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Interactions between arctic fox (*Vulpes lagopus*) and red fox (*Vulpes vulpes*) in alpine habitats in Norway – activity patterns and avoidance mechanisms

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Preface

This thesis is part of the ECOFUNC project (Understanding ecosystem functionality, expansion, and retreat of species on the Scandinavian mountain tundra under multiple drivers of change), funded by the Norwegian Research Council (grant 244557). In addition, the Interreg Project “Felles Fjellrev 2” financed data collection in Sylan and Lierne, while camera trap monitoring in Børgefjell was collected under “Ecosystem Børgefjell” funded by the Norwegian Environment Agency**.**

Thanks to my supervisor Nina Eide, for letting me take part of this project and for your helpful advice during the writing process. Thanks to my supervisor Vidar Selås, for helping me with statistics, the writing, and for always keeping your door open. A BIG thanks to my supervisor Lars Rød-Eriksen, for all your help with the fieldwork, the data analysis, the statistics and the writing. Thanks for your patience, and thank you for putting up with me and Johanna locked inside a small cabin at Hardangervidda for 3 days during the storm!

Thanks to Johanna Skrutvold, for being such a good friend and study partner. Who would have known that a random meeting at the beach at Galápagos would lead to such a good partnership? Thanks for literally helping me to push the right buttons, in Excel, Minitab, JMP, Word and so on, I don’t know what I would do without you! Thanks to my parents – all three of you, for your endless love and support. A special thanks to you mom, for your valuable proofreading.

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Thanks to all of you! You are all highly appreciated!

Ås, 15th May 2017

Hanne Jaasund

Abstract

The arctic fox (*Vulpes lagopus*) population in Fennoscandia declined drastically in the beginning of the 20th century. In contrast, the red fox (*Vulpes vulpes*) population expanded rapidly during the 20th century. Fragmentation, dampened rodent cycles and increased interspecific competition with the red fox have been suggested to explain the non-recovery of the arctic fox. It is well documented that the arctic fox in most cases avoid contact with the red fox. In this study, baited camera traps were used to investigate if the arctic fox avoid the red fox in its search for food, spatially or temporally. Two hypotheses were addressed, and I investigated if: 1) there is a negative relationship between arctic fox activity and red fox activity at the baits, and 2) the time between red fox and arctic fox observations will increase with increasing activity of red fox at the bait, and activity of arctic fox and red fox will be temporally segregated.

I found a significant negative relationship between days with arctic fox observations and days with red fox observations, and my first hypothesis was hence accepted. Mean time between a visit of red fox and arctic fox was also considerable higher than mean time between a visit of an arctic fox and a red fox, indicating that the arctic fox is more cautious of the red fox than vice versa. However, the time between red fox and arctic fox observations decreased with increasing red fox activity, and my second hypothesis was hence rejected. I found no temporal segregation of arctic fox and red fox activity, and arctic fox activity patterns seemed not to be affected by red fox activity. The contradictory results of this study suggest that the interactions between the arctic fox and red fox are complex and varied. The competition will likely vary with resource availability, and individual differences in sex, age and size of the foxes will also likely affect the outcome of direct, physical competition. Since the results of this study indicate that arctic foxes not always avoid areas where encounters with red foxes are likely, it could be interesting to further investigate if the arctic fox's response to risk is more reactive than predictive. The results of this study suggest that the avoidance behaviour of the arctic fox might not be as consistent as previously thought. In that case, new approaches should be considered and investigated for further conservation of the arctic fox.

Sammendrag

Bestanden av fjellrev (*Vulpes lagopus*) i Fennoskandia gikk kraftig tilbake i begynnelsen av 1900-tallet, og bestanden har til tross for fredning ikke tatt seg opp igjen. I motsetning, økte bestanden av rødrev (*Vulpes vulpes*) kraftig i løpet av 1900-tallet. Fragmentering, svekkede smågnagersykluser og økt interspesifikk konkurranse med rødreven har blitt framsatt som forklaringer på hvorfor bestanden av fjellrev ikke har tatt seg opp igjen. Det er godt dokumentert at fjellreven i de fleste tilfeller unngår nærkontakt med rødreven. I denne studien ble viltkamera og åter brukt til å undersøke om fjellreven unngår rødreven, i tid eller rom. To hypoteser har blitt testet: 1) det er et negativt forhold mellom aktivitet av fjellrev og aktivitet av rødrev, og 2) tiden mellom et rødrevbesøk og det neste besøket av fjellrev vil øke med økende rødrevaktivitet på åtet, og aktivitet av fjellrev og rødrev vil være adskilt i tid.

Resultatene bekreftet den første hypotesen da det ble funnet et signifikant negativt forhold mellom dager med fjellrevobservasjoner og dager med rødrevobservasjoner. Gjennomsnittstiden mellom et besøk av rødrev og fjellrev var også betydelig høyere enn gjennomsnittstiden mellom et besøk av fjellrev og rødrev, noe som indikerer at fjellreven i større grad frykter rødreven enn omvendt. Tiden mellom rødrev- og fjellrevbesøk sank imidlertid med økende rødrevaktivitet, og den andre hypotesen ble dermed forkastet. Resultatene tydet heller ikke på at aktiviteten til fjellreven var adskilt i tid fra aktiviteten til rødreven, og fjellrevens aktivitetsmønster ble ikke påvirket av aktivitet av rødrev. De tvetydige resultatene i denne studien indikerer at interaksjonene mellom fjellrev og rødrev er komplekse og varierte. Konkurransen vil trolig variere med mattilgang, og individuelle forskjeller i kjønn, alder og størrelse vil trolig påvirke utfallet av et fysisk møte. Siden disse resultatene indikerer at fjellreven ikke alltid unngår områder der det er sannsynlig å møte rødrev, ville det vært interessant å utforske nærmere mulighetene for at fjellrevens risikorespons er mer reaktiv enn prediktiv. Resultatene av denne studien indikerer at fjellrevens atferd ovenfor rødreven ikke er like entydig som tidligere antatt. Dersom dette er tilfellet, burde nye innfallsvinkler vurderes og undersøkes for videre bevaringsarbeid av fjellreven.

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1. Introduction

In nature, the activity of an organism will affect the surrounding environment, including other organisms (Begon et al. 1996). The interactions among organisms in an ecosystem, are many and diverse (Begon et al. 1996). Food resources will often be limited, either periodically or permanent (Beeby & Brennan 1997). When such a limitation occurs, organisms that exploit the same resources will interact with each other in the form of competition (Begon et al. 1996; Krebs 2009). Competition between two different species, so-called interspecific competition, may lead to exclusion of one of the species from the habitat (Ayala et al. 1973; Begon et al. 1996; Connell 1983). In other cases, the two species may be able to coexist in the same habitat, due to the occupation of slightly different niches (Ayala 1971; Connell 1983; Krebs 2009).

