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The expansion of red foxes (*Vulpes vulpes*) into alpine areas

– Effects of human-induced subsidies along roads, and consequences for ground-nesting birds

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Preface

This thesis is part of the NINA project ECOFUNC, funded by the Norwegian Research Council (2015-2019). With several work packages, the project aims to understand ecosystem functionality, expansion and retreat of species in the Scandinavian mountain tundra. My part of the project (linked to work package 2) was to investigate the relationship between generalist species expansion into alpine areas and access to human subsidies from roads. The red fox is used as a model species for expanding generalists in this thesis. My master thesis is closely linked to Lars Rød-Eriksen's (NINA) PhD work under this research project. Fieldwork is part of the cooperation, and the results presented in this thesis will be utilized in his future modelling work.

First, I would like to thank my supervisor, Nina E. Eide (NINA), for letting me be a part of the ECOFUNC project and for guidance and thorough feedback during the writing process. Thanks to my supervisor Vidar Selås for constructive feedback and for helping me with statistical analyzes.

Finally, great thanks to Lars Rød-Eriksen for invaluable effort with preparations before the fieldwork and for guidance, participation and pleasant lunch breaks during fieldwork. I am also grateful for feedback throughout the writing process and for engagement over the past year.

Thank you!

Abstract

During the past century, the red fox (*Vulpes vulpes*) has gradually increased its presence in alpine habitats, threatening endangered species such as the arctic fox (*Vulpes lagopus*). Several factors have been suggested as underlying mechanisms: increased access to ungulate carcasses, the absence of top predators and increased productivity in mountainous areas. My main objective in this thesis was to investigate if human-induced subsidies along roads could be identified as one of the contributing factors, i.e. driving red fox expansion into alpine areas.

Potential food resources were registered along road segments on the European highway 6 over Dovrefjell. The occurrence of red foxes at camera traps were used to record the species' relation to the highway. I further investigated potential spillover effect of the road, aiming to estimate predation rate on ground nesting birds (using 90 artificial nests) in relation to the highway.

Along the road segments, we registered 547 items considered as potential edible garbage, and 17 road-killed small game animals. My results indicated that red foxes were exploiting these human-induced subsidies along the road. The number of days before a bait was detected by a red fox, increased with distance to the road. Surprisingly, no predation on the artificial nests was observed.

I suggest the lower response time of red foxes closer to the European highway to be explained by a higher red fox density along the road, due to higher food availability. I conclude that the red fox can benefit from available food along roads and suggests that roads may increase red fox density and survival in areas with initially low productivity. Roads are thus likely to be a contributing factor in driving the red fox expansion into alpine areas.

Based on my results, aiming to reduce roads' positive effect on the red fox and its expansion into alpine areas, I suggest two measures to reduce the availability of food, by: 1) more frequent removal of garbage and road-kills along the road, and 2) raise awareness on the ecological side effects among motorists who throw garbage.

Sammendrag

I løpet av det siste århundret har rødreven (*Vulpes vulpes*) gradvis økt sin tilstedeværelse i alpine områder, og er således en økende trussel mot truede arter, slik som fjellrev (*Vulpes lagopus*). En rekke faktorer er foreslått som bakenforliggende mekanismer: økt tilgang til hjortedyrkadaver, fraværet av topp-predatorer og økt produktivitet i fjellområder. Mitt hovedmål var å undersøke om menneske-tilførte subsidier langs vei kunne identifiseres som en av de bakenforliggende mekanismene som driver rødrevens ekspansjon til alpine områder.

Registrering av potensielle matressurser ble registrert langs veg-segmenter på Europaveg 6 over Dovrefjell. Forekomsten av rødrev ved åte-kameraer ble benyttet for å registrere artens tilknytning til motorvegen. Jeg undersøkte også en potensiell tilleggs-effekt av veien, med mål om å estimere predasjonsrate på bakkehekkende fugler (ved bruk av 90 kunstige reir) i forhold til nærhet til veien.

Langs veg-segmentene registrerte vi 547 elementer ansett som potensielt spiselig avfall, og 17 påkjørte småvilt. Mine resultater indikerte at rødreven utnyttet disse menneske-tilførte subsidiene langs veien. Antall dager før et åte ble oppdaget av en rødrev, økte med avstand til veg. Overraskende nok, ble ingen av de kunstige reirene predatert.

Jeg foreslår at den lavere tidsresponsen ved nærhet til Europavegen kan forklares med høyere rødrev-tetthet langs veien, grunnet større mattilgang. Jeg konkluderer med at rødreven kan dra nytte av tilgjengelig mat langs vei og at veier kan øke rødrevens sannsynlighet for overlevelse i områder med opprinnelig lav produktivitet. Veier er dermed en sannsynlig medvirkende faktor til ekspansjonen av rødrev til alpine områder.

Basert på mine resultater, med mål om å redusere den positive effekten veier kan ha på rødrev og dens ekspansjon til alpine områder, foreslår jeg to tiltak for å redusere tilgjengeligheten til mat, ved: 1) hyppigere rydding av søppel og påkjørt vilt langs vei, og 2) øke bevisstheten rundt de økologiske bivirkningene blant bilister som kaster søppel.

Table of contents

Introduction 1
Methods 4
  Study area 4
  Study design 5
  Explanatory variables 8
  Statistical analyzes 8
Results 9
Discussion 17
Conclusions 21
Recommendations 22
References 23

Introduction

Land-use change is the largest threat against biodiversity (Sala et al. 2000). Part of that is development of infrastructure, which in terms of roads, railroads, drainage and electricity supply is the underlying structure and foundation of a functioning society. Continual development of infrastructure influences both habitats and wildlife, leading to substantial environmental impacts (Millenium Ecosystem Assessment 2005; UNEP 2001) and destruction of wildlife habitats (Sala et al. 2000). Infrastructure also causes direct mortality of wildlife species through collisions with both vehicles and the infrastructure itself (Bevanger & Brøseth 2004; Erritzoe et al. 2003; Forman & Alexander 1998; Rolandsen et al. 2015).

The mortality caused by infrastructure can provide carcasses as an easily available food source for scavengers (Benitez-Lopez et al. 2010), and function as an external resource subsidy, as it comes in addition to the natural prey base (Newsome et al. 2015). Along roads in particular, subsidies might also be provided in form of edible waste (Balestrieri et al. 2011) that motorists throw out or leave at car stops. Like other generalist species, the red fox (*Vulpes vulpes*) can take advantage of such human-induced subsidies, being capable of changing diet composition and switch to alternative prey, adjusted to the available food supply and prey population changes in an area (Delibes-Mateos et al. 2008; Jedrzejewski & Jedrzejewska 1992; Leckie et al. 1998; Meisner et al. 2014; Pagh et al. 2015). Although characterized as a boreal forest species, the red fox is highly adaptable to various environments and is today the most widespread carnivore in the world (Gloor et al. 2001; Jedrzejewski & Jedrzejewska 1992; Kurki et al. 1998).

