Patterns of reproduction and body condition in Red fox (*Vulpes vulpes*)

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Master Thesis

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2014

Applied ecology

Lakselv, May 16, 2014

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Abstract

Scandinavian red fox populations are commonly considered to be driven by the cyclicity of small rodent populations. It was recently suggested that the red fox' general dependency of voles is becoming less pronounced due to larger availability of alternative food resources. Several factors has been suggested to increase red fox' carrying capacities. In my study I explored current patterns in age, sex, reproduction, body condition and morphometrics in relation to abundance of food and population densities. I also investigated possible selective effects of hunting by baiting.

My study area consisted of six municipalities in Hedmark County, Norway, and comprised significant divergences in landscape productivity and altitude. I autopsied 106 red foxes killed between January and April, 2012.

The majority of red foxes autopsied were shot at bait hunting stations. Most of them were killed during March and the sex ratio was not different from 1:1. A large proportion of the foxes were juveniles and there were more juvenile males than females. Males were significantly heavier and larger than females, but with no differences in weight and length between adults and juveniles.

Bait hunting tended to select for individuals with high body condition and the average number of embryos were higher in individuals shot outside bait stations. Females had a significantly higher body condition than males and barren females a higher body condition than non-barren females. Body condition in males was positively correlated to abundance of small rodents the previous autumn. The distribution of adult females decreased with increasing fox abundance.

Autopsied red foxes were mostly in average condition with low variation in body fat. The relatively small proportion of reproducing females, along with an increased body condition of males shot at bait stations compared to other hunting methods, indicates a food limited fox population.

Furthermore, to understand the potential management options possible to reduce the threats to other species, and the potential cascade effects by promoting new assemblages of species in different ecosystems, I stress the importance of continued monitoring of the red fox.

1. Introduction

The relationships between body condition, reproductive success and food availability in vertebrates are complex and not easily disentangled. Body condition in mammals refers to an individual's energetic state. Energy is usually stored as fat reserves and the amount of fat that an individual carry is directly related to its fitness (Schulte-Hostedde et al. 2001). Individuals with larger fat reserves are therefore likely to have better fasting endurance and thus higher probability of survival than individuals with smaller reserves (Millar & Hickling, 1990). Body condition also affects reproductive attributes. In female mammals, reproductive traits such as litter mass and litter size increase with body condition (see e.g. Dobson & Michener, 1995; Tannerfeldt & Angerbjörn, 1998).

Scandinavian red fox populations are commonly considered to be driven by a bottom-up process, in other words by the availability of food (See e.g. Englund, 1970). Food availability affect their reproductive success, body condition and survival (Englund, 1970). Hence, these parameters respond in large to the cyclicity of small rodent populations (Englund, 1970; Lindström & Hörnfeldt, 1994; Kjellander & Nordström, 2003). Lindstöm (1983, 1989) described positive correlations in growth rate, ovulation rate, mean litter size and adult spring densities with increasing vole densities in Sweden. Furthermore, these correlations appeared to be more pronounced in northern latitudes (see Englund, 1970; Elmhagen & Rushton, 2007). Recently, Selås & Vik (2006) suggested that the red fox' general dependency of voles is becoming less pronounced due to larger availability of alternative food resources in winter. The availability and abundance of food in winter has been described to be limited by the winter's severity, that is; low temperatures, deep snow, and long durations of snow cover (Barton & Zalewski, 2007).

In the first half of the 20th century, the Scandinavian red fox population was relatively low, but during the 1940's, it increased considerably. The red fox population size remained high from 1945 throughout 1975, followed by an epizootic of sarcoptic mange in the late 1970's and 1980's (Selås & Vik, 2006). The reduction in red fox during the sarcoptic mange and several eradication experiments has revealed the red fox' role as a keystone predator. From this, the red fox showed positive responses through intraguild predation and competition on prey species such as mountain hares (*Lepus timidus*; Danell & Hörnfeldt, 1987; Marcström et al. 1989), tetranoids (*Tetranoidae* spp.; Marcström, Kenward & Engren, 1988; Kauhala, Helle & Helle, 2000) and roe deer (*Capreolus capreolus*; Lindström, et al. 1994) as well as goshawk (*Accipiter gentilis*; Selås, 1998) and pine marten (*Martes martes*; Lindström et al. 1995; Smedshaug et al. 1999). Also, the recently described expansion of red fox into northern latitudes and higher altitudes, has led to a high interspecific competition between red fox and arctic fox (*Alopex Lagopus*), limiting the southern distribution of the arctic fox population (Hersteinsson & MacDonald, 1992; Elmhagen et al. 2002; Tannerfeldt et al. 2002; Herfindal, et al. 2010; Killengreen, et al. 2011).

Hersteinsson & MacDonald (1992) suggested that regional warming positively affected red fox populations, through a general increase in food availability due to expanded boundaries in to northern latitudes and higher altitudes. Furthermore, increased supplies of anthropogenic food items (Serafini & Lovari, 1993; Panek & Bresinski, 2002) due to contemporary consumerism could lead to increased carrying capacities (Hjeljord, 1980). Furthermore, a general increase and expansion of ungulate populations, may produce larger amounts of exploitable ungulate offal (Jedrzejewski & Jedrzejewska, 1992; Smedshaug & Sonerud, 1997; Selås & Vik, 2006). Moreover, the reestablishment of the Scandinavian wolf (*Canis lupus*) population has resulted in reduced seasonal variations in biomass from moose carcasses, and a higher carcass availability in spring which in term may lead to an increase in red fox survival and reproduction (Wikenros, et al. 2013). Arable, as well as silvicultural clear cuts may also positively influence demographic traits and individual performance in red fox as small rodents and voles are more abundant in these habitats (see e.g. Kurki, et al. 1998; Savola, et al. 2013).

Most of the research conducted on the red fox in Scandinavia had been completed by the end of the 1980s. In light of the recently suggested development in carrying capacities, it is reasonable to assume that several factors influencing individual performance and body characteristics may have changed during the last decades. In order to predict the future development of the red fox, it is important to improve our understanding of current factors that may affect their survival and reproduction.

The aim of my study was thus to investigate recent patterns in reproduction, body morphometrics and body condition of the red fox in a highly diverse environment in south-eastern Norway, comprising a considerable altitude gradient, with significant divergences in landscape productivity and habitat types. By conducting necropsies on red foxes supplied by Hedmark County hunting and fishing association, I obtained information about body condition, body fat, and reproduction parameters as well the sex and age of the red foxes. I will try to document and explain patterns in these individual characteristics related to sex and age structures as well as availability of rodents, fox population density, the relative presence of households and possible selective effects of different hunting methods.