The distribution of arctic fox (*Vulpes lagopus)* and red fox (*Vulpes vulpes*) is mainly separate, but areas of overlap exist in North America and in Eurasia (Hersteinsson & Macdonald 1992). The arctic fox population declined drastically throughout Fennoscandia in the beginning of the 20th century (Linnell et al. 1999). Overharvesting has been suggested to be the main reason for this dramatic decline, due to the good business of fur trade at the time (Hersteinsson et al. 1989; Linnell et al. 1999; see also Selås & Vik 2007). In contrast, the red fox population expanded rapidly during the 20th century (Hersteinsson & Macdonald 1992; Linnell et al. 1999; Selås & Vik 2006), possibly as a result of increased food availability in winter (Hjeljord 1980; Killengreen et al. 2011; Selås & Vik 2006). Overlapping in time, the populations of forest-living ungulate species increased, likely due to the eradication of large carnivores (Selås & Vik 2006). This increase may have led to improved availability of food in the form of cervid carcasses, and this has been suggested as a main cause of the rapid red fox expansion (Henden et al. 2014; Hjeljord 1980; Selås & Vik 2006). Additionally, larger carnivores like lynx (*Lynx lynx*) and wolves (*Canis lupus*) kill red foxes (Palomares & Caro 1999), and the eradication of these big carnivores may also have led to a mesopredator release effect, allowing the red fox population to grow and expand (Elmhagen & Rushton 2007; Elmhagen et al. 2010; Prugh et al. 2009).

In Norway, the arctic fox was protected by law in 1930 (Hersteinsson et al. 1989; Linnell et al. 1999), but has despite the protection failed to recover (Elmhagen et al. 2000; Linnell et al. 1999; Tannerfeldt et al. 2002). Many hypotheses have been suggested to explain this non-recovery. The arctic fox population in Fennoscandia is naturally fragmented, and anthropogenic processes have further increased the level of fragmentation (Herfindal et al. 2010). Subsequent Allee effects may have prevented the recovery of local arctic fox populations, and may also have decreased the arctic fox's resilience against the red fox (Herfindal et al. 2010). Since arctic fox dens often are found in low productive areas at high altitudes (Dalerum et al. 2002; Frafjord 2003; Killengreen et al. 2007; Linnell et al. 1999; Selås et al. 2010), lemmings and other small rodents are very important prey for the arctic fox (Bjärvall et al. 1997; Dalén et al. 2005; Ims & Fuglei 2005; Jędrzejewski & Jędrzejewska 1992). Dampened rodent cycles during the 1980s and 1990s are believed to have limited the arctic fox's reproduction during this period (Angerbjörn et al. 2001; Cornulier et al. 2013; Elmhagen et al. 2000). The fluctuating rodent cycle has been proven to affect both arctic fox and red fox reproduction, and arctic foxes will usually not reproduce in years with low densities of rodents (Angerbjörn et al. 1991; Elmhagen et al. 2011; Hjeljord 1980; Ims & Fuglei 2005; Meijer et al. 2013; Tannerfeldt & Angerbjörn 1998).

Increased interspecific competition with the red fox is believed to be an important explanation for the arctic fox's non-recovery (Hersteinsson et al. 1989; Tannerfeldt et al. 2002). The arctic fox and red fox have more or less the same diet, morphology and behaviour, and it is therefore likely that the two species will compete in areas where they coexist (Frafjord et al. 1989). Both direct and indirect competition are documented. Direct competition include competition for the best dens and hunting grounds (Hersteinsson & Macdonald 1992; Tannerfeldt et al. 2002), avoidance (Hamel et al. 2013; Tannerfeldt et al. 2002) and intraguild predation where the red fox kill and eat the arctic fox (Frafjord et al. 1989; Lourenço et al. 2014; Pamperin et al. 2006). Indirect competition includes exploitation of the same food resources (Tannerfeldt et al. 2002).

Interspecific killing between mammalian carnivores, where individuals of the larger species kill and possibly eat individuals of the smaller species, is common in nature (Palomares & Caro 1999). This is also the case regarding red fox (5-10 kg) and arctic fox (3-5 kg) (Audet et al. 2002; Bjärvall et al. 1997; Frafjord et al. 1989). Resource availability might affect the occurrence of both interspecific killing and consumption (Lourenço et al. 2014; Palomares &

Caro 1999). It is thus likely that the interspecific competition between the arctic fox and red fox will vary with resource availability, as Henden et al. (2010) demonstrated in a theoretical population model on the two fox species.

Results from studies with both wild and captured animals suggest that the arctic fox in most cases simply avoid close contact with the red fox (Frafjord et al. 1989; Hamel et al. 2013; Rudzinski et al. 1982; Tannerfeldt et al. 2002). Rudzinski et al. (1982) found that the activity of arctic foxes decreased when red foxes were present, and that the red fox dominated the arctic fox in 8 out of 9 cases of encounters. Predation risk and interference competition can strongly affect animals behaviour, and their spatial distribution (Ripple & Beschta 2004). Typical predator avoidance mechanisms include occupation of refugia, alteration of foraging habitats (spatial avoidance) and alteration of activity periods (temporal avoidance) (Brodie Jr et al. 1991).

In this thesis, I investigate the relationship between arctic foxes and red foxes in alpine habitats. I investigate if the arctic fox is avoiding the red fox, spatially or temporally. Based on current knowledge, I expect to find that red foxes impact arctic foxes negatively. Thus, I expect that baits frequently visited by red foxes will be less used by arctic foxes, and that time between a visit of red fox and arctic fox at the bait will increase with increasing red fox activity. I will also explore red fox’s and arctic fox’s daily activity patterns, to investigate if the arctic fox is using temporal avoidance as an avoidance mechanism. Two main hypotheses have been addressed:

1) There is a negative relationship between arctic fox activity and red fox activity at the baits.
2) The time between red fox and arctic fox observations will increase with increasing activity of red fox at the baits, and activity of the arctic fox and the red fox will be temporally segregated.

2. Materials and methods

2.1 Study areas

The study was conducted in five different mountain areas in Norway; Saltfjellet, Børgefjell, Lierne, Sylan and Hardangervidda (figure 2.1).

Figure 2.1: Overview of the five different study areas.

Saltfjellet national park (2102 km^2) is located in Nordland county (66°35'2.2"N 15°20'44.9"E). The study area is situated within the north boreal and low alpine vegetation zone (Moen 1999).

Børgefjell national park (1447 km^2) is an alpine mountain area located on the border between Nord-Trøndelag and Nordland county, close to the Swedish border (65°2'22.7"N 13°49'58.2"E). The study area is situated within the north boreal and low alpine vegetation zone (Moen 1999). In Norway, Børgefjell represents the mountain area with the highest activity of arctic fox (Ulvund et al. 2016).

Lierne national park (333 km^2) is located in Nord-Trøndelag county, on the border between Norway and Sweden **(**64°23'46.3"N 13°25'22.1"E). The study area is situated within the north boreal and low alpine vegetation zone (Gaarder et al. 2007; Moen 1999).