During the 20th century, the red fox gradually increased its northern and altitudinal limit and extended its distribution to the mountain tundra habitats (Elmhagen et al. 2002; Hersteinsson & Macdonald 1992; Linnell et al. 1999; Post et al. 2009). The expansion is suggested to be driven by several factors; increase of ungulate carrions (Henden et al. 2014; Selås & Vik 2007), diminishing of apex consumers (predators on top of the food chains) likely causing a mesopredator-release effect (Elmhagen & Rushton 2007), and an increase in ecosystem productivity (Hersteinsson & Macdonald 1992; Killengreen et al. 2011).

Microtine rodents is by far the most important prey for red foxes (Anda 2015; Leckie et al. 1998; Lindström & Hörnfeldt 1994; Pagh et al. 2015). However, subsidized food like carrion and edible garbage have also proved to be an important source of food (Anda 2015; Ghoshal et al. 2016; Kaikusalo & Angerbjörn 1995; Killengreen et al. 2012; Meisner et al. 2014; Pagh et al. 2015), particularly in winters with deep snow (Jedrzejewski & Jedrzejewska 1992), when rodents are less available (Halpin & Bissonette 1988; Lindström & Hörnfeldt 1994). In comparison with arctic foxes (*Vulpes lagopus*), red foxes require a greater amount of nutrition, due to their larger body size (Hersteinsson & Macdonald 1992). As red fox distribution is related to habitat productivity (Barton & Zalewski 2007), human-induced subsidies may serve as external subsidies that affect red fox reproduction and survival, resulting in expansion into habitats with initially low productivity (Henden et al. 2010; Henden et al. 2014; Kaikusalo & Angerbjörn 1995; Killengreen et al. 2011; Newsome et al. 2015).

An effect of red fox expansion can be increased competition and predation pressure on other species, which could have severe impacts on both abundance and the dynamics of affected species' populations (Andren & Angelstam 1988; Elmhagen 2003; Kurki et al. 1998). The expansion of red foxes into alpine areas is considered one of the most important threats to the critically endangered arctic fox in Scandinavia, acting through both increased competition and predation (Frafjord 2003; Selås & Vik 2007; Tannerfeldt et al. 2002). Furthermore, the red fox is capable of limiting mountain hare (*Lepus timidus*) populations (Lindström et al. 1994; Marcström et al. 1989; Smedshaug et al. 1999), and is an important predator on lambs (*Ovis aries*) (Lund 1963; Rødven & Hansen 2015).

The red fox is also an important predator on ground nesting birds (Bergin et al. 1997), having great influence on reproduction success and breeding numbers (Fletcher et al. 2010). Nests along roads are expected to be more vulnerable to predation due to increased encounter-rate by predators (Bergin et al. 1997), as roads are utilized by predators for travelling through the landscape (Coffin 2007), and for searching for road-kills (Forman & Alexander 1998). This expectation of a potential spillover effect agrees with nest predation increasing and reproductive success decreasing with increased degree of landscape fragmentation (Andren & Angelstam 1988; Paton 1994; Pedersen et al. 2011).

In this thesis, I investigate whether there are any impacts of human-induced subsidies along road segments on a European Highway (E6) over Dovrefjell, a Norwegian mountain plateau. I record red fox distribution along road segments in order to test whether roads have influence on the occurrence of red fox, i.e. are driving the species expansion to mountainous habitats. I also investigate potential spillover effects of the roads, setting up artificial nests along the same road segments. The E6 highway is expected to be a source of substantial amounts of road-killed animals and disposal of garbage. Hence, I predict that the abundance and occurrence of red fox is positively correlated with proximity to the road and access to such subsidies along the road. Based on the assumption that red fox density is higher along roads, I further predict a higher frequency of nest predation at nests close to the road compared to nests far from the road.

Methods

Study area

The study was conducted in the south-central part of Norway in an alpine mountain pass, along the European Highway 6 (E6) in Dovrefjell (Fig. 1). The average number of vehicles passing the study area each day on the E6 is 1.965 (Statens Vegvesen 2015). The study was conducted in and outside of protected areas along the road; Dovre National Park (289 km^2; 62^{o}05´00´´N, 9^{o}32´00´´E) on the southeast side and Dovrefjell-Sunndalsfjella National Park (1693 km^2; 62^{o}16´00´´N, 9^{o}13´00´´E) and Fokstumyra Nature Reserve (18.2 km^2; 62^{o}12´00´´N, 9^{o}27´00´´E,) in the northwest. Parallel to the highway, on the north side, with a varying distance from 20 to 1000 meter from the road, is a railroad, which may contribute to the total amount of subsidies, i.e. carcasses (Rolandsen et al. 2015; Statistisk sentralbyrå 2015). Similarly, power lines are present in my study area, and which may provide carcasses due to bird collisions (Bevanger & Brøseth 2004). The presence of other types of infrastructure may have had an influence on my data; however, due to the scope of my thesis, the potential influence was not taken into account. Other roads, such as small country roads, are present within my study area, most of them not usable in winter. These where assumed to provide little to no subsidies.

The study area is situated in the north boreal- and low alpine zone. The lower areas are dominated by birch (*Betula pubescens*) woodland and sparse coniferous forest. Above the timberline (approximately 1000 m.a.s.l.); the land is characterized by willow shrubs (*Salix* spp.), dwarf birch (*Betula nana*), bilberry (*Vaccinium myrtillus*) and juniper (*Juniperus communis*). The study area ranges from 900 to 1100 m.a.s.l, is snow covered between 175-225 days per year, and has a short growing season of about 110-120 days (Moen 1999).

