The relative effect of intraguild predation and carcass availability on red fox (*Vulpes vulpes*) abundance by a re-colonizing wolf (*Canis lupus*) population

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Abstract

In this study the effects of intraguild predation (IGP) and increased carcass availability on red fox abundance were investigate from the re-colonising wolf population in south-eastern Norway. I conducted a field experiment with 24 artificial carcasses placed in high and low wolf-use areas to investigate the carcass utilization by red fox. Differences in red fox density were investigated by the use of red fox track data from 451 transect lines in high and low wolf-use areas. I found that there was less red fox in high wolf-use areas and that the difference was most apparent close to human impact. In remote areas far from human impact there was no difference in red density between high and low wolf-use areas. Further, the utilization of carcasses was significantly lower in high wolf-use areas than low wolf-use areas. These results strongly indicate that IGP of wolves limit red fox abundance, and that the bottom up effect of increased carcass availability do not compensate for the effect of IGP.

Introduction

Interactions between members of the predator guild may range from intraguild predation (IGP: Polis & Holt 1992) to facilitation (Selva *et al.* 2003; Wilmers *et al.* 2003a). Today, there is a strong foundation in the literature on the extent and significance of IGP (Polis & Holt 1992; Palomares & Caro 1999; Caro & Stoner 2003), both with regard to the potential of IGP to alter the behaviour (Switalski 2003; Hunter *et al.* 2007), and limit population abundance of the species exposed to killings (Krefting 1969; Berger & Gese 2007). This might in turn have strong effects on prey communities (Palomares *et al.* 1995; Crooks & Soule 1999; Sæther 1999; Terborgh *et al.* 1999).

The mesopredator (medium sized predators) release hypothesis reflects the top down effect of a large predator killing the smaller predator, manifested by an increase in the numbers of the smaller predator following large declines in the abundance of the top predator (Soulé *et al.* 1988; Litvaitis & Villafuerte 1996). However, the relative strength of IGP on the victim species is equivocal. Some studies show that the strength of top down predation is mediated by bottom up effects like the degree of fragmentation and landscape productivity (Crooks & Soule 1999; Elmhagen & Rushton 2007). Such bottom up factors are likely to be important since food availability is known to impact mesopredator densities (Lindström 1989a; Angerbjorn *et al.* 1991; Selås & Vik 2006). When top predators re-establish after years of absence, the IGP once again could cause top down effects on mesopredator populations.

Mesopredators could also benefit from top predators subsidies' such as increased carcass availability (Wilmers *et al.* 2003a). In theory however, even such a predictable and available food source, would at some point be given up by the mesopredator if the risk of encountering top predators and being killed is too high (Lima 1998; Caro 2005). On the other hand the victim species could manage to balance the risk by adjusting its behaviour (e.g increased vigilance), and thereby increase the use of this energetically advantageous food source (Switalski 2003).

The red fox (*Vulpes vulpes*) is a widespread mesopredator known to be involved in interactions with larger predators (Scheinin *et al.* 2006; Van Etten *et al.* 2007), and even killed by them, e.g. wolves (*Canis lupus*) and lynx (*Lynx lynx*) (Jedrzejewski & Jedrzejewska 1998; Helldin *et al.* 2006). The red fox is an opportunistic generalist predator and scavenger (Jedrzejewski & Jedrzejewska 1992; Henry 1996; Leckie *et al.* 1998; Elmhagen *et al.* 2002), and has the ability to shift between different food sources depending on the availability (Kjellander & Nordstrom 2003; Dell'arte *et al.* 2007). In spite of this flexibility, a reduced availability of prey may limit the density of red fox populations (Lindström 1989a; 1994a; Barton & Zalewski 2007), and under harsh climatic conditions in the winter season, shortage of prey might be compensated for by an increased use of carcasses (Cagnacci *et al.* 2003; Selås & Vik 2006). During the period when top predators were eradicated from Norway and Sweden, the red fox population experienced a large population increase. This has been attributed both to the mesopredator release effect (Elmhagen & Rushton 2007), and to an increase in ungulate numbers and thereby an increase in available carcasses in snow rich-winters (Selas and Vik 2006). In southern Scandinavia the abundance of red fox is closely linked to human impact factors (Elmhagen & Rushton 2007), with the highest densities of red fox occurring in fragmented areas with agricultural land and human settlement (Kurki *et al.* 1998; Kauhala *et al.* 2006).

