The impact of climate change on interspecific competition between invasive species in northern ecosystems

The competition between the arctic fox (*Vulpes lagopus*) and the red fox (*Vulpes vulpes*)

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Abstract

Effects of climate change are globally perceivable, especially in the arctic and this is often referred to as arctic amplification. Climate change could affect interspecific competition in northern ecosystems in terms of changes in direct competition, spatial competition, competition for food sources and anthropogenic factors affecting interspecific competition. The interspecific competition between the red fox (*Vulpes vulpes*) and the arctic fox (*Vulpes Lagopus*), the topic of this essay, occurs in overlapping regions in North-America and Eurasia. In captivity, a strong dominance of the red fox over the arctic fox was observed in direct physical confrontations. In Fennoscandia the arctic fox population is at a low level since hunting in the early nineteenth century and is in competition with the red fox for more than hundred years. In contrast, in Alaska and Canada the arctic fox populations are stable and are facing the rise of the red fox since a relatively short period. The use of particular dens by arctic foxes seems to be mostly negatively influenced by red fox abundance and altitude and to a lesser extent by distance from the forest. In terms of food, there is overlap between the diet of the arctic fox and the red fox. Lemmings and voles are the main food sources for both fox species. These two food sources are dealing with annual fluctuations in abundance, influencing the number of offspring of the arctic fox. The dependency of both the red fox and the arctic fox on lemmings and voles makes the two species vulnerable for changes in annual fluctuating cycles of voles and lemmings by climate warming. Human disturbances (in the form of infrastructure, food distribution or both) have a huge negative impact on the abundance of the arctic fox and the red fox and could amplify affects caused by climate change. If the red fox becomes more abundant at higher altitudes in Fennoscandia and more abundant at higher latitudes in Alaska and Canada due to climate change, the arctic fox will probably seek shelter at even higher altitudes and even higher latitudes to prevent (direct) competition with the red fox. This process would amplify the existing niche differences between the species. There is a limit to the escape possibilities of the arctic fox in Fennoscandia, due to the limited altitude of the mountains.

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Introduction

The global effects of climate change are perceivable worldwide, especially in the arctic (Post *et al.* 2009; IPCC, 2014). In the arctic region, the warming is above average compared to the global increase in temperature. This process of faster warming temperatures in the arctic is also known as arctic amplification. The warming in the arctic could have effects on snow cover, vegetation and survival of certain species. Climate change can influence processes on multiple levels and various ways in an ecosystem. The huge scale of the impact of climate change is sometimes difficult to assess, due to the various aspects of an ecosystem that can be affected by climate change. For example, climate change can influence an ecosystem in such way that for some species the ecosystem becomes uninhabitable by a shortage of food or habitat loss (Post *et al.* 2009). The effects of climate change on habitat, food sources or other provisions of species could also change the interactions with other species. Effects of climate change may also include the introduction of new predators or enabling a higher level of competition within a species. Two species, each affected by climate warming, could change their interactions towards each other as an effect of climate change. This can be an increase or decrease in existing interspecific competition between two species or the introduction of new forms of interspecific competition. Climate change can lead to a shift of the competitive balance between species, alongside various other effects (Poloczanska 2008).

Interspecific competition occurs if there is any competition, in the widest sense of the term, between two different species. Interspecific competition could involve competition over reproduction sites, food sources or habitats in general and can manifest itself in agnostic behaviour or in more avoiding behaviour towards the other species. Eventually interspecific competition could lead to changes in diets of species or even changes in habitats and distribution of species (Tannerfeldt *et al.* 2002). Interspecific competition is therefore a process of many different aspects. For example, food sources and habitats could both be influenced by climate change as well as by interspecific competition. People can also have their effect on interspecific interactions, for example by providing anthropogenic food sources for species or reducing the geographical range of one or both species (Savory *et al.* 2014). In turn, people can also be affected by the climate, for example by some areas becoming more accessible for human activities. Because of the complex interplay between climate change and interspecific competition, one process can be obscured by the other process. In this essay I will discuss the effects of current and future climate change on interspecific competition in northern ecosystems, especially between the red fox (*Vulpes vulpes*) and the arctic fox (*Vulpes Lagopus*).

In order to make the interplay between interspecific competition and climate change more clear, I will first discuss in each chapter one of four aspects of interspecific competition between the arctic fox and the red fox. At the end of each chapter the effect(s) of climate change on this specific aspect of interspecific competition will be covered. The four aspects of interspecific competition I will address in this essay are direct competition, spatial competition, competition for food sources and anthropogenic factors affecting interspecific competition. In order to reduce the scale of this essay, it will focus on the interspecific competition of two specific species: the red fox and the arctic fox. I've chosen for these two species because the interspecific competition between the two fox species is relatively well studied. The interspecific competition between the species has been studied on a regular basis in the last thirty years in multiple northern ecosystems. The species live together in northern ecosystems on different continents (America and Eurasia) in different conditions. The locations where the two fox species live together include Scandinavia, Newfoundland (Canada), Prudhoe Bay (Alaska) and Yamal Peninsula (Russia) (Rodnikova *et al.* 2011; Gallant *et al.* 2012; Gallant *et al*. 2013; Hamel *et al*. 2013; Savory *et al.* 2014). The competition between both species could be an example of interspecific competition of predatory terrestrial species in northern ecosystems. Beside the role of climate change I will also look at the differences of the interspecific competitions between the different regions where the arctic fox and the red fox occur. In the end I will discuss the total effect of climate change on the interspecific competition of the fox species for all the regions.

Direct competition

Interspecific competition between species is most visible in examples of direct competition. Direct competition manifests itself in agnostic behaviour, including threats, chases and direct physical fights. The dominance of species may have an influence on the interspecific competition between two species. In this chapter I will first discuss the direct competition between the red fox and the arctic fox in captivity. Afterwards I will discuss direct competition between the two fox species in the wild.
To get an insight into the degree of competition between the arctic fox and the red fox one can first look at their dominant attitude in relation to the other species. The interspecific competition and dominance of the red fox and arctic fox in captivity has been studied by Rudzinski *et al*. (1982). For this study behavioural interactions of artic foxes (originally from Prudhoe Bay, Alaska) and red foxes (originally from North and South Dakota) were studied in an enclosure of 40500 square meters. During nine trials, the effects of the introduction of a red fox female and later a red fox male into an enclosure with a male-female pair of arctic foxes were studied. In the case of 8 out of 9 trials, the red foxes dominated the arctic foxes. This occurred during agonistic encounters and in the form of replacements of resting, denning and foraging sites. There was no direct competition for provided food sources. Overall the arctic foxes lost their preferred natural den to the red foxes. A difference in the activity of the artic foxes was visible before the introduction of the red fox (phase A) and after the introduction of the red foxes (phase B and C), which can be seen in figure 1. There was agonistic behaviour like chases and threats between the two species, but no direct physical fights (Rudzinski *et al*. 1982). A dominant attitude of the red fox towards the artic fox was clearly observable, though without direct fights.