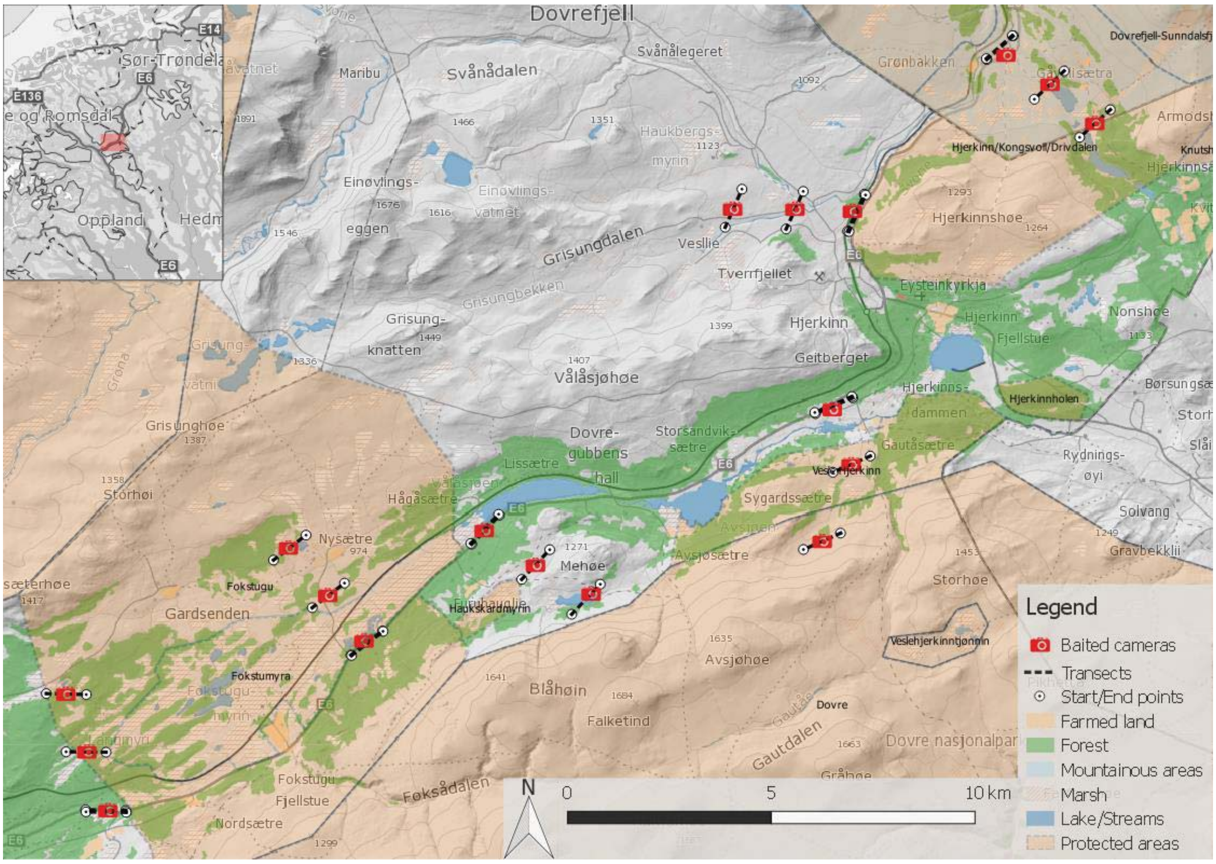

Figure 1. Map showing the study area in Dovrefjell. The camera traps and transect lines along the road are spread out randomly, although with a minimum of 3 km between each segment. The remaining camera traps and transect lines are placed in parallel to the road transect at a distance of 1500 and 3000 meters from the road. Map layers acquired from Statens kartverk.

Study design

The fieldwork was conducted between April and October 2015. 2015 was a low phase of the rodent population cycle in Dovrefjell (Framstad 2016). Information of this is relevant, as lack of rodents is believed to increase the red foxes' need for alternative prey, carcasses and anthropogenic food supply (Jedrzejewski & Jedrzejewska 1992; Leckie et al. 1998; Selås & Vik 2006).

Recording access to garbage and road-kills

Along six km of the road (six segments of one km, with a minimum distance of three km between each segment, see Fig. 1) we intended to count the number of potential food sources for scavengers, both in form of edible garbage and road-kills. All human-induced items with characteristics as a solid food item for humans were considered as potential edible food for red foxes. As it was impossible to investigate which items had previously contained food or leftovers, we did not distinguish between whether the goods had content or not. Our intention was to see whether the road was providing food available for the red fox, and if the numbers could be set in context with red fox distribution and activity along the same segments. We walked each road segment three times (in May, July and October, corresponding to late winter, summer and autumn), and conducted the registration of garbage and road-kills on both sides of the road each time.

Distribution and activity of scavengers

To examine the relationship between the highway and red fox activity, 18 baited camera traps were installed at three different distances to the road (~50 m, 1500 m and 3000 m). The camera type used for this project was Reconyx HyperFire PC800 (Reconyx, Inc, Wisconsin, USA). The cameras were placed at approximately one meter above the snow, angled towards the bait (~20 kg frozen offal of reindeer), 4-6 meters away (Fig. 2 and 3).

Cameras and baits were placed in late April. Two weeks later, we visited all the traps, replaced all the memory cards in the cameras and replenished the baits. All cameras were removed from the field after approximately one month in total (26-30 days). There were no leftovers of any of the baits. For the camera traps, we used a 5-minute interval in addition to motion sensor pictures for the first two weeks. For the last two weeks, we decided to use the 5-minute interval only, as an easier way of statistic use. However, we included the motion sensor pictures of red fox for the first period to increase the quality of the data. During the camera trap experiment, the ground was covered by snow in most parts of the study area.

Figure 2. Example of a set-up of one of the baited camera traps.

In total 146 779 pictures were manually analyzed, and all necessary information (species, number of individuals, bait present or not) from each picture was recorded into an Excel datasheet. Herbivores and small birds (mainly great tit (*Parus major*)) were not registered. Only a minor part of the pictures had to be excluded due to some sort of failure, like overexposure, snow covered lens or that the camera had fallen down.

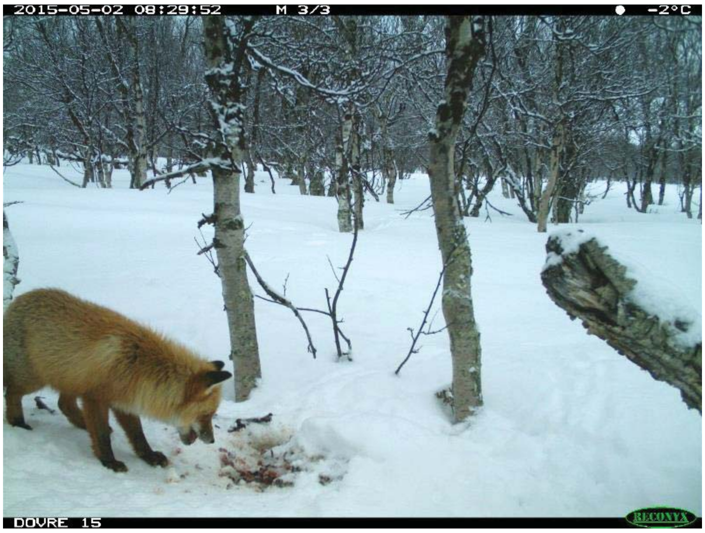

Figure 3. Example of a red fox visiting a bait station and captured by one of our wildlife cameras.