Today wolves from the Finnish-Russian population have re-colonised as top predators in south-central Scandinavia (Wabakken *et al.* 2001; Vilà *et al.* 2003; Linnell *et al.* 2005), with unknown impact on the red fox population. As the red fox is considered to be a keystone predator in the Scandinavian boreal forests (Angelstam *et al.* 1984; Lindström 1989b), the re-colonisation of a top predator may contribute essentially to shaping the dynamics of the boreal forest ecosystem. From the mesopredator release hypothesis and increased carcass availability hypothesis two contradicting predictions can be made for the effect of re-establishing wolves on the red fox population dynamics; either 1) red fox density decreases due to the effect of IGP from wolves, or 2) increased use of carcasses by red fox causes a positive response of red fox density.

In this study, I aimed to investigate the relative impact of the two effects on the red fox population in south-central Norway. The question was approached at two levels. First, I conducted a field experiment to investigate differences in carcass utilization between high and low wolf-use areas. Then, I analyzed landscape scale data on red fox abundance, to investigate the numerical responses to wolf re-colonization. I predict that the red fox show increased use of carcasses in high wolf-use areas. However, I don't expect this bottom up effect to be strong, and I predict that the red fox suffers from IGP and show decreased densities in high wolf-use areas.

Methods

Study area

The study area was located in south-eastern Norway confined by the borders of Hedmark county and a northern limit at latitude N61°51′ (Figure 1). The northern boundary was set on basis of topography and suitable wolf habitat: north of the border the landscape is more alpine, with no known resident wolves. The total study area of 20300 km^2 was part of a wildlife monitoring project by The Norwegian Association of Hunters and Anglers (NJFF), and had forest areas with both high and low wolf-use. Boreal coniferous forests cover most of the study area, with valleys (down to 200 m a.s.l) and mountain areas (up to 1000 m a.s.l) in the north, and a lower average altitude with hills and slopes in the south. Almost all agricultural land is located at low altitudes in proximity to the valley bottoms, with the areas most intensively used for agriculture found in the south of the study area. The forests are intensively managed for commercial timber production with a high density of gravel roads and a mosaic of clear-cuts and stands of varying age classes giving a semi-wilderness landscape (Hamre 2006). The climate is typically continental and the normal average winter temperature (November – March) is – 7°C with an average monthly precipitation of 45 millimetres (The Norwegian Meteorological Institute; www.met.no). The human population density averages 16 km^{-2}, but is generally < 1 km^{-2} in the high wolf-use areas (Wabakken *et al.* 2001). All main prey species of wolves in Scandinavia are present, but the wolf diet consists almost exclusively of moose (*Alces alces*); 95% of the consumed biomass in the study area (Pedersen *et al.* 2005). Since 1998 wolves have been present in the study area in a few packs and scent marking pairs (Sand *et al.* 2007). The estimated wolf population size was 19-23 individuals in the 2006-2007 winter season, where 12-14 individuals were split into two packs and one scent marking pair (Wabakken *et al.* 2007).

Carcass utilization experiment

Selection of areas and stations

I sampled carcass utilization by red fox at four stations in each of three different wolf pack territories (hereafter termed high wolf-use areas) and at four stations in each of three different control areas with no known wolf territories (hereafter termed low wolf-use areas), giving a total of 24 stations investigated. The selection of three high wolf-use areas were based on all known wolf pack territories within the study area from 2003 to 2006, and were defined as the area covered by a wolf pack or a scent marking pair continuously for the last 2 years or more. The territory borders were defined by a Minimum Convex Polygon (MCP) of the border points of the annual winter territories, since the territory borders changed between years. The territory borders were provided by the Swedish-Norwegian monitoring project of wolves on the Scandinavian Peninsula (information about the monitoring: Wabakken *et al.* 2001). In order to select three low wolf-use areas, MCPs of the same size and shape as the wolf territories were placed on maps of low wolf-use areas. I made adjustments to the borders where necessary to follow natural terrain obstacles to the wolves, such as large rivers or lakes.

The 4 stations in each of the tree high and low wolf-use areas were randomly selected, but with the limitation that 1) the stations had to be more than 3 kilometres away from each other, and 2) more than 500 meters away from snow-cleared roads. This was done to reduce the probability of attracting the same fox to two different stations. The minimum distance between stations was chosen based on red fox home range size (Overskaug *et al.* 1995; Frafjord 2004; Kauhala *et al.* 2006), and the distances to snow cleared roads was chosen to avoid human disturbance.