2. Material and methods

2.1 Study area

My study was conducted in Hedmark County, south-eastern Norway, in the municipalities of Engerdal, Trysil, Åmot, Elverum, Stange and Hamar (61°15´N, 11°30´W; Figure 1). The municipalities were situated in a north-south gradient, comprising highly productive agricultural areas in the southern region, which gradually turned in to poor alpine areas with low productivity in the northern region. With a total land area of approximately 8300 km^2, ranging in altitude from 120 to 1460 meters above sea level, the study area covered a wide range of habitats, predominantly consisting of boreal coniferous forest (68%; Moen, 1998; Norwegian forest and landscape institute, 2011). Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated the forest, with scattered occurrences of Birch (*Betula* spp.). Most of the coniferous forest had been logged and replanted through the last 200 years, creating a mosaic pattern of even aged stands (see e.g. Aasetre & Bele, 2009).

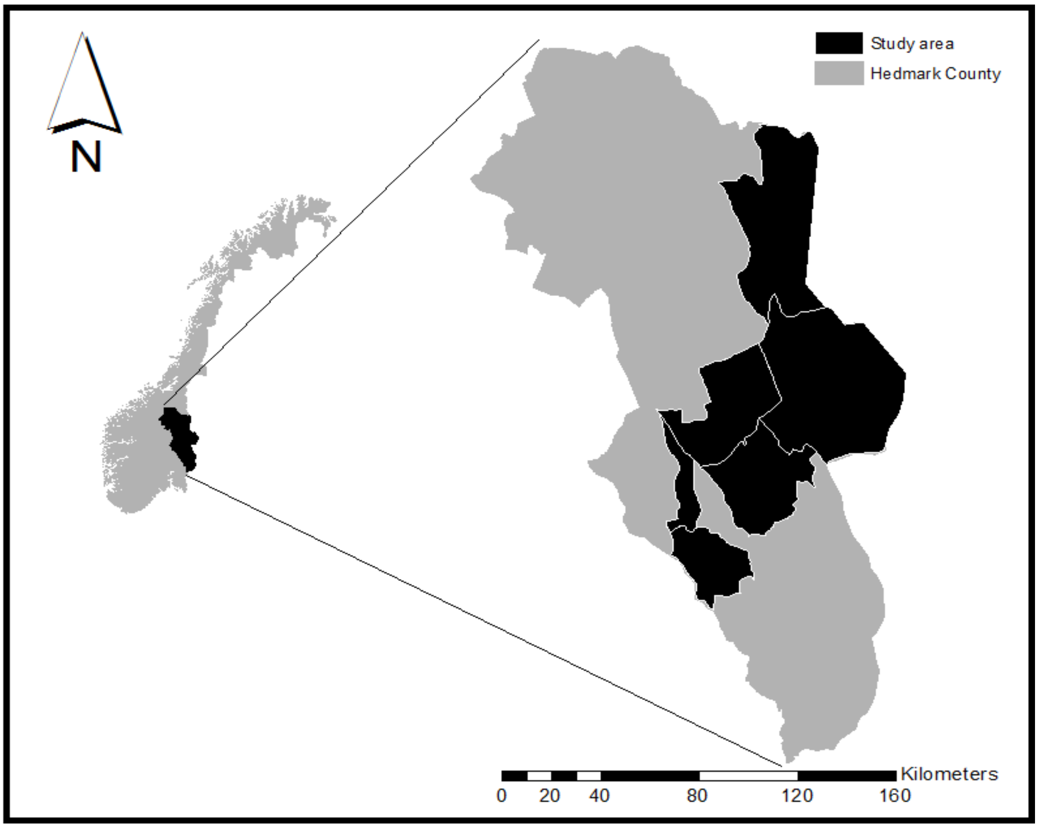

Figure 1 Map of Hedmark County with the study area colored black

Both free-ranging domestic sheep (*Ovis aries*) and semi-domestic reindeer (*Rangifer tarandus*) were present in the study area. Sheep was present in all municipalities, while reindeer only in Engerdal municipality. Moose (*Alces alces*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) were all present throughout the study area. In 2011, approximately 2750 moose, 15 red deer and 130 roe deer were killed during hunting within the study area (Statistics Norway, 2012), leaving considerable amounts of exploitable offal (Jedrzejewski & Jedrzejewska, 1992; Smedshaug & Sonerud, 1997; Selås & Vik, 2006). Mountain hare (*Lepus timidus*) forest grouse (*Tetraonid* spp.), and voles (*Arvicolidae* spp.) were common species of prey found throughout the study area. Lynx (*Lynx lynx*) was present throughout the study area, while wolf (see Wabakken et al. 2012), wolverine (*Gulo gulo*) and brown bear (*Ursus arctos*) were primarily found in the north and eastern parts.

Anthropogenic food items was a potential source of nutrition (Serafini & Lovari, 1993; Panek & Bresinski, 2002; Selås & Vik, 2006; Balestrieri, Remonti, & Prigioni, 2011), as all of the municipalities had human settlements. The human population density decreased with increasing latitude, encompassing densities of 86 people pr. km^2 in the southernmost municipality and 0.7 people pr. km^2 in the northernmost municipality (Statistics Norway, 2012b).

2.2 Data collection

Through the project "På sporet av rødreven" ("Tracking the red fox"), managed by Hedmark County hunting and fishing association, I obtained 106 red fox carcasses during the winter of 2012. All red foxes were killed with rifles or shotguns using seven different hunting strategies; shooting at a baits, chasing with dogs, shooting at dens, hunting with game calls, flushing with people, baited box-traps and stand hunting, respectively (see Table 3).

I conducted necropsies on all specimens to acquire information about body measurements and body fat indices for both sexes. Reproduction parameters were collected only for females. All collected samples from the necropsies were frozen at -20°C until further analysis. Not all measurements were possible to obtain for each individual because of damages from hunting or advanced decomposition.

2.2.1 Exterior body

Eleven exterior body measurements were made for each individual; Sex, body weight, length, width and circumference of the head, circumferences of neck and chest, body length, tail length, total length (body and tail) and length of the rear leg. Nine individuals were already skinned by hunters and therefore not measured. I measured the weight to the nearest decigram using a spring scale whilst a measuring tape and slide gauge were used to measure the length-, width- and circumference parameters down to the nearest millimetre.

2.2.2 Body fat

For all specimens, I visually assessed the amount of fat surrounding the kidney, mesenteries, pericardium and cardiac. The assessment of fat surrounding the spine was done by palpation between vertebras of the thoracic curve without removing the fur. Each assessment was scored on a scale of 1 (no fat) to 5 (totally covered by fat). See further details in (Cavallini, 1996).