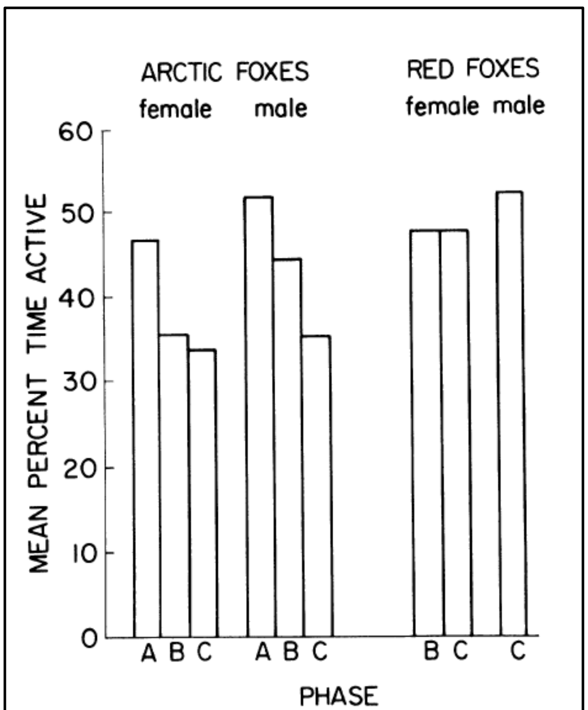

Figure 1: The mean percentage of time in which the foxes were active for all nine experiments. During phase A, only the arctic foxes were in the enclosure. During phase B the red fox female was introduced and in phase C the red fox male was introduced in the enclosure. From: Rudzinski *et al.* 1982. Behavioural Interactions of Penned Red and Arctic Foxes. *The Journal of Wildlife Management* **4**: 877-884.

A second study on interspecific competition and dominance between the red fox and arctic fox in captivity used farm-bred foxes of both species from Finland (Korhonen *et al.* 1997). The enclosures for this study were much smaller in compare with the previous study. The degree of dominance was scored on the basis of dominant and submissive behaviour, for example fights that have been converted into a dominance score between 0 and 1. The study showed that the dominance between the two species changed between different periods. In the first period after weaning from August to September, the arctic fox was dominant over the red fox. In return, during the gestation period and the period after the pregnancy of both species, the red fox was dominant over the arctic fox. The red fox appears to gain dominance in the maturation process of both species. A big difference between the foxes captured in the wild (used in the previous mentioned research) and the captive foxes from a farm (used for this study) is the weight difference between the foxes. In the wild, the red fox is almost twice as large as the arctic fox. By means of the fox fur industry, the arctic foxes are heavier than the red foxes by selection in genetic characteristics. Despite these differences, the mature red fox was still dominating the mature arctic fox during the research. So despite the differences in weight between the species during the study and in natural situations in the wild, the red fox was still dominant over the arctic fox in the adult stage. These results are therefore in accordance with the results from the previous study in 1982 (Rudzinski *et al*. 1982; Korhonen *et al.* 1997). The fact that during this study physical fights were observed may be contributed to the smaller enclosure and the resulting higher density of foxes. Overall, the research from Rudzinski *et al.* seems a more credible representation of a natural situation of interspecific competition between both species than the latter research.

The degree of dominance between the arctic fox and the red fox was also studied in the wild. An example of a direct physical confrontation between the red fox and the arctic fox is the killing of arctic fox pups by a red fox. Such an event is described in two studies (Frafjord *et al.* 1989; Tannerfeldt *et al.* 2002) from Scandinavia. The first study observed seven aggressive interactions between the red fox and the arctic fox throughout Sweden and Norway. During two of those aggressive interactions one or more arctic foxes were killed by red foxes. The study described an observation of an adult arctic fox killed by red foxes and an observation of an artic fox cub killed by a single female red fox. There were no indications that arctic foxes were killed for food or for takeover of a (breeding) den. The study from Tannerfeldt *et al.* analysed the den use of reproducing red foxes and arctic foxes in Sweden. In two cases where an arctic fox den was situated near a red fox den, the juveniles of the arctic foxes were killed by red foxes. Both studies describe dominant behaviour of the red fox, sometimes resulting in the dead of the arctic fox. Another example of a confrontation between the arctic fox and the red fox, whereby arctic fox pups disappeared (and were probably killed) occurred on the Yamal Peninsula (Russia) (Rodnikova *et al.* 2011). This study observed a single takeover of an arctic fox den by a red fox, whereby the juveniles of the arctic fox disappeared. These three studies combined, there is a strong indication that killing of arctic foxes by red foxes is scarce, but present in both Scandinavia and Russia. These events support the hypotheses that wild red foxes dominate the arctic foxes in direct physical confrontations.

This dominant attitude of the red fox may have effects on the behaviour of the arctic fox. Home ranges of the red fox could keep the arctic fox at distance. This possibility was tested in a spatially explicit individual based model, created to simulate the populations dynamics of arctic foxes in northern Sweden (Shirley *et al.* 2009). The model included (annual) fluctuations in population sizes of some prey of the arctic fox, also known as microtine cycles. The population dynamics of the arctic fox were simulated with the model with the help of microtine cycles and red fox home range avoidance behaviour. The model that included only microtine cycles was insufficient to simulate the population decline that was observed in the wild. However, with the inclusion of red fox home range avoidance behaviour, the model was capable of matching the population dynamics of the wild. A certain degree of avoidance behaviour therefore seems likely for the arctic fox with respect to the red fox, at least in Fennoscandia. I will come back on this subject later in chapter 2 about spatial competition.

No studies were found about the pressure of other predators, for example wolverines and grizzly bears, on the populations of both the arctic foxes and the red foxes in the northern ecosystems, with exclusion of the previous mentioned articles about the aggressive behaviour of the red fox towards the arctic fox that resulted in the dead of arctic foxes. It is therefore not possible to draw conclusions about the role of other predators on the populations of both the arctic foxes and the red foxes in the process of interspecific competition between the two species.

Direct competition and climate change

The previous mentioned articles all support the thesis that wild red foxes dominate arctic foxes in direct physical confrontations (Rudzinski *et al*. 1982; Frafjord *et al.* 1989; Korhonen *et al.* 1997; Tannerfeldt *et al.* 2002; Rodnikova *et al.* 2011). Apparent avoidance behaviour of red fox home ranges by arctic foxes could leave its mark on the population dynamics of the arctic fox (Shirley *et al.* 2009). Traditionally the arctic fox is distributed in the polar region in North-American and Eurasian arctic tundra regions. The zone of overlap between the arctic fox and the red fox is relatively small in compare with the overall habitat of the red fox, which can be seen in figure 2. In Fennoscandia, the arctic fox usually breeds in small numbers above the tree line. The red fox are abundant all across Fennoscandia (Frafjord *et al.* 1989).

Figure 2: The geographical distribution of the red fox (*Vulpes vulpes)* and the arctic fox *(Alopex lagopus).* Overlap between the two species is visible in North-American and Eurasian arctic tundra regions. From: Hersteinsson and Macdonald 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64:** 505-515.

The differences between the arctic fox and the red fox lie mainly in adaptation to colder temperatures and regions above the tree line. The arctic fox is in comparison with the red fox more adapted to extreme cold, with a smaller body size in general and for example smaller and more rounded ears, a smaller neck and a smaller tail (Hersteinsson and Macdonald 1992). If relative cold regions would warm up because of climate change, areas previously only occupied by the arctic fox could become accessible for the red fox. Thus, the geographical distribution of the red fox in Scandinavia, Russia, Alaska and Canada could strongly be influenced by climate warming. If the northern limit of the red fox's geographic range would move towards the north by means of climate change, the chance of interactions resulting in agnostic behaviour between the arctic fox and the red fox increases. Aggressive behaviour between the two species is already taking place in at least Fennoscandia and Russia. The number of deadly interactions between the red fox and the arctic fox could also increase by climate change. If one only looks at direct physical competition between both species, however, there is already a clear distinction in dominance visible. This distinction appears to increase as climate change creates more overlap and therefore a greater risk of physical confrontations between the two species, which the arctic fox will probably lose.