The surrounding area of the stations might differ in suitability for red fox, and may be confounded with red fox utilization of carcasses. In order to compare the degree of human impact and habitat types between high and low wolf-use stations I created a 3 km radius buffer around each station (n = 24, overlapping buffers were merged: Figure 1). Within the buffers a total of 1000 points were randomly distributed and I measured distances to human impact factors and type of habitat at each point by using ArcGIS 9.2 (Environmental Systems Research Institute, Inc. ESRI). Human impact was defined as the distances to nearest agricultural land, residential house, paved road, gravel road and cabin. Habitat type was classified as forest, bog, open area (mostly mountains), and water (lake or river). I found no difference between high and low wolf-use stations in relation to human impact (all $p > 0,995$) or habitat type (all $p > 0.600$) and thus assumed that the variation did not bias the results. The maps were provided by the Norwegian Mapping and Cadastre Authority.

Experiment

Carcass utilization was investigated by the use of artificial carcasses (bait) to attract red fox during winter conditions (November-December 2007). The bait consisted of entrails and meat from hunted moose, frozen in 20 kg blocks. Bait was allocated at the same time at two different stations in a high wolf-use area and at two stations in a low wolf-use area. The four baits allocated simultaneously were monitored for 5 consecutive days by sensor triggered digital cameras (CamTrakker Digital 6.0/CamTrak South, Inc). The cameras were modified with improved insulation and external batteries and a strong strobe flash secured clear photographs at night. The cameras were programmed to take one picture every 5th minute when activity at bait triggered the infra-red sensor. All photographs were time and date stamped. In addition red fox tracks within radii of 10 metres and 100 metres from the station were recorded at the end of the 5 days period. This was done because preliminary tests revealed that red fox could be present near by the station, but not close enough to be captured by the camera. In addition this registration could give indications on the behavior around the station. This was particularly apparent once pieces of bait were spread out by scavengers. The registration of red fox tracks was also done to reduce potential bias caused by camera malfunction.

I repeated the monitoring after the 5 days period at four new stations, until all 24 stations were investigated. The tracking conditions were good throughout the experiment and it was possible to classify presence and absence of red fox tracks both at 10 m and 100 m distances from all stations. Human disturbance was not observed at any station, and all stations were included in the analysis of tracks.

The cameras were not fully operational at three stations (1 in high and 2 in low wolf-use areas). In addition there were very few photographs of red foxes ($n = 6$). To handle this low sample size I classified of the photograph data as either presence or absence of red fox at the station (i.e. at 0 m from the station), resulting in data of presence and absence within three distances for the analysis (i.e. 0 m from photo, 10 m and 100 m from tracking).

Numerical responses

The analysis of a potential numerical response to wolf re-colonisation was based on data of red fox tracks from the wildlife monitoring project by The Norwegian Association of Hunters and Anglers (NJFF). Inside the study area a total of 451 fixed transect lines of 3 kilometres length were inspected once each winter (March-April) from 2003 to 2006 (Figure 2). The field personnel consisted mainly of volunteers, such as local hunters. Not all transect lines were inspected every year (due to new lines being added during the project or bad tracking conditions), giving a total of 1401 observations. The annual MCPs of winter territory borders of wolves (see above) were used to classify each transect line as either being in a low wolf-use area or in a high wolf-use area. In total 238 (17%) observations on 137 (30%) transect lines were in a high wolf-use area. A red fox density index was calculated by number of tracks crossing the transect line per kilometre divided by the number of days since last snowfall (track/km/day).

Statistical analyses

I used generalized linear models (GLM) to analyse the response of red fox to wolf re-colonisation. In the analyses of the carcass experiment I used a binomial error term and logit link function in the model to compare the probability of red fox presence between the high and low wolf use areas at the different distances form the station (i.e. 0 m, 10 m and 100 m). In the analyses of the numerical response I used a poisson error and log link function in the model. The transect lines were randomly distributed in forest habitats in the study area with varying distance to human impact. I expected that distance to human impact could be confounded with the presence of red fox (see e.g. Kurki *et al.* 1998). To correct for this I included human impact as a covariable in the models. The human impact variables used were the same as for the carcass utilization experiment. Due to the correlation structure between the human impact variables (Table 1), I conducted a principal component analysis (PCA) and used the first two components (PC 1 and PC2) as an index of human impact. The first two ordination axis explained a total of 72.9% of the variation (PC1 = 49.3% and PC2 = 23.6%). The score showed that PC1 was associated with agricultural land (r = 0.849), residential houses (r = 0.836) and paved roads (r = 0.832), wile PC2 was associated with cabins (r = 0.791) and gravel roads (r = 0.602). The correlation matrix was appropriate to use since all measurements had the same units and scale (Quinn & Keough 2006), and the variation in mean values of the variables reflect the biological important differences in relation to red fox density (long distances in PC1; the important variables, and short distances to PC2; the less important variables). Six observations were excluded because of outlying high values of PC1 (i.e. PC1 >7), yielding a total of 1395 observations with a PC1 < 5 for the analysis. I used wolf-use (high and low), PC1, PC2, years (4 levels; 2003-2006), and all two-way interactions as fixed factors in the full model. Since the transect lines were investigated repeatedly by year, year nested within track line was used as a repeated factor. I based the final model selection on the significance of each variable (Type III test of fixed effects, P < 0.05) using a backward procedure.