2.2.3 Reproduction

The reproductive organs were collected from all vixens; reproductive tracts including the ovaries were cut at the cervix. The uteri were visually examined for embryonic swellings. Embryos were counted, and afterwards sectioned and opened longitudinally along with reproductive tracts without embryonic swellings. Subsequently, all placental scars were counted and scored on a color scale from 1 (barely visible/light grey) to 6 (distinct/almost black). Dark, uniformly distributed scars were considered as a measure of litter size at birth the previous mating season (Englund, 1970; Lindström, 1981, 1994).

2.2.4 Age

The lower jaw was collected from all specimens. If the mandibular canines were damaged, I collected the upper jaw instead. I carefully extracted the canine tooth from the jaw using forceps, or by hand. The root of the canine was then longitudinally ground down to approximately half its thickness using a grinding machine, and later smoothed by hand using sandpaper (coarseness 400). The prepared canine tooth was examined under a stereoscopic microscope at 16x magnification. When studying the cross section of the root I counted the number of dark lines (*cementum annuli*), representing years since birth. The method is further described in (Roulichová & Anděra, 2007). In Swedish land areas located at the same latitude as Hedmark County the assumed average birth date of red fox litters is *medio* April (Lindström, 1987). Based on my observations of embryo size in females shot in April, I assumed births in Hedmark County to occur a few weeks later. I could thereby calculate the age of the specimens simply by adding the months between date of birth and date of death to the previously counted *cementum annuli*.

2.2.5 Abundances of rodens, human population and red fox

Rodent abundance data from the autumns of 2010 and 2011 were supplied by "Rypeforvaltningsprosjektet" (Andersen, et al. 2013) - A national project responsible for, amongst other tasks, the yearly monitoring of willow grouse in Norway from 2006 to 2011. For each of the two years about 840 kilometers divided in about 280 unique transect lines were surveyed in Hedmark County. While walking the transect lines the voluntary field personnel primarily registered ptarmigan observations, but were asked to note down whether they also observed small rodents or not. Transect lines were plotted in Arc GIS (ESRI, 2011), converted to points centered on the middle of the transect, and interpolated using Kriging spatial analyst tool (See Fortin & Dale, 2005). Kriging is an advanced geostatistical procedure that generates an estimated surface from scattered set of points with z-values. The Kriging tool then fits a mathematical function to a specified number of points within a specified radius, to determine the output value for each location. In this case the z-values were defined as a binomial value of either 1 (rodents present) or 0 (rodents absent) and the specified output points were the kill positions of red fox, which were assigned a interpolated indexed value of rodent abundance. Indexed rodent abundance from the autumn of 2011 were used as a measure of food availability on all responses except for placental scars, where food availability was represented by indexed rodent abundance from the autumn of 2010.

Fox abundance data from the late autumn of 2011 and early winter of 2012 were obtained through the national carnivore monitoring project (Tovmo & Brøseth, 2012). During the study period approximately 1160 kilometers divided in 386 unique transect lines were surveyed in Hedmark County. Voluntary field personnel primarily registered snow tracks from lynx and other large carnivores, but were asked also to record any crossing red fox tracks. The amount of red fox tracks registered was divided by the amount of days since last snowfall creating an index of fox tracks seen per 3 km line walked. The index value for each transect-line was plotted in Arc GIS and interpolated using Kriging spatial analyst tool, assigning individual values to each kill position.

All human households were plotted in Arc GIS. To create a measurement of human settlement density, I conducted a fixed 95% Kernel analysis (Worton, 1989). Based on locations of households derived from digital maps of Hedmark County, I created 6 km^2 large raster cells covering the whole study area. Each red fox kill position was given a individual Kernel value based on the distance from, and density of households. Kernel values were highest at households and decreased with increasing distance.

2.2.6 UTM

To investigate possible spatial patterns, I included the UTM coordinates of kill sites as two separate parameters; one for the east-west coordinate and one for the north-south coordinate (hereafter referred to as "EW" and "NS"). These parameters could act as control variables if spatial related unmeasured factors had an influence on the studied response variables.

2.3 Statistical analysis

2.3.1 Exploratory analysis

I checked the correlation of all variables using a correlation matrix in R (R Core Team, 2013). Highly correlated variables were removed prior to further analysis (Table 1). Furthermore, all variables were checked for normal distribution plotting histograms showing frequencies of observations. Non-normal distributions were transformed for further analysis.

Because 81.1% of the foxes were shot during bait hunting (Table 3), I pooled all other hunting methods and created a binomial parameter for further analysis. Thus, I investigated the effect of bait hunting compared to all other hunting methods.

Chest, head, and neck circumferences were strongly correlated with body weight. Total length (body including tail) was highly correlated to body length (body without tail). I kept body weight and body length, and excluded the other variables prior to further analysis (Table 1). Although width and length of the head and length of legs were not highly correlated to other parameters, I considered them redundant for further analysis and were therefore removed (Table 1). To create an alternative measure of body condition, I created a standardized parameter by dividing body length by body weight ("body condition" = "body length" / "body weight").

In *a priori* analysis, the kidney fat showed the largest variation amongst the adipose tissue observations, and was therefore selected to represent the total amount of body fat in further analysis. Moreover, Winstanley, Saunders, & Buttermer (1998) found that kidney fat indices show a good correlation with total body fat and overall nutritional condition. Fat measures from the mesenteries, pericardium, cardiac and spine, where thus removed (Table 1).

Because of the relatively small sample size of both embryos (9) and placental scars (9), I chose to create binomial variables, representing presence or absence of reproduction indicators in female uteri; one variable for embryos and one for placental scars. Also, as a result of the small sample size, I chose to test biologically possible single predictors on the presence of embryos and placental scars (Table 2) in females using a Wilcoxon rank sum test (Wilcoxon, 1945) instead of conducting a full model selection.

Interpolated fox abundance and kernel house densities were strongly correlated. Also, when studying the kill positions, the majority were in close proximity of houses. This is most likely due to the lenience of maintaining bait hunting stations and hunting on your own private property. Hence, I chose to remove the house density parameter prior to further analysis (Table 1).

Table 1 List of variables kept and variables excluded for further analysis

Parameters kept	**Parameters discarded**
Body weight	Head circumference
	Neck circumference
	Chest circumference
Body length (tail excluded)	Total length (including tail)
	Leg length
	Head length
	Head width
Kidney fat	Mesenteric fat
	Subcutaneous spinal fat
	Pericardial fat
	Cardiac fat
Fox abundance	House density

2.3.2 Model selection

I conducted model selections for 5 responses; age, sex, kidney fat, body condition and bait, respectively (Table 2). General linear models (GLM) were used to fit all models. Model selection was conducted in R, using the "AICcmodavg" package (Mazerolle, 2013). All models Based on literature reviews, biological plausible combinations and forward selections, I created a set of candidate models using combinations of several predictor variables; combinations of six predictors were tested on age, kidney fat and body condition, five predictors on sex and nine predictors on bait (see Table 2). Furthermore, I selected the most parsimonious model for all predictors based on Akaike Information Criterion with a correction for finite samples (AICc; see e.g. Burnham & Anderson, 2002). I considered a ΔAICc>2 as a cutoff for identifying the best models.

