Ecol Res (2008) 23: 889–896
DOI 10.1007/s11284-007-0452-2

ORIGINAL ARTICLE

Manuela Panzacchi · John D. C. Linnell
Giulia Serrao · Sveinung Eie · Morten Odden
John Odden · Reidar Andersen

Evaluation of the importance of roe deer fawns in the spring–summer diet of red foxes in southeastern Norway

Received: 23 May 2007 / Accepted: 13 November 2007 / Published online: 26 December 2007
© The Ecological Society of Japan 2007

Abstract Red fox *Vulpes vulpes* predation on roe deer *Capreolus capreolus* fawns has the potential to strongly affect prey population dynamics, but it is unclear whether this relationship is symmetrical or not. We analysed the spring–summer diet of adult foxes and of their cubs in a fragmented agricultural area of southeastern Norway, where a parallel study showed that the predator kills annually 25% of the radio-monitored roe deer fawns. The overall diet was highly varied and was dominated by small mammals (33% volume), especially *Microtus agrestis*, and medium-large mammals (25%), largely represented by fawns. The frequency of occurrence (FO) of fawns in the diet of adult foxes was highest in early spring, thus, supporting previous studies showing that the predator started actively hunting for fawns from the very beginning of the birth season. During the summer, the FO of both fawns and small mammals markedly declined, while that of berries and invertebrates increased. As expected for central-place foragers, cubs consumed a higher proportion of large prey items compared to adults. In particular, 25% of scats from cubs—versus 9% from adults—contained roe deer remains, suggesting a high profitability of fawns for vixens raising offspring. However, considering the wide food spectrum and the availability of several large prey items in our study area, it seems unlikely that the importance of fawns to the diet and population dynamics of red foxes could be as great as the impact of the predator on roe deer populations. This asymmetrical relationship implies that there are unlikely to be any stabilising feedback mechanisms in the predator–prey relationship.

Keywords Alternative prey · Meso-predators · Optimal foraging theory · Predator–prey interactions · Voles

Introduction

The red fox (*Vulpes vulpes*) is widely regarded as being one of the most important keystone species within the boreal forest ecosystem of Fennoscandia (Lindström 1989a, b; Lindström et al. 1994; Smedshaug et al. 1999). Within a food web context, the red fox is among the species with the greatest number of linkages. Perhaps uniquely among all mammalian predators, it is closely linked to at least three trophic levels and feed upon diverse taxonomic groups. Vegetation, mainly in the form of fruits and berries, is common in its diet, as are insects, earthworms, amphibians, small mammals and birds. Even insectivores are often killed, but less often eaten, and red fox predation on smaller meso-predators has been well documented (Lindström et al. 1995; Palomares and Caro 1999; Linnell and Strand 2000, 2002). What is especially interesting about red foxes is the fact that they also interact with species far larger than themselves, thus, linking food webs normally associated with small (stoats *Mustela vision* and weasels

---

M. Panzacchi · S. Eie
Biology Department, Norwegian University
of Science and Technology, 7491 Trondheim, Norway

J. D. C. Linnell · G. Serrao · J. Odden
Norwegian Institute for Nature Research,
Tungasletta-2, 7485 Trondheim, Norway

M. Odden
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences, 1432 Ås, Norway

R. Andersen
Museum of Natural History and Archaeology,
Section of Natural History, Norwegian University
of Science and Technology, 7491 Trondheim, Norway

Present address: M. Panzacchi (✉)
Italian Wildlife Institute, Via Stradelli Guelfi 9,
40064 Ozzano dell'Emilia, Bologna, Italy
E-mail: manuela.panzacchi@bio.ntnu.no
Tel.: +39-051-6512229
Fax: +39-051-796628

Present address: G. Serrao
Department of Environmental Science "G. Sarfatti",
University of Siena, Via Mattioli 8b, Siena, Italy

Mustela erminea), medium (pine martens *Martes martes*, racoon dogs *Nyctereutes procyonoides*) and large predators (wolves *Canis lupus* and lynx *Lynx lynx*). The interaction between red foxes and large predators is complex, as they can be prey (Linnell et al. 1998), vectors for diseases (Degiorgis et al. 2001) or competitors.