In order to investigate to which extent the effect of wolf presence changed with time, I also conducted a set of follow-up analysis. From the dataset I selected the transect lines that had changed from being a low wolf-use area to being a high wolf-use area during the 4 years period. Each line was classified by the number of years with wolf presence (e.g. low wolf-use = 0, first year with high wolf-use = 1, second year with high wolf use = 2). Only two transect lines had a 3rd year with wolf presence, and were excluded, resulting in a total of 30 transect lines that changed from 0 to 2 years of presence for the analysis. I used the red fox density index (DI) in year 0 to estimate the change after 1 and after 2 years of wolf presence $\log(DI_{t+1}) - \log(DI_t)$ and $\log(DI_{t+2}) - \log(DI_t)$ respectively. This normally distributed growth rate index was used to compare the development of tracks between years (3 levels; 2004-2006) and year with wolf presence (2 levels; 1 year and 2 years) in a mixed model with line as random factor (all analysis were performed in SAS 9.1; Institute, Inc., Cary, NC. All mixed models were done by using the GLIMMIX Macro in SAS 9.1).

Results

Carcass utilization

According to the carcass weight loss and recordings of red fox tracks by the station a total of 17 of the 24 baits were not scavenged on. The probability to scavenge on a bait was higher in low wolf-use areas (11 out of 12) than in high wolf-use areas (6 out of 12; $\chi^2_{1,4} = 5.46$, $p = 0.020$). Two different red foxes where photographed at stations both in high and low wolf-use areas. However, the odds to observe red fox at 10 m distance from the station was 15.0 times (95% C.L. = [1.9, 115.8]) higher in low than in high wolf-use areas ($\chi^2_{1,4} = 7.021$, $p = 0.008$). At 100 m radius from the station there was red fox tracks by all stations in low wolf-use areas, while only at 25% (95% C.L. = [10%, 51%]) in high wolf-use areas ($\chi^2_{1,4} = 7.434e{+}13$, $p<0.0001$; Figure 3).

By analysing only the stations were I know there has been a red fox present in at least 100 m distance 67% of the baits in high wolf-use areas had red fox present also at 0 m, compared to only 17% in the low wolf-use areas. This contrast was, however, not significant ($\chi^2_{1,4} = 2{,}525$, $p = 0{,}112$).

Numerical response

Red fox density was significantly associated to the interaction between the presence of wolves and human impact described by the first principal component ($F_{1,943} = 5.00$, $p = 0.026$; Table 2; Figure 4). In general there was less red fox in high wolf-use areas than in low wolf-use areas. The interaction effect showed that the difference in red fox density between high and low wolf-use areas was most apparent in areas close to human impact, i.e. were the red fox density also was highest. In addition red fox density varied considerably between years ($F_{3,943} = 23.62$, $p < 0.0001$; Table 2; Figure 3).

There was no correlation between the growth rate of red fox and presence of wolves ($F_{1,28} = 0.00$, $p = 0.968$). In accordance with the density model year was a significant predictor of the growth rate ($F_{1,28} = 9.75$, $p = 0.0006$; Table 3).

Discussion

This study strongly indicated that wolves significantly limited the red fox density, but the strength of the effect depended on the distance to human impact. The negative effect on red fox density was most apparent in close distance to human impact factors, factors associated with high density of red fox in low wolf-use areas. However, wolf presence did not change the red fox density significantly within the two years timeframe investigated. Furthermore, in contrast to the prediction the red fox did not utilize carcasses in high wolf-areas at a higher rate, which minimizes the possibility of bottom up effects of wolf presence.

To my knowledge, this is the first time large-scale effects of a top predator re-colonisation have been found on mesopredator densities in Scandinavia. One study of Helldin *et.al.* (2006) points in the same direction and discuss the potential of limiting effects by Lynx re-colonisation on red fox populations. My study indicates that the density of red fox in low wolf-use areas is almost twice as high as the density in high wolf-use areas in close distance to human impact. These findings are in support to the mesopredator release hypothesis (Soulé *et al.* 1988; Crooks & Soule 1999).