Table 2 Illustrates all responses analyzed with predictors tested and the number of candidate models used in model selections

Response	Family	Predictors	N candidate models
Age	binomial	sex, date shot, NS, EW, fox abundance, rodent abundance	23
Sex	binomial	date shot, NS, EW, fox abundance rodent abundance	10
Kidney fat	poisson	sex, date shot, NS, EW, fox abundance, rodent abundance	24
Body condition	gaussian	sex, date shot, NS, EW, fox abundance, rodent abundance	15
Bait	binomial	sex, date shot, NS, EW, fox abundance, rodent abundance, age, body condition, kidney fat	15
Sex	binomial	date shot, NS, EW, fox abundance, rodent abundance	10
Embryos	binomial	fox abundance, rodent abundance, kidney fat, body condition, bait	5
Scars	binomial	rodent abundance 2010	1

3. Results

3.1 Descriptive analysis

A total of 106 of the shot red foxes were autopsied from January throughout April, 2012, (56 females and 50 males). The sex ratio was not different from 1:1 (X^2=0.34, df=1, p=0.56). Out of the 106 red foxes, the majority (81.1%) were shot on bait hunting stations, whereas the remaining foxes were shot through a variety of other hunting methods (Table 3). More than half of the individuals autopsied were shot during March (Figure 2).

Table 3 Number and percentage of autopsied fox shot using different hunting methods in Hedmark County, 2012

Hunting method	N shot	% shot
Shoting at baits	86	81.1
Chasing with dogs	2	1.9
Shooting at dens	6	5.7
Hunting with game calls	7	6.6
Flushing with people	1	0.9
Baited box traps	1	0.9
Stand hunting	3	2.8

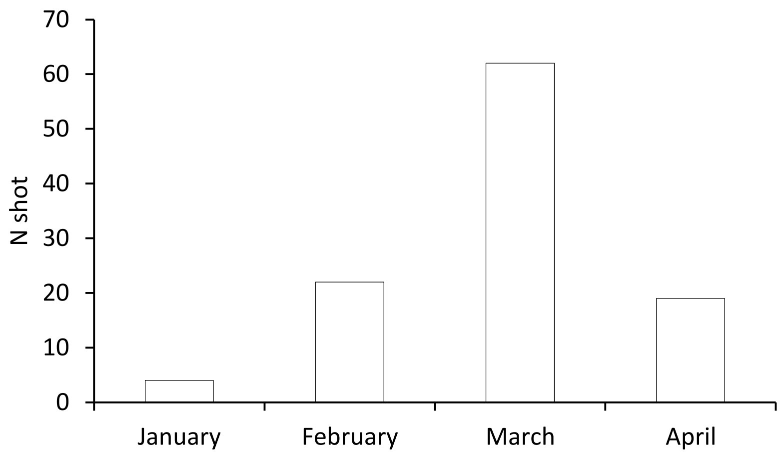

Figure 2 Numbers of autopsied red foxes shot per month in Hedmark County in 2012

Most of the autopsied foxes were juveniles (64%). The proportion of juvenile males were significantly larger than the proportion of juvenile females (X^2=3.59, df=1, p=0.05; Table 4).

Table 4 The number and proportion of fox autopsied in Hedmark County in the winter of 2012 divided by sex and age.

Age	Females		Males		Total	
years	*N*	*%*	*N*	*%*	*N*	*%*
< 1	31	55	37	74	68	64
1 - 2	15	27	7	14	22	21
2 -3	3	5	4	8	7	7
3 - 4	2	4	0	0	2	2
4 - 5	1	2	1	2	2	2
unknown	4	7	1	2	5	5

The individual difference in body weight spanned from 3.4 kg (smallest adult female) to 7.7 kg (largest juvenile male) and males were significantly heavier than females ($x^2_{1,95}$=27.86, p<0.001; Table 5). Furthermore, individual difference in body length spanned from 54.2 cm (smallest juvenile male) to 87 cm (largest adult male). Although the smallest individual was a male, the average length of females were significantly less than males ($x^2_{1,95}$=9.503, p<0.01; Table 5). There were no weight difference between ages (correcting fox sex dimorphism; p>0.1; Table 5), and no difference in body length between adults and juveniles ($x^2_{1,90}$=0.012, p=0.91; Table 5)

Table 5 Average, minimum and maximum measurements of body weight and body length in autopsied red foxes in Hedmark County in 2012, divided by sex and age.

Parameter	Measure unit	Average	Min measured	Max measured
Weight	*kg*	5.36	3.4	7.7
Females	*kg*	4.98	3.4	6.7
Males	*kg*	5.78	4.4	7.7
Juveniles	*kg*	5.48	3.9	7.7
Adults	*kg*	5.12	3.4	6.9
Body length	*cm*	71.8	54.2	87
Females	*cm*	70.5	62	80
Males	*cm*	73.3	54.2	87
Juveniles	*cm*	71.8	54.2	80
Adults	*cm*	71.9	62	87

When checking reproduction indicators in females, 9 uteruses contained placental scars, 9 contained embryos, and 32 uteruses had no signs of impregnation in the current or previous mating season. The number of embryos found in pregnant females ranged from 2 to 6, whereas the number of placental scars ranged from 2 to 8.

3.2 Results of model selections

3.2.1 The effect of bait hunting

To establish if there were any factors influencing the frequency of individuals shot at bait hunting stations, I conducted a model selection where the most parsimonious model consisted of age and body condition and rodent abundance as predictors (Table 6).

Table 6 Output from model selection based on AICc, displaying the top five models and the intercept model explaining the selective effect of bait hunting.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
age+body condition+rodent abundance	4	81.94	0	0.71	0.71	-36.73
age+body condition*rodent abundance	5	84.08	2.14	0.24	0.95	-36.68
age+body condition	3	88.61	6.67	0.03	0.97	-41.17
age+rodent abundance	3	89.42	7.48	0.02	0.99	-41.58
body condition+rodent abundance	3	91.32	9.38	0.01	1	-42.53
intercept model	1	100.93	18.99	0	1	-49.45

Bait hunting did not select for a specific age ($X^2_{1,99}$=0.17, p=0.68). Both adult and juvenile foxes shot at bait hunting stations had the same body condition as foxes shot outside bait hunting stations (ad: logit slope ± SE = 0.18 ± 0.28, p=0.52; juv: logit slope ± SE = 0.22 ± 0.20, p=0.28). Furthermore, rodent abundance were significantly higher in bait hunting areas than in areas where other hunting methods were used ($X^2_{1,102}$=0.72, p<0.05; Figure 3).