Sylan is a mountain area situated on the border between Norway and Sweden (63°0'26.3"N 12°11'3.7"E), in Sør-Trøndelag county. Sylan is classified as protected landscape. The study area is situated within the low alpine vegetation zone (Moen 1999).

Hardangervidda (60°5'56.2"N 7°29'16.7"E) is located within Hordaland, Telemark and Buskerud county. The study area is situated along Riksvei 7 (Rv. 7), in the low alpine vegetation zone (Moen 1999). Most of the study area is situated within Hardangervidda national park (3422 km^2).

2.2 Data collection

The fieldwork was conducted during late winter of 2016 (March to May). Camera traps with 15–20 kg blocks of reindeer slaughter remains were deployed. The cameras (Reconyx HyperFire PC800) were placed ~4 m from the baits, facing north to avoid sun glare. One camera at Hardangervidda was never found, and pictures from another was excluded because of picture failures. Pictures from cameras deployed at Saltfjellet, Sylan, Lierne and Børgefjell were provided by the Norwegian Institute for Nature Research (NINA). In total, pictures from 49 cameras were used in the analyses (10 at Hardangervidda, 13 at Børgefjell, 12 at Saltfjellet, 8 at Lierne and 6 at Sylan). The cameras were programmed to take pictures every 5 minutes. At Hardangervidda and Saltfjellet, pictures were also taken whenever movement was registered. The cameras were active between 8 (Saltfjellet) and 30 days (Børgefjell and Hardangervidda). The baits were consumed after 8 days in average. Thus, the first 8 days with pictures in all areas were used in the analyses, to adjust for the difference in days the cameras were active.

The cameras were placed systematically at Hardangervidda and Saltfjellet, in proximity to the main road (Rv. 7 at Hardangervidda and E6 at Saltfjellet). Distance to the road varied from 0 to 3 km. At Lierne, Børgefjell and Sylan, the cameras were deployed randomly within the mountain area.

A total of 106 727 pictures from Børgefjell were manually analysed. For each picture, species, number of individuals, and the condition of the bait were recorded. Empty pictures with no animals present were also recorded. A few pictures had to be excluded because of failure – where the camera lens was covered by snow/dew, or where the camera had tilted. Pictures from Hardangervidda, Sylan, Lierne and Børgefjell were analysed by NINA. Extracting the pictures taken the 8 first days only, a total of 113 628 pictures provided by cameras from the five different mountain areas were used in the statistical analyses.

2.3 Explanatory variables

To investigate my first hypothesis, the following explanatory variables were used: number of days with red fox observations, total number of red fox observations, mean hours of red fox, distance to road (m), distance to buildings (m), distance to forest (m), elevation (m.a.s.l.), number of days with available carcass and mean temperature (°C). All the explanatory variables were defined for each camera trap in the five different mountain areas. Distance to forest was found using the raster dataset AR50 provided by the Norwegian Institute of Bioeconomy Research (NIBIO) (Norsk institutt for skog og landskap 2015). Using the line measuring tool in QGIS (QGIS Development Team 2016), the direct line between the camera traps and the nearest forest larger than 1 km^2 was measured. Forest is defined as an "area with at least 60 trees per hectare which are or may become 5 metres tall, and which should be evenly distributed over the area" (Norsk institutt for skog og landskap 2015). The line measuring tool in QGIS (QGIS Development Team 2016) made it easy to find the distance to the nearest road at Hardangervidda and Saltfjellet, where the cameras were deployed in close proximity to the main road. Distance to road at Lierne, Sylan and Børgefjell, and distance to buildings in all the five areas, were extracted from N50 maps from the Norwegian Mapping Authority (Kartverket 2016), using GRASS GIS 7.0 (GRASS Development Team 2016). Each camera recorded temperature for every picture taken, and mean temperature for the 8 days' period at each camera trap location was later calculated. Elevation was provided by Google Earth, by importing a gpx-file containing the coordinates for the different camera traps. Number of days with available carcass was defined as number of days where the bait was still present and visible.

To investigate my second hypothesis, I used the explanatory variable "Red fox +/- 1 hour", defined as number of hours with visits of red fox at the bait, in a period of +/- one hour before and after a visit of arctic fox.

2.4 Statistical analyses

To investigate the relationship between activity of arctic fox and red fox, I used linear regression. “Days with arctic fox” represented the response variable, defined as number of days with arctic fox observations – out of the eight days the cameras were active. “Days with red fox” was used as explanatory variable, defined as the number of days with red fox observations – out of the eight days the cameras were active. The chosen significance level for all statistical analysis was 0.05. This analysis was performed in the statistical software Minitab 17 (State College 2010).

To further investigate which factors affected the activity of the arctic fox, I used a generalized linear model (Poisson distribution and log link) corrected for over-dispersion. Again, “Days with arctic fox” was used as response variable. Pearson correlation tests were used to check for correlation. This analysis was performed in the statistical software JMP Pro 13.0.0 (SAS Insitute Inc 2007).

Linear regression supported the investigation of my second hypothesis, concerning time between observations of red fox and arctic fox related to red fox activity. In this analysis, only data from Børgefjell were included, as Børgefjell was the only area where several of the cameras recorded both species. Time (hours) between a red fox observation and the subsequent arctic fox observation was applied as response variable. “Red fox +/- 1 h” functioned as explanatory variable. Time between observations of red fox and arctic fox was compared to time between observations of arctic fox and red fox, using a two-sample t-test.

To investigate red fox and arctic fox daily activity, mean number of observations of the two species were calculated for every hour in a day (0–23), in each of the five different mountain areas. Mean number of observations of both species for every hour in a day were also calculated for every individual camera. Simple line plots were made in Excel to compare activity between the different areas. Average visitation hours per day in each of the five different mountain areas were also calculated, and simple line plots were made in Excel.

3. Results

The total number of arctic fox and red fox observations were highly variable between the different mountain areas (Table 3.1). Most observations of red fox were registered at Hardangervidda, while the majority of observations of arctic fox were registered at Børgefjell. Lierne represents the area with the lowest number of fox observations in total.

Table 3.1: Total number of pictures with fox observations in each of the five mountain areas.

Mountain area	Number of cameras (number of pictures)	Total number of arctic fox observations	Total number of red fox observations	Number of locations with both species
Børgefjell	13 (27680)	207	158	5
Hardangervidda	10 (24527)	46	693	0
Saltfjellet	12 (31679)	80	219	1
Sylan	6 (12702)	17	48	1
Lierne	8 (17040)	11	3	1
Total	49 (113628)	361	1121	8

The activity of red fox and arctic fox peaked between day 3 and 4 in all the different mountain areas (Figure 3.1). The activity of arctic fox was higher than the activity of red fox at Saltfjellet, Lierne and Børgefjell, while red fox activity was considerable higher than arctic fox activity at Hardangervidda. At Sylan, the activity of red fox increased steadily from day 4 to day 8, while arctic fox activity was more varied. The activity of arctic fox and red fox highly overlapped in all areas, except at Lierne, where there was no overlap (Figure 3.1).