In the Elmhagen (2007) study the mesopredator release effect was mediated by the agricultural expansion, linking the effect of top predators to productive areas. Although on a much smaller scale the findings in my study supports the assumption that the effect of top predators depend on landscape productivity. In my study the effect of wolves decreased with increasing distance to agricultural land, indicating that both bottom up effects of landscape productivity and top down effect of wolf presence affect red fox densities.

In addition my study supports the common understanding that red fox abundance is a matter of distance to productive areas like agricultural land (Kurki *et al.* 1998; Kauhala *et al.* 2006), and the fact that wolves kill red fox (Jedrzejewski & Jedrzejewska 1998; Palomares & Caro 1999). However, the interaction of the two effects (Wolf use x PC1) implies that the encounter rate of the two species plays an important role. In the Helldin (2004) report he found that red foxes stayed more in the vicinity of agricultural land and resident houses after lynx establishment, but he found no spatial separation between the two species. A spatial separation between red fox and wolves is more likely. The wolf territories in Scandinavia have lower density of agricultural land, built up areas (>200 inhabitants and <200m between the buildings), and roads than areas outside wolf territories. In addition wolves avoid areas with a high degree of human activity (Karlsson *et al.* 2007). As a consequence, the territory borders often make a boundary towards human impact. The borders follow valley bottoms, rivers and large roads, where almost all agricultural land and human settlement is found. Hence, a high number of encounters between wolves and red fox are likely to take place in the border of wolf territories as wolves patrol their area. In addition wolf prey density could play an important part. In Hedmark County moose aggregate in winter browsing areas (November-March) in the valley bottoms and the aggregation effect is most evident in areas with presence of wolves (Gundersen 2003). The high densities of wolf prey along parts of the territory borders increases the probability of wolves encountering red fox.

When Selås & Vik (2006) found a delayed effect on red fox abundance after the eradication of top predators they argue that this is due to the increase in ungulate numbers and subsequently available carcasses in snow rich winters. It is not likely to find the same relation today because the ungulate populations are almost exclusively regulated by hunting (e.g. 95% of the deaths in moose populations: Pedersen *et al.* 2005) which results in very few carcasses available, even in snow rich winters. In addition their study was in absence of top predators, making the consumption of carcasses less risky to the red fox. However, when wolves re-establish in Hedmark County today they have to establish in areas of heavily managed moose populations. Due to the high kill rates (number of moose killed in wolf territories averages 100-130 a year: Sand *et al.* 2007) the number of moose shot by hunters might be reduced, and the main cause of deaths could alter from hunting towards wolf kills. This provides a more predictable food supply for the scavengers, and could be important for the red fox survival in harsh winters. When Wilmers (2003b) investigated this effect he found a large variation between species in the ability to utilize wolf-killed and hunter-killed carcasses. The ability was depending on the characteristics of the species in relation to the dispersion of the carcasses. When he found that wolf subsidises scavengers (Wilmers *et al.* 2003a), the effect might vary in strength between areas and species. One possible explanation to the lack of bottom up effect of increased carcass availability in the present study might be because most red fox (adults) are territorial and the actual subsidies within their territory is too low to make an effect. On the other hand red foxes with home ranges connected to a moose aggregation area could benefit more than others due to the high rate of wolf-kills in this part of the territory. The results from the carcass experiment do not support this prediction; since the red fox do not show an increased use of carcasses in high wolf-use areas. In addition the moose aggregation areas probably have an even higher number of encounters between wolf and red fox than the areas investigated in the experiment.

In a monitoring project on carcass use in eastern Poland it was found that the red fox preferred kills of predators (mainly wolves) rather than dead ungulates (Selva *et al.* 2005). In my experiment I used artificial carcasses comparable to dead ungulates, and this could have biased the results if the red fox in high wolf-use areas systematically follow wolves to utilize their kills. This is hardly the case over long distances since the red fox is territorial, and at least not to an extent where it affects red fox abundance.

From the experiment I was not able to estimate any foraging behavioural aspects that could explain the difference in carcass utilization. However, the placement of stations in the experiment was limited by the minimum distance to gravel roads (> 500m). This resulted in a placement of stations relatively far from human impact (e.g. the mean distance to agricultural land was 2.3 ± 1.3 km (± SD). In these remote areas the red fox density was less affected by wolf presence than in areas closer to human impact. This opens up to the possibility that differences in density might not be the single explanation. Some sort of foraging behavioural aspects is also likely. This assumption is strengthened by the trend found in the change of presence from 100 m to 0 m between the high and low wolf-use areas.