To get an overview of all activities, both pictures with and without bait present were included in the data.

Along the 18 transects we also performed snow tracking in late April, recording tracks and scats of red foxes. Our intention was to compare the intensity of red fox activity in different distances from the road. However, after tracking once on each transect, we decided not to continue this part of the study, mainly due to poor tracking conditions (early snowmelt).

Estimating nest predation rates

An experiment was conducted to compare the predation rate on nests with different distances to the road (same distances as for the camera traps). In July, 90 artificial nests, each with one egg of common quail (*Coturnix coturnix*) and one fake egg of plastic clay, was placed (and slightly hidden in the vegetation) along the 18 transects described above. Two of the transects were changed slightly for practical reasons. Five nests were placed on each transect, with a 250 meters distance between each nest. The artificial egg of plastic clay was, based on bite marks in the clay, meant to be used as a source for assessing the nest predator. In addition to the fake egg, camera traps were set up on 36 nests to aid in identification of the nest predator. All nests were revisited and removed after approximately three weeks. The method was based on a successful study from Finnmark county (Jacobsen 2014).

Explanatory variables

In addition to the highway, the proportion of forest was tested as an explanatory variable. Red foxes' attraction to forest is well-documented (Killengreen et al. 2012; Kurki et al. 1998; Røhnebæk 2004), and a comparison of these two factors could therefore contribute in explaining the strength of red foxes' attraction to road. The proportion of forest surrounding each camera trap was found using AR50 (1:50 000) maps (Skog og landskap 2015). Data was extracted within a 500-meter buffer (radius) around each camera position using GRASS GIS 6.4.4 (GRASS Development Team, 2014).

Statistical analyzes

Linear regression and multiple regression models were used to test the number of days with bait present against both baits' distance to road and proportion of forest within 500 meters from the bait. Further analyzes was given to the red fox only.

The response variable "days to find bait" (also called "response time") gives the number of days between activation of the camera until the first picture of red fox was taken. This variable was log-transformed in the analysis to obtain normally distributed residuals. The response variable "visitation days" describes the number of days with at least one picture of red fox. Linear regression was used to analyze the relationship between these two response variables and the baits' distance to road and the proportion of forest within 500 meters from the bait. Using a multiple regression model, I also tested each response variable against both distance to road and proportion of forest.

To test for a direct relationship between human-induced subsidies and red fox activity, I compared the two response variables with the number of potential edible garbage and the number of road-kills. Due to the small sample size (six segments), I used nonparametric statistic when conducting this analysis (Kendall's rank correlation). All data analyses were performed by use of the statistical computer program JMP (version Pro 12).

Results

<u>Recording access to garbage and road-kills</u>

During the three periods recording potential food source along the highway, we found 547 items considered as potential edible garbage (Table 1) and 17 road killed animals (Table 2). Potential edible garbage was very diverse, but consisted mostly of fruit and packings from chocolate, energy bars, snacks and fast food. Road killed animals consisted of 15 birds (thrushes (*Turdidae*), pipits (*Anthus* spp.), ptarmigans (*Lagopus* spp.) and Eurasian magpie (*Pica pica*)), and two mountain hare.

Table 1. Number of garbage considered as potential edible items for red foxes, found along the six road segments and the month it was found. Kilometer reference, in brackets, refer to air distance (km) to nearest village (Dombås).

Road segment (distance)	Period			Total
	1 (May)	2 (July)	3 (Oct)	
1 (4.6 km)	41	12	53	106
2 (12.2 km)	45	14	35	94
3 (16.6 km)	53	21	28	102
4 (25.4 km)	46	13	18	77
5 (29.6 km)	38	18	24	80
6 (33.9 km)	52	16	20	88
Total	275	94	178	547

Table 2. Number of road-kills found along the six road segments, and the month the road-kills were found. Kilometer reference, in brackets, refer to air distance (km) to nearest village (Dombås).

Road segment (distance)	Period			Total
	1 (May)	2 (July)	3 (Oct)	
1 (4.6 km)	0	0	4	4
2 (12.2 km)	1	0	1	2
3 (16.6 km)	0	1	1	2
4 (25.4 km)	2	0	1	3
5 (29.6 km)	3	0	0	3
6 (33.9 km)	1	0	2	3
Total	7	1	9	17

Distribution and activity of scavengers

The baits were removed faster with decreasing distance to the road (Fig. 4). There was a significant relationship between the number of days with bait present and the baits' proximity to the road (R^2 = 0.27, P = 0.026).