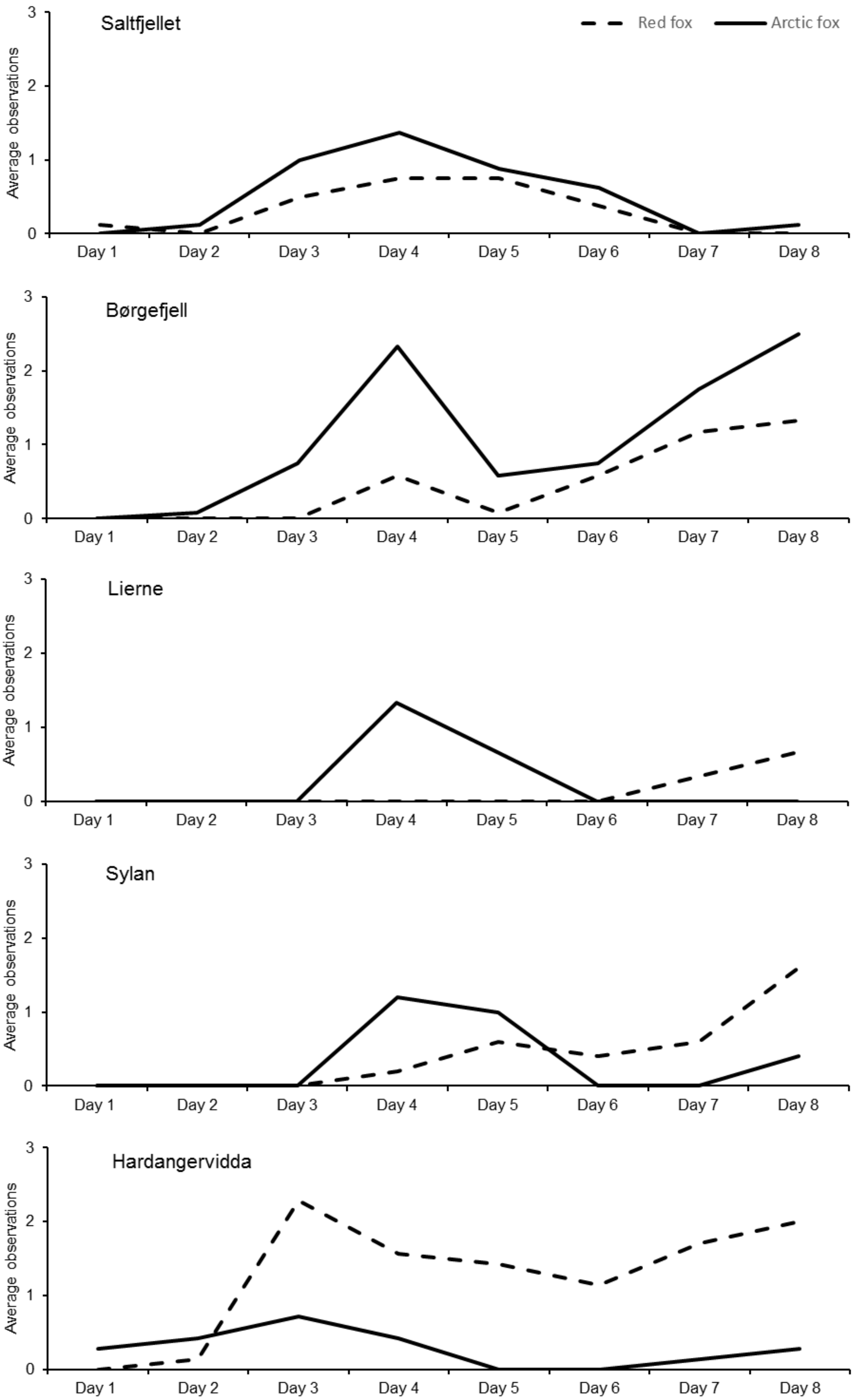

Figure 3.1: The daily activity patterns (average visitation hours per day) of arctic fox and red fox in each mountain area.

There was no significant relationship between the number of days with observations of red fox and arctic fox when all locations were included (Estimate = - 0.134, $F_{1,48} = 0.94$, $R^2_{adj} < 0.01$, p = 0.336). When excluding all locations without any fox observations, the number of days with arctic fox observations decreased with increasing number of days with red fox observations (Table 3.2, Figure 3.2).

Table 3.2: Linear regression model showing a significant negative relationship between number of days with arctic fox observations (response) and number of days with red fox observations. Only locations with fox observations (n = 35) were included.

Explanatory variable	**Estimate**	**SE**	**t**	**p**	**R^2**	**R^2adj**
Intercept	2.068	0.366	5.658	<0.0001		
Days with red fox	-0.371	0.153	-2.417	0.0213	0.150	0.125

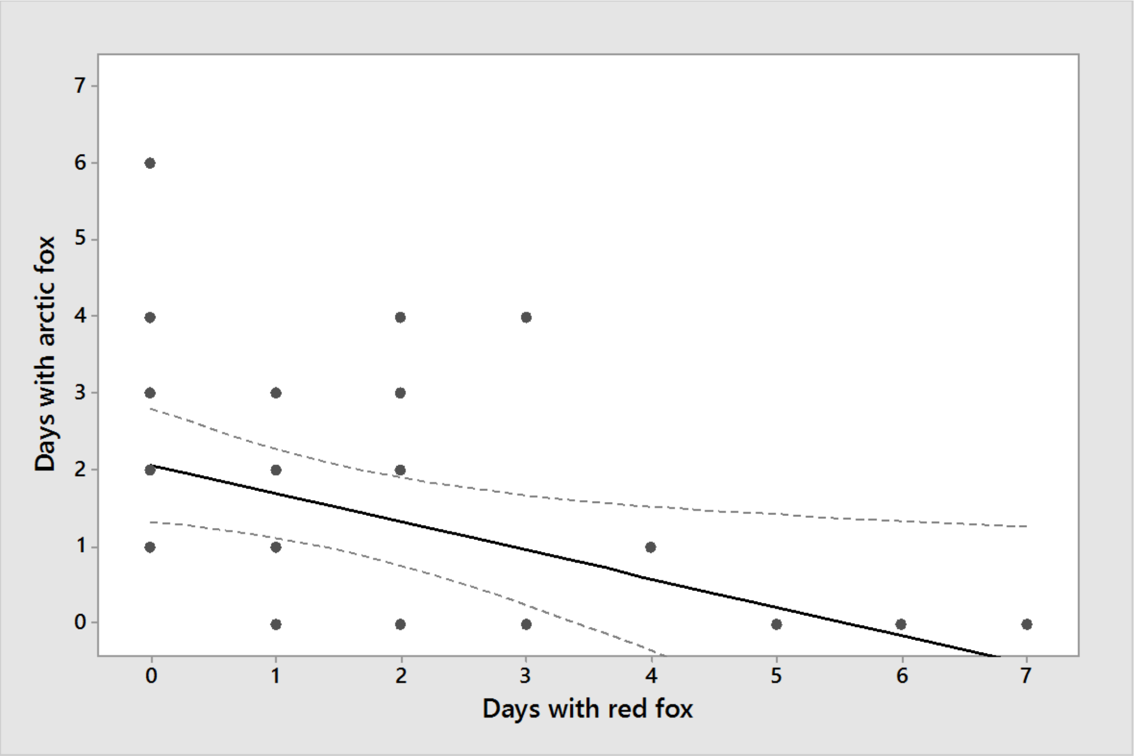

Figure 3.2: Results from a linear regression analysis, showing a negative relationship between number of days with arctic fox observations and number of days with red fox observations. Only locations with fox observations (n = 35) were included.