Spatial competition

Spatial competition between the arctic fox and the red fox is manifested via competition for dens of both species. A certain distribution of dens based on quality or preference for dens by the fox species could indicate interspecific spatial competition. In this chapter I will first discuss the differences between dens of the arctic fox and the red fox. Thereafter I will discuss the locations of dens of both species relative to the other species and other spatial factors. Finally I will discuss the general level of spatial competition between the fox species and the effects of climate change on this process.
There is no consensus about potential differences between the (natal) dens of arctic foxes and the (natal) dens of red foxes. A study from Smits and Slough, that studied natal dens of both species on the Yukon Coastal Plains, Canada, found no differences in size between the natal dens of both species (Smits and Slough 1993). However, a more recent study from Frafjord has shown that the dens of arctic foxes are larger, have more lush vegetation and have more den openings in compare with dens used by red foxes (Frafjord 2003). The den area in square meters and the number of openings could play a role in den choice of arctic foxes. Den area is also addressed in a research from Dalerum *et al.* in Sweden. During this study the arctic foxes used only the largest dens available. However, there was no statistically significant partial effect on arctic fox den use by den area in square meters. For red foxes, there was a statistically significant partial effect on red fox den use by den area in square meters (Dalerum *et al.* 2002). A high number of entrances of a den is another characteristic that seems to be preferred by arctic foxes. Arctic foxes were using dens with significant more openings in compare with red fox dens during a study in Sweden. The number of openings was even a statistically significant partial effect on arctic fox den use. For red foxes there was no significant effect of number of entrances on den use. A study from Norway found a huge difference between the number of openings of arctic fox dens and red fox dens (Frafjord 2003). The number of red fox den entrances was only twelve percent of the number of entrances in arctic fox dens. In the article, protection (against the red fox), conservative behaviour (reuse of dens from previous years) or maintaining multiple microclimates are mentioned as possible explanations for the multiple entrances in an arctic fox den. The most recent study on this topic concluded that arctic foxes had a preference for dens with many entrances and good springtime access in the period of reproduction of red foxes. This study was conducted on Hershel Island in north Yukon, Canada (Gallant *et al*. 2013). A successful den for an arctic fox, as defined in the likelihood of many offspring, seems to include many accessible entrances and covers a large area.

In view of interspecific competition, den takeovers by the other species are especially interesting. In the case of the arctic fox and the red fox, for both species it is known that they are able to take over or occupy a nest of the other species. In Canada, on the Yukon Coastal Plains, arctic foxes were able to occupy an abandoned nest of red foxes (Gallant *et al.* 2012). However, these examples of takeovers of red fox dens are probably caused by periods of limitations in food availability, wherein the red fox disappeared from the den. During a study in Sweden, dens that were created by red foxes were not used by arctic foxes. However, dens dug by arctic foxes were quite in demand by both species (Dalerum *et al.* 2002). There are no known examples of takeovers of already occupied dens in both studies. Thus, there seems to be a two-way exchange possible between the dens of arctic foxes and dens of red foxes, but a takeover of an arctic den by a red fox is more likely and more frequently observed. There seems to be no prohibitive difference between the dens of the arctic fox and the red fox that would prevent acquisitions of a den by the other species. Possible differences in the number of entrances or den area seem too small to preclude den takeovers.

The location of a den in the landscape can play an important role for a fox. Dens of foxes are usually located at elevated sites (in the tundra), associated with a more deeper layer of unfrozen soil through greater irradiation and good drainage. In Fennoscandia, the arctic fox usually breeds above the tree line, however the red fox breeds all across the region (Frafjord *et al.* 1989). Red foxes are suggested to have a larger home range. Because of their larger body size and higher resting metabolic rate they need more food and thus a larger prey area than arctic foxes (Gallant *et al*. 2013). The altitude of red fox dens and arctic fox dens is also a characteristic that differs between the dens of the species. Two studies compared the altitude of arctic fox dens and red fox dens in Sweden and Norway (Linnell *et al*. 1999; Tannerfeldt *et al.* 2002). For the study in Norway, the occupied dens of red foxes were significantly situated at lower altitudes than the occupied dens of arctic foxes. A Study from Tannerfeldt *et al.* Sweden observed the same pattern (figure 3). The location of a den has its influence on prey availability, protection, interactions with predators and interactions with the own species. The spatial behaviour of the arctic fox relative to the red fox was studied in four different studies in Sweden and Norway. The studies compared locations of dens of reproducing arctic foxes and their distance to a red fox den. The overall presence of the red fox around the arctic fox dens was also compared between dens of reproducing arctic foxes. The study in Sweden from Tannerfeldt *et al.* concluded that reproducing arctic foxes had more often dens in locations with no breeding red foxes in the proximity of eight square kilometres (Tannerfeldt *et al.* 2002). In the same study, in three cases involving reproducing arctic foxes near a red fox den, two times the juveniles of the artic foxes were killed. A study in Norway confirms this pattern. In this study the arctic fox dens, producing at least once litters in the period of 1980 until 2001, were situated further from red fox dens in compare to arctic fox dens without any pups (Frafjord 2003). The reproduction success of the arctic fox is linked in both studies with the vicinity of red fox dens. A second study from Norway tested the recolonization success of the arctic fox in the abundance of the red fox. For locations with a few recorded observations of red foxes, there were no observation of any arctic fox. The recolonization success of the arctic fox was zero in areas were the red fox was not removed. This study therefore proposes to reduce the red fox populations to accomplish a potential re-introduction of the arctic fox in regions in Scandinavia (Hamel *et al*. 2013). The final study that covered the influence of red fox abundance on artic fox den choice checked 27 different known arctic fox dens in the period of 2001 until 2005 in Norway. From these 27 dens, 14 were used by arctic foxes during the time period of the study. The used dens were further away from red fox habitats in compare with the unused arctic fox dens (Selås *et al.* 2010). In each of the four previous mentioned studies on spatial behaviour of the arctic fox relative to the arctic fox, the effect of red fox populations on the use of particular dens of Arctic foxes seems to be strongly present. The presence of red foxes is already enough to make a den such less attractive to the arctic fox, that the arctic fox stays away from these dens.

However, research in Yukon, Canada, shows contradictory results (Gallant *et al.* 2012). Here most dens in the research area were taken by the arctic fox. The relative abundance of both species didn't change during the last forty years. The takeover of dens of the other species was similar for both species. Change in occupancy by red foxes to arctic foxes occurred for 9.8% of the dens. Change in occupancy by arctic foxes to red foxes occurred for 8.2% of the dens. The research shows a stable situation of arctic and red fox dens sympatrically in the same area for a longer time period, with a similar proportion of exchanges between dens of the two species. This difference in compare with the other studies may be due to specific characteristics of the region or the relatively high abundance of arctic foxes and low abundance of red foxes in compare to Fennoscandia. The previously mentioned differences in altitude of dens between the species is suggested to be linked with red fox avoidance behaviour of the arctic fox (Linnell *et al*. 1999; Tannerfeldt *et al.* 2002). The traditional differences between the niches of the arctic fox and the red fox, for example in altitude, could be amplified by the interspecific competition between the species and the following arctic fox behaviour. Two other studies focused on the preference of the arctic fox for certain characteristics, for example altitude above tree line. Arctic foxes used dens that were significantly situated at higher altitudes in compare with unused arctic fox dens (Selås *et al.* 2010). The altitude above tree line was even qualified as one of the two most important variables that determined the den use. The other variable was the previously mentioned abundance of red foxes (Frafjord 2003).