My analyses did not reveal when wolf presence significantly affected the red fox density. The number of lines investigated was only 30, and none of them had more than 2 years of wolf presences. The overall effect of wolf presence came mainly from lines that already were in a high wolf-use area when the monitoring started. Some of these lines have had wolf presence for more than 20 years (Wabakken *et.al* 2001). This indicates that the yearly effect is relatively weak and future monitoring should take this into account by placing more lines into areas were wolves are allowed to establish.

In the Elmhagen (2007) study of historical data (1828-1917) both Eurasian lynx and wolves were included as the top predators behind the mesopredator release effect. In Hedmark County lynx are present both the high and low wolf-use areas (Odden *et al.* 2006). When I found an effect by another single top predator in this study, this could be an additional effect to the lynx killings. In such a situation the potential of cascading effects is obvious (Palomares *et al.* 1995; Crooks & Soule 1999; Sæther 1999; Terborgh *et al.* 1999). This is likely since the red fox is considered a key stone predator in the boreal forests and even small changes in red fox abundance could affect prey numbers (Lindström *et al.* 1994b; Smedshaug *et al.* 1999; Kjellander & Nordstrom 2003). The re-colonising wolves could cause cascading effects, and in concert with lynx the effect on red fox prey species could be significant.

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Tables

Table 1. Correlation matrix of the distances to human impact variables. The distances were measured from the starting point of each track line (n = 451) to the nearest variables (n =5).

	Agricultural land	Paved road	Gravel road	Cabin
Paved road	0,72			
Gravel road	0,22	0,21		
Cabin	0,10	0,05	0,32	
Residential house	0,60	0,58	0,34	0,19

Table 2. Parameter estimates of the log regression model estimating red fox density. From the full model backward selection ($p < 0.05$) was used to exclude non significant factors.

Variable	Class	Estimate	SE
Intercept		-1.2762	0.1042
Wolf	0	0.3545	0.0899
Wolf	1	0	
PCR1		-0.0297	0.0522
Year	2003	0.1749	0.0946
Year	2004	0.2711	0.0884
Year	2005	0.6501	0.0828
Year	2006	0	
PCR1*Wolf	0	-0.1300	0.0581
PCR1*Wolf	1	0	

Table 3. Parameter estimates of the growth rate model used to estimate the effect of wolf presence.

Variable	Class	Estimate	SE
Year	2004	–0.1083	0.1457
	2005	0.0840	0.0624
	2006	–0.1726	0.1121
Number of years with wolf	1	–0.0681	0.0721
	2	–0.0630	0.0961