A generalized linear model also revealed a significant negative relationship between days with arctic fox observations and the explanatory variables days with red fox observations and distance to road (n = 35) (Table 3.3; illustrated in Figure 3.3). There was a tendency for a positive relationship between days with arctic fox and days with available carcass (Table 3.3). Days with arctic fox observations decreased with increasing number of days with red fox observations, and increased with increasing distance to road (Figure 3.3). The highest number of days with arctic fox observations (3–4 days) were recorded at locations far from the road, and with few days with red fox observations. Locations closer to the road, with more days with red fox observations resulted in fewer days with arctic fox observations (0–1 days). Distance to forest, distance to buildings, and elevation were not significant, and were hence excluded from the model. None of the explanatory variables were correlated.

Table 3.3: Generalized linear model (Poisson distribution and a log link, corrected for over-dispersion) (n = 35), showing number of days with arctic fox observations related to number of days with red fox observations, distance to road and number of days with available carcass (bait).

Explanatory variable	**Estimate**	**SE**	**χ^2**	**p**
Intercept	-0.3490	0.6030	0.3530	0.5527
Days with red fox	-0.3722	0.1650	7.0750	0.0078
Distance to road	0.0001	< 0.0001	4.5720	0.0325
Days with available carcass	0.1416	0.0830	3.1440	0.0762

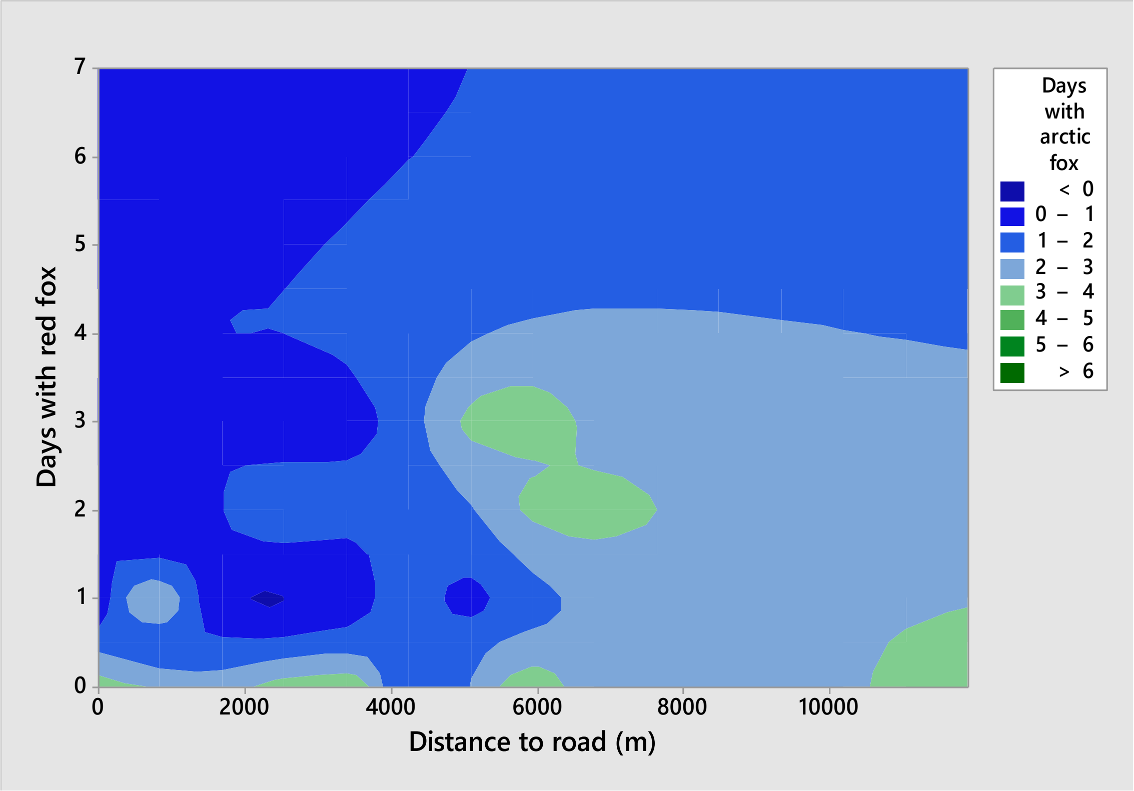

Figure 3.3: Contour plot that shows that the number of days with arctic fox were highest far away from the road, and where number of days with red fox on the baited camera traps were few.

The results revealed a moderate but significant negative relationship between time between visits of red fox and arctic fox, and red fox activity at the bait (Table 3.4, Figure 3.4). This means that the time before arctic foxes returned to the bait after a visit of red fox, was shorter at baits with high red fox activity.

Table 3.4: Results of a linear regression analysis showing a negative relationship between time between a visit of a red fox and the subsequent visit of arctic fox (response), and red fox activity (n = 43).

Explanatory variable	**Estimate**	**SE**	**t**	**p**	**R^2**	**R^2adj**
Intercept	31.728	3.961	8.01	< 0.0001		
Red fox activity +/- 1 hour	-5.194	1.717	-3.03	0.0043	0.183	0.163

