Master's thesis

NTNU
Norwegian University of Science and Technology

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A battle of the mountains: Intraguild competition between arctic fox *Vulpes lagopus* and red fox *Vulpes vulpes*

Master's thesis in Biology
Supervisor: Henrik Jensen
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July 2019

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ABSTRACT

The arctic fox (*Vulpes lagopus*) is a threatened species in Fennoscandia. Intraguild competition with the red fox (*Vulpes vulpes*) is considered one of the main threats for their existence in this area. Several conservation actions, including supplemental feeding of the arctic fox, red fox culling and a captive breeding and release reintroduction programme have been implemented. Over the last decade, these actions have led to growth in the remaining Fennoscandian arctic fox populations. In this study I examined components of a conceptual model framework suggesting that the competitive strength of the two species is dependent on their relative population sizes, meaning that the red fox is the dominant competitor at small arctic fox population sizes, while the arctic fox is the dominant competitor at large arctic fox population sizes. The study was conducted at Finse mountain plateau, where arctic foxes have been released from 2009 until 2012. Fox activity was recorded using movement-triggered wildlife cameras at feeding stations. The arctic fox population size in the study area was estimated, and I investigated the effect of arctic fox activity and population size on the red fox activity. I also looked for avoidance behaviour between the two species by comparing the time duration between visits of individuals of the opposite species.

My results show that red fox activity is not affected by arctic fox activity nor the population size of arctic fox. However, there seems to be a trend towards a negative relationship between the activity of the two species. A possible reason for these findings could be that the arctic fox population size is too small to be expected to have an impact on the red fox activity, as the largest estimated arctic fox population size in the study period was way below the estimated carrying capacity in the area. Neither did I find any evidence of avoidance behaviour between the two species, or that the population size affected their visiting patterns at the feeding stations. This could, according to the conceptual model, suggest that the arctic fox population is large enough to have become the dominant competitor and hence do not avoid the red fox. The contradicting results in my study area stress the need for a better understanding of the relationship between arctic fox and red fox. The conceptual model framework should be tested covering several subpopulations with contrasting densities of the two species. Knowledge about the intraguild interactions between the arctic fox and red fox is important for the future management and conservation of the arctic fox in Fennoscandia and provides a better understanding of intraspecific interactions between intraguild predators. If the arctic fox does not become the dominant competitor when reaching viable population sizes, the Norwegian management plan will not succeed in the long term and must be revised.

SAMMENDRAG

Fjellreven (*Vulpes lagopus*) er en truet art i Fennoskandia. Konkurranse med rødreven (*Vulpes vulpes*) er regnet som en av hovedtruslene for fjellrevens utbredelse. Flere bevaringstiltak har blitt satt i gang for å redde fjellreven, både støttefôring av fjellreven, uttak av rødrev og et avls- og reintroduksjonsprogram. Gjennom de siste tiårene har disse tiltakene ført til en vekst i de gjenværende fjellrevpopulasjonene i Fennoskandia. I dette studiet undersøkte jeg deler av et konseptuelt modell-rammeverk som foreslår at konkurransestyrken til de to artene avhenger av deres relative populasjonsstørrelse, nemlig at rødreven er den dominante konkurrenten ved små populasjonsstørrelser av fjellrev, mens fjellreven er den dominante konkurrenten ved store populasjonsstørrelser av fjellrev. Dette studiet ble utført i området rundt Finse, der det har blitt sluppet ut fjellrever fra 2009 til 2012. Revenes aktivitet ble registrert med viltkameraer med bevegelsessensor ved fôringsstasjoner. Populasjonsstørrelsen til fjellreven ble estimert, og jeg undersøkte effekten av fjellrevaktivitet og populasjonsstørrelse av fjellrev på rødrevaktivitet. Jeg så også etter unngåelsesatferd mellom de to artene ved å sammenligne hvor lang tid det gikk mellom besøk av de ulike artene på fôringsstasjonene.

Resultatene mine viser at rødrevaktivitet verken er påvirket av fjellrevaktivitet eller populasjonsstørrelse av fjellrev. Det ser derimot ut til at det er en trend mot et negativt forhold mellom aktiviteten til de to artene. En mulig årsak til disse funnene kan være at populasjonsstørrelsen av fjellrev i området er for liten til at det kan forventes at den har noen effekt på rødrevaktiviteten, siden den største populasjonsstørrelsen av fjellrev i studieperioden var under den estimerte bæreevnen til området. Jeg fant heller ikke noe bevis for unngåelsesatferd mellom de to artene, eller at populasjonsstørrelsen av fjellrev påvirket besøksmønstrene deres ved fôringsstasjonene. Dette kan, ifølge det konseptuelle rammeverket, bety at fjellrevpopulasjonen *er* stor nok til å være den dominante konkurrenten og derfor ikke unngå rødreven. De motsigende resultatene mine viser behovet for en bedre forståelse av forholdet mellom fjellreven og rødreven. Det konseptuelle modell-rammeverket burde testes med flere subpopulasjoner med forskjellige tettheter av de to artene. Kunnskap om interaksjonene mellom rødreven og fjellreven er viktig for den videre forvaltningen og bevaringen av fjellrev i Fennoskandia og kan gi bedre forståelse av intraspesifikke interaksjoner mellom predatorer. Hvis fjellreven ikke blir en dominant konkurrent mot rødreven når den når bærekraftige populasjonsstørrelser, vil ikke den norske forvaltningsplanen lykkes i det lange løp, og det må gjøres endringer i forvaltningsmålene.

Keywords: Avoidance behaviour, exclusion, conservation, reintroduction, niche overlap, interspecific competition, alpine, boreal

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Ragnhild Thorseth Grevskott,

Trondheim, June 2019

CONTENTS

1 INTRODUCTION

1.1 BACKGROUND

A variety of conservation and reintroduction programmes are carried out to conserve species, habitats and ecosystems throughout the world. In many cases, local extinctions require significant management actions to help species recolonize their native habitat (Adams, 2008; Kleiman, 1989). Globally, many reintroduction programmes trying to reintroduce captive-bred individuals to their former habitats fail (Jule et al., 2008; Snyder et al., 1996). One reason for the numerous failures of reintroduction programs is that the factor that made the population go extinct in the first place was not removed or changed before the species is reintroduced, and in the long-term, this factor may eventually again lead to extinction of the population (Jule et al., 2008). Such factors could include interactions between the threatened species and other species within a guild, such as interspecific competition for food, breeding localities and other common resources, as well as predation on competitors within the same guild (Linnell & Strand, 2000; Polis et al., 1989; Sergio & Hiraldo, 2008).

The arctic fox (*Vulpes lagopus*) has a circumpolar distribution and a global population size of several hundred thousand individuals (A. Angerbjörn & Tannerfeldt, 2014), which is believed to be robust and viable in most areas. However, the arctic fox is listed as ‘critically endangered’ in Norway (Henriksen & Hilmo, 2015) and ‘endangered’ in Sweden (ArtDatabanken, 2015). The population was close to extinction in year 2000 with only 40-60 adult foxes left in Fennoscandia. (Henriksen & Hilmo, 2015). To increase the population size in Norway, several comprehensive conservation actions were initiated in 1998. These were supplemental feeding of the arctic fox, culling of red fox (*Vulpes vulpes*) and a captive breeding and reintroduction programme which started in 2005. Today, the arctic fox population in Fennoscandia consists of minimum 304 individuals in reproductive age (Ulvund & Wallén, 2018).

Historically, the arctic fox was a common species in northern Europe, but it was intensively hunted for its valuable fur since the beginning of the 20th century (Collett, 1912). The population suffered drastic decline, and this intensive hunting is believed to be the main factor for its reduced distribution and numbers (Hersteinsson et al., 1989; Linnell et al., 2004; Loison et al., 2001). As a response, the arctic fox became protected by law in 1928, 1930 and 1938, in

Sweden, Norway and Finland, respectively. Despite protection, the population remained at a low density for over 85 years.

Three main ecological drivers are believed to contribute to the failure of recovery of the arctic fox population in Fennoscandia. These threats are small and fragmented populations with very limited gene flow (Herfindal et al., 2010), reduced food availability due to disruptions of rodent cycles (Anders Angerbjörn et al., 2001; Henden et al., 2008), and increased competition with the larger red fox (Frafjord et al., 1989; Hamel et al., 2013).

The Scandinavian action plan from 2017 for conservation of the arctic fox stresses the need to continue the conservation measures that have been conducted during the recent years: population supplementation through the arctic fox captive breeding and reintroduction programme, supplementary feeding through feeding dispensers made exclusively for the arctic fox, as well as red fox culling (Eide et al., 2017). Several studies also suggest that culling of red fox should be done in areas where the two species' distributions overlap to reduce interspecific competition (Hamel et al., 2013; Hof et al., 2012; Linnell & Strand, 2000). However, culling is a short-term initiative which will not be a permanent solution as red fox dispersal from low-elevation areas is expected to increase in the future (Elmhagen et al., 2017). Increased competition from the red fox may prevent the arctic fox from reaching viable population numbers. If this is the case, the captive-breeding and reintroduction programme will not succeed in the long-term, since the goal of the management plan is to have viable populations that are independent of any further management actions (Eide et al., 2017).

Historically, the arctic fox and red fox showed little range overlap (Hersteinsson & MacDonald, 1992). Where they both existed, the arctic fox occupied the more marginal habitats (high alpine and high arctic tundra areas). In contrast, in places without red fox, for example in Greenland, Iceland and Svalbard, the arctic fox is found in urban, inland and coastal areas as well as from the high arctic to the more temperate areas (i.e. Southern Greenland and Iceland; Figure 1) (Szor, 2006).