Figures

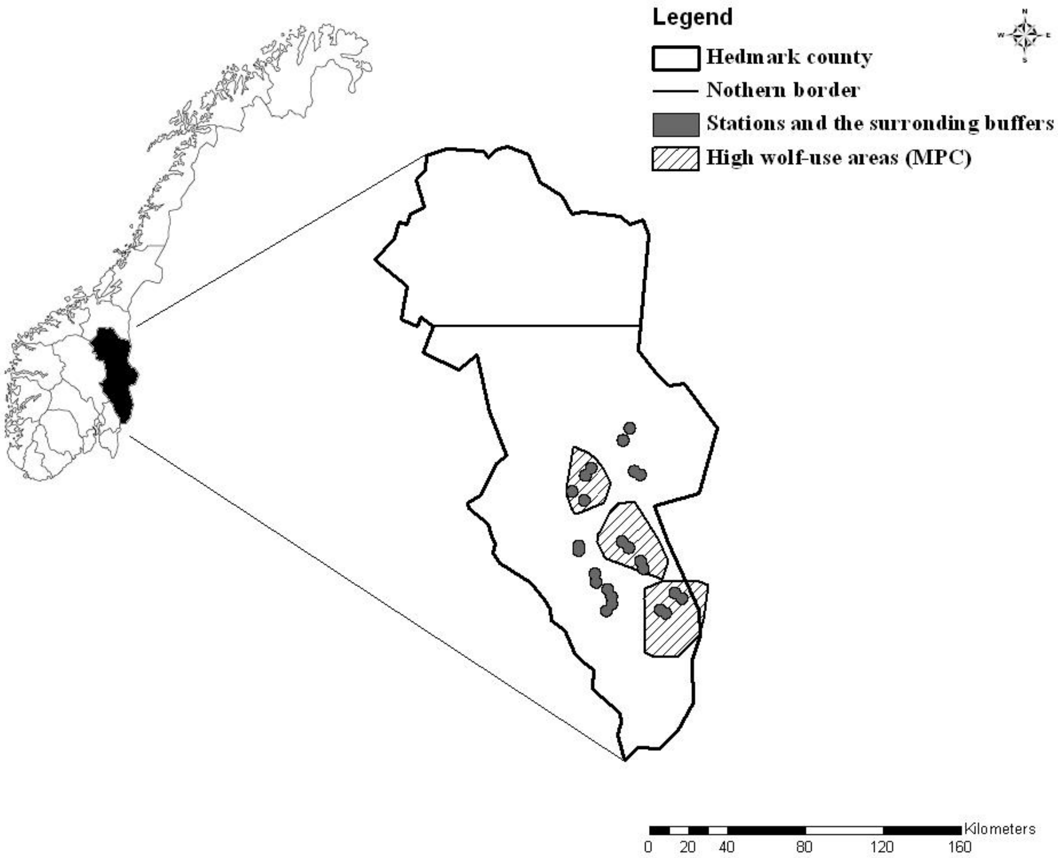

Figure 1. Map of the study area and the location of the carcass utilization experiment. In the experiment the wolf territory borders were used as high wolf-use areas (MCP). The buffers outside high wolf-use areas are in low wolf-use areas (MCP)

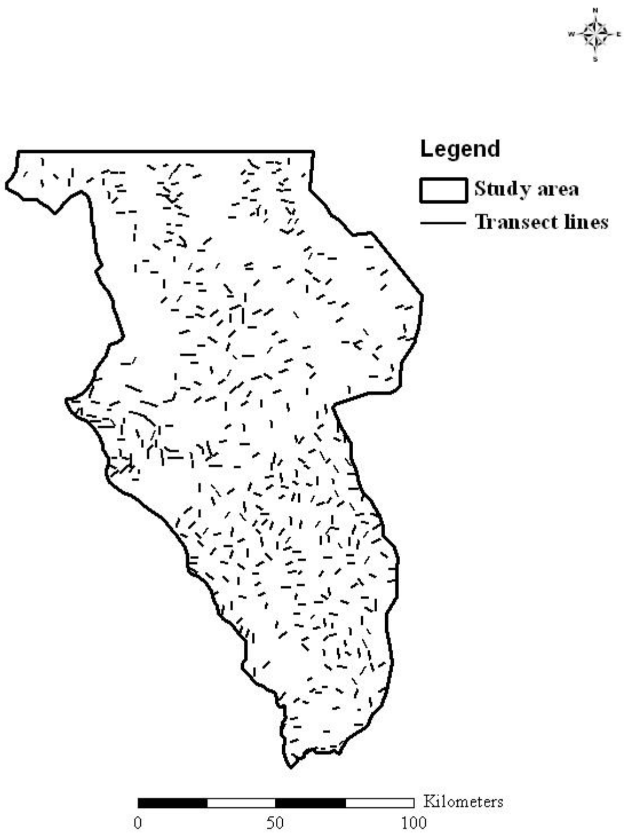

Figure 2. Map of transect lines (n = 451) used to estimate red fox density. Each line is 3 km long.