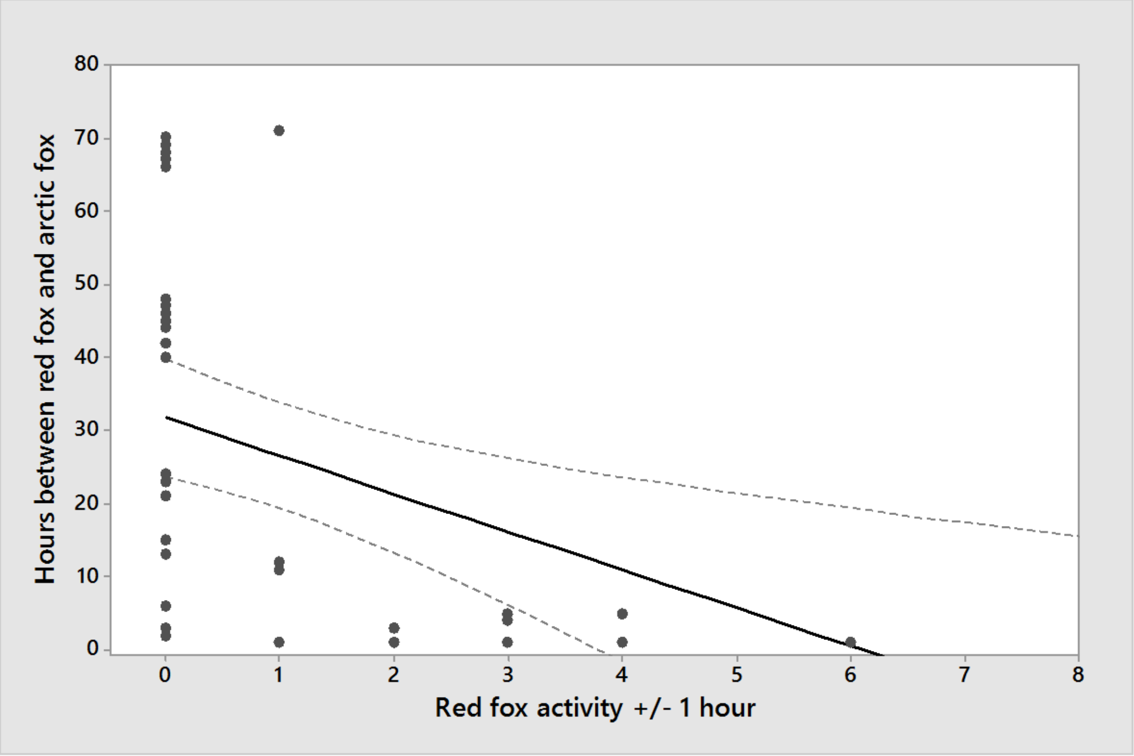

Figure 3.4: Time between a visit of a red fox and the subsequent visit of arctic fox, related to red fox activity at the bait (n = 43).

Time between observations of red fox and arctic fox was generally higher than time between observations of arctic fox and red fox (Figure 3.5). Mean number of hours between red fox and arctic fox visitations were 28.2 (CI = [20.18,36.2]), while mean number of hours between arctic fox and red for visitations were 11.2 (CI = [4.27,18.06]). A two-sample t-test confirmed that there was a difference in mean between the two samples (T_{74} = 3.27, p = 0.002).

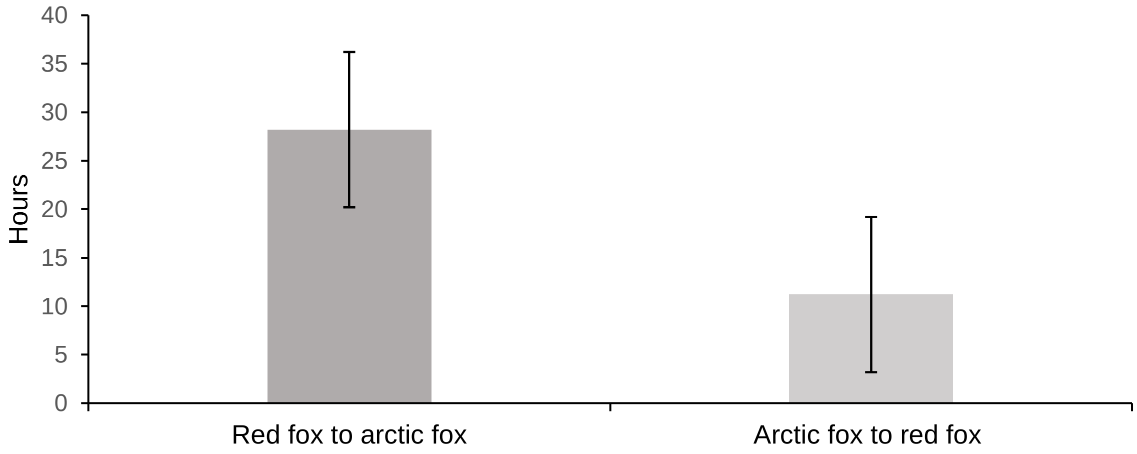

Figure 3.5: Mean hours between a visit of red fox and arctic fox, and mean hours between a visit of arctic fox and red fox. Error bars represent the 95 % confidence interval.

Figure 3.6 shows red fox and arctic fox average activity within each hour during a day, in each of the five mountain areas. In general, red foxes were more active during the day than arctic foxes. The peaks of arctic fox activity appeared during the night (between 2 and 5 a.m.), and in the evening.

A visualisation of arctic fox and red fox's daily activity at each camera trap location (n = 35) is presented in figure 3.7, organized with increasing red fox activity on the x-axis, and increasing arctic fox activity on the y-axis. Locations with the highest activity of both species are located in the upper right corner of the figure. The activity of arctic foxes was punctual in all locations, with activity peaks at night and/or in the evening. Red fox activity overlapped with arctic fox activity at many locations, and the patterns of arctic fox activity seemed not to be affected by red fox activity.