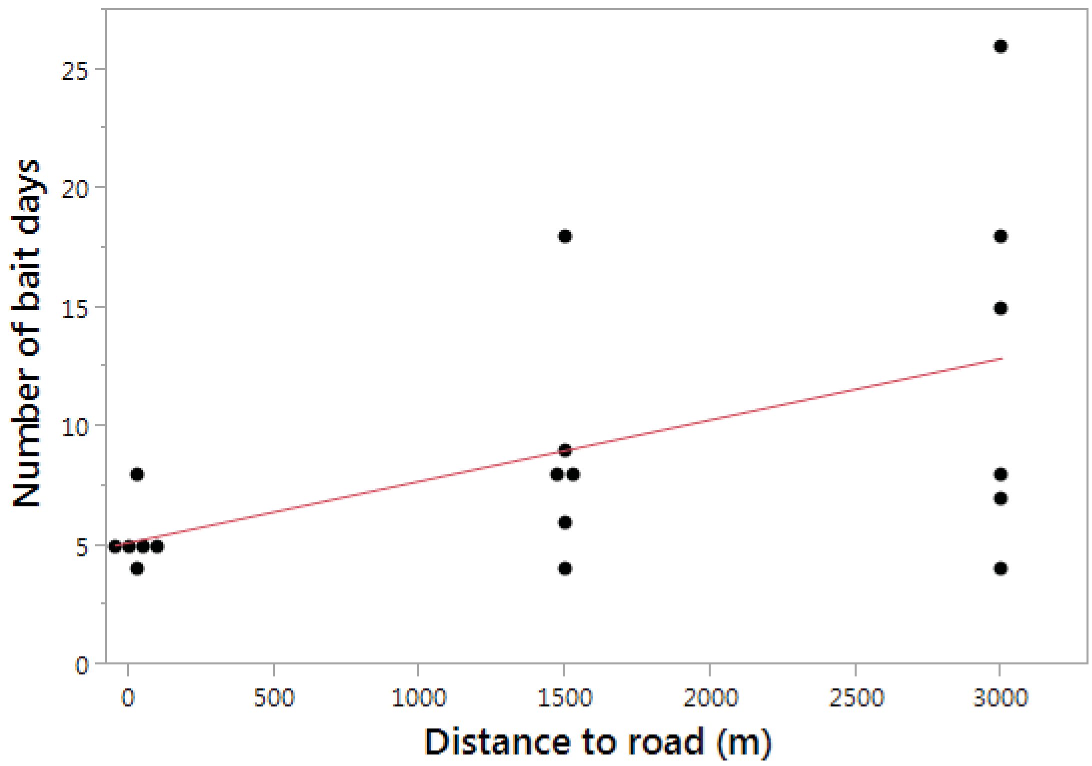

Figure 4. The mean number of days before the baits (n = 18) was gone, divided into the three different distances to the road.

The proportion of forest within 500 meters from the baits did not affect the number of days with bait present ($R^2 = 0.02$, $P = 0.567$).

Red fox, common raven (*Corvus corax*), hooded crow (*Corvus cornix*) and Eurasian magpie were the most frequent scavengers on the baited camera traps, see table 3 for other species recorded.

Table 3. The number of visitation days at the baits of the various scavengers, divided into the three different distances to the highway.

Species	Distance		
	~ 50 m	1500 m	3000 m
Red fox	35	30	22
Common raven	19	31	26
Hooded crow	43	47	17
Eurasian magpie	32	3	3
European pine marten (*Martes martes*)	0	0	2
Wolverine (*Gulo gulo*)	0	2	2
Rough-legged buzzard (*Buteo lagopus*)	1	3	1
Golden eagle (*Aquila chrysaetos*)	2	5	4
White-tailed eagle (*Haliaeetus albicilla*)	2	0	1
European herring gull (*Larus argentatus*)	0	1	0

Visitation days of red foxes were not significantly related to the distribution of garbage found along the road segments (Kendall's Rank Correlation, t = -0.33, P = 0.348), or the distribution of road-kills (t = 0.08, P = 0.837). Nor was red foxes response time significantly related to the distribution of garbage (t = 0.07, P = 0.845) or road-kills (t = 0.42, P = 0.289).

The number of days the red fox used to find the baits increased with increasing distance to the road (Fig. 5). The statistical relationship between the response time of red foxes and the baits distances to road was highly significant, with a p-value at 0.007 (Table 4).

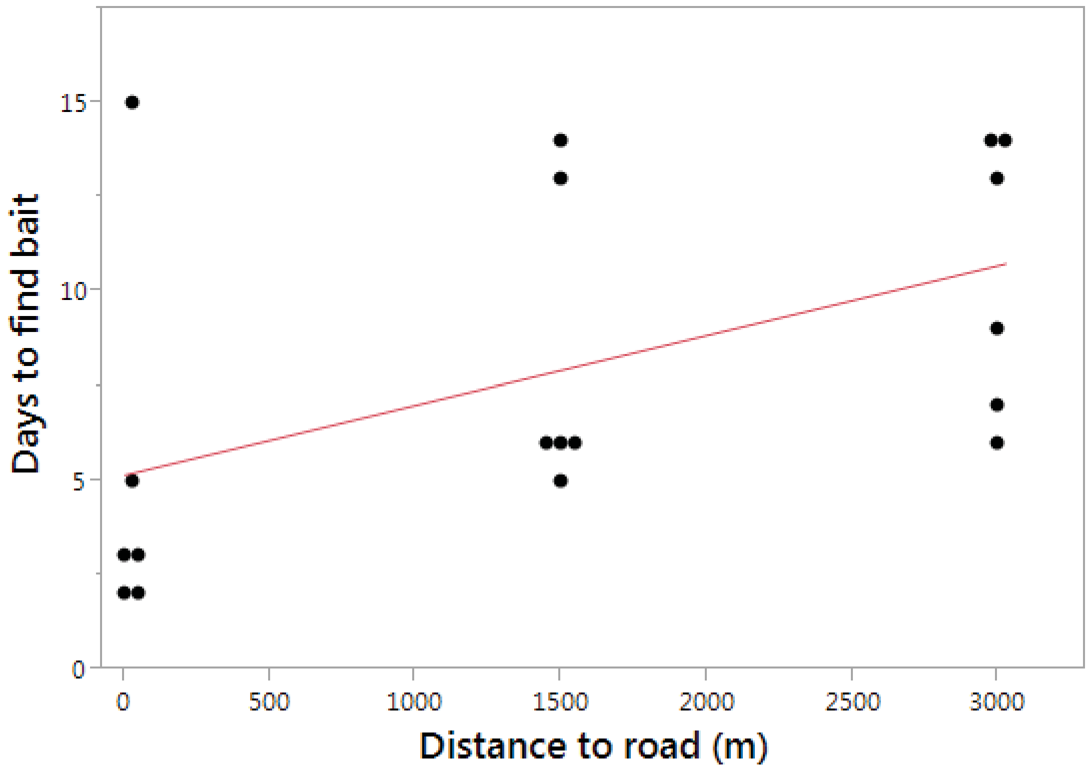

Figure 5. Response time of red foxes (number of days before the bait was found) in relation to the distances between the baits and the road.

Table 4. Linear regression model with the log-transformed data of the response time of red foxes (number of days before the bait was found) as response variable and the baits' distance to road as explanatory variable showing a clearly significant coefficient of determination. $R^2 = 0.37$

Explanatory variable	Estimate	SE	t	P
Intercept	0.60175	0.089421	6.73	< 0.001
Distance to road	0.00014	0.000046	3.09	0.007

The relationship between the number of days with visits of red foxes at the baits and the bait's distance to road was not significant ($R^2 = 0.07$, P = 0.280; Fig. 6). Nor was there a correlation when using only visitation days when bait was still present ($R^2 = 0.01$, P = 0.637).