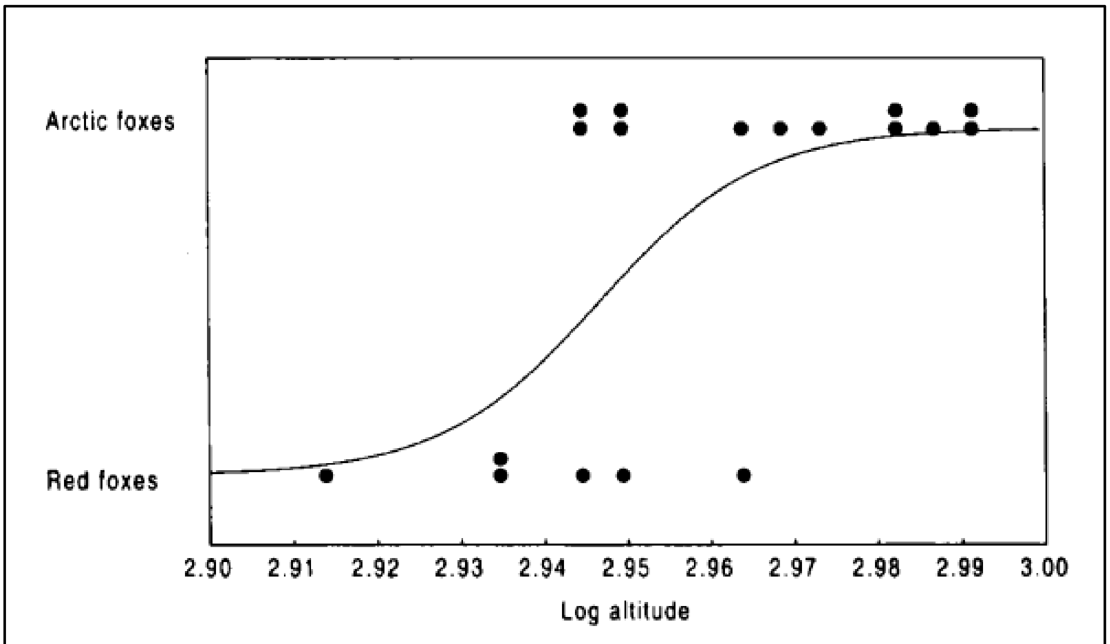

Figure 3: the altitude of dens used by breeding arctic and red foxes in the period of 1986 until 2000 in Vindelfjällen, Sweden. The twelve dens of breeding arctic foxes were situated at significantly higher altitudes (mean=932 m; SD=39) than the six dens of breeding red foxes (mean=872 m; SD=34). From: Tannerfeldt *et al.* 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132**: 213-220.

A last variable that could have an effect on the spatial distribution of arctic fox or red fox dens is the distance from a forest. This variable is tested for both red foxes and arctic foxes in a study in Sweden from Tannerfeldt *et al.* (Tannerfeldt *et al.* 2002). The dens of arctic foxes were situated significantly further away from a forest than the dens of the red foxes. Anthropogenic spatial factors caused by humans, like roads and (vacation) cabins will be discussed in chapter 4.

Spatial competition and climate change
In general, the preference of arctic foxes for specific dens seems to be mostly influenced by red fox abundance (with dens and overall presence) and altitude. Distance from a forest was also a characteristic with a significant effect on the spatial distribution of arctic fox and red fox dens. These variables can be influenced by each other, for example red fox avoidance behaviour could drive the arctic fox to dens at a higher altitude and a longer distance from a forest. Despite the apparent avoidance behaviour, observed by arctic foxes in Fennoscandia, situations with a stable relative abundance of both species are still existing in Yukon, Canada. A future study based on behaviour and spatial distribution in this region could shine a light if the avoidance behaviour of the Scandinavian arctic fox is also present by Canadian arctic foxes. The den itself seems to be more attractive for arctic foxes if the den has multiple accessible entrances and includes a large area. In the perspective of climate change, the most rapidly affected variable influencing spatial competition is the abundance of red foxes. If climate change would move the northern limit of the red fox's geographic range towards the north in Yukon and towards more higher altitudes in Fennoscandia, the abundance of red foxes and red fox dens in the shared habitats with arctic foxes would increase. The effects of climate change on the spatial competition of the arctic fox and the red fox arise primarily from the red fox avoidance behaviour of the arctic fox, discussed in chapter 1. The red fox is also capable to chase away the arctic fox, but also to kill arctic fox juveniles and even to take over the arctic fox's dens. To keep enough distance from the red fox, the arctic fox could populate dens at an even higher altitude, further away from forest (with red foxes) or improve the protective characteristics of its own den if that's possible. In regions where it's possible for the arctic fox to establish itself in more northern regions, where the red fox abundance is lower, a gradual migration to more northern regions is a possible outcome. However, climate change hasn't disturbed the competitive balance of the red fox and the arctic fox in Yukon, Canada during the last four decades, despite the intense climate warming in the western arctic of North-America (Gallant *et al.* 2012). So a larger population of arctic foxes and a smaller population of red foxes are able to live sympatrically without major changes in den use during a longer period. However, in the future climate change could disrupt this sympatric coexistence of the arctic fox and the red fox in Yukon by increased numbers of red foxes migrating to the region. The arctic fox would thereby move to more northern areas. The dominant red fox in Fennoscandia, a region with a relative small population of arctic foxes seems already to have huge impact on the spatial distribution of the arctic fox. If the red fox becomes more abundant in Fennoscandia at higher altitudes, the arctic fox could seek shelter at even higher altitudes to prevent (direct) competition with the red fox and amplify the existing niche differences between the species. However, there is a limit to the possibilities for the arctic fox in Fennoscandia to avoid the red fox, due to the limited altitude of mountains. The differences in spatial competition between Fennoscandia and North-America could be influenced by population sizes of both species or food abundance in the region, which will be addressed in the next chapter.

Competition for food sources

Competition for food sources is an example of potential indirect competition between the arctic fox and the red fox. Research on overlap of food sources between the species has been done on basis of a faeces analysis. With the help of the faeces of the foxes, one can classify the types of the food foxes have eaten. Also the proportion of the food source in the diet of the fox species can be determined. Research in Sylane, on the border of Norway and Sweden, has been looking at 518 pieces of faeces of arctic foxes and 60 pieces of faeces of red foxes (Frafjord 1995). The faeces were collected from eight different dens of Arctic foxes in August 1984 and two dens of red foxes in August 1985. Besides the arctic fox faeces in Sylane, also 100 faeces of arctic foxes at Finse, south Norway, were studied. The food found in the faeces reflects in particular the diet of the fox cubs, because the fox cubs spend the most time in and around the dens of foxes. As can be seen in Figure 4, the most abundant food source found in faeces of arctic foxes was lemmings, with an average for all dens of

73.9 percent. For the faeces of the red foxes, the most abundant food source was vole with an average for all dens of 89.5 percent. However, for this research the sample size for the red fox faeces was smaller and derived from one location (only in Sylane), thus less reliable. The differences between the food sources of the fox species in this research comprises mainly in the numbers of lemmings and voles. Other food sources were rare in the faeces of both species and do not appear to play an important role in the summer diet of the foxes. Thus, these data suggest that the arctic fox has a preference for lemmings, while the red fox appears to have a preference for voles. The arctic foxes in the lowermost dens ate less lemmings than the rest of the foxes at higher altitudes. This raises the question whether the difference in most eaten food source between the two species could be explained by differences in hunting grounds at different altitudes. Lemmings are scarcer under the tree line than above (Frafjord 1995). Thus altitude could also play a role in competition in food sources, besides the role of altitude in spatial competition (see chapter 2).