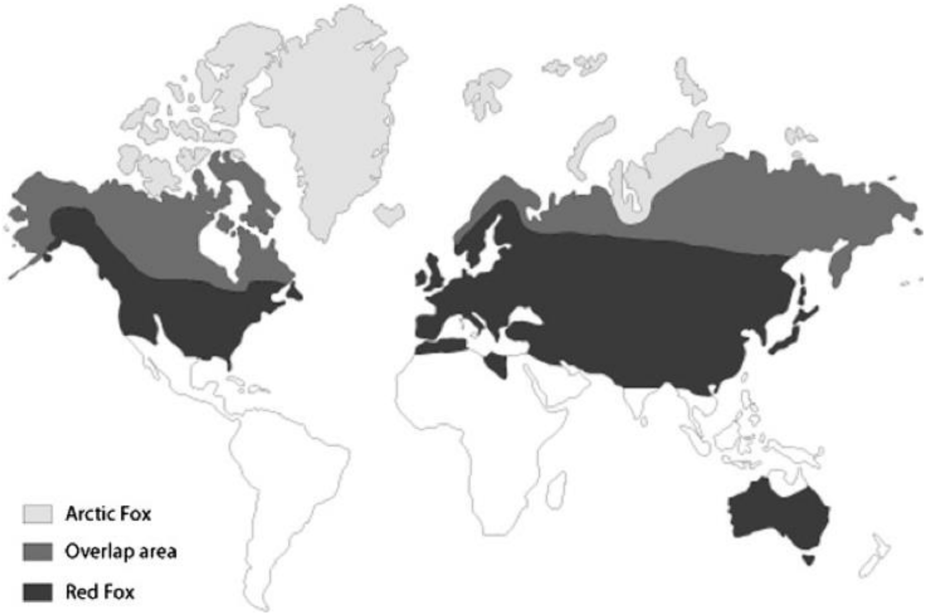

Figure 1. The distributions of arctic fox *Vulpes lagopus* and red fox *Vulpes vulpes*, retrieved from Szor (2006).

Arctic and red foxes have very similar fundamental food niches (Elmhagen et al., 2002; Frafjord, 1993). However, the red fox is not as well adapted to harsh climatic and marginal arctic environments as the arctic fox (Hersteinsson & MacDonald, 1992), it is rather dependent on an environment with a more stable food supply (Elmhagen et al., 2002). The red fox distribution northwards and high-elevation expansion is likely limited by climate and temporal and spatial distribution of food. Hersteinsson and MacDonald (1992) suggested that the arctic fox distribution southwards and at lower elevation is limited by the red fox. During the last decades, the red fox has expanded its range above the tree line in Fennoscandia (Henden et al., 2014; Killengreen et al., 2011). The reason for this is not fully known, but both climate change, increased amount of infrastructure in mountainous areas and increased amounts of carcasses from semi-domesticated reindeer (*Rangifer tarandus*) are believed to contribute to their expansion towards higher elevation (Elmhagen et al., 2017). This has resulted in an increased overlap zone for arctic and red fox distribution, which threatens the arctic fox distribution by competition for resources (Dalerum et al., 2002; Frafjord, 2003; Linnell et al., 1999) and intraguild predation (Frafjord et al., 1989).

The competitive exclusion principle (Hardin, 1960) states that two species with completely overlapping ecological niches cannot coexist over time, and that one species will eventually lead to the extinction of the other. Most literature suggests that the red fox presence affects the arctic fox distribution negatively (Elmhagen et al., 2017). In Fennoscandia, the red fox has been found to exclude the arctic fox from dens in low elevation areas, and use them for breeding (Dalerum et al., 2002; Frafjord, 2003; Linnell et al., 1999). Herfindal et al. (2010) found that the arctic fox breeding success in Fennoscandia was also negatively associated with increased risk of red fox presence. In Alaska, Stickney et al. (2014) observed arctic fox population decline and concurrent red fox population increase. However, some studies do not find these patterns. Two studies from northern Canada found no contractions of arctic fox distribution due to red fox presence, even though interspecific interactions were observed (Gallant et al., 2012; Gauthier et al., 2013). The discrepancies in the literature calls for further research to understand how these fox species influence each other.

The mechanisms of the interspecific interactions between the arctic fox and the red fox are not well studied. Some studies show that the red fox can kill the arctic fox (Frafjord et al., 1989; Pamperin et al., 2006), but how frequent this happens remains unknown. There is, however, not much knowledge about how often they encounter each other in areas where their distributions overlap. Red fox avoidance towards larger canids is well documented (Leo et al., 2015; Scheinin et al., 2006; Voigt & Earle, 1983), and research investigating if the same avoidance patterns exist between the smaller arctic fox and the larger red fox is needed to understand the mechanisms of their interactions.

Researchers involved in the Arctic fox National monitoring programme in Norway have established a conceptual model framework about how the competitive strengths of the arctic fox and red fox are expected to relate to the relative population size of the two species (Figure 2) (pers.com, Nina Eide & Arild Landa 2019).

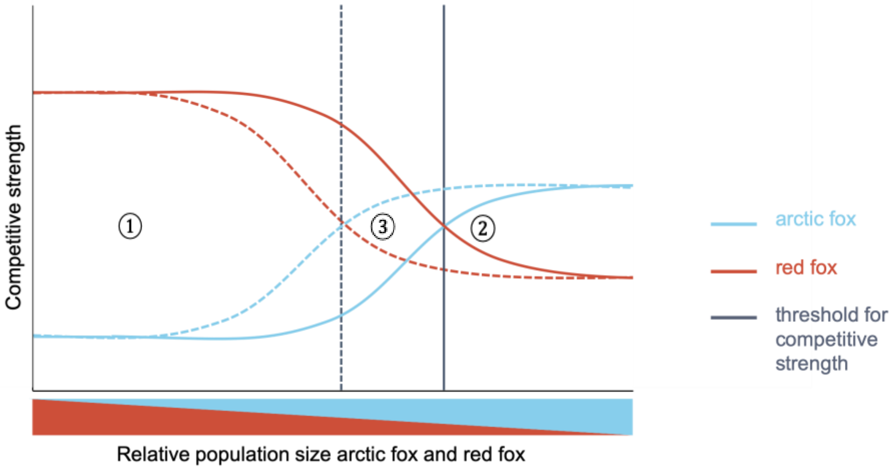

Figure 2. The predicted relative competitive strengths of red fox (*Vulpes vulpes*) and arctic fox (*Vulpes lagopus*) as a function of the relative population size of the two species. Solid lines represent the predicted competitive strengths when none of the species are affected by supplemental feeding, while the dotted lines represent the predicted competitive strengths when the arctic fox is supplementary fed. ① Low arctic fox to red fox population ratios, the red fox is the dominant competitor, ② High arctic fox to red fox ratios, reaching a threshold where the arctic fox becomes the dominant competitor, ③ Expected change in the threshold for competitive strength due to exclusive feeding of the arctic fox.

The model framework states that the competitive strengths of the two species are dynamic and dependent on their relative population size. At low arctic fox to red fox population ratios ①, the red fox is the dominant competitor, able to outcompete the arctic fox in areas where their distributions overlap. However, increasing the proportion of arctic fox to red fox population sizes is expected to change this relationship reaching a threshold where the arctic fox becomes dominant and is able to outcompete the red fox ②. This hypothesized change in interspecific relations with population size has not yet been investigated.

With the ongoing supplemental feeding of the arctic fox, the threshold for where the arctic fox is able to outcompete the red fox is according to the conceptual model framework predicted to shift, setting the threshold for competitive strength at lower relative densities of arctic fox ③. The feeding dispensers are built to be exclusive for the arctic fox but are frequently visited by other trespassing carnivores, such as red fox or mustelids (*Mustelidae*). They are equipped with camera traps to register occurrence of the two fox species (see description under section 2.3), making it possible to monitor their activity.

1.2 OBJECTIVES AND HYPOTHESIS

The main purpose of this study was to use the conceptual model framework (Figure 2) to examine interactions between the arctic fox and the red fox in areas where their distributions overlap. I examined how these interactions change at different population sizes of arctic fox at the Finse mountain plateau.

I hypothesized that the red fox should be differently affected by the arctic fox depending on the population size of arctic fox. I investigated this in space and time by exploring the activity of the two species at the arctic fox supplementary feeding stations. Firstly, I predicted that the arctic fox activity does not affect the red fox activity negatively at low population sizes of arctic fox. However, at large population sizes of arctic fox, I expected that the red fox activity would be negatively affected by arctic fox activity. Secondly, I predicted that the arctic fox would show avoidance behaviour towards the red fox at small population sizes of arctic fox, while such avoidance behaviour towards the red fox would disappear at large arctic fox population sizes.

2 METHODS

2.1 STUDY AREA

The study was conducted at the Finse mountain plateau. It is located centrally in southern Norway in the border zone between Buskerud, Hordaland and Sogn og Fjordane counties (Figure 3). This study area was chosen due to the absence of red fox culling, which made it possible to study interactions between the species while avoiding that culling affects the results. Parts of the study area are within Hallingskarvet national park, which is a protected area for nature and wildlife covering 450 km^2 (Forskrift om verneplan for Hallingskarvet, 2006). The ecosystem is characterized by long winters and low to middle alpine climate (Moen, 1999). Typical vertebrate species in the area are lemmings and other small rodents (*Rodentia*), mountain hare (*Lepus timidus*), rock ptarmigan (*Lagopus mutus*), willow ptarmigan (*Lagopus lagopus*), small mustelids, reindeer, arctic fox, red fox, passerines (*Passeriformes*), ducks (*Anseriformes*), and waders (*Charadriiformes*) (Høiland et al., 2005).