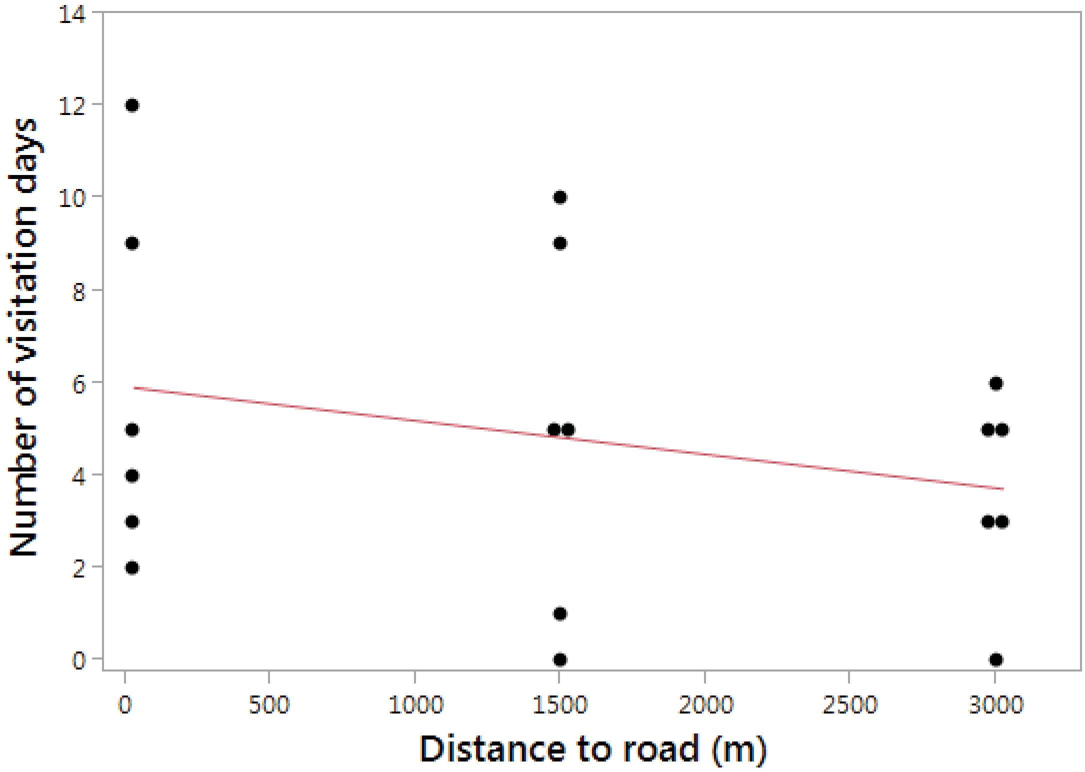

Figure 6. The relationship between the number of visitation days for red fox on baits and the bait's distances to road.

The proportion of forest within 500 meter from the baits was not a significant predictor for the response time of red foxes (R^2 = 0.09, P = 0.215; Fig. 7), or number of red fox visits at a bait (R^2 =0.09, P = 0.238; Fig. 8). I also tested the number of visitation days in relation to forest, only when bait was still present. This revealed a tendency of increased number of visitation days with increased proportion of forest (R^2 = 0.17, P = 0.090).

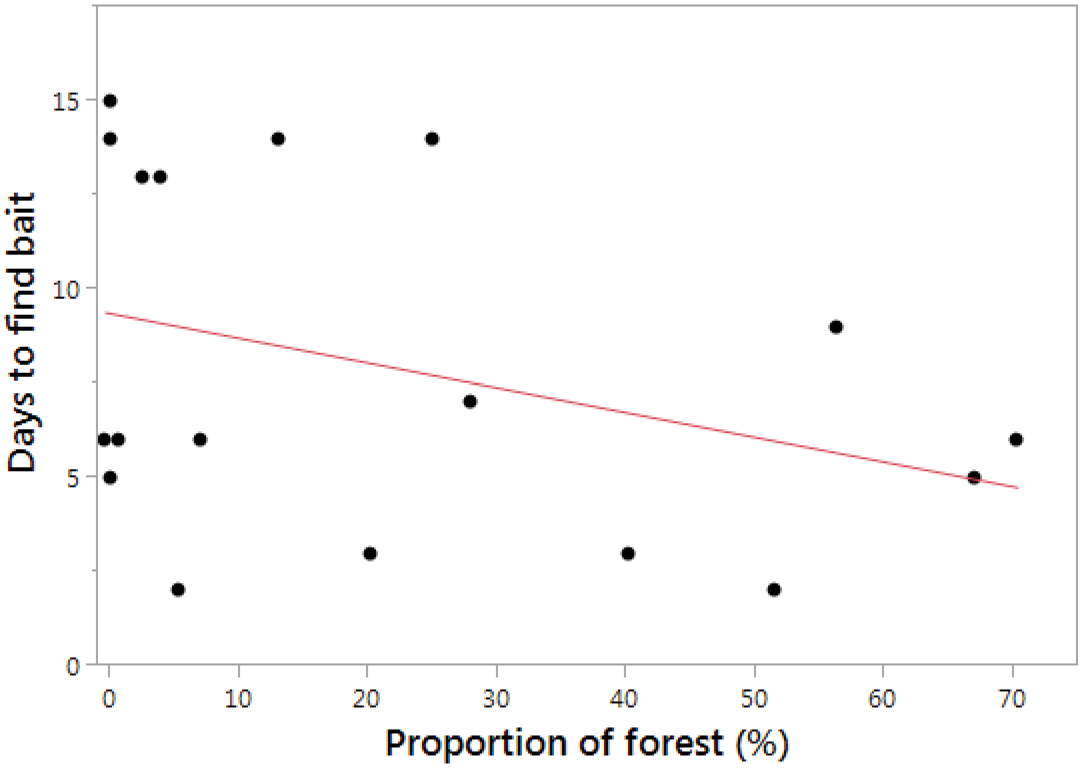

Figure 7. Response time of red foxes (number of days before the bait was found) in relation to the proportion of forest within 500 m from the bait.