	Arctic fox			Red fox	
	Finse	mean	*SD*	mean	*SD*
Lemmings	94	73.9	12.1	10.6	3.5
Voles	3	21.3	13.8	89.5	3.5
Birds	2	6.6	5.4	3.6	1.2
Eggshell		1.8	3.5	1.4	1.9
Reindeer		1.1	2.2		
Berries		0.5	1.5		
Arctic fox	1				
Sheep	1				
No. of scats	100	518		60	

Figure 4: the percentages (mean and standard deviation) of the occurrence of food in the faeces of arctic foxes and red foxes in Finse (the first column) and Sylane (column two to five). From: Frafjord 1995. Summer food habits or arctic foxes in the alpine region of southern Scandinavia, with a note on sympatric red foxes*. Annales Zoologici Fennici* **32**: 111-116.

The differences between food sources of the red fox and the arctic fox were described in an article from Elmhagen *et al.* (2002) in Scandinavia. This study examined the faeces of foxes of both species for four years, during the summers of 1993 and 1996 until 1998 in the Vindelfjällan natural reserve. The researchers have been looking at 293 pieces of faeces of arctic foxes and 177 pieces of faeces of red foxes. The faeces are collected from 15 different dens of arctic foxes and 9 dens of red foxes. The results from the study from Elmhagen *et al.* are partly consistent with the results of the article from Frafjord. The arctic foxes in the study from Elmhagen *et al.* also ate more lemmings in compare with the red fox. The red fox ate in turn more voles, as in the study from Frafjord, but also more birds. The number of lemmings, voles and birds were all correlated with altitude in this study. Lemmings were positively correlated with altitude, but voles and birds had a negative correlation with altitude. The study calls altitude-segregation as a plausible explanation for the differences in diet between the red fox and the arctic fox. However, the overlap in food-niches is according to the researchers consistently high in most summers. This could partly be due to the comparable response of the arctic fox and the red fox to temporal changes in the availability of prey. The researchers conclude that the fox species have a similar "virtual" food niche, but spatial segregation causes the differences in the observed diet (Elmhagen *et al.* 2002). An explanation for the spatial segregation could be the spatial competition between the arctic fox and the red fox, mentioned in chapter 2, or a preference of the arctic fox for lemmings, a prey mostly living at high altitudes. The most recent article in which the overlap of food sources of the arctic fox and the red fox are described comes from Savory *et al.* in 2014. This article describes the determination of the diet of ten arctic foxes and ten red foxes from Prudhoe Bay, Alaska, with the help of tissue samples (hair and blood) (Savory *et al.* 2014). Besides the caught living animals, also nine dead red foxes and three dead arctic foxes were used to obtain hair, bone and muscle samples. Stable isotope ratios from the winter coat hair were used to determine the diet in the late summer. To determine the diet during late winter, blood samples or muscle samples obtained from foxes in April and May were used. In general the study included 13 late summer and 13 late winter red fox measurements and 10 late summer and 11 late winter arctic fox measurements. The distribution of food sources in the diets of the red fox and arctic fox in late summer and late winter can be seen in figure 5.

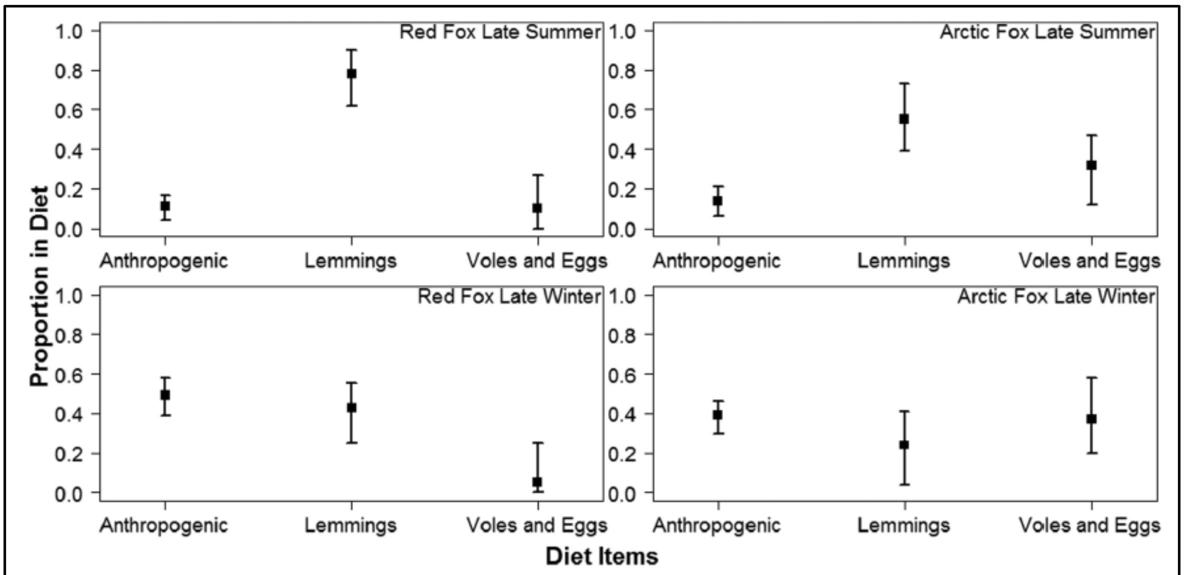

Figure 5: The distribution of food sources in the diets of the red fox (left) and arctic fox (right) in late summer (above) and late winter (below). The food sources are divided in the groups anthropogenic food, lemmings and voles and eggs. From: Savory 2014. Anthropogenic food use and diet overlap between red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. *Canadian journal of zoology* **92**: 657-663.

The season wherein the research was done made a difference in diet for both fox species. This finding is also important in the analysis of the previously mentioned articles, all of which were conducted in the summer. The number of lemmings in the diet of the arctic fox and the red fox was lower in late winter in compare with late summer. In contrast to the previous two studies from Scandinavia, the red fox ate most lemmings in comparison with the arctic fox in both summer and winter. The content of voles in the diet of the fox species was also in contrast to the aforementioned studies from Scandinavia. The red fox ate hardly any eggs and voles in both late winter and late summer. The arctic fox ate eggs and voles especially in late winter. The striking differences between the studies of food sources in Scandinavia and this research from Alaska could be caused by the difference in research methods (analyses of faeces and the analyses of stable isotope ratios), a difference in food sources between habitats on different continents, a difference between the diet of fox pups (more represented in the Scandinavian studies) and the diet of adult foxes (represented in the study from

Alaska) or a combination of these factors. The availability of anthropogenic food sources could also influence the diets of both fox species. The influence of humans on the competition between the arctic fox and the red fox will be further discussed in chapter 4. The researchers also addressed the differences in the abundance of lemmings and voles by annual fluctuations (Savory *et al.* 2014). However, the study could not draw conclusions about the diet of the fox species in specific years. Prey of the arctic fox and the red fox often have cyclic fluctuations.