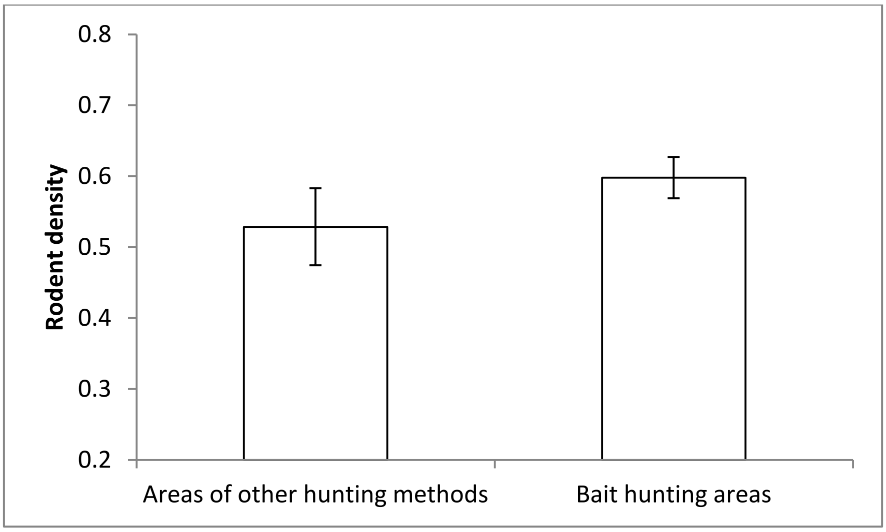

Figure 3 The average rodent abundance in areas of bait hunting and areas where other hunting methods were used with 95% confidence intervals.

As there were only five observations of adult foxes shot outside bait hunting stations, and since the slope for juveniles and adults was close to identical, I chose to plot the effect of body condition and rodent abundance regardless of age. The frequency of red foxes getting killed at bait hunting stations tended to increase with increasing body condition (logit slope ± SE = 0.21 ± 0.16, p=0.19; Figure 4).

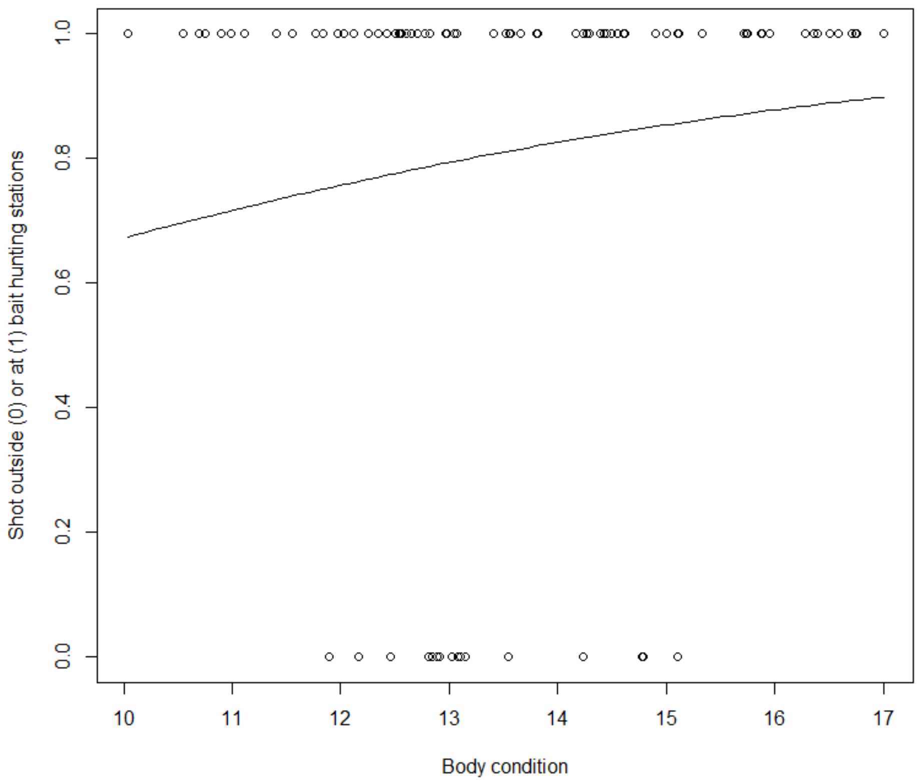

Figure 4 The frequency of individuals getting shot at or outside bait hunting stations explained by body condition.

3.2.2 Body fat, body condition, age structure and sex structure.

The most parsimonious model explaining the variation in kidney fat was the intercept model; Hence, I found no relationships between any of my predictors and the amount of fat surrounding the kidneys (Table 7).

Table 7 Output from model selection based on AICc, displaying the top six models explaining variations in kidney fat in foxes autopsied in Hedmark County, 2012.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
intercept model	1	294.74	0	0.17	0.17	-146.35
sex	2	295.5	0.76	0.12	0.29	-145.69
date shot	2	296.14	1.39	0.09	0.37	-146.01
EW	2	296.74	1.99	0.06	0.44	-146.31
fox abundance	2	296.78	2.04	0.06	0.5	-146.33
NS	2	296.79	2.04	0.06	0.56	-146.34

Sex was clearly the most important factor explaining body condition (ΔAICc=14.5); Females had a significantly higher body condition than males ($X^2_{1,93}$=18.77, $p<0.001$). To look for other explanations of variation in body condition I chose to run one model selection for males and females separately. No predictors could help explain the variation in female body condition, as the model selection favoured the intercept model (Table 8).

Table 8 Output from model selection based on AICc, displaying the top six models explaining variation in female body condition.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
intercept only	2	209.38	0	0.22	0.22	-102.57
NS	3	210.72	1.34	0.11	0.34	-102.11
EW	3	210.81	1.43	0.11	0.45	-102.16
date shot	3	211.09	1.71	0.1	0.54	-102.29
rodent 2011	3	211.1	1.72	0.09	0.64	-102.3
rodent 2011 + NS	4	211.28	1.9	0.09	0.72	-101.22

The most parsimonious model explaining male body condition was rodent abundance in combinations with several parameters (see Table 9). According to Arnold (2010), if a model has an addition of only one parameter to its competitor and the parameter is not significant, that parameter is likely spurious. Thus, I only focused on the effect of rodent abundance.