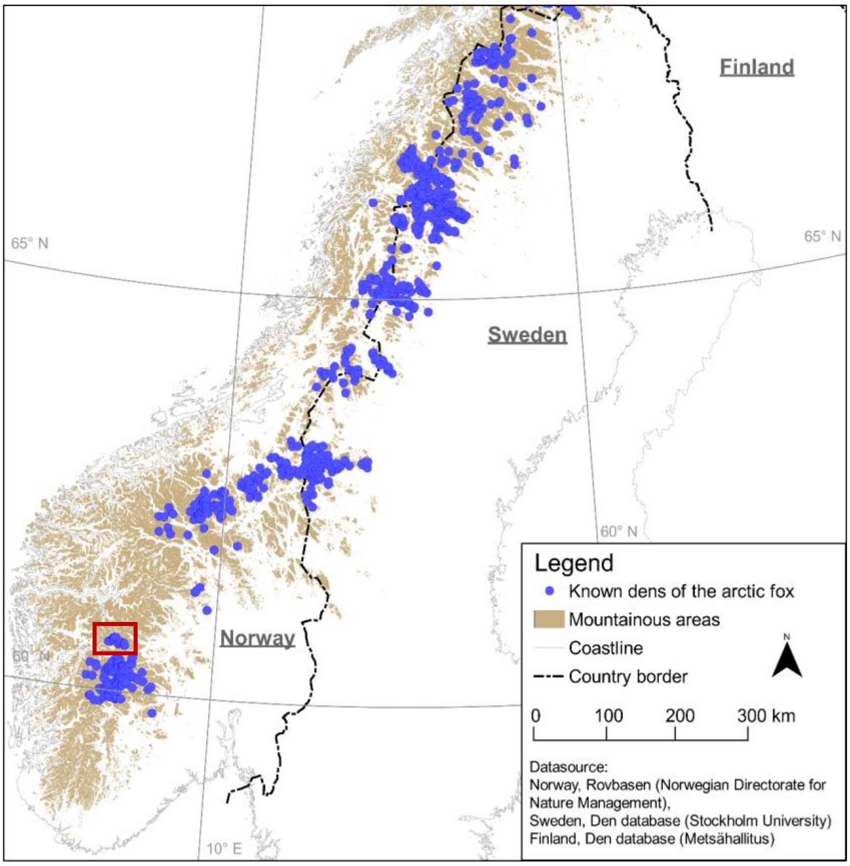

Figure 3. Map of Southern Norway showing the study area Finse mountain plateau (in the red square) and known arctic fox den sites.

2.2 SPECIES DESCRIPTION

ARCTIC FOX

The arctic fox is a relatively small canid (3-5 kg) inhabiting the arctic and alpine tundra (Audet et al., 2002). It is described as a generalist, and when living in inland climate as in most of Fennoscandia, it heavily depends on lemmings as its main food source (Elmhagen et al., 2000). Rodent cycles in Fennoscandia are in general repeated with a three to five-year interval (Anders Angerbjörn et al., 1995; Henden et al., 2009). One arctic fox pair has capacity to raise as much as 19 cubs in a single breeding season during rodent peaks, whereas the arctic fox rarely reproduces during periods of low rodent density (Tannerfeldt & Angerbjörn, 1998). When rodent availability is high, the population can increase rapidly, but this is typically followed by a crash when rodent density declines (Tannerfeldt & Angerbjörn, 1998).

RED FOX

The red fox is a slightly larger canid (3-8 kg) and a boreal generalist, inhabiting a large variety of habitats throughout the world (Hoffmann & Sillero-Zubiri, 2016). It is a common species in Fennoscandia, and its distribution there is limited by harsh climatic conditions (K. A. Bartoń & Zalewski, 2007; Elmhagen et al., 2017). As a generalist it is feeding opportunistically and is shown to have overlapping food niche with the arctic fox (Elmhagen et al., 2002).

2.3 DATA COLLECTION

The study took place in the late winter (February to May) over eight years (2010-2017). At Finse mountain plateau, the arctic fox population was re-established by the release of captive-bred pups during a four-year period (2009-2012; n=71). These individuals were the foundation for the present Finse population (Ulvund et al., 2018). Fox scats were collected annually during winter time for DNA identification of individuals. Annual arctic fox breedings were recorded, pups were captured and marked with HPT12 Biomark PIT-tags (injected between the shoulder blades) for lifelong identification by the captive breeding programme and DNA samples were collected from ear tissue (Landa et al., 2017). Already marked adults were also identified when possible. The captive-bred pups previously released to the area, were additionally marked with four coloured Dalton Rototag ear tags for identification through pictures and direct observations. (Landa et al., 2017).

Supplemental feeding stations for the arctic fox were installed in the study area in 2010. Based on the size difference in arctic and red foxes, the feeding station entrances were designed to exclude the red fox and exclusively feed the arctic fox (Figure 4a). The feeding stations are filled with dog food (Landa et al., 2017), monitored monthly by the local rangers, and equipped with movement-triggered digital wildlife cameras (PC800 HyperFire semi-covert camera trap, Reconyx, Wisconsin, USA) and Biomark PIT-tag readers (FS-2001, Biomark, Idaho, USA; Figure 4a) (Landa et al., 2017).

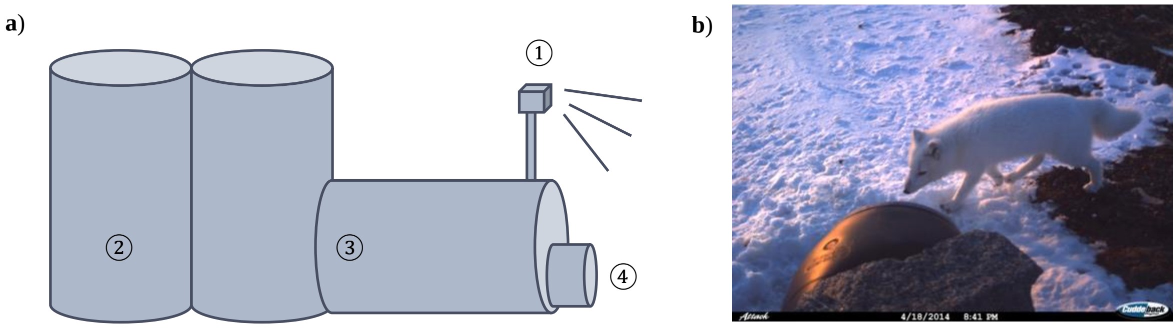

Figure 4. a) Diagram showing a feeding station built exclusively for the arctic fox, made of two vertical and one horizontal positioned barrels. ① Movement-triggered digital wildlife camera, ② Dog food available inside the barrel, ③ A Biomark PIT-tag reader placed between the horizontal and the first vertical standing barrel, ④ Entrance. **b**) A picture taken by a movement-triggered wildlife camera in front of a feeding station.

The Biomark PIT-tag readers were placed between the horizontal and the first vertical standing barrel of the feeding station (Figure 4a), and registered arctic fox individuals that had been marked with PIT-tags when present inside the feeding station. Information about which arctic fox individual and the date and time of the visit were extracted from the Biomark PIT-tag readers.

The movement-triggered wildlife cameras were placed pointing towards the entrance of the feeding stations (Figure 4a). Nine locations had two feeding stations and cameras, while four locations had one of each. The locations with two cameras were treated as one location since they were quite close to each other (from 30 m to 768 m) and thus not independent. Coordinates for the merged locations were obtained by calculating the mean of the coordinates from the two feeding stations. The movement triggers were set to medium sensitivity to be able to detect the movement that corresponds to foxes and reduce the number of empty pictures. The cameras were set to record only once a minute during periods of continuous movement. Flash was automatically activated at night.

Pictures from 13 locations in the study area were used to determine the occurrence of different species outside the feeding stations (Figure 4b; Appendix 1). Due to regular inspection of the cameras and feeding stations, the cameras were assumed to be active during the whole study period unless otherwise specified (Appendix 1). Between 2010 and 2017, 74 969 pictures were captured, where 55 803 yielded observations of foxes. Originally, there were feeding stations with cameras at 18 locations. Five of those locations were excluded from this study because there was no activity (no pictures) for four or more years during the study period.

A number of different variables were obtained from the pictures. Filename, date and time were extracted into excel files using ad hoc software (Rød-Eriksen, 2013). For each picture, animal occurrences were registered by identifying the species and number of individuals present. Pictures without foxes were removed from the dataset. For arctic foxes, fur colour and ear tags were also registered for identification of individuals when possible.

Analysing camera data from eight whole years is time consuming and was not within the scope of a Master's thesis. Hence, the winter time was selected for this study as these months are considered the most marginal time of year for the foxes due to low food availability (Selås & Vik, 2006). Rodent abundance data for Finse mountain plateau during the study period was collected from the Norwegian terrestrial surveillance programme (Framstad, 2017).

2.4 DATA ANALYSIS

MEASURING SPECIES ACTIVITY

The fox activity at the feeding stations was assumed to mirror the fox activity in the area. I measured the *red fox activity* and *arctic fox activity* at the feeding stations at each location during the study period. This was done by summing the number of days per month with fox presence of either species at each feeding station (range = 0-31 days with activity). By choosing day as the unit for measuring fox activity, information about activity within days was lost. A Pearson´s correlation test showed that the number of hours and number of days per month with fox activity were highly correlated (r = 0.84, Appendix 2) and hence the number of days per month with visits was chosen for further analyses.

ESTIMATING ARCTIC FOX POPULATION SIZE

I was provided results of the estimations of the arctic fox population at Finse. The *arctic fox population size* at Finse was estimated for each year of the study period, using all available data on arctic fox individuals that were marked, released and then recaptured by Biomark PIT-tag readers, ear tags read by cameras at feeding stations, DNA and/or wild capture of foxes. A Capture mark-recapture model (CMR) with robust design was run with the software MARK v8.2 (White & Burnham, 1999). 'Encounter histories' were built from the arctic fox individual data described above. Years were set as primary occasions (n = 8, 2010 to 2017) and the winter months (n = 3, March to May[1]) were set as secondary occasions. Rodent abundance data was included in the model to account for potential differences in survival within the study period. The difference in probability of capture and recapture was also included in the model, given by equation 1:

$$p(group * time) = c(group * time), \qquad 1$$

where *p* is the probability of the first capture, *c* is the probability of recapture, time is the years in the study period (2010-2017) and the groups are captive-released and wild-born individuals.