A study from Shirley *et al.* tried to incorporate the impact of cyclic fluctuations on the arctic fox in a model (Shirley *et al.* 2009). The effects of red foxes and cyclical fluctuations in populations of lemmings and voles on arctic foxes were identified during the study. The cycles of lemmings and voles have, according to the study, a significant negative effect on the arctic fox populations, also in the absence of red foxes. During peak years for the prey of arctic foxes, like lemmings and voles, there was a spike in the number of pups of the arctic fox. A same correlations was seen during a study of the number of arctic fox pups and rodent abundance (Strand *et al.* 1999). The study analysed 675 pieces of faeces in winter and summer of arctic foxes in south-central Norway. In years with a high rodent abundance there was an increased production of arctic fox pups. There was no association between rodent abundance and the number of adult arctic foxes. Thus the cycles of the main food sources of both fox species, namely lemmings and voles, have also a huge effect on the level of competition for food sources. A study from Hof *et al.* (2012) tried to implement the biotic interactions of both the red fox and lemmings on the arctic fox in a species distribution model. In this model, there was no clear relationship between the number of lemmings and the distribution of the arctic fox. There was a peak visible for arctic foxes in an area with a low number of lemmings. The study discussed the intertwined processes of availability, seasonality, preference of both fox species and relative importance of the different preys. All these processes made it harder to compose the most accurate model, including all the prey of the red fox and the arctic fox. The model is therefore questionable, because lemming seem at least an important part of the diet of the arctic fox. A specific process in the food collection of both fox species is hoarding. The process of hoarding could partially neutralize the effects of climate change, because the fox species could use their reserves to bridge periods of scarcity. This process was studied for the arctic fox in Newfoundland, Canada, with observations of nine red foxes in the period of 1978 until 1982 and analyses pieces of faeces of red fox in 1983 on Baccalieu island (Sklepkovych and Montevecchi 1996). Additionally, one arctic fox in Funk island was studied in 1988. The study emphasizes the flexibility of both species in the case of changing food availability. Both species used larder hoarding, the storage of large numbers of prey in and/or around the fox den. The hoarded prey were consumed in large numbers during winter. The larder hoarding behaviour of the foxes is associated with the superabundance of prey (applicable during this study) and could reduce the temporal impact of food availability.

Competition for food and climate change

In general, there seems to be certainly overlap between the diet of the arctic fox and the red fox. Lemmings and voles are both main food sources for both species. There is no consensus about the amounts of these two food sources in the diets of the fox species in the different articles. However, the three studies from Scandinavia on the distribution of food sources between red foxes and arctic foxes have corresponding results. The lemming is the most important food source for the arctic foxes in Scandinavia. Voles are the most important food source for the red fox in Scandinavia. Lemmings and voles were differently distributed in a study from Alaska, wherein the red fox mostly consumed lemmings and the arctic fox mostly consumed voles. Both main food sources, lemmings and voles, are dealing with annual fluctuations in abundance. These fluctuations are directly influencing the number of pups produced by arctic foxes. The abundance of food sources plays an important role in the reproduction process of the arctic fox. The abundance of some food sources, for example lemmings, is also correlated with altitude. The distribution of arctic foxes in areas at higher altitudes, discussed in chapter 2, could amplify or even cause the observed differences in the proportion of food sources in the diet of the red fox and the arctic fox. The processes behind the distribution of food sources are numerous and the impact of these processes on the final distribution is difficult to estimate. Altitude, annual fluctuating cycles of food sources, seasonal differences and differences between habitats could all influence the proportion of food sources in the diets of the red fox and the arctic fox. The competition of food sources is in my view strongly influenced by the spatial distribution of the arctic fox and the red fox. The amount of food sources seems in most habitats sufficient to supply both fox species. The kind of food the arctic fox consumes is highly influenced by red fox abundance and to a lesser extent by the cyclical fluctuations of the two main food sources of both species, lemmings and voles (Shirley *et al.* 2009). The effects of climate change on lemming and vole populations could heavily affect both arctic and fox population. Both fox species are strong dependent on their two main food sources. If one of the two main food sources of the foxes will decrease in supply by climate change, both fox species could be rapidly affected. The dependence on only two food sources could strongly influence the competition between the red fox and the arctic fox in a year with small lemming and vole populations. Lemmings and voles are dependent on long and cold winters and are therefore extra vulnerable to a relative small change in the climate (Ims and Fuglei 2005). A third different food sources, like birds or eggs could become more important by a vole or lemming crash. In general, competition for food sources between the red fox and the arctic fox is the form of competition that seems the most vulnerable for climate change. The effect of climate change on food sources could therefore have a huge impact on the interspecific competition of the fox species in particular and for the whole food web in northern ecosystems in general.

Anthropogenic factors influencing interspecific competition

The effects of human activity on the arctic fox in general and the interspecific competition of the arctic fox and the red fox in particular can be divided in three categories. The first effect of human activity is the effect on available food supplies for the arctic fox and the red fox. Humans can complement the food sources for both species in the form of human garbage, road kills or residues after fishing. A second effect of human activities originates from hunting foxes or hunting the prey of foxes. The last form of human impact of foxes is the influence of human infrastructure, that could affect the abundance of the arctic and the red fox. First I will address the food affiliated effects of human activity on the interspecific competition of the arctic fox and the red fox. Afterwards I will discuss the effects of human infrastructure on the spatial distribution and interspecific competition of the arctic fox and the red fox.
The interspecific competition between the arctic fox and the red fox could have its origin in the human hunting activity on reindeer. A study from Norway analysed the hunting statistics from the period 1821 until 1960 (Selås and Vik 2007). This analysis was done following the idea that the level of reindeer (*Rangifer tarandus*) hunting could affect the population dynamics of arctic foxes and red foxes. The reindeer population increased between 1920 until 1950, whereby also the number of hunted reindeers increased, which can be seen in figure 6. The number of hunted red foxes and hunted arctic foxes was unfortunately not be distinguished in the statistics. However, after a strong decrease in arctic foxes in the period 1905 until 1910, most hunted foxes were probably red foxes. The bounties for red foxes are visible in figure 6. The bounties for red foxes were introduced in Norway in 1879. However, the red fox population increased after the introduction of the bounties regulations. The researchers in the study attribute this apparent contradiction to the decrease in large predators and the increase in forest-living ungulate species. According to the researchers, the stable red fox population benefitted from the increasing reindeer populations starting in the 1920's until the 1950's, visible in figure 6. The red fox population could increase due to the increased availability of reindeer carcasses. The study linked both the over-hunting of reindeer and the success of the red fox to the absence of an increase of the arctic fox population in Norway (Selås and Vik 2007).

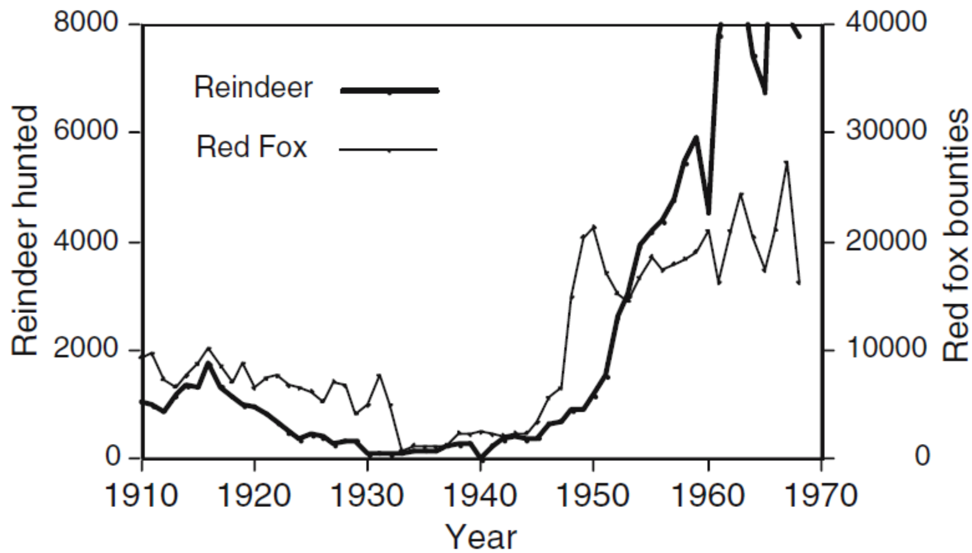

Figure 6: The number of hunted reindeer and hunted foxes (mainly red foxes) killed in the period of 1910 until 1970. From: Selås and Vik 2007. The arctic fox *Alopex lagopus* in Fennoscandia: a victim of human-induced changes in interspecific competition and predation? *Biodiversity and conservation* **16**: 3575-3583.