Table 9 Output from model selection based on AICc, displaying the top five models and the intercept model explaining variations in male body condition.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
rodent abundance + date shot + EW	5	162.2	0	0.16	0.16	-75.33
rodent abundance + date shot	4	162.33	0.13	0.15	0.32	-76.66
rodent abundance + EW	4	162.54	0.34	0.14	0.45	-76.77
rodent abundance	3	163.29	1.1	0.09	0.55	-78.35
rodent abundance + date shot + EW + fox abundance	6	163.42	1.22	0.09	0.64	-74.6
intercept model	2	169.28	7.08	0	1	-82.5

Body condition in males increased with increasing rodent abundance (slope ± SE = 5.41 ± 1.83, $p<0,01$; Figure 5).

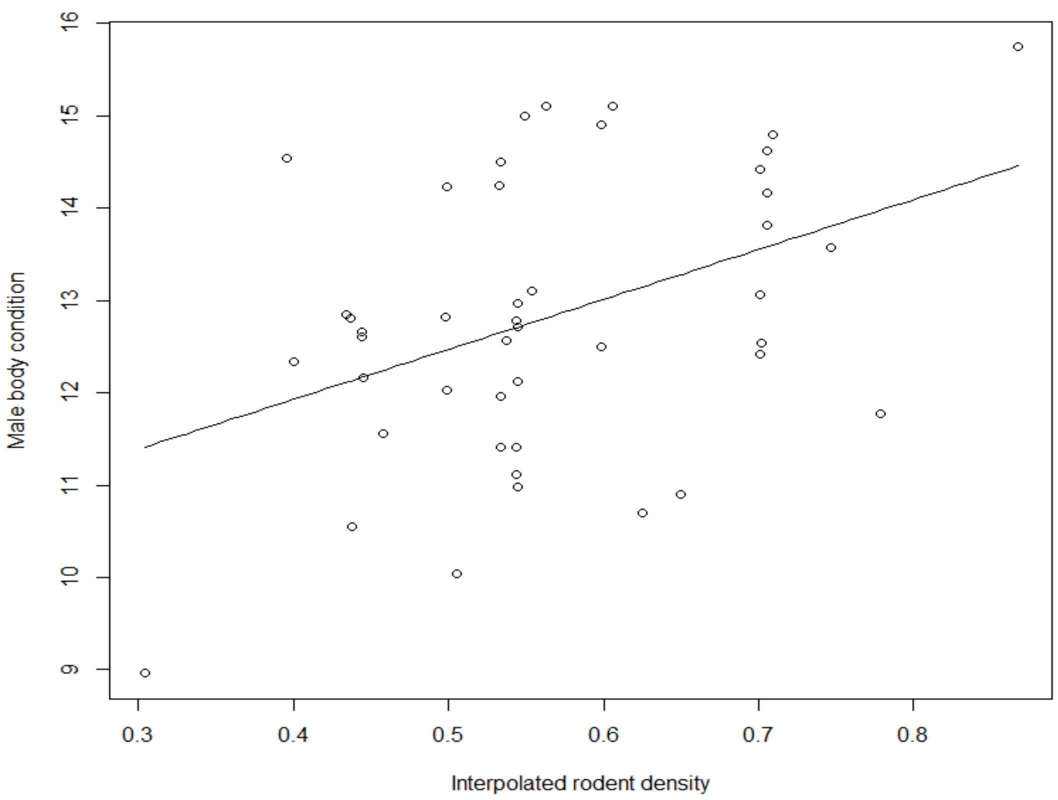

Figure 5 The relationship between male body condition and interpolated rodent abundance.

Fox abundance and sex best explained the age structure of the population (Table 10). The distribution of both male adults and juveniles was unaffected by fox abundance (logit slope ± SE = 0.07 ± 0.55, p=0.89; Figure 6), whilst the proportion of adult females decreased with increasing fox abundance (logit slope ± SE = -1.52 ± 0.58, p<0.01; Figure 6).

Table 10 Output from model selection based on AICc, displaying the top five models and the intercept model explaining variations in age in autopsied foxes in Hedmark County, 2012

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
fox abundance + sex	3	125.91	0	0.16	0.16	-59.83
fox abundance + sex + rodent abundance	4	126.57	0.66	0.12	0.28	-59.08
fox abundance + sex + date shot	4	126.86	0.95	0.1	0.38	-59.22
fox abundance + sex +EW	4	127.46	1.54	0.08	0.46	-59.52
fox abundance + sex + NS	4	127.9	1.99	0.06	0.52	-59.74
intercept model	1	131.07	5.16	0.01	0.97	-64.52

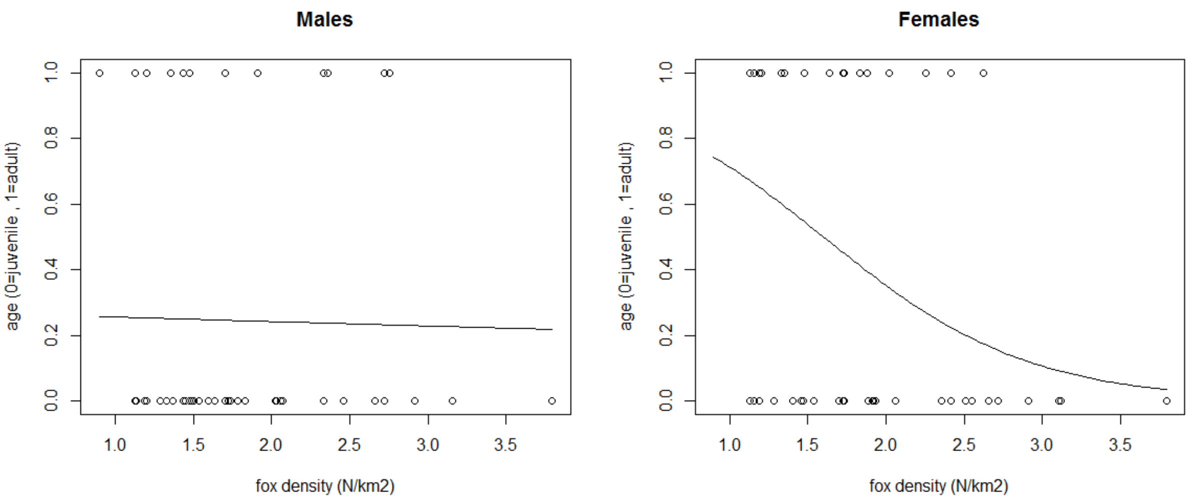

Figure 6 The relationship between fox abundance and age for both males and females.

None of the candidate models could explain the sex structure of the red foxes killed in Hedmark County in 2012. Hence, the model selection favoured the intercept model (Table 11).