The Biomark PIT-tag readers were only properly active for four of the eight years in the study period (2013-2016). The expected differences in the probabilities of capture throughout the years were accounted for in the model with the *time* variable. In 2017 the Biomark PIT-tag readers worked for around one week, and 5 individual foxes were detected during this time period. These are included in the analyses. Due to assumptions of no movement in or out of the study area and no deaths or births in the closed capture recapture model, the pups were excluded in their first winter in the population size estimates.

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[1] February is counted as a winter month in this study, but not included in these models as captive-bred pups were released in February at the latest, which conflicts with the assumptions of no movement in or out of the study area, deaths or births in the closed capture recapture model.

Model selection was done using the Akaike information criteria corrected for small sample size (AICc) by looking at the normalized AICc model weights for the models with Δ AICc < 2 (Burnham & Anderson, 2002). To account for model uncertainty for the population estimates, parameter estimation was done with model averaging for the models with Δ AICc < 2. *Arctic fox population size* was mean centred prior to the statistical analyses to make the model intercepts biologically meaningful and to avoid extrapolation.

OTHER RELEVANT COVARIATES

Den distance (distance to the nearest active arctic fox den, given in km) was expected to have effect on the fox activity at feeding stations. The distance was calculated for all locations each year of the study period based on the yearly den surveys done for the arctic fox monitoring programme. A den was considered active if there were clear signs that it was being used regularly by one or more arctic foxes (for details, see Ulvund et al., 2018).

Elevation of the feeding stations was included as it was expected to affect the amount of activity of the arctic fox and red fox (Linnell & Strand, 2000). As a boreal species the red fox is expected to be more present in areas of lower elevation. Elevation was mean centred prior to the statistical analyses.

MODELLING FOX ACTIVITY

The *red fox activity* was used as the response variable to investigate if the *arctic fox activity* affects the *red fox activity* differently depending on the arctic fox population size. The distribution of the response variable was right skewed. A generalized linear mixed effect model was applied. The response variable had much more zeros than expected in a Poisson distribution (Appendix 3), so a zero-inflated model with negative binomial distribution was used. The function ‘glmmTMB’ from the R package ‘glmmTMB’ (Brooks et al., 2017) was used for modelling. All the explanatory variables (*arctic fox activity, arctic fox population size, elevation and den distance*) were checked for collinearity using Pearson´s correlation (Appendix 4). In the full model, *arctic fox activity* and *arctic fox population size* were set as continuous fixed effects, while *elevation* and *den distance* were included as covariates. To account for non-independence due to the nested structure of the data, *location* and *year* were set as random factors. The ‘r2’ function from R package ‘sjstats’ was used to obtain the marginal and conditional R^2 values for the final model (Lüdecke, 2019). Marginal R^2 (R^2_m) and conditional

R^2 (R^2_c) represent the variance explained by the fixed factors and covariates in the model and by the complete model, respectively (Nakagawa & Schielzeth, 2013).

The full model also included the interaction between *arctic fox activity* and *arctic fox population size*. Rodent abundance data was not included as an explanatory variable in the modelling as the *arctic fox population size* estimates were already corrected for rodent abundance. Backwards stepwise removal of non-significant terms using a likelihood ratio test (LRT) was done with the drop1 function to obtain final models. For determining whether the covariates and fixed factors in the final model explained any significant proportion of the variance in the response, the final model was contrasted with separate models where the final model's covariates and fixed factors were excluded one at a time (Zuur et al., 2009). The model was run using restricted maximum likelihood to obtain parameter estimates and their uncertainties.

MEASURING TIME BETWEEN VISITS

To test for avoidance behaviour between the species, I examined whether the time that elapsed from one visit to the next (with no visits between) differed depending on the species on the current visit and the species of the last visit to the feeding station. I assumed that a longer *time between visits* for one of the species following the other species would suggest avoidance behaviour.

The visits of arctic fox that were followed by a visit of red fox (AF ⟶ RF) were extracted from the dataset, and the same was done with the visits of red fox that were followed by a visit of arctic fox (RF ⟶ AF). Each observation (picture) of a species was here counted as a visit. The time between the last visit of one species to the first visit of the other, *time between visits* was measured for every occurrence (n = 257 AF ⟶ RF, n = 258 RF ⟶ AF).

Since the camera data from feeding stations did not provide information on individual level, PIT-tag readers at two of the feeding stations were used to obtain the time between different individuals of arctic fox (AF ⟶ AF) for comparing any signs of interspecific avoidance with intraspecific visit patterns between arctic foxes. A total of 62 individuals were recorded by the PIT-tag readers during the time when the readers were active, and the time between the last visit of one individual to the next individual was measured for all occurrences (n = 2629). I wanted to be able to look for any possible avoidance among arctic foxes without any relation, as mates, siblings or parents/cubs were not expected to avoid each other. There were several arctic fox individuals that followed each other at one feeding station more than a hundred times during the study period, and also many individuals that followed each other a number of times. These could be assumed to be familiar with the scent markings of each other and not expected to avoid each other. Thus, only observations of individuals that appeared after each other only one time in the whole study period were kept in this dataset (which gave n = 205). I was not able to measure the time that elapsed between different red fox individuals which visited the feeding stations, as it was not possible to distinguish red fox individuals in this study.

While the movement-triggered wildlife cameras recorded movement in front of the feeding station, the PIT-tag reader recorded individuals inside the feeding stations (pers.com Arild Landa 2019; Figure 4). Despite the different sources for the data, the two types of data were assumed to be very similar as the arctic fox is assumed to be present at feeding stations due to food intake inside the feeding stations.

MODELLING AVOIDANCE BEHAVIOUR

The *time between visits* distributions were right skewed. A generalized mixed effect model with negative binomial distribution was run with ‘glmmTMB function’ from the ‘glmmTMB package’ (Brooks et al., 2017). The *time between visits* was set as the response variable, *species* combinations type (AF ⟶ RF, RF ⟶ AF, AF ⟶ AF) as fixed factor and *arctic fox population size* (popsize AF) as continuous fixed effect. Due to the nested structure of the data, *location* and *year* were set as random factors. Model selection was done in the same way as for the modelling of fox activity. The ‘r.squaredGLMM’ function from R package ‘MuMIn’ was used to obtain the marginal and conditional R^2 values for the final model (K. Bartoń, 2018).

The maximum time between two visits was 736 hours, which equals to one month (30.7 days). For time intervals that long, the visit of one fox is not expected to affect the visit of the next fox. Since these extreme observations could potentially be driving the model, an ecological approach was applied to make a threshold for which time interval to include after a visit. Henry (1977) used a 48-hour limit for smell detection when studying red foxes, as the scent markings were assumed to last for two to three days. An assumption in this study was that the foxes leave scent markings when visiting a feeding station, and that if they avoid individuals or species, they would do so based on scent markings. Additionally, the daily activity patterns of the two species varied throughout the day (Appendix 5). To avoid any bias towards periods of day with less or more fox activity, the unit for the threshold should be full days (e.g. 24, 48, 72 hours). Hence, a model with only the observations < 48 hours was included in the analysis.

The arctic fox and red fox could also have different activity patterns throughout the day, which could again affect their visiting patterns at the feeding stations. Their visiting patterns were therefore investigated by plotting their occurrences at the feeding stations during all hours of the day. The abovementioned software MARK v8.2 (White & Burnham, 1999) was used for estimating the arctic fox population size. Otherwise, the software R version 3.5.1 (R Core Team, 2018) was used for all data exploration and statistical analyses.

3 RESULTS

During the study period (February to May) there were a total of 55 803 pictures of foxes, 1689 of red foxes and 54 114 of arctic foxes. Summing all the feeding stations, the number of days with fox visits during the study period was 11 424 in total, 93 days with red fox and 11 331 days with arctic fox (Appendix 6). In average per feeding station, this equals to 0.24 days with red fox visits per month and 8.72 days with arctic fox visits per month (range: red fox = 0-6; arctic fox = 0-31 days per month with visits at feeding station). Of a total 380 months included in the analysis, 47 months had red fox activity while 268 months had arctic fox activity. The fox activity of both species varied a lot between the years in the study period (Appendix 7). The estimated population size ranged from 8 to 32 individuals during the study period, with a mean of 26 adult individuals.

3.1 FOX ACTIVITY

I found no statistical evidence that red fox activity was affected by arctic fox activity nor population size of arctic fox (Figure 5; Appendix 8). However, there seems to be a tendency for a negative relationship between the activity of the two species, as there were no instances where there was recorded high activity of both species in one month at a given location (Figure 5b).

Even though I did not find a clear relationship between the arctic fox activity and the red fox activity, the red fox activity at the feeding stations was reduced with shorter distances to the nearest active arctic fox den. The red fox activity increased with 1.02 days of activity per month (± 1.01 days, p = 0.017) per additional kilometre separating a feeding station and the nearest arctic fox den (Table 1).

Table 1. Parameter estimates and their standard errors for the best ranked model fitted with restricted maximum likelihood. The response variable red fox activity (RF activity) is the number of days with red fox occurrence at a feeding station during one month and year at one location in the study period. The explanatory variable is the distance to the nearest active arctic fox den (den distance; km). Conditional R^2 (R^2_c) and marginal R^2 (R^2_m) are given for all models and represent the explained proportion of variance by both fixed and random effects and fixed effects only, respectively. The parameter estimates of each fixed factor (Estimate), standard errors (SE), z-statistics (z) and p-value (P) for the explanatory variable obtained from likelihood ratio test are given. The estimates are given on log-scale. * $p < 0.05$.