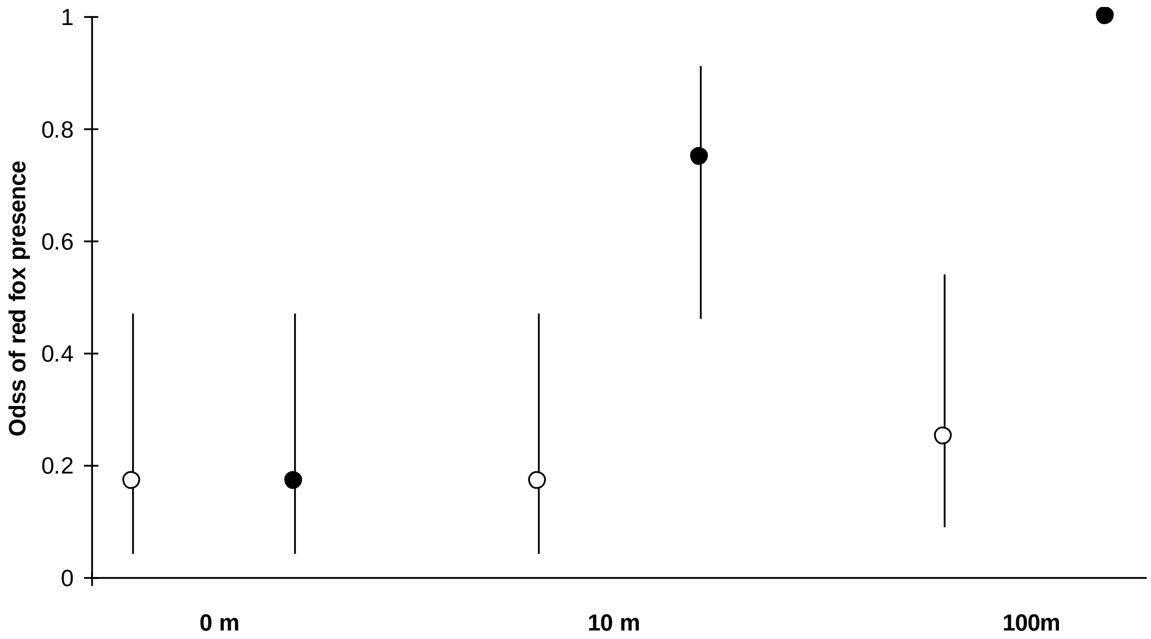

Figure 3. The odds (estimate, 95% CL) to observe red fox in high and low wolf-use areas at 0 m, 10 m and 100 m distance from the stations. The hollow circles are high wolf-use areas, the filled circles low wolf-use areas.

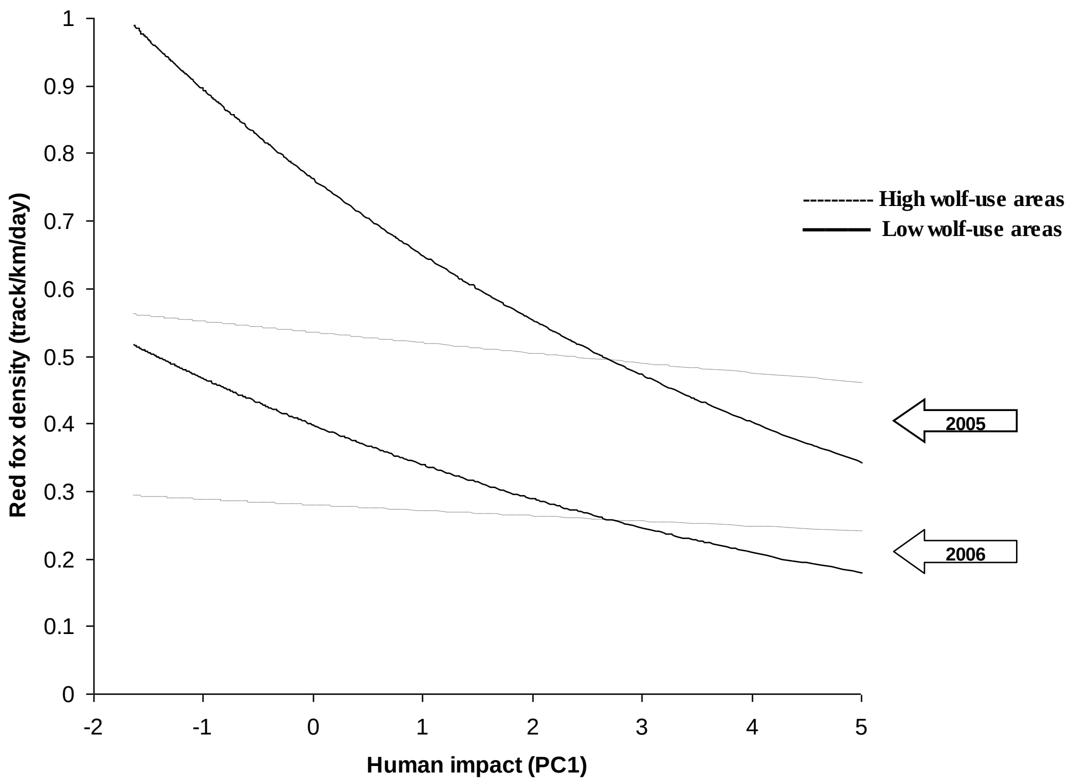

Figure 4. The model prediction of the effect of the interaction between wolf use and human impact on the red fox density. Human is defined by the first principal component (PC1) and is related to agricultural land, resident houses and paved roads. The human impact scale (-2 to 5) correspond to distances from human impact, e.g. for agricultural land in the range from 0 meters to approximately 5000 m. Only the year with the highest density (2005) and the year with the lowest density (2006) are shown.