Foxes can compete with larger carnivores indirectly, by consuming the meat of large prey killed by their competitors (Selva et al. 2005), and directly through their impact on shared prey species. This latter effect is most pronounced on the impact that red foxes have on roe deer (*Capreolus capreolus*) fawns. Repeated studies throughout Scandinavia have confirmed that red foxes can kill significant numbers of fawns (Aanes and Andersen 1996; Jarnemo et al. 2004) and that this predation can elevate neonatal mortality rates above that which is expected in the absence of predation (Andersen and Linnell 1998; Jarnemo and Liberg 2005). From 2001 to 2004, we studied the survival of radio-monitored roe deer fawn in southeastern Norway and have found that 58% of fawn mortality is due to red fox predation, with annual predation rates of 25% (Panzacchi et al. 2007a). Our studies have gone further and have attempted to understand the complexity of this predator–prey relationship, especially with respect to habitat (Panzacchi et al. 2007b) and alternative prey (Panzacchi et al. 2007c, d), of which earlier studies have indicated the importance (Kjellander and Nordström 2003).

While our roe-deer-centred studies have indicated the importance of red foxes for fawn mortality and, thus, for the ungulate's population dynamics, the question remains as to whether roe deer fawns are of any real importance for the predator. A symmetric relationship would affect potential feedback mechanisms and, therefore, the stability of the predator–prey relationship. Earlier studies on red foxes have indicated that, because of their generalist nature with fluctuating food preferences, red fox predation may be important for prey, even though the prey may be of no real significance for the foxes (Macdonald 1977).

This study aimed to investigate red fox diet during the period when roe deer fawns are available as prey (spring and summer) in a study area where we conducted a parallel study on fawn mortality. In this specific study site, we previously showed that foxes tend to specialise on roe deer fawns and, thus, predation rates are high from the very beginning of the birth season (Panzacchi et al. 2007a). We aimed to test the following predictions. P1: based on existing knowledge concerning red foxes in south-central Scandinavia (Lindström 1989a, b), we predicted that small mammals would dominate red fox diet and that their occurrence in diet would reflect their seasonal availability. P2: because red foxes tend to function as temporary specialist predators on roe deer fawns in this study area, we expected that the newborn ungulates would be a major component of fox diet and that their occurrence in diet will be high from the beginning of the birth season. P3: because of the northern latitude of this study area, we expect that invertebrates and plant material would be of minor importance to red fox diet.

Study area

The study was conducted in southeastern Norway, in the counties of Østfold and Akershus (Aurskog-Høland, Enebakk, Høbol, Rælingen, Spydeberg and Trøgstad municipalities). The area consists of a fine mosaic of agricultural land (24%), water (11%) and forest (65%), which is both coniferous and deciduous. During the study period (May–August 2003 and 2004) the average temperature ranged from 10°C to 15°C and rainfall of 31 to 115 mm rain/month were recorded (Meteorologisk Institutt 2006). Indirect measurements suggest that the study area is inhabited by a relatively large roe deer population, as about 1.5 roe deer are killed every year per km^2, and by a large red fox population, as an extensive track count study showed that the number of tracks crossing a 1-km transect during winter is about twice as high as the number of roe deer tracks (Panzacchi et al. 2007b). Among the potential prey for the red fox, the study area is occupied by at least 11 species of voles, mice and shrews (Panzacchi et al. 2007c), moose (*Alces alces*), hares (*Lepus timidus*), *Mustelidae* such as weasel (*Mustela nivialis*) and mink (*M. vison*), *Tetraonidae* such as black grouse (*Tetrao tetrix*) and capercaillie (*T. urugallus*), a range of passerines and waterfowl, in addition to domestic sheep, domestic cats and domestic rabbits. In addition to red foxes, the main predators of roe deer fawns in the study area are Eurasian lynx (*L. lynx*) and domestic dogs; wolves (*C. lupus*) and golden eagles (*Aquila chrysaetos*) have been recorded in the study area but never killed radio-monitored roe deer fawns (Panzacchi et al. 2007a). In accordance to previous studies, which showed that small mammals show multi-annual cycles only approximately above 60°N latitude (Hanski et al. 1991), in our study area population, the dynamics are relatively stable (G. Sonerud, personal communication).

Methods

Collection and analysis of red fox scats

During May–August 2003 and 2004, a total of 171 red fox scats were collected, stored in plastic bags and frozen at −20°C. Of these, 147 apparently fresh scats were collected by walking six transects (1–6-km long) previously cleared from old scats or while carrying out routine radio-tracking of red foxes (Linnell 2007, unpublished data). In addition, in two occasions during the course of spring and summer, we visited two red fox breeding dens. Here, we collected a total of 24 scats, which were attributed to red fox cubs due to their smaller size. Scats analysis was performed by following the methods suggested by Reynolds and Aebischer

(1991). Faeces were broken down in water and microscopic fragments were separated from macroscopic ones using a sieve with mesh size of 0.5 mm. The microscopic residuals were sampled to count earthworms' *chaetae*, while macroscopic fragments were dried and identified by sampling. The discrimination among different *taxa* of medium-large mammals (different species of ungulates, mustelids, insectivores and domestic animals) was done by a microscopic hair analysis of the cuticle, section and medulla using a 400× microscope (Teerink 1991). The identification of different species of small mammals (mice, voles and rats) was possible only when jaws or teeth were found, and it was done by comparison with reference material. We estimated the number of small mammals in one scat by counting the number of jaws or teeth (Lockie 1959).