A recent study on another continent looked at the more direct effects of human presence on the food distribution of the red fox and the arctic fox (Savory *et al.* 2014). The human presence near the oil fields in Prudhoe Bay could have enhanced the presence of the red fox in the same area. The proportion of the anthropogenic food in the diet of the arctic fox and the red fox was already addressed in figure 5. The researchers concluded that, especially in the winter, the red fox benefitted from the food supply through human activities. The red fox uses anthropogenic food sources during the whole year, five times as much in winter as in summer. There was also a significant use of anthropogenic food by the arctic fox. In late winter the proportion of anthropogenic food for the red fox was 49%, against 39% for the arctic fox. The diet of the arctic fox was more diverse, including more eggs and voles, and therefore less dependent on the human food sources. Anthropogenic food sources are also mentioned in an article from Selås *et al.* on the use of dens of the red fox and the arctic fox (Selås *et al.* 2010). The study tried to make a model to reconstruct the arctic fox abundance for dens with and without litters. The model included the abundance of human infrastructure, including number of (vacation) cabins, kilometres of roads and kilometres of trails. The researchers expected for all three examples of human infrastructure in general a link with garbage. Specific for trials the researchers expected a correlation with remains of fishing and specific for roads a correlation with carcasses by road kills. The best fitting model for den use in general contained less human infrastructure within 7 by 7 kilometre squares. For dens with litters, the model for den use contained less human infrastructure within 15 by 15 kilometre squares. The study suggests the effect of human infrastructure is coupled with a higher abundance of red foxes near the human infrastructure, where the foxes consume the more stable human food sources. In a different article the probability of colonization of the arctic fox according to the closest road is tested (Hamel *et al.* 2013). Asphalt roads had also in this article a strong negative impact on the recolonization of the arctic fox, comparable with the abundance of the red fox. The researchers suggest the effect of the presence of roads is due to a sum of several factors. Roads are often located along the coast, through forests and past human settlements. All these three factors would deter the presence of arctic foxes.

Anthropogenic factors and climate change

In general, human disturbances (in the form of infrastructure, food distribution or both) have a huge impact on the abundance of the arctic fox and the red fox and therefore on the interspecific competition between both species. In both Alaska and Scandinavia, human activity had a huge influence on the abundance of the arctic fox and on the food distribution of both fox species by providing anthropogenic food sources. The red fox seems to make better use of anthropogenic food in compare with the arctic fox. Climate change could increase the presence of human activity in certain locations, for example by increasing the number of suitable locations for (oil) industry. Around new shipping routes new industry could be constructed, including new roads to secure the accessibility. However, the human influence could be limited by strong regulation regarding waste and human presence in general. The human impact is not negligible, as shown in the studies where the influence of red foxes and human infrastructure on the arctic foxes is comparable. Climate change seems to me rather a reason for stricter regulation or at least a second look at human activity in the habitats of both fox species, than the cause of even greater influence on the interspecific competition between the arctic fox and the red fox. The effects of human presence on interspecific competition between the red fox and the arctic fox are in my opinion easier to prevent or to reverse in compare with the effects of climate change on interspecific competition between the fox species. Processes such as changes in population sizes of the most important food sources of the red fox and the arctic fox and changes in distribution of the red fox and the arctic fox are in my view the most important long-term effects on the interspecific competition, both mostly affected by climate change. However, because of the vague line between anthropogenic influence and influence of climate change on interspecific competition, it’s difficult to assign effects to one of both categories. For example, the distribution of anthropogenic food sources could accelerate the increase in the number of red foxes in Yukon by means of climate change, Canada.

Conclusion and discussion

The process of interspecific competition is characterized by a complex web of multiple influencing factors. Two studies on interspecific competition in captivity with controlled conditions observed both a strong dominant attitude of the red fox in relation to the arctic fox. The red fox dominates the arctic fox in direct physical confrontations. The interspecific competition between the arctic fox and the red fox in the wild is mostly studied in three different regions. These three regions are Fennoscandia, Prudhoe Bay (Alaska) and Yukon (Canada) (Gallant *et al.* 2012; Gallant *et al*. 2013; Hamel *et al*. 2013; Savory *et al.* 2014). I have found only one article about the interspecific competition between the red fox and the arctic fox in Yamal Peninsula, Russia (Rodnikova *et al.* 2011). This is probably caused by the inaccessibility of Russian literature. It is therefore not possible for me to draw conclusions about the state of interspecific competition between the red fox and the arctic fox in the Russian tundra. Particularly the differences between interspecific competition in the regions in the North-American arctic and the regions in Fennoscandia are important to keep in mind. Despite that the arctic fox population in Fennoscandia has a protected status since 1940, the population is at a low level since hunting in the early nineteenth century and has not recovered (Shirley *et al.* 2009). In contrast, in Alaska and Canada, the arctic fox populations are stable and dealing since a relatively short period with the rise of the red fox. During the last forty years, little has changed according to research into the competitive balance between the two species in northern Yukon (Herschel Island and the coast of the mainland). In Prudhoe Bay, Alaska, red foxes were for the first time observed in 1988 (Savory *et al.* 2014). Thus, the length in time in which the two species occur together in Europe and America differs strongly. Also the degree of human interference in the areas differs. In Fennoscandia, human interference seems present on a bigger scale in compare with Alaska with roads, cabins and fishing. However, there is no research available about the distance between arctic fox and red fox dens and human infrastructure or constructions in Alaska. This distance has been studied in

Fennoscandia. It is therefore not yet possible to make a good comparison between the influence of human infrastructure or constructions on the distribution of fox dens in Alaska and Fennoscandia.

The presence of arctic foxes in Fennoscandia is most influenced by the presence of the red fox and human influence. The arctic fox was not possible to adapt to the increased reindeer populations and red fox populations that have emerged in the period from the 1920s to the 1950s. The enhanced presence of the red fox in Fennoscandia has a negative influence for the arctic fox on its spatial distribution and reproduction. (Linnell *et al*. 1999; Tannerfeldt *et al.* 2002; Frafjord 2003; Elmhagen *et al.* 2002; Savory *et al.* 2014). The dominant position of the red fox makes a stable healthy arctic fox population of similar size of the red fox population unlikely, even with the least human interference. Only a reduction of the red fox population, as proposed by Selås and Vik (2007), seems to be a possibility to reintroduce the arctic fox. Climate change could have another negative effect on the arctic fox, but also on the red fox by the effects of climate warming on food sources of the species. Global warming will affect the lemming population, a key species in the food web and one of the main food sources for the arctic fox and the red fox. It is difficult to estimate if the arctic fox or even the red fox is able to adapt to huge changes in the food web and therefore their diet. The cycles in the populations of voles and lemmings are traditionally influencing the number of pups of the arctic fox. Thus, possible changes in the availability of food sources for fox species by climate change is another factor, besides the relative large red fox population and human interference, that poses a threat to the survival of the arctic fox in Fennoscandia.

The situation around food sources in Prudhoe Bay, Alaska, has similarities and differences with the situation in Fennoscandia. Lemmings were still one of the main food sources for both species, however voles were only a crucial food source for arctic foxes. The anthropogenic food proportion in the winter diet of both fox species was comparable with the proportion of lemmings in the diet of both fox species in winter. The anthropogenic food proportion in the summer is really small and comparable with the proportion of voles and egg in the diet. However, the effects of climate change on the lemming populations are similar to the effects in Fennoscandia and bring the same concerns for food shortage for both the arctic and the red fox in both regions. The situation of the arctic fox in Alaska is less endangered in compare with its species in Fennoscandia by a more stable situation with less red foxes and less human interference. The arctic fox population in Alaska is less vulnerable to changes in the ecosystem by climate change by the relatively stable situation in the last forty years.