Response variable	**Explanatory variable**	**R^2_c**	**R^2_m**	**Parameter**	**Estimate**	**SE**	**z**	**P**
Red fox activity	den distance	0.422	0.030	Intercept	-3.316	1.260	-2.632	0.017 *
				den distance	0.068	0.090	0.018	

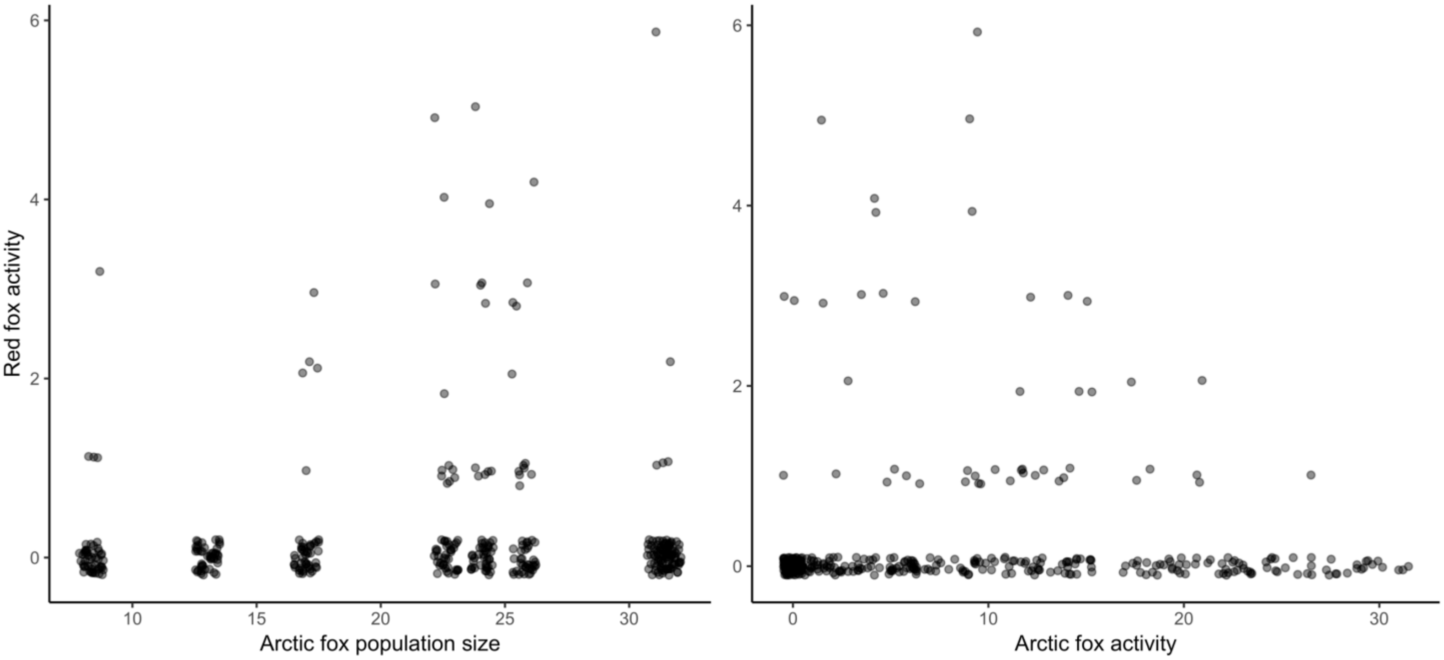

Figure 5. The y-axis shows red fox activity at Finse mountain plateau as the number of days in one specific month (n = 4 months) with red fox activity occurred at a specific location (n = 13 locations) in a specific year (n = 8 years). Red fox activity is plotted against **a)** arctic fox population size at Finse mountain plateau. **B)** arctic fox activity (measured the same way as red fox activity) at the same location in the same month and year as the red fox activity. The points in the graphs are jittered to visualize the clusters in the data by adding random noise. The scale of the jittering is: height = 0.1, width = 0.5.

3.2 AVOIDANCE BEHAVIOUR

When all observations were included, the model describing the variation in the time between visits best only included the species combination (Table 2; Appendix 9). The arctic fox population size did thus not explain a significant amount of the variation in the data (Figure 7a, Appendix 9). The expected times between visits for the three species were 1.7 ± 0.3 hours for RF ⟶ AF, 1.0 ± 0.3 hours for AF ⟶ AF and 1.1 ± 0.1 hours for AF ⟶ RF (Figure 6a). This means that the arctic fox used more time returning to the feeding station after a red fox last visited the feeding station than when an unknown arctic fox had visited. The arctic fox also used more time returning to the feeding station after a red fox visited than the red fox did after an arctic fox last visited the feeding station, which suggests avoidance behaviour from the arctic fox towards the red fox. However, as explained previously, the model including all observations was affected by many extreme observations likely to have little ecological importance.

Table 2. Parameter estimates and their standard errors for the best ranked model fitted with restricted maximum likelihood. The response variable 'time between visits' is the time duration (hours) between visits of different foxes. The fixed factor 'species' gives which combination of species were observed, arctic fox followed by arctic fox (AF ⟶ AF), arctic fox followed by red fox (AF ⟶ RF) and red fox followed by arctic fox (RF ⟶ AF). Conditional R^2 (R^2_c) and marginal R^2 (R^2_m) are given for all models and represent the explained proportion of variance by both fixed and random effects and fixed effects only, respectively. The parameter estimates of each fixed factor (Estimate), standard errors (SE), z-statistics (z) and p-value (P) for the explanatory variable obtained from likelihood ratio test are given. The estimates are given on log-scale. ** p <0.01.

Response variable	**Explanatory variable**	R^2_c	R^2_m	**Parameter**	**Estimate**	**SE**	**z**	**P**
Time between visits ~	species	0.067	0.745	Intercept	0.529	0.316	11.181	0.003 **
				species AF ⟶ AF	-0.572	0.270	-2.117	
				species AF ⟶ RF	-0.442	0.143	-3.089	

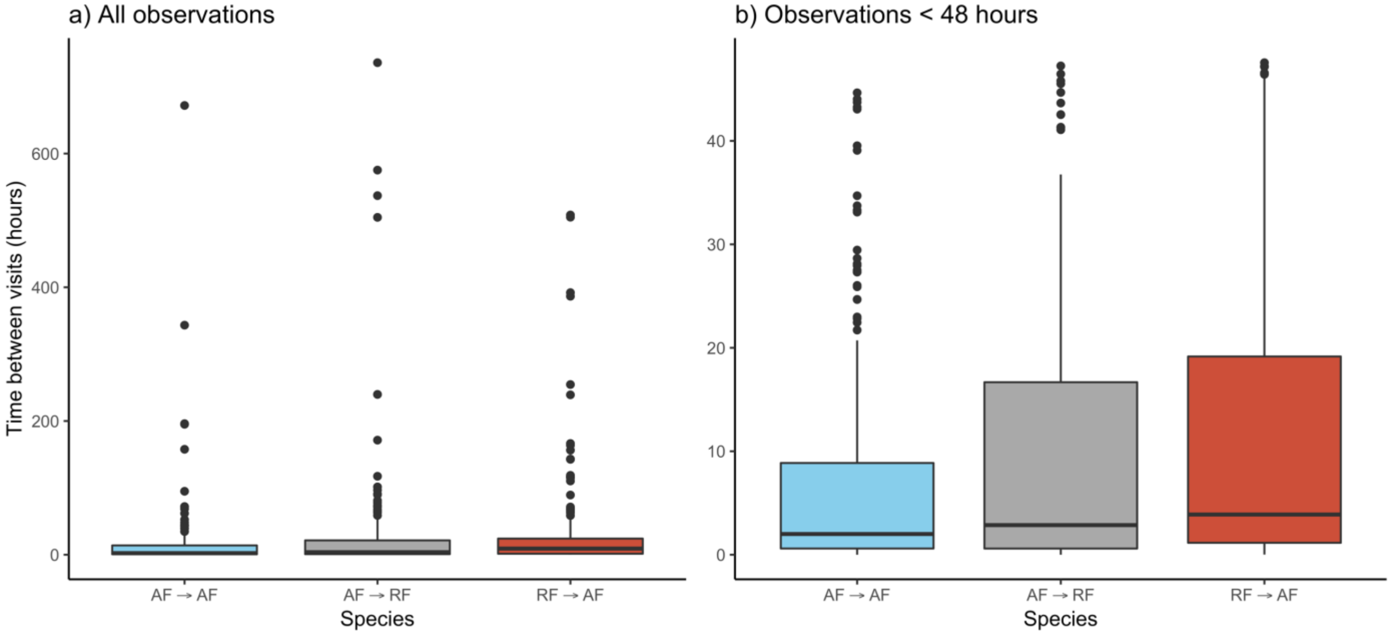

Figure 6. The time interval between visits of different foxes at feeding stations for arctic fox. Boxes represent the interquartile range with the whiskers showing lowest and highest values and outliers are shown with black dots. The horizontal lines represent the medians. Times between visits of different individuals of arctic fox (AF ⟶ AF) (n=217) were obtained from Biomark PIT-tag readers (n=2). The time between arctic fox to red fox visits and red fox to arctic fox visits (AF ⟶ RF, n = 255; RF ⟶ AF, n = 257, respectively) were obtained from movement-triggered wildlife cameras (n=11). **A**) All observations included. **b**) Intervals between visits exceeding 48 hours were excluded, which gives n = 205 for AF ⟶ AF, n = 228 for AF ⟶ RF and n = 207 for RF ⟶ AF.

