different models.

GLME analysis

		Estimate	SE	z	p	Odd ratio
Probability of rodents per scat	Intercept	5,153	2,017	2,554	0,010	
	Week	-0,134	0,069	-1,946	0,051	0,873
	Year2014	0,140	0,298	0,469	0,638	1,150
WFE for rodents	Intercept	3,146	1,454	2,164	0,030	
	Week	-0,102	0,050	-2,031	0,042	0,902
	Year2014	0,131	0,220	0,596	0,551	1,140
Probability of birds per scat	Intercept	-0,110	3,213	-0,034	0,972	
	Week	-0,018	0,111	-0,166	0,868	0,981
	Year2014	-1,233	0,489	-2,522	0,017	0,291
WFE for birds	Intercept	1,254	3,295	0,381	0,703	
	Week	-0,127	0,116	-1,094	0,274	0,880
	Year2014	-1,035	0,510	-2,029	0,042	0,354

Appendix 5

Table 5. Estimate values resulting from the differences of $\delta^{13}C$ and $\delta^{15}N$ between the different years.

	Estimate	Std. Error	t value	P(>|t|)
C_2007	-23,532	0,193	-121,642	< 2e-16 ***
C_2008	-0,493	0,230	-2,141	0,034 *
C_2009	-0,570	0,212	-2,683	0,008 **
C_2010	-0,551	0,220	-2,506	0,013*
C_2011	-0,410	0,233	-1,761	0,081 .
C_2012	-0,992	0,246	-4,024	<0,0001 ***
C_2013	-0,898	0,230	-3,9	<0,0001 ***
C_2014	-0,591	0,212	-2,782	0,006**
N_2007	8,34	0,437	19,076	<2e-16 ***
N_2008	0,045	0,520	0,088	0,93
N_2009	0,467	0,480	0,973	0,332
N_2010	-0,087	0,497	-0,177	0,86
N_2011	0,012	0,527	0,024	0,981
N_2012	-0,183	0,557	-0,33	0,742
N_2013	0,988	0,520	1,899	0,060 .
N_2014	0,245	0,480	0,51	0,610