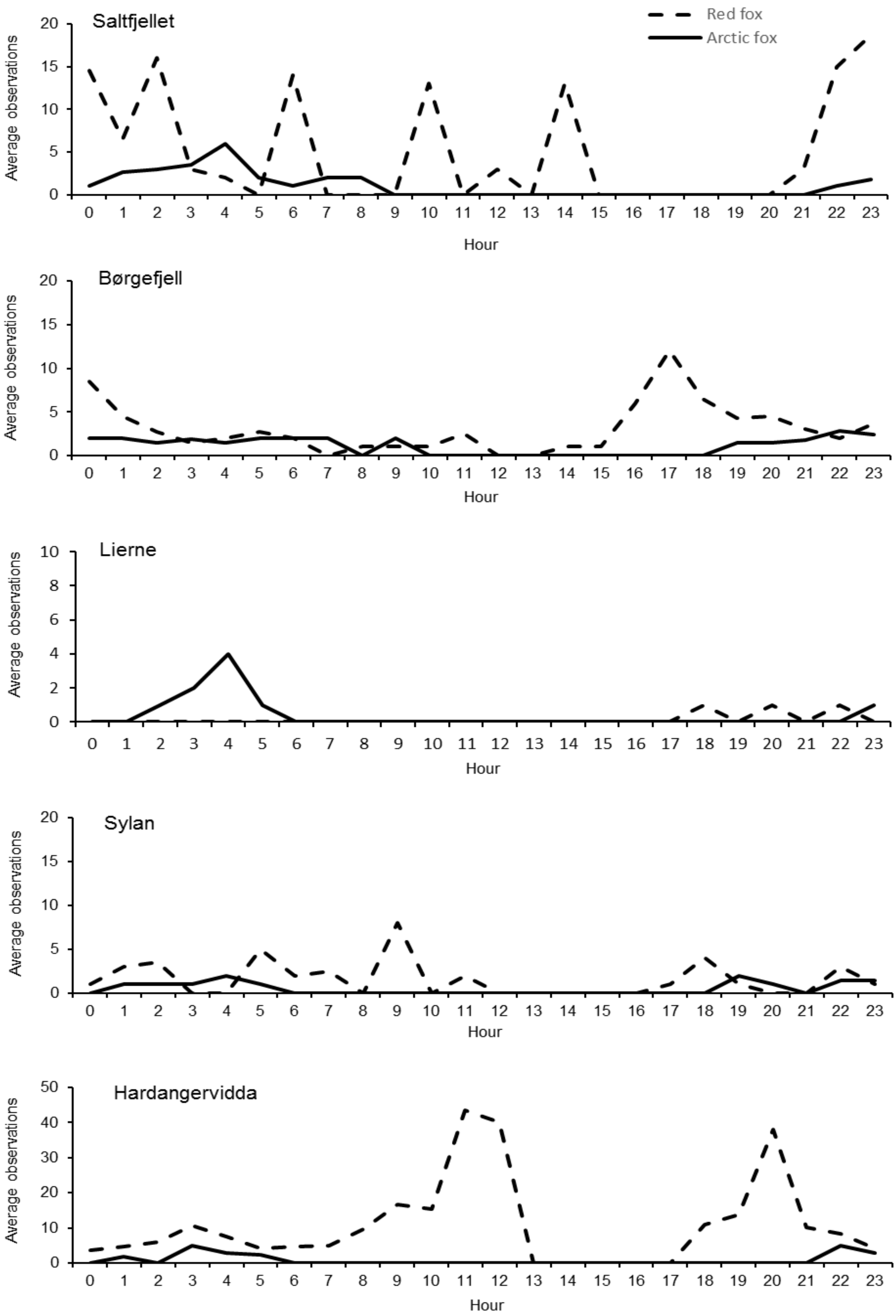

Figure 3.6: Arctic fox and red fox average daily activity (24 hours) in each of the 5 mountain areas. Note the different values on the y-axis between the different areas.

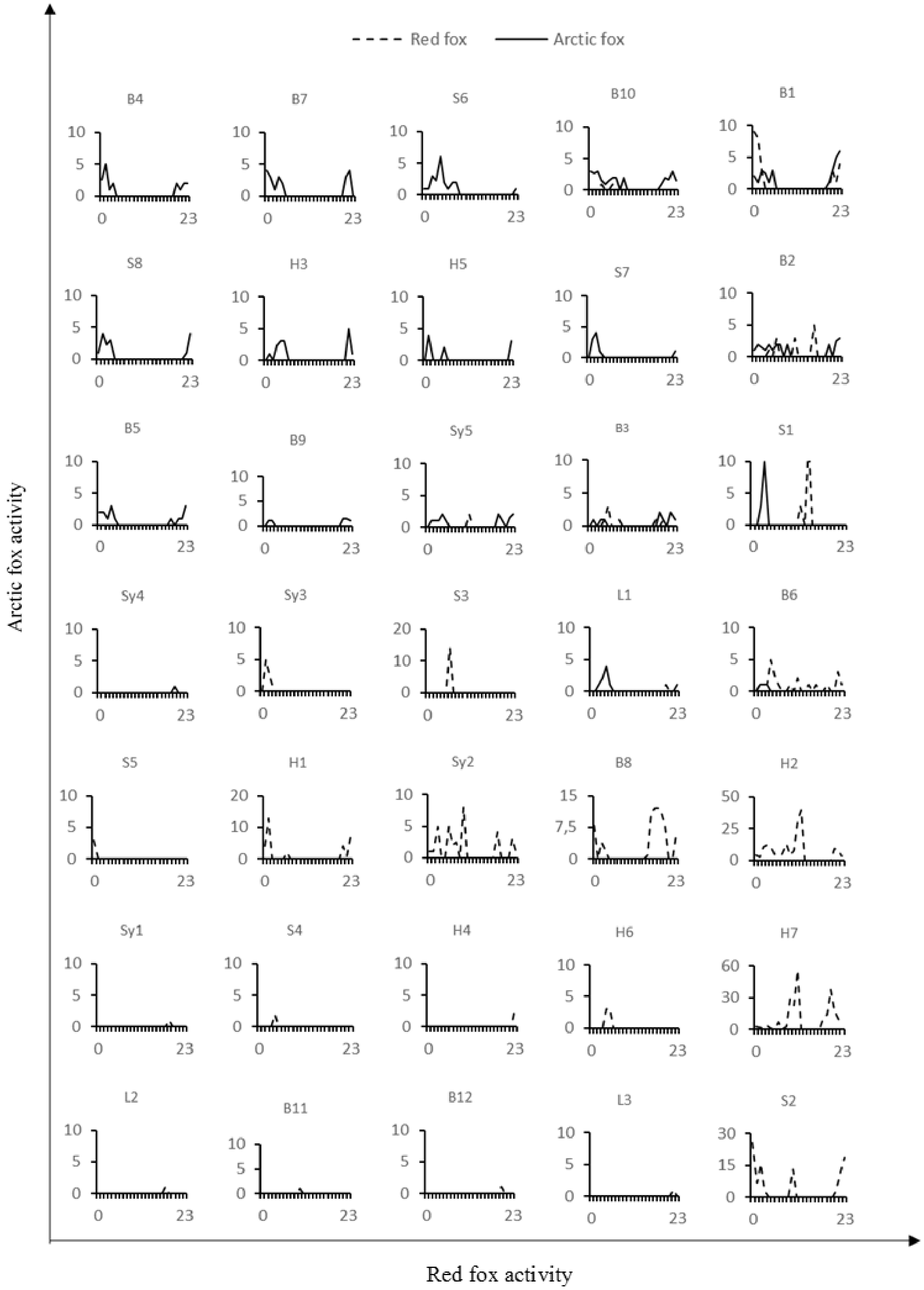

Figure 3.7: Arctic fox and red fox activity during a day at each location in the 5 different areas. Locations are organized after arctic fox and red fox activity with increasing red fox activity at the x-axis, and increasing arctic fox activity at the y-axis. The small figures are named with mountain area of the location: S = Saltfjellet, B = Børgefjell, L = Lierne, Sy = Sylan, H = Hardangervidda. Note the different values on the y-axis of the small figures for each location.

4. Discussion

The negative relationship between days with arctic fox observations and days with red fox observations suggests that the arctic fox is avoiding the red fox spatially, and my first hypothesis was hence accepted. It is likely that arctic foxes will avoid baits frequently visited by red foxes. Many studies confirm that there are negative interactions between red foxes and arctic foxes. Hersteinsson and Macdonald (1992) concluded that the arctic fox's southern distribution limit is determined by interspecific competition with the red fox, and studies on den use suggest that arctic foxes avoid high quality dens at lower altitudes to avoid the red fox (Frafjord 2003; Linnell et al. 1999). Hamel et al. (2013), using a similar study design as I did, found no observations of arctic foxes at sites with just a few daily observations of red fox. Similarly, Killengreen et al. (2012) found that red foxes may exclude arctic foxes from carcasses during winter. In my study, longer mean time between visits of red fox and arctic fox than between visits of arctic fox and red fox, also indicates that the arctic fox is more cautious of the red fox than vice versa. While the linear regression regarding days with arctic fox observations and days with red fox observations in my study showed some significance, the relationship was rather weak. At some camera traps with many observations of red fox, many arctic fox observations were also registered, sometimes also within the same day. This indicates that the competition between the two species are ambiguous and varied.