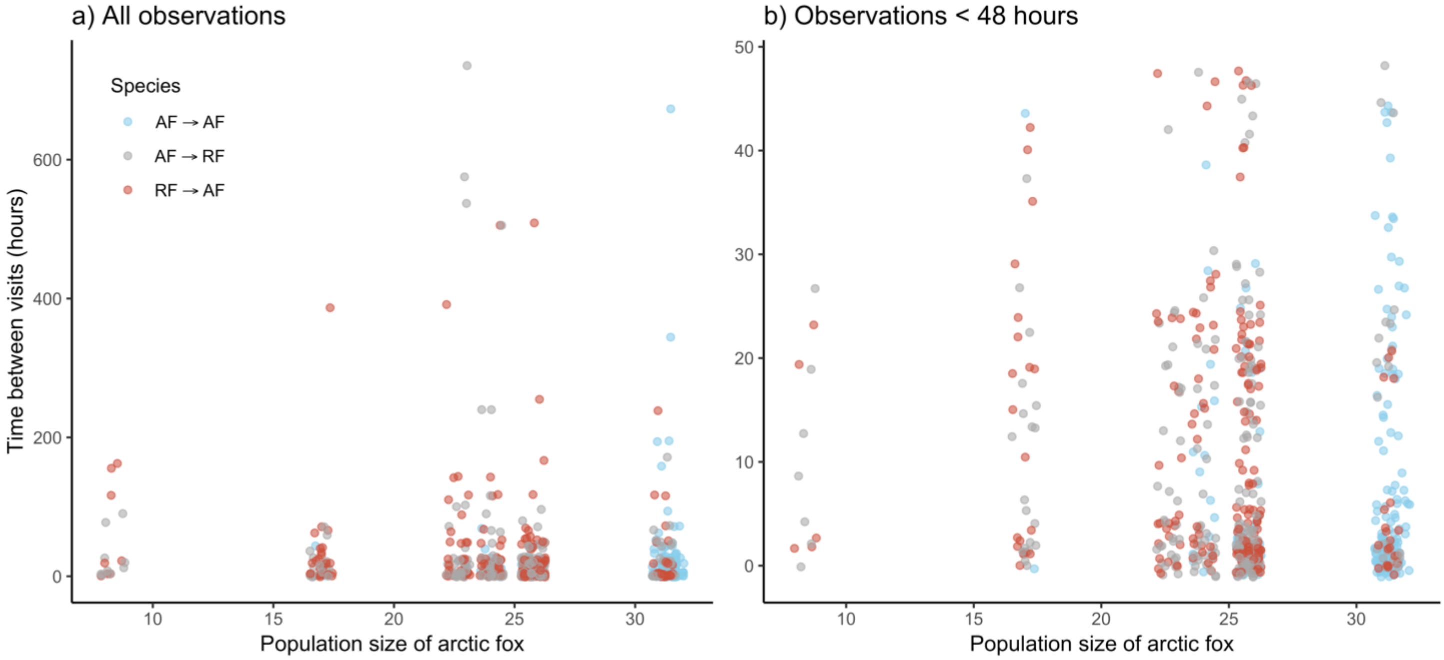

Figure 7. The time interval between visits of different foxes at feeding stations for arctic fox, plotted against the population size of arctic fox. Times between visits of different individuals of arctic fox (AF ⟶ AF) (n=217) were obtained from Biomark PIT-tag readers (n=2). The time between arctic fox to red fox visits and red fox to arctic fox visits (AF ⟶ RF, n = 255; RF ⟶ AF, n = 257, respectively) were obtained from movement-triggered wildlife cameras (n=11). **A**) All observations included. **b**) Intervals between visits exceeding 48 hours were excluded, which gives n = 205 for AF ⟶ AF, n = 228 for AF ⟶ RF and n = 207 for RF ⟶ AF. The points in the graphs are jittered to visualize the clusters in the data by adding random noise. The scale of the jittering is: height = 1.3, width = 0.5.

When only observations < 48 hours were included in the model, the model containing only the intercept was the model describing the variation in the data best, suggesting that neither the species combination nor the arctic fox population size explained any significant proportion of the variation in the time between visits (Figure 6b and 7b; Appendix 10). This means that no avoidance behaviour between the two species was found.

4 DISCUSSION

Overall, there was not very much red fox activity in the study area. I found no evidence for a negative relationship between the red fox activity and the arctic fox population size nor arctic fox activity, although there was a tendency for a negative relationship between the arctic fox activity and the red fox activity. Neither did I find evidence of avoidance behaviour between the two species, or that the arctic fox population size affected their visiting patterns at the feeding stations.

4.1 FOX ACTIVITY

This study shows that the red fox was not affected differently by the arctic fox at different arctic fox population sizes, contrary to my hypothesis and the conceptual model framework. A possible reason for these findings could be that the competitive strength of the arctic fox does not increase with arctic fox population size and that the arctic fox is not able to affect the red fox negatively. This would be supported by the former established hypothesis that the distribution of the arctic fox is limited by the distribution of the red fox, while the distribution of the red fox is limited by climate and food availability (Hersteinsson et al., 1989), as well as anthropogenic subsidies (Elmhagen et al., 2017).

As there were only 0.24 days per month with red fox presence on average during the study period, this could also imply that the study area is located above the distribution limit of the red fox. As previous studies have shown, red foxes mostly use dens at the lower distribution limits for the arctic fox (Dalerum et al., 2002; Frafjord, 2003; Linnell et al., 1999), which could mean that the red fox is only roaming the area occasionally in search for food while they occupy dens at lower elevations. If this is the case in this study, the red fox would not be expected to have much impact on the arctic fox.

There are several important aspects to consider when interpreting these results. First, during my study period, the largest estimated arctic fox population size was 32 individuals in reproductive age. The researchers involved in the Arctic fox monitoring programme in Norway have estimated the population size of arctic fox at their carrying capacity based on hunting data from the 19th century and extensive habitat surveys (Eide et al., 2010). The carrying capacity at the Finse mountain plateau is roughly estimated to be around 70-100 adult arctic fox individuals (Nina E. Eide, unpubl. data). Therefore, the relative population size of the arctic fox could be too small to have any detectable effect on the red fox distribution and activity in the area (towards the left side of the conceptual model framework, Figure 2, ①). However, it is challenging to estimate the arctic fox population sizes at carrying capacities, as the carrying capacities are influenced by many factors in the ecosystem. The realised niche for the arctic fox could have changed since the 'saturated' population sizes were estimated based on hunting statistics from late 1800s, and if the estimated arctic fox carrying capacity is over- or underestimated, the comparison of the present population size with the estimated carrying capacity could be of less significance.

Possible differences in interactions due to seasonality is also an interesting aspect that could contribute further to the understanding of the interactions between the two species. Climatic conditions could prevent the red fox from moving into high elevation areas in winter time. Firstly, previous studies have shown that the snow depth is limiting the prey availability in high elevation areas (Barton et al 2007; Halpin & Bissonette,1988; Jedrzejewska & Jedrzejewski, 1998), which could lead to the red fox foraging at lower elevation in winter time. Secondly, red fox movement into mountain areas in winter time could be limited by their low insulation properties compared to the arctic fox (Irving et al., 1955; Klir & Heath, 1992; Scholander et al., 1950). Thirdly, Cagnacci et al. (2004) found that red foxes selected lower elevational and forested habitats during winter time. Together, this suggests more red fox activity in high elevation areas in summer time compared to winter time. The inter-annual variation in red fox activity is controlled for by setting *year* as a random effect in my models, but since this study only looked at the winter months, it is not possible to draw any further conclusions on intra-annual variation (e.g. between seasons). If the suggestion about more red fox activity in summer time is true, the effect of one species on the other could be more prominent in summer time and thus lead to this study not being able to find possible effects. Additionally, summer is also a vulnerable period for the breeding arctic foxes as their pups are small. Contrary to this, Dalén et al. (2004) investigated how the spatial overlap between arctic and red foxes changed between seasons and found that they overlap more in winter time than in summer time, as the red fox distribution expanded and the arctic fox retreated to higher elevation during the summer. Differences in the red fox activity throughout the year should be investigated in future studies, and comparing the species' effect on each other in summer and winter time would be interesting.

4.2 AVOIDANCE BEHAVIOUR

The two different modelling approaches (all observations and observations < 48 hours) show different results regarding how the time between visits of different foxes was affected by arctic fox population size. The model including all observations showed a difference in the times between visits for the different species combinations. This relationship was not found in the model including only observations < 48 hours. The model including all observations was, as mentioned above, affected by many extreme observations which likely have little ecological importance regarding my hypothesis. These observations were from very long time intervals between two visits, in which the visit of one fox is not expected to affect the visit of the next fox. Hence, I focused on the model excluding these observations.

The results showing no avoidance behaviour between the species and no changes in behaviour with increasing population size of arctic fox could be interpreted in several ways. Looking at the conceptual model framework, this would give reason to expect that the arctic fox population is large enough not to avoid the red fox, as avoidance was expected only at small arctic fox population sizes. However, the red fox did not show any signs of avoidance behaviour towards the arctic fox. Also, as mentioned above, the arctic fox population size is not believed to be above the threshold for their competitive strength to have overcome that of the red fox at Finse in the study period.

The decision about setting a threshold for the inclusion of observations of times between visits based on ecological knowledge was difficult. There was clearly need for a threshold considering what time interval to include between two fox visits, as intervals sometimes reached a month between two visits, and thus the first visitor would no longer be expected to affect the next visitor. No research on the lasting of scent markings in canids was found, and the 48-hour limit was set based on one personal observation (Henry, 1977). This means that the threshold for the lasting of scent markings could be too long or short in this study.

Several studies have looked at avoidance behaviour in red fox towards larger canids (Gese et al., 1996; Leo et al., 2015; Scheinin et al., 2006; Voigt & Earle, 1983). Generally, they show that the red fox (the smallest canid in all studies) avoids the larger canids. However, the red fox does not necessarily avoid the ll markings of other canid species, as assumed it should do for the arctic fox in this study. Scheinin et al. (2006) found that the red fox avoided direct encounters with the golden jackal (*Canis aureus*), but that they did not avoid their scent markings. Leo et al. (2015) looked at red fox avoidance towards dingo (*Canis dingo*) odour at feeding stations and found that the red fox fed more apprehensively with presence of dingo odour, but that they did not avoid the area. It remains unknown if the same avoidance patterns exist for the arctic fox towards the red fox. In our study, only six pictures with both species present were observed at the feeding stations (0.01 % of all pictures with foxes), which could suggest that the red fox and the arctic fox do not frequently encounter in direct meetings. On the other hand, what was not considered in the predictions for avoidance behaviour in this study was that the scent markings of the foxes could, instead of repel the other species, actually attract them. The scent markings of conspecifics or competitors with overlapping food niches could potentially lead to carcass remains or other food sources (Smith, 2008). Which, if any, avoidance patterns exist for the arctic fox towards the red fox, would need further investigation.