Food supply seems to be most vulnerable to climate change in northern ecosystems and could have a huge effect on the distribution of species and therefore the (direct) interspecific competition. The food supply for specific the arctic fox and the red fox is perhaps more vulnerable than the food supply for other species by the already existing (annual) fluctuating cycles of food sources of the foxes. The interspecific competition between the arctic fox and the red fox is probably influenced by climate change in an earlier stage in compare with species with more stable food sources. The arctic fox is in comparison with the red fox more adapted to extreme cold conditions. Climate warming could lead to less harsh conditions, making it possible for the red fox to survive in former inaccessible areas. Anthropogenic food sources provide an alternative food source for the red fox, increasing the survival chances of the red fox in harsh conditions. In general, climate change has consequences on interspecific competition, mainly by effects on food availability and resulting changes in distribution. Climate change could enable red fox abundance at higher altitudes in Fennoscandia and abundance at higher latitudes in Alaska and Canada. The arctic fox will probably try to prevent (direct) competition with the red fox by seeking shelter at even higher altitudes and higher latitudes. The existing niche differences between the species would be amplified by this process. Due to the limited altitude of the mountains, the arctic fox cannot continue to avoid the red fox in the future in Fennoscandia.

The changes in spatial distribution may ultimately result in more physical confrontations between species that could result in fatalities by one of the species, as observed in several studies for the arctic and the red fox (Frafjord *et al.* 1989; Tannerfeldt *et al.* 2002). For a more complete picture of interspecific competition more research has to be done on the situation on Yamal Peninsula (Russia), where only one observation of a den takeover by a red fox is known. Also the influence of human interference on the spatial distribution of dens of arctic and red foxes in Prudhoe Bay (Alaska) needs further research, to complement the research on competition for food sources between the species in this region. In Newfoundland, Canada, the distribution of food sources between the red fox and the arctic fox remains unknown and needs further study, in addition to testing for the presence of red fox avoidance behaviour among the arctic fox in Canada.

Bibliography

Figures

Front cover:
Die besten Naturfotografien des Jahres; available at https://www.greenpeace-magazin.de/nachrichtenarchiv/die-besten-naturfotografien-des-jahres Accessed on February 10, 2016.

Figure 1:
Rudzinski *et al.* 1982. Behavioural Interactions of Penned Red and Arctic Foxes. *The Journal of Wildlife Management* **4**: 877-884.

Figure 2:
Hersteinsson, P. and Macdonald, D. W. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64:** 505-515.

Figure 3:
Tannerfeldt *et al.* 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132**: 213-220.

Figure 4:
Frafjord 1995. Summer food habits or arctic foxes in the alpine region of southern Scandinavia, with a note on sympatric red foxes. *Annales Zoologici Fennici* **32**: 111-116.

Figure 5:
Savory 2014. Anthropogenic food use and diet overlap between red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. *Canadian journal of zoology* **92**: 657-663.

Figure 6:
Selås and Vik 2007. The arctic fox *Alopex lagopus* in Fennoscandia: a victim of human-induced changes in interspecific competition and predation?. *Biodiversity and conservation* **16**: 3575-3583.

Literature

1. Post, E. *et al.* 2009. Ecological dynamics across the arctic associated with recent climate change. *Science* **325**: 1355-1358.

2. IPCC (2014) Climate Change 2014; Available at https://www.ipcc.ch. Accessed on February 5, 2016.

3. Poloczanska, E. S. *et al.* 2008. Modeling the response of populations of competing species to climate change. *Ecological Society of America* **89:** 3138-3149.

4. Tannerfeldt, M. *et al.* 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132:** 213-220.

5. Savory, G. A. *et al.* 2014. Anthropogenic food use and diet overlap between red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. *Canadian Journal of Zoology* **92:** 657-663.

6. Rodnikova, A. *et al.* 2011. Red fox takeover of arctic fox breeding den: an observation from Yamal Peninsula, Russia. *Polar Biology* **34:** 1609-1614.

7. Gallant, D. *et al.* 2012. Arctic fox versus red fox in the warming Arctic: four decades of den surveys in north Yukon. *Polar Biology* **35:** 1421-1431.

8. Gallant, D. *et al.* 2013. Natal den selection by sympatric arctic and red foxes on Herschel Island, Yukon, Canada. *Polar Biology* **37:** 333-345.

9. Hamel, S. *et al.* 2013. Disentangling the importance of interspecific competition, food availability, and habitat in species occupancy: Recolonization of the endangered Fennoscandian arctic fox. *Biological Conservation* **160:** 114-120.

10. Rudzinski, D. R. *et al.* 1982. Behavioural interactions of penned red and arctic foxes. *The journal of wildlife management* **46:** 877-884.

11. Korhonen, H. *et al.* 1997. Inter- and intraspecific competition between the fox species *Alopex lagopus* and *Vulpes vulpes*: an evaluation trial under penned conditions. *Polar Biology* **17:** 330-336.

12. Frafjord, K. *et al.* 1989. Interactions between arctic and red foxes in Scandinavia: predation and aggression. *Arctic* **42:** 354-356**.**

13. Shirley, M. D. F. *et al.* 2009. Modelling the spatial population dynamics of arctic foxes: the effects of red foxes and microtine cycles. *Canadian Journal of Zoology* **87:** 1170-1183.

14. Hersteinsson, P. and Macdonald, D. W. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* **64:** 505-515.

15. Smits, C. M. M. and Slough B. G. 1993. Abundance and summer occupancy of arctic fox, *Alopex lagopus*, and red fox, *Vulpes vulpes*, dens in the northern Yukon territory, 1984-1990. *The Canadian field-naturalist* **107:** 13-18.

16. Frafjord, K. 2003. Ecology and use of arctic fox *Alopex lagopus* dens in Norway: tradition overtaken by interspecific competition? *Biological Conservation* **111:** 445-453.

17. Dalerum, F. *et al.* 2002. Distribution, morphology and use of arctic fox *Alopex lagopus* dens in Sweden. *Wildlife Biology* **8:** 187-194.

18. Linnell, J. D. C. *et al.* 1999. Use of dens by red *Vulpes vulpes* and arctic *Alopex lagopus* foxes in alpine environments: Can inter-specific competition explain the non-recovery of Norwegian arctic fox populations? *Wildlife Biology* **5:** 167-176.

19. Selås, V. *et al.* 2010. Arctic fox *Vulpes lagopus* den use in relation to altitude and human infrastructure. *Wildlife Biology* **16:** 107-112.

20. Frafjord, K. 1995. Summer food habits of arctic foxes in the alpine region of southern Scandinavia, with a note on sympatric red foxes. *Annales Zoologici Fennici* **32:** 111-116.

21. Elmhagen, B. *et al.* 2002. Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology* **80:** 1274-1285.

22. Strand, O. *et al.* 1999. Dietary and reproductive responses of arctic foxes to changes in small rodent abundance. *Arctic* **52:** 272-278.

23. Hof, A. R. *et al.* 2012. How biotic interactions may alter future predictions of species distributions: future threats to the persistence of the arctic fox in Fennoscandia. *Diversity and distributions* **18:** 554-562.

24. Sklepkovych, B. O. and Montevecchi W. A. 1996. Food availability and food hoarding behaviour by red and arctic foxes. *Arctic* **49:** 228-234.

25. Ims, R. A. and Fuglei E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* **55:** 311-322.

26. Selås, V. and Vik, J. O. 2007. The arctic fox *Alopex lagopus* in Fennoscandia: a victim of human-induced changes in interspecific competition and predation? *Biodiversity and conservation* **16:** 3575-3583.