Red foxes seemed in general to be more active during daytime than the arctic fox, while peaks of arctic fox activity were mainly focused at night and in the evening. Although only explored visually at the scale of each camera trap, these results are consistent with the results from a study conducted by Eberhardt et al. (1982), who also found a nocturnal activity pattern of adult arctic foxes. Peaks of red fox activity were more inconsistent and widely spread throughout the day. Servín et al. (1991) found the same activity pattern as I did among red foxes, but highlighted differences in males and females. While females mainly displayed a nocturnal activity pattern, males were active during both night and day. In my study, arctic fox activity patterns seemed not to be affected by the intensity of red fox activity – their activity seemed to peak during night time and in the evening, regardless of whether or not red foxes were present. Temporal spacing of activity can make coexistence of species possible (Linnell & Strand 2000). For example, subordinate predators of the African predator guild avoid their dominant kleptoparasites and predators by minimizing their temporal overlap of activity (Hayward & Slotow 2009). I investigated if temporal avoidance could be a possible mechanism behind the coexistence of arctic fox and red fox. My results did not reveal any consistent temporal segregation of activity. Thus, the arctic fox was unlikely using temporal avoidance as an avoidance mechanism. However, more data with precise statistical analyses are needed to fully address this question.

Regarding my second hypothesis, I expected that time between a visit of a red fox and an arctic fox would increase with increasing red fox activity at the bait. Instead, the regression analysis showed exactly the opposite – time between a visit of a red fox and an arctic fox decreased with increasing red fox activity. The average activity of the two species highly overlapped in time, suggesting that high activity of red foxes at the bait did not necessarily lead to low activity of arctic foxes. At some camera traps, many observations of both species were registered. These results indicate that arctic foxes do not fear the red fox as much as I expected. A challenge here is that if the arctic fox activity is constant, then increased red fox activity will reduce the average time between red fox and arctic fox observations. Thus, it is hard to tell if the results of my study derived from arctic foxes not avoiding red foxes, or if the result is coincidental. This problem makes it difficult to draw any conclusions based on these results, and an improved study design with more data in space and time should be developed for further investigations.

As Tannerfeldt et al. (2002) suggested, arctic foxes are likely to avoid close contact with the red fox if the red fox represents a competitor and possible predator. Broekhuis et al. (2013) distinguish between reactive and predictive response to risk, and studied cheetah's (*Acinonyx jubatus*) response to risk related to their predators, lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). A reactive response is defined as an animal's knowledge of actual, real-time risk, and a predictive response is defined as an animal's preventive response to a potential risk (Broekhuis et al. 2013). They concluded that cheetahs did not avoid areas intensively used by lions, and that the cheetahs instead adjusted their behaviour according to the current, real-time risk. In other words, they found that the cheetah's way of dealing with their predators, were reactive instead of predictive. The relationship between cheetahs, lions and hyenas should probably not be directly compared to the relationship between arctic foxes and red foxes, but there are some similarities. The body size of the cheetah is smaller than the body size of lions and hyenas, and intraguild predation where lions and hyenas kill cheetah cubs are common (Broekhuis et al. 2013). However, there are also important differences, one of them being that an adult cheetah will be able to outrun a lion or hyena, in the case of an attack. It is unlikely that an arctic fox would be able to outrun a red fox. Still, it would be interesting to investigate further if the arctic fox's response to risk posed by red foxes is more reactive than predictive. My results show that the arctic foxes did not always avoid areas where encounters with red foxes were likely, and a possible reactive response mechanism by the arctic fox could be worth to investigate. Broekhuis et al. (2013) argues that if subordinate species were to completely avoid dominating predators, they would lose many feeding opportunities. Reactive response mechanisms should thus be important and relevant for coexisting carnivores such as arctic fox and red fox, especially in low productive habitats.

Competition between arctic fox and red fox may vary between different habitats, and food availability is a factor that is likely to affect the intensity of competition (Henden et al. 2010). If the food availability is low, the arctic fox may be forced to risk encounters with red foxes at carcasses, in order to fulfil their nutritional needs. In 2016, when the fieldwork of my study was conducted, the rodent cycle was probably in its low phase at Børgefjell (Ulvund et al. 2016), where most cameras registered both species. Low food availability could thus explain the results from Børgefjell, where arctic foxes seemed to avoid the red fox to a lesser extent than expected. However, the rodent cycle was probably also in its low phase at Sylan and Lierne (Ulvund et al. 2016), where only one camera recorded both species. The rodent cycle was probably in its increasing phase at Hardangervidda and Saltfjellet (Ulvund et al. 2016). Higher availability of rodents could possibly explain why no cameras recorded both species at Hardangervidda. When enough food is available, the arctic fox can avoid the red fox to a higher extent. Size, age and sex of the individual foxes will also likely affect the outcome of direct psychical competition (Palomares & Caro 1999). A large, male arctic fox has for example been observed chasing a female red fox (Frafjord et al. 1989).

The negative linear relationship between days with arctic fox observations and days with red fox observations was significant, but rather weak. A larger dataset with more observations, preferably with data ranging over several years, would give a stronger and more reliable result. I am also aware that the significant positive relationship between arctic fox observations and distance to road could have been affected by a considerably longer distance to road at Børgefjell than in the other areas, where most of the arctic fox observations were made.

My results suggest that the avoidance behaviour of the arctic fox might not be as consistent as previously thought. Knowledge of the interactions between the arctic fox and the red fox is crucial for the further conservation of the arctic fox. If the arctic fox is avoiding the red fox to a lesser extent than previously thought, the measures regarding red fox control should be reconsidered. However, I only investigated interactions between arctic fox and red fox related to their search for food, and competition for dens was not investigated. The competition for dens is likely more severe than competition for resources, because dens are impossible for a red fox and an arctic fox to share. Thus, the red fox may pose a great threat to the arctic fox in this context, and red fox control could still be an important measure to conserve the arctic fox.

In conclusion, the results of my study suggest that the interactions between arctic foxes and red foxes are complex and varied. Further studies are needed to investigate if the arctic fox's response to risk posed by red foxes is more reactive than predictive. Further studies with an improved study design are also needed to investigate activity patterns and temporal avoidance mechanisms. If the arctic fox is really avoiding the red fox to a lesser extent than previously thought, new approaches should be considered and investigated for further conservation of the arctic fox.

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