Table 11 Output from model selection based on AICc, displaying the top six models explaining variations in sex in autopsied foxes in Hedmark County, 2012

Predictors	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
intercept model	1	148.65	0	0.26	0.26	-73.3
rodent abundance	2	150.08	1.44	0.13	0.38	-72.98
EW	2	150.11	1.46	0.12	0.51	-72.99
fox abundance	2	150.41	1.76	0.11	0.61	-73.15
NS	2	150.69	2.04	0.09	0.7	-73.29
date shot	2	150.72	2.07	0.09	0.8	-73.3

3.2.3 Reproduction

I found embryos in nine females. Three out of nine were adults whilst six were juveniles. Naturally, all females with observed placental scars were adults. I found no significant relationships between the presence of placental scars in females and rodent abundance the previous season ($p>0.1$). I found a significant difference in the average number of embryos per female between individuals shot at bait stations and those not ($W=276$, $p<0.01$; Figure 7). I also found that non-barren females in average had poorer body condition than barren females ($W=232$, $p<0.05$; Figure 8).

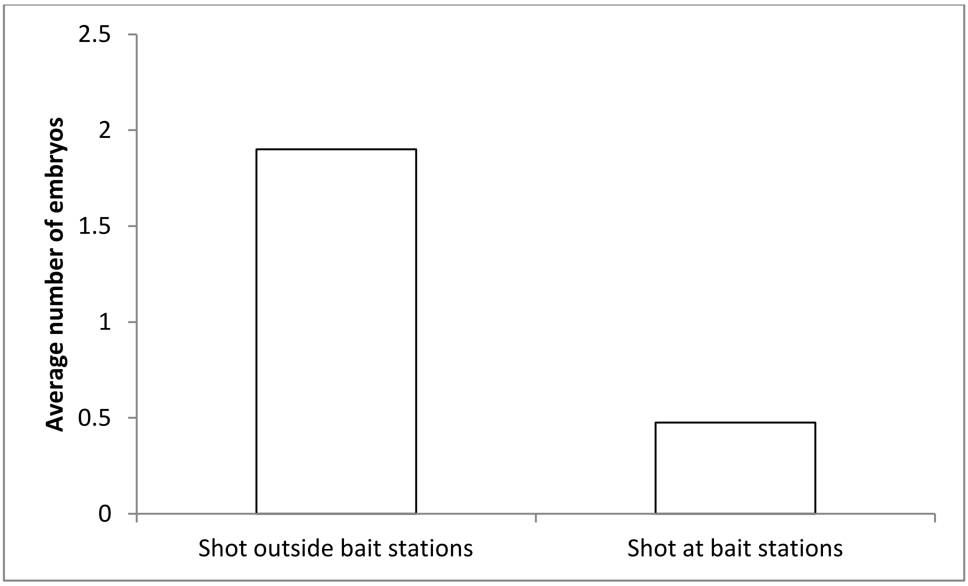

Figure 7 The average number of embryos observed in autopsied females shot at bait hunting stations and outside bait hunting stations in Hedmark County, 2012

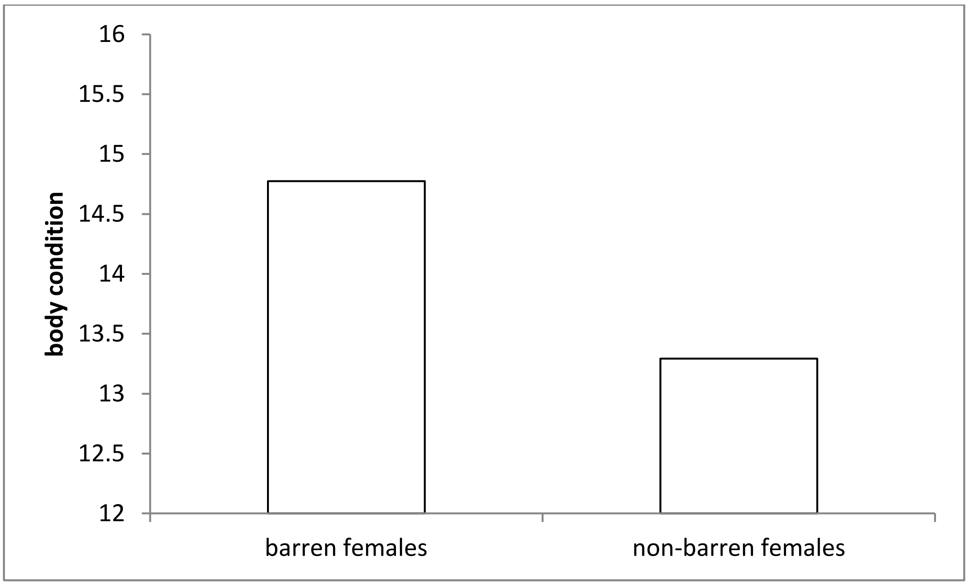

Figure 8 The average body condition of barren and non-barren females autopsied in Hedmark County, 2012

4. Discussion

Most of the red foxes autopsied were killed during March and the sex ratio was not different from 1:1. A large proportion of the foxes were juveniles and there were more juvenile males than females. Males were significantly heavier and larger than females, but with no differences in weight and length between adults and juveniles. Furthermore, the majority of red foxes were shot at bait hunting stations.

My results show that bait hunting might select for individuals with better body condition, though not statistically significant. The possible selection for individuals with better body condition was not related to either age or sex, although females had higher average body condition than males. Selection for certain individuals or traits might occur when using bait stations as a facility for hunting (see e.g. Lindström, 1982; Galby & Hjeljord, 2010). Galby & Hjeljord (2010) found that males were shot in excess at bait hunting stations early and mid-winter and that equal proportions of males and females were shot in early spring. Their study was conducted further south in Norway, and the fox population is likely more dense in these areas (see Lindström, 1982). I can only speculate that there were more young males without territories, floaters, compared to the Hedmark area. A higher mortality and natal dispersal in my area could possibly explain the more even sex ratio compared to the previous study. Migration in juvenile red fox is likely to occur between 6 and 12 months of age (Soulsbury et al. 2008). Red fox can migrate over large distances in a short period of time, especially young males in intermediate densities (T. Willebrand, personal communication, May 15, 2014). 64% of my data consisted of juvenile individuals. This could strongly bias the spatial parameters based on the kill site, as it is hard to know if individuals are passing by or stationary in the area of measurement.

Lindström (1982) suggested that hunger, as a result of low food availability, could positively influence bait hunting as a collection method. Assuming that scarcity of food was the main reason for red foxes to utilize bait hunting stations in Hedmark County, it is interesting that individuals killed here also had a higher body condition than individuals killed outside bait hunting stations. One explanation could be that red foxes frequently visit bait hunting stations without getting killed due to a varying temporal presence of hunters. If so, baits could be a stable food resource over time, contributing to an increased body condition. Moreover, the fact that my data was skewed towards juveniles coincide with this theory, as juveniles are suggested to be bolder and less experienced than adults (Lindström, 1982). Thus they might have a lower threshold for approaching bait hunting stations.