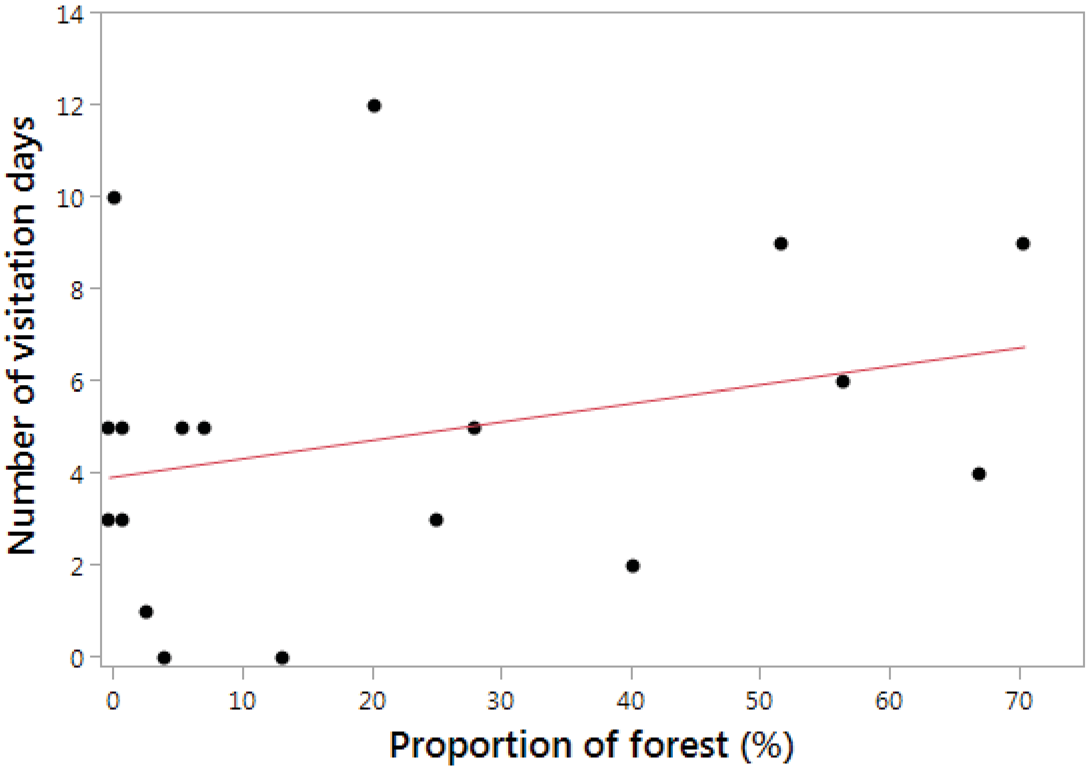

Figure 8. The relationship between the number of visitation days for red fox on baits and the proportion of forest within 500 m from the bait.

In a multiple regression model with both distance to road and proportion of forest as explanatory variables, only distance to road was a significant predictor for red foxes response time (Total R^2 = 0.41; Distance to road, P = 0.013; Proportion of forest, P = 0.355). None of the two variables were significant predictors for visitation days of red foxes in the multiple regression model (Total R^2 = 0.13; Distance to road, P = 0.385; Proportion of forest, P = 0.325).

Estimating nest predation rates

None of the nests (n = 90) were predated during the study period. There was no findings of bite marks on the plastic clay, nor any pictures of predators on the camera traps set by the nests.

Discussion

The road did supply easy available food in the form of edible garbage and road-killed animals. Hence, the road may function as a source of food for species utilizing such subsidies. Like most estimates of subsidies along roads (Teixeira et al. 2013), these values are underestimates, due to the high incidence of potential biases, such as persistence probability. Guinard et al. (2012) found a high daily persistence probability at 0.976 ± 0.003, while Antworth et al. (2005) experienced that 72.6 % of bird carcasses disappeared within 36 hours. Injured animals dying at distance from the roads should also be taken into account.

When it comes to encounter probability of road-kills, a capture-recapture experiment of bird carcasses along roads (Guinard et al. 2012) found high encounter probabilities (0.957 ± 0.007). The experiment was conducted on foot, as in this study, and we can therefore expect a comparable encounter probability. As garbage was more visible and easier to detect, garbage encounter probability is expected to be at approximately the same level. In addition to biases above, it was apparent that litter picking had been conducted along some of the segments before our counting's. Our findings, therefore, exclusively represent the provision of food along the road, at that particular time of recording. However, our findings confirm that roads supply available food for scavenging species in the form of road-kills (Bruinderink & Hazebroek 1996; Forman & Alexander 1998) and edible garbage.

Despite the risk of being killed by vehicles (Ashley & Robinson 1996; Lode 2000) when scavenging (Jones 1980), roads are frequently utilized as a source of food for scavengers (Antworth et al. 2005; Santos et al. 2011) and may provide an easy and energy efficient way to fill nutritional needs. This corresponds with the faster removal of the baits closer to road, which must be interpreted as higher frequency of scavenging activity along the road, as found by Lambertucci et al. (2009). The time of removal was not affected by proportion of forest, which strengthens the prediction that scavenging activity is related to the road itself, and not its location. A number of scavenging species, including red fox, exploited the deployed baits that were distributed throughout the study area. Red fox, common raven, hooded crow and Eurasian magpie, all generalists, had a double-digit number of visitation days at the baits close to the road.

The red fox is capable of benefit greatly from external resource subsidies (Ghoshal et al. 2016; Henden et al. 2010; Kaikusalo & Angerbjörn 1995), and responds with increased presence and growth rate to increased food supply (Kaikusalo & Angerbjörn 1995; Lindström

1989). I did, however, not find a direct relationship between red fox occurrence and distribution of edible garbage or road-killed animals. Although a positive relationship was expected, the prediction could also have turned out the opposite way, with less subsidies in areas with high scavenging activity, as scavengers remove subsidies from the road (Antworth et al. 2005; Santos et al. 2011). Anyway, due to the abundance of likely biases above, the counted numbers of garbage and road-killed animals are not a representative distribution of human-induced subsidies along these road segments. A much better mapping of garbage and road-kills is required to get grip on those relationships.

However, the red foxes needed fewer days to detect the baits located close to the road, which suggest that red foxes moved more frequently along the road compared to the surrounding areas, indicating some sort of attraction to the road. Human-induced subsidies, like our findings, is the most reasonable explanation for this attraction, as red foxes are known to scavenge for road-killed animals (Forman & Alexander 1998) and can benefit greatly from available garbage (Doncaster et al. 1990; Ghoshal et al. 2016). As red foxes are capable of switching from their regular choice of food resource when other food sources increases in availability (Aryal et al. 2010), my results may also suggest that the road supplied a more stable and easier source of food than the surrounding areas. The low phase of the rodent population cycle in the study area this year (Framstad 2016) may have increased the importance of road kills and garbage along the road.