4.3 THE CONCEPTUAL MODEL FRAMEWORK

In this study two different approaches were used to test the conceptual model framework introduced above (see section 1.1; Figure 2), and the results are contradicting each other. On one side, the activity results show that the arctic fox does not affect the red fox negatively, which could, assuming that the conceptual model framework is true, be explained by the small population size of arctic fox in the area compared to the assumed carrying capacity. On the other side, the avoidance results suggest that the arctic fox does not avoid the red fox, which according to the conceptual model framework would be explained by the arctic fox populations being large enough to not be affected negatively by the red fox.

Based on these contradicting results, the conceptual model framework does not seem to be applicable for the present arctic fox and red fox populations at Finse mountain plateau. The only literature that was found supporting that the competitive strength of a species increases with increasing population size was for wolves (*Canis lupus*) living in packs. Cassidy et al. (2015) found that relative pack size in wolves improved the odds of one wolf pack displacing another pack. Although this study only looked at intraspecific interactions, one could expect that their competitive strength would also increase against other species. The arctic foxes mostly live in pairs of two and are only known to form packs very occasionally when food resources are very abundant (Eide et al., 2004; Elmhagen et al., 2014). Due to this, it may not be expected that the competitive strength of the arctic fox will increase with increasing arctic fox population size. Since the arctic fox does not usually live in packs, but rather solitary or in pairs, the competitive strength towards the red fox could be assumed to be more on individual scale than on population scale. However, a larger arctic fox population would mean more occupied territories, which would lead to the red fox experiencing higher levels of interspecific competition simply due to more frequent encounters with resident arctic foxes when moving within the arctic fox distribution. This would be expected regardless of the conceptual model framework and would also be true for the effect of red fox on arctic fox.

Since this conceptual model framework has not been studied elsewhere, the results from this study provides both methods that can be used for further testing of the different aspects of the framework, as well as results for the present Finse population. Although the results from this study are not directly applicable for the conceptual model framework, more research should be done to fully understand the intraguild interactions between the two species. Other methods may also be applied to further disentangle the interactions of the two species. Studies in Fennoscandia are particularly important as the outcome of the ongoing reintroduction project relies on this framework to be true, meaning that culling of the arctic fox is only needed at small population sizes of arctic fox, especially when they are supplementary fed. With the ongoing climate change and a warming Arctic, and due to the expected northwards and high elevation expansion of the red fox, findings from the testing of this conceptual model framework could in the future also be important for the distribution of the two species distributions other places in the world.

4.4 LIMITATIONS & FUTURE STUDIES

Firstly, when looking at the interspecific interactions between the red fox and the arctic fox in the future, it would be useful to include several subpopulations with contrasting densities of the two species. It is an evident limitation that this study only included one mountain area. This would increase the power of the study and contribute further to the understanding of the underlying mechanisms of the interactions between the two species. Collecting data in populations of arctic fox that are larger and closer to the carrying capacity would be essential when testing the conceptual model framework. However, this is not yet possible to test in Fennoscandia, as none of the subpopulations in Fennoscandia are close to their natural densities at the estimated carrying capacity (pers.com, Nina E. Eide, 2019). Also, large amounts of data are collected on the arctic fox from the national monitoring programme (Ulvund et al., 2018), but very little data is available for estimating the red fox populations size. To be able to design a balanced study in the future, data on the red fox population size should be collected.

Secondly, I assumed that the red fox is attracted to the feeding stations in the same way as the arctic fox, even though it cannot go inside and get access to the food. It could be that the red fox is not that attracted to the feeding stations or that it learns that there is no available food there, so this assumption must be handled with caution. This could have led to an underestimation of the red fox activity in the area and could thus be another explanation for the low amount of red fox activity at the feeding stations. However, the red fox activity did not decline throughout the study period (Appendix 7), which could be an indication that it is nevertheless attracted to the feeding stations. It would be possible to test this assumption by comparing the data from the feeding stations with wildlife camera data from open baits available for both species are placed out in the field (Hamel et al., 2013; Lars Rød-Eriksen, unpubl. data). A high correlation between the feeding station data and the open bait data would be an indication that the red fox is equally attracted to both.

Thirdly, as mentioned above, the time between visits is not necessarily the best way to measure avoidance behaviour, as I assumed that the foxes avoid each other’s scent markings. If the general pattern is that canids do not avoid scent markings as supported by several studies (Gese et al., 1996; Leo et al., 2015; Scheinin et al., 2006; Voigt & Earle, 1983), but rather avoid direct encounters, then another study design would be needed. To better understand the interference interactions of the two species, an experimental study could be done to investigate how the arctic fox reacts to scent markings from conspecifics and red foxes compared live red foxes, as done in Scheinin et al. (2006).

Lastly, the lemming abundance in the study area was used to account for difference in probability of detection in different years when estimating arctic fox population size. This made it impossible to study the effect of the lemming cycles on the red fox, as the lemming abundance could not be used in the models containing estimated arctic fox population size. The lemming abundance in the study area is, however, expected to affect the red fox activity in the area as more activity is expected in years with high lemming abundance. For future studies, the study setup should allow to control for the lemming abundance for both species.

5 CONCLUSION

In this study I evaluated competitive relationship between the arctic fox and the red fox and found no relationship between arctic fox population size and red fox activity. Neither did I find any difference in the visit patterns of the two species and conclude that most likely the population size was too small to enable detection of any change in the interspecific relationship between the arctic fox and the red fox. Overall, the conceptual model framework needs further testing with data from regions with arctic fox populations that are closer to their estimated carrying capacity to get a better understanding of the intraguild interactions between the two species.

Knowledge about the intraguild interactions between the arctic fox and red fox is important for the future management and conservation of the arctic fox in Fennoscandia and provides a better understanding of intraspecific interactions between intraguild predators. If the conceptual model framework is supported in future studies and the arctic fox is able to affect the red fox negatively when reaching large population sizes, reintroduction of arctic fox could be done without the red fox culling that is today implemented in many areas as the distribution of the two species overlap. However, if the arctic fox does not become the dominant competitor towards the red fox when reaching viable population sizes and the red fox expansion into high elevation areas continues in the future, the Norwegian management plan will not succeed in the long term and must be revised.

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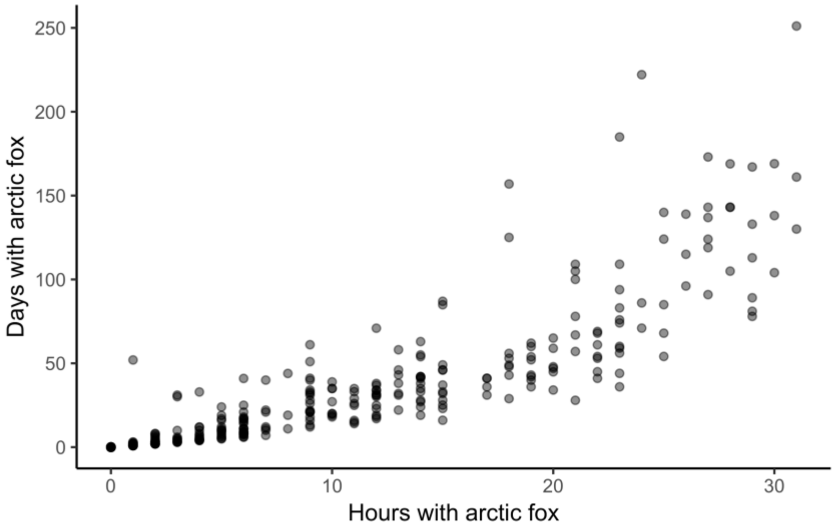
APPENDIX 1

Number of pictures captured at feeding stations at different locations at Finse from 2010 to 2017. NAs are representing cameras that were not active during that particular year.

Location	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**
Dyrhaugane	397	414	1484	5042	424	55	6594	2712
Flakavatn	*NA*	393	107	2426	246	719	244	0
Larsadalen	62	266	178	610	6	2	597	247
Lengjedalen Midt	0	0	708	793	10	13	4312	798
Lengjedalen Vest	0	0	575	28	0	386	763	301
Memorge	72	682	2	352	117	4478	2215	1137
Omnsbreen	*NA*	*NA*	*NA*	*NA*	523	35	3986	1680
Sandå 1507	373	723	409	2734	206	8	2413	1676
Sandå 3-4	80	558	738	1427	215	2	1538	317
Såtedalen	346	396	676	1380	467	964	4371	1032
Såtehjellane	8	125	44	81	76	115	835	576
Tverrå	315	735	818	2621	319	55	2064	1408
Namnlause	6	75	15	105	*NA*	*NA*	*NA*	*NA*
SUM	1653	4367	5754	17599	2609	6832	29932	11884

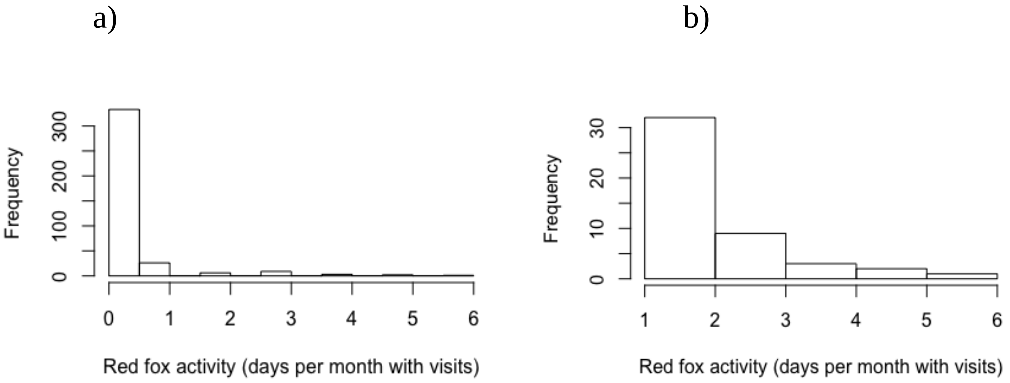
APPENDIX 2

The relationship between two different ways of measuring arctic fox activity at a feeding station per month (r = 0.84). X-axis shows the number of days with arctic fox visits per month and the y axis shows the number of hours with arctic fox visits per month. The study period was four months (February, March, April, May) in eight years (2010-2017).