Furthermore, areas where foxes were shot at bait hunting stations had a higher abundance of rodents than areas where other hunting methods were used. Therefore, another possibility is that the relatively high abundance of rodents the previous autumn caused a higher individual body condition in red foxes residing in areas of bait hunting. This coincides with the fact that body condition in males increased with increasing rodent abundance. Moreover, taking into consideration that my measure of body condition was based on individual body length and weight, this theory is supported by the findings of Lindström (1983). Lindström found that growth rate in young vixens shot in the winter was correlated with vole abundance the previous autumn.

I find it interesting that only body condition in males and not females responded to the abundance of rodents, as there were no difference in average rodent abundance on the kill positions for females and males. However, juvenile males tend to leave their natal home ranges and disperse further than females (Jensen, 1973; Englund, 1980). This may also imply that females tend to emigrate less frequently, and thus not roam far enough to exploit available food resources such as rodents in the same manner as males. The fact that females in average had a significantly higher body condition than males could also imply that females generally reside within a limited territory with sufficient resources of food. Lindström (1989) found territory size to be constant, regardless of food availability, which implies that a fox territory is large enough to provide sufficient amounts of food in periods with limited resources (Englund, 1970).

Individuals with larger fat reserves are likely to have better fasting endurance and thus higher survival than individuals with smaller reserves (Millar & Hickling, 1990). Hence, I expected parameters reflecting food availability to affect the amount of kidney fat. The abundance of small rodents the previous autumn did not explain the variation in kidney fat. This concurs with the findings of Lindström (1983), which states that although voles were a major food resource, there was no positive relationship between vole abundance and fat deposits. Nevertheless, Lindström did find a positive correlation between abundance of berries and subcutaneous fat thickness, revealing plant production as an important factor influencing the amount of body fat in red foxes. Thus vegetation, but possibly also offal from ungulates (Jedrzejewski & Jedrzejewska, 1992; Smedshaug & Sonerud, 1997; Selås &

Vik, 2006), could have contributed to fat deposits in red foxes. As such, subcutaneous fat is possibly more sensitive to variation in energy intake than kidney fat, and could be a more appropriate indicator of starvation. This might further explain why none of my predictors could explain the amount of fat surrounding the kidneys. A priori analysis also showed a very low variation in the amount of kidney fat between individuals. This may suggest that, as all foxes were shot in winter, the generally lower abundance of available food this time of year (Barton & Zalewski, 2007) might have affected all foxes, or that the level of kidney fat is actually saturated.

Reproduction in red fox vary amongst years in relation to food abundance (Lindstöm, 1982). Englund (1970) observed a lower rate of reproducing females with scarcity of rodents the previous autumn. In years with low rodent abundance 88% of sub adults and 67% of adults did not reproduce. In my study 86% of adults and 82% of juveniles did not reproduce the spring of 2012. Initially this strongly suggest a scarcity of food. However, the autumn of 2011 was a peak year for rodent abundance in Norway (see e.g. Flagstad et al., 2011), implying that as much as 46% and 87% of juveniles and adults, respectively, possibly should reproduce the following spring.

Considering the above mentioned, the explanation of the low proportion of non-barren females could be some kind of sampling bias selecting for barren females. When a female invest in reproduction, she might avoid high-risk food sources and therefore have a higher threshold for approaching bait hunting stations. This theory is supported by the fact that my results showed a higher average number of embryos in females culled outside bait hunting stations. If non barren vixens avoided bait hunting stations to a larger degree than barren ones, this might have lead to a lower food availability, and thereby explain the observed lower body condition in non barren compared to barren females. Moreover, the first observation in embryonic swellings was observed February 26. At that time the swellings were small and barely visible, thus females culled prior to this date might not show signs of impregnation.

My results showed no relationship between rodent densities of 2010 and the presence of placental scars in vixens. An obvious source of error is the time passed between the measured rodent density and the time of death, which is almost 1,5 years. The possibility of migration in this time period and the low sample size does not cause for further speculations.

Englund (1970) found a proportion of 3.9 sub adults per adult in early summer following years with high rodent abundances, and a proportion of 0.8 sub adults per adult in years following autumns with low rodent abundance. In my study it would have been 3 young per two adults using about 60% young in the killed sample. This is a high value, but the monitoring of rodents in Hedmark County supported a vole peak in the period previous to the red fox collection. Thus it is possible that there were no bias towards young in my data material.

The distribution of male adults and male juveniles was unaffected by fox abundance whilst the amount of adult females decreased with increasing fox abundance. The relationship between adult females and fox abundance could be explained by territoriality in adult foxes. During the mating season the female is thought to stay within the territory while males has been described to leave the territory due to a high level of promiscuous behavior (Baker et al. 2004). Furthermore, fox abundance is likely to be higher closer to resident houses because of the increased availability of anthropogenic food items (Balestrieri, Remonti, & Prigioni, 2011). Therefore, adult males might reside in such areas when activity levels are high during mating. This coincides with the low number of pregnant adult females shot at bait hunting stations (N=2).

Conclusion

This study shows recent patterns in body condition and reproduction in a red fox population in Southeastern Norway. Autopsied red foxes were mostly in average condition with low variation in body fat. The relatively small proportion of reproducing females, along with an increased body condition of males shot at bait stations compared to other hunting methods, indicates a food limited fox population.

The red fox is considered a keystone predator in several ecosystems (Smedshaug et al. 1999). It has also been labeled as one of the largest threats to other species, such as the endangered arctic fox (Selås & Vik, 2007; Angerbjörn et al. 2013). Global warming and increased access to anthropogenic food items may increase the carrying capacity of the red fox, through enhanced body condition and increased reproductive output and winter survival. It is therefore important to continue monitoring the red fox, to understand the potential management options possible to reduce the threats to other species, and the potential cascade effects by promoting new assemblages of species in different ecosystems.

5. Acknowledgements

This thesis concludes my master’s degree in Applied Ecology at Hedmark University College. First of all, I want to use this opportunity to thank everyone who made this five year study an unforgettable experience. Special thanks to my supervisor Morten Odden, for his help, guidance and encouragement throughout the process of planning and writing this thesis. Thanks to Mathea Storihle for a great effort and companionship during the data collection. Thanks to Lars Rød Eriksen for substantial technical guidance and to Tomas Willebrand and Torfinn Jahren for their constructive feedbacks. Thanks to Hedmark County hunting and fishing association and the project “Tracking the red fox” for supplying the data needed, and thanks to all other people helping out with the practical and technical realization of this project. Also, thanks to my mom for constantly worrying about my, and the thesis’ well being, and thanks to my wonderful girlfriend for all her encouragement and support.

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