The number of red fox visitation days was not related to the baits' distance to road. As red foxes are territorial (Doncaster & Macdonald 1991; Meia & Weber 1995; Niewold 1980; Sargeant 1972), the number of red foxes using the area surrounding each bait are limited. Each bait will therefore benefit the territorial individuals, and number of visitation days will be strongly affected by the territorial foxes' utilization of each bait. The number of visitation days should therefore not be related to the distribution of red foxes in the area. There was nevertheless a tendency of visitation days of red foxes increasing with proximity to the road. If the road supplied a more stable and easier source of food than the surrounding areas, the tendency may be explained by increased overlap between neighboring red fox habitats (Meia & Weber 1995) and larger family groups within each territory (Lindström 1989; von Schantz et al. 1984).

Although red foxes have strong holds in forest (Killengreen et al. 2012; Kurki et al. 1998; Røhnebæk 2004), the proportion of forest in proximity to the baits was not an important factor explaining red foxes response time, suggesting that the road had a far stronger impact on the red fox distribution in my study area. This strengthens the suggestion above that the road itself, and not the road's location, functioned as a strong attraction. Moreover, not just for scavengers in general, but this was also valid when I tested exclusively for red foxes.

As the red fox has higher nutritional needs, compared to an alpine adapted species as the arctic fox, the red fox will also need a larger home range to fulfill its needs in such habitats. This will require more time both for foraging and defending of the larger home range (Hersteinsson & Macdonald 1992), which is a disadvantage in low productive habitats. However, as food availability is a main factor for home range size, the disadvantage might be mitigated if food availability increases (Barton & Zalewski 2007; Lucherini & Lovari 1996) as a result of subsidies from roads. If a road supplies a considerable amount of external resources, the red fox may therefore decrease its home range size due to increased efficiency in foraging near the road. A response of smaller habitat sizes would potentially increase the number of red fox territories and further increase the red fox density near the road. A higher red fox density close to the road could explain the shorter response time at the baits in proximity of the road.

As the food availability in winter is the limiting factor for red fox distribution in alpine habitats (Barton & Zalewski 2007; Hersteinsson & Macdonald 1992), human-induced subsidies in winter may possibly be a deciding factor for red fox winter survival, and subsequent expansion into these habitats. Red foxes are known to increase their scavenging when temperatures drop (Selva et al. 2005), which probably applies especially in years when rodents are less abundant and the red fox must switch to alternative prey or food supply (Halpin & Bissonette 1988; Jedrzejewski & Jedrzejewska 1992; Leckie et al. 1998). In low productivity areas, with limited availability of alternative prey, human-induced subsidies may occur as the determining factor for survival and reproduction. The amount of infrastructure-induced subsidies between seasons was not investigated in this study, however, bird collisions with power lines in alpine habitats are most important in winter and spring (Bevanger & Brøseth 2004). The number of collisions between cervids and trains are in addition at their peak during the winter months (Rolandsen et al. 2015). An increased food availability wintertime in alpine habitats may increase the importance of infrastructure-caused subsidies for red foxes.

The nest experiment resulted in no predation rate. As the method was based on a successful experiment from Finnmark county (Jacobsen 2014), the lack of findings was surprising. Earlier studies on nest predation along roadsides proposed a lower predation rate of artificial nests compared to natural nests, suggested to be explained by the lack of scent, and possibly also the direct visible encounter of, incubating females (Bergin et al. 1997). However, it does not explain the complete lack of results, as most nest experiments with artificial nests has proved successful (Bergin et al. 1997; Pescador & Peris 2007; Svobodova et al. 2007). An error source could be the low number of artificial nests, as the studies above used a far larger number. However, related to these studies, a predation rate between 23 % and 76 % could be expected. A predation rate of 0 % was therefore unexpected.

Svobodova et al. (2007) did not find a higher nest predation success along roads in their study. Their suggestion was that roads might become less important in highly fragmented areas, as was the case in their study area and in contrast to mine. As their study area was exclusively in forest landscape with a higher habitat productivity, one might also expect subsidies along roads to become less important compared to alpine habitats. In another study, Pescador and Peris (2007) found a negative relationship between nest predation rates and traffic density. Road classified with high traffic density (12,499 vehicles each day) had lower nest predation close to the road, while road classified with medium traffic density (1674 vehicles each day) had higher nest predation close to the road. The lower predation rate along the road with high traffic density was suggested to be explained by the higher level of disturbance that left a narrower time frame for scavenge, as well as being in greater danger of being killed themselves. As the E6 in our study fits well with medium traffic density (1965 vehicles each day), I would expect a higher nest predation close to the E6. Further assessments of potential method faults will be considered before future nest experiments in the ECOFUNC project.

Conclusions

Human-induced subsidies along roads increase the total amount of available food. This applies to species benefiting from such subsidies, like the red fox and other generalists. Increased food availability may increase the carrying capacity, and thus the density of such species, which in turn could have negative effects for their competitors and prey. Winter survival seems to be the key factor for red foxes to establish in alpine areas, due to limited food availability. For this reason, a road’s impact on red fox survival in alpine areas will likely be strongly affected by the amount of subsidized food in winter. In this study, I suggest that the lower response time for red foxes closer to the road, was due to a higher density of red foxes along the highway. I further consider the human-induced subsidies along the European highway in Dovrefjell to be of considerable amount, as I suggest these resources to be the most reasonable explanation for the red fox attraction to the road. I conclude that roads can function as an important source of food for red foxes in years with low rodent abundance, and may increase the probability of red fox survival in areas with initially low productivity. Hence, roads are likely to be a contributing factor in driving the red fox expansion into alpine habitats.

Recommendations

Our tracking experiment gave no results, due to poor tracking conditions. Anyway, I recommend tracking experiments of generalists' movement in the context of all infrastructures in alpine regions, for a better understanding of how the infrastructure affects their way of exploiting resources in areas with low productivity.

I emphasize the need for further research to understand the full relationship between roads and generalists in alpine habitats, which could add an important basis for future management. In order to investigate the suggestion of higher red fox densities along roads, I suggest density in alpine areas to be compared between areas with and without roads.

I also recommend future studies to aim to quantify the volume of human-induced subsidies along roads in alpine habitats. Due to biases, like the potentially low persistence probability (Antworth et al. 2005), the less accurate and efficient survey by car (Guinard et al. 2012) and the actual volume of leftovers in garbage, future segments should be surveyed on foot at least once a day. In addition, one such experiment must obtain overview of the timing of litter picking along the road, so this does not occur as a source of error.

Based on my results, aiming to reduce roads' positive effect on the red fox and its expansion into alpine areas, I suggest two measures to reduce the availability of food, by: 1) more frequent removal of garbage and road-kills along the road, and 2) raise awareness on the ecological side effects among motorists who throw garbage.

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