APPENDIX 3

The distribution of red fox activity given by the number of days per month with at least one red fox visit at a feeding station made exclusively for the arctic fox. a) shows the distribution of the red fox activity and b) shows the distribution of the red fox activity with zero-observations removed for better visualization.



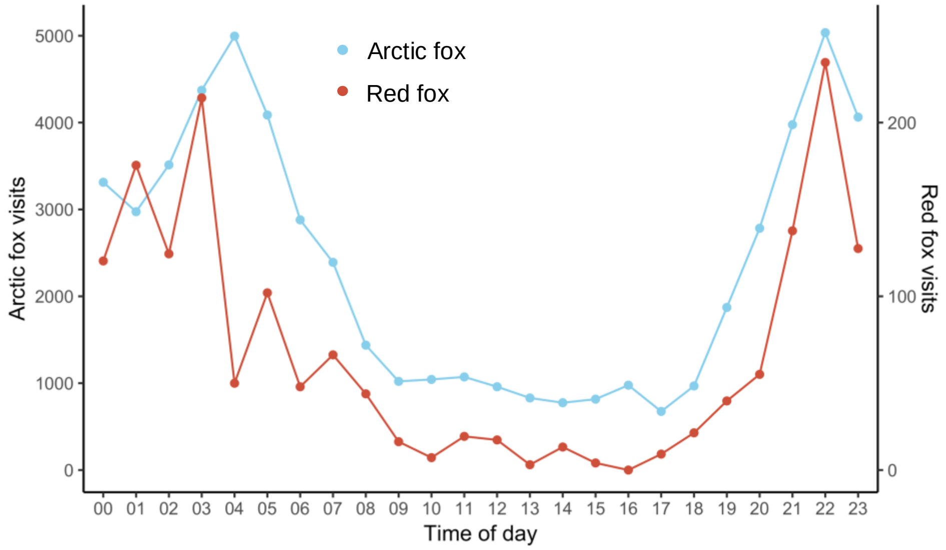
APPENDIX 4

Correlation matrix for explanatory variables used in modelling red fox activity at feeding stations.

	Arctic fox activity	Elevation (m)	Den distance (km)	Popsize AF
Arctic fox activity	1			
Elevation (m)	0.26	1		
Den distance (km)	-0.33	-0.44	1	
Popsize AF	-0.05	0.00	0.06	1

APPENDIX 5

The amount of arctic fox and red fox activity at feeding stations at different times of day. Note that the graph has two y axis, the left axis is the total number of arctic fox visits at each hour during the day, while the y axis is the total number of red fox visits during the day.



APPENDIX 6

Total number of days with visits of a) arctic fox and b) red fox at feeding stations at Finse during the study period. The feeding stations were equipped with movement-triggered wildlife cameras and the pictures were used to determine the species visiting the feeding station. February, March, April and May are the month included. *Na*s represent years where the cameras were not active at a given location.

a)

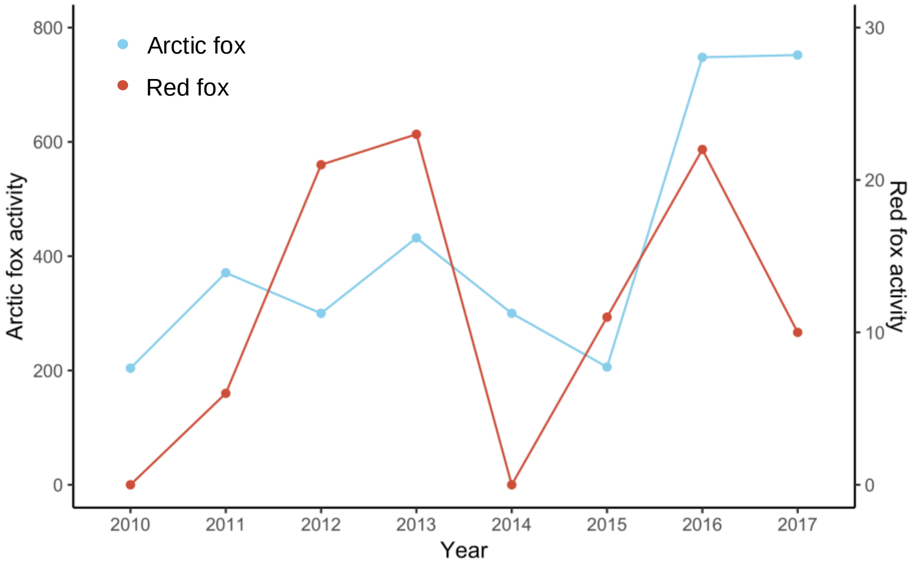
Location	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**
Dyrhaugane	30	57	65	68	25	3	105	111
Flakavatn	*NA*	42	4	39	24	25	14	0
Larsadalen	6	22	9	7	0	1	54	40
Lengjedalen Midt	0	0	24	24	1	7	41	75
Lengjedalen Vest	0	0	19	3	0	38	39	63
Memorge	10	19	1	32	25	86	78	84
Omnsbreen	39	53	33	44	28	1	76	53
Sandå 1507	22	14	41	72	20	0	85	60
Sandå 3-4	31	56	47	60	53	26	64	73
Såtedalen	3	28	8	8	27	0	0	0
Såtehjellane	63	62	49	74	46	9	88	85
Tverrå	0	18	0	1	*NA*	*NA*	*NA*	*NA*
Namnlause	*NA*	*NA*	*NA*	*NA*	51	10	104	108
Average	18.5	30.9	25.0	36.0	25.0	17.2	62.3	62.7

b)

Location	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**
Dyrhaugane	0	0	0	2	0	0	0	0
Flakavatn	*NA*	1	0	7	0	0	0	0
Larsadalen	0	0	0	0	0	0	0	0
Lengjedalen Midt	0	0	11	9	0	0	10	4
Lengjedalen Vest	0	0	4	0	0	10	6	0
Memorge	0	0	0	1	0	0	3	1
Omnsbreen	0	1	2	0	0	0	0	5
Sandå 1507	0	0	1	0	0	0	0	0
Sandå 3-4	0	0	0	0	0	0	1	0
Såtedalen	0	0	0	0	0	0	0	0
Såtehjellane	0	1	0	0	0	1	2	0
Tverrå	0	3	3	4	*NA*	*NA*	*NA*	*NA*
Namnlause	*NA*	*NA*	*NA*	*NA*	0	0	0	0
Average	0.0	0.5	1.8	1.9	0.0	0.9	1.8	0.8

APPENDIX 7

The total amount of fox activity in the different years of the study period. The y-axis represents the total amount of days in the study period with fox activity at a feeding station, summed for all locations.



APPENDIX 8

Model selection using the likelihood ratio test (LRT) for step-wise removal of non-significant terms from the full model. The full model included the variables red and arctic fox activity (RF activity; AF activity), measured as the number of days with occurrence of the species at a feeding station during one month at one location, estimated population size of arctic fox (popsize AF) in the study area (Finse mountain plateau) for each year in the study period (2010-2017), elevation (meters above sea level) and the distance to the nearest active arctic fox den (den distance; km). Pr(>Chi) is the p-value for the LRT. * = $p < 0.05$.

Full model	**Single term deletions**	**Df**	**LRT**	**Pr(>Chi)**	
RF activity ~ AF activity + popsize AF + elevation + den distance + AF activity × popsize AF	elevation	1	0.025	0.874	
	den distance	1	5.427	0.020	*
	AF activity × popsize AF	1	0.403	0.526	
RF activity ~ AF activity + popsize AF + den distance + AF activity × popsize AF	den distance	1	5.519	0.019	*
	AF activity × popsize AF	1	0.395	0.530	
RF activity ~ AF activity + popsize AF + den distance	AF activity	1	1.1794	0.277	
	popsize AF	1	0.0015	0.969	
	den distance	1	5.3505	0.021	*
RF activity ~ AF activity + den distance	AF activity	1	1.178	0.278	
	den distance	1	5.565	0.018	*
RF activity ~ den distance	den distance	1	5.6865	0.017	*

APPENDIX 9

Model selection using the likelihood ratio test (LRT) for step-wise removal of non-significant terms from the full model. The response variable was the time that passed between the visits of different species (red fox; RF and arctic fox; AF) and different individuals of arctic fox (time between visits). The explanatory variables were the species present at the last and the present visit (AF ⟶ AF, AF ⟶ RF, RF ⟶ AF) and the estimated population size of arctic fox at Finse mountain plateau (popsize AF). ** $p < 0.01$.

Full model	**Single term deletions**	**Df**	**LRT**	**Pr(>Chi)**	
time between visits ~ species * popsize AF	species:popsize AF	2	3.020	0.22	
time between visits ~ species + popsize AF	species	2	11.513	0.003	**
	popsize AF	1	0.011	0.918	
time between visits ~ species	species	2	11.575	0.003	**

APPENDIX 10

Model selection using the likelihood ratio test (LRT) for step-wise removal of non-significant terms from the full model. The response variable was the time that passed between the visits of different species (red fox; RF and arctic fox; AF) and different individuals of arctic fox (time between visits). The explanatory variables were the species present at the last and the present visit (AF ⟶ AF, AF ⟶ RF, RF ⟶ AF) and the estimated population size of arctic fox at Finse mountain plateau (popsize AF).

Full model	**Single term deletions**	**Df**	**LRT**	**Pr(>Chi)**
time between visits ~ species * popsize AF	species:popsize AF	2	3.825	0.148
time between visits ~ species + popsize AF	species	2	2.207	0.332
	popsize AF	1	1.313	0.252
time between visits ~ popsize AF	popsize AF	1	2.779	0.096

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