Analysis of red fox diet

The red fox diet was analysed using the frequency of occurrence (FO), defined as the proportion of scats containing a given food item with respect to the total sample size (Leckie et al. 1998). Even though this is a common way to present results of diet analyses, and it is useful in order to test how often a given food item was ingested, this method is not a good estimator of the nutritional importance of the different prey categories. All methods for extrapolating from occurrence in faeces to biomass or energy consumed are fraught with a range of errors and assumptions (Reynolds and Aebischer 1991). In order to obtain an estimate of the contribution in terms of the volume of each prey species, we used the estimated ingested volume (EIV) method described by Kruuk and Parish (1981), and we categorised the EIV of each prey item in each scat into the following categories: < 5, 6–25, 26–50, 51–75, 76–95, > 96%. This method has been widely used in meso-predator diet studies (e.g. Lucherini and Crema 1994). However, in order to compare the relative contribution of different prey categories to the estimated total volume ingested, the EIV have been converted into whole scat equivalents (WSEs) described by Angerbjörn et al. (1999). The WSE is a modified FO calculated with the estimated volume (in our case, EIV) of each prey category. For example, one scat with 60% voles and 40% berries plus another scat with 40% voles and 60% berries were considered to be equivalent to one scat with 100% voles and another with 100% berries. This method has the advantage of maintaining the same unaltered sample size and, thus, allows for a direct comparison of the different proportions ingested.

In order to combine FO with volume and, thus, provide a better visualisation of the composition of a typical red fox meal (Fig. 1), we estimated the average volume (AV) of each food item in a scat, defined as the total volume of a given food item in all scats divided by the number of scats containing that food item (e.g. Ciampalini and Lovari 1985).

Statistical analyses

In order to assess the feeding habits of adult red fox during the course of spring and summer, we divided the sample in two periods: 15th May–15th July ($n = 51$) and 16th July–30th August ($n = 96$). Differences in FO and WSE were tested by using contingency tables specifying the number of scats where a given food item was present or absent, as suggested by Angerbjörn et al. (1999). The relative importance of different food items was assessed by determining which group gave the major cell contribution to the total χ^2 value in a chi-square test (Dalgaard 2002). Since the proportions of different food items in a scat are interdependent, we tested for variations in

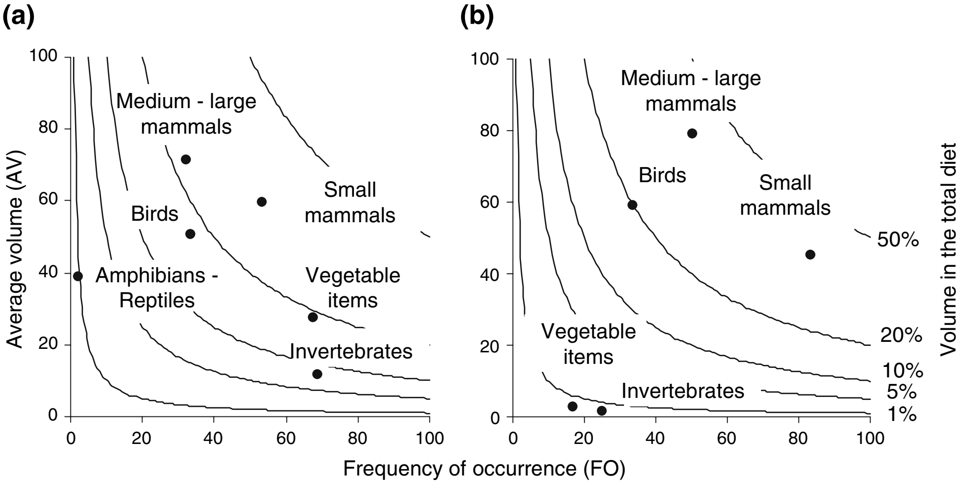

Fig. 1a, b Representation of the diet of adult red foxes (**a**) and cubs (**b**) in southeastern Norway during May–August 2003 and 2004. Each figure illustrates the relationship between the frequency of occurrence (FO) and the average volume (AV) of the main food items. The isopleths indicate the relative volume of the considered food item with respect to the total volume of all food items. For example, in **b**, birds occur in 33% of the scats and account for 60% of the volume of each of those scats; they represent about 20% of the volume in the overall spring–summer diet of red fox cubs the overall diet composition between two periods by applying log-linear likelihood models (*G* tests) on contingency tables (Reynolds and Aebischer 1991). Logistic regression analyses were performed in order to test for factors affecting the occurrence (presence/absence) of roe deer and small mammals in red fox scats. The category "amphibians–reptiles" was always of insignificant importance in the red fox diet and, thus, it was not included in these analyses. All analyses were conducted by using the statistical software R, version 2.2.1 (R Development Core Team 2006).

Indices of abundance of small mammals and roe deer fawns

Parallel to the study of the red fox diet, two other research projects were carried out during the same period in the study area: a capture-mark-recapture study of small mammals (Panzacchi et al. 2007c) and a study on the mortality of 98 radio-monitored roe deer fawns, which took place from 2001 to 2004 (Panzacchi et al. 2007a, b). The index representing the temporal availability of small mammals was calculated as the number of different individuals captured per trap-night during May–August 2003. In order to obtain a reliable estimation of the availability of potential prey for the red fox, we calculated an index of abundance by considering only those species which have been both trapped and found in the scats: *Apodemus* spp. ($n = 70$), *Clethrionomys* spp. ($n = 161$) and *Microtus* spp. ($n = 98$).

The daily availability of vulnerable roe deer fawns was estimated by adopting the method suggested by Mayfield (1975) and Jarnemo et al. (2004). Hence, we calculated the number of roe deer fawns actually alive and radio-monitored every day, corrected according to the red fox preference for different age classes of roe deer fawns. For further details, see Panzacchi et al. (2007a, b). Considering that 21 out of 98 fawns captured in the study area were killed by red fox during the first 2 months of life, that in several cases the carcasses of predated radio-collared fawns were recovered inside fox dens and that in several cases red foxes had been observed killing or attempting to kill roe deer fawns during the study period, we assume that all roe deer remains detected in the red fox scats belong to the newborn ungulates. Hence, we assume that scavenging on roe deer that had died during the winter was finished by May and that scavenging on roe deer killed by lynx during the early summer is insignificant (Linnell and Teurlings 2007, unpublished data).

Results

Red foxes in our study area had a surprisingly varied diet, with 18 species of mammals, five bird orders, two species of amphibians and reptiles plus a wide range of invertebrates, berries, fruits and other vegetation (Table 1). However, the relative contribution of the different food items to the overall red fox diet varied in relation to age class (i.e. adults vs. cubs) and season (i.e. spring vs. summer).

Diet of adult red foxes and cubs

Since the diet of adult red foxes did not vary between 2003 and 2004 in terms of EIV (WSE: $G = 3.400$, $df = 4$, $p = 0.493$) or FO ($G = 1.721$, $df = 4$, $p = 0.787$), the data were pooled for the analyses. The relative proportion of the main food items to the overall diet of adult foxes was uneven in terms of volume ($\chi^2 = 28.079$, $df = 4$, $p < 0.001$). The major contribution to the χ^2 value was given by the category "small mammals," which, thus, constituted the largest proportion of the diet of adult red foxes during spring and summer (WSE = 32%, Table 1). The field vole *M. agrestis* occurred in the diet more frequently than any other small mammals, but the proportion of the larger-sized *Arvicola terrestris* was also substantial. Medium-large mammals were the second major components of the diet of adult red foxes and, among these, roe deer largely dominated. Among birds, *Passeriformes* and *Galliformes* accounted for the main part of the overall spring–summer diet. The relative importance of the main food items in the overall diet of adult red foxes differed not only in terms of ingested volume, but also in FO ($\chi^2 = 74.059$, $df = 4$, $p < 0.001$). The category medium-large mammals occurred in the diet less frequently than expected (major contribution to the χ^2 value), while "invertebrates" had the highest FO, occurring in 69% of the scats (second major contribution to the χ^2 value).

The overall diet of adult red foxes differed significantly from the diet of cubs at the dens both in terms of volume (WSE: $G = 13.930$, $df = 4$, $p = 0.008$) and FO ($G = 22.55$, $df = 4$, $p < 0.001$). Cubs consumed an overall higher proportion of large prey (mammals and birds) compared to adults (WSE: $\chi^2 = 6.684$, $df = 1$, $p = 0.010$). Small mammals ($\chi^2 = 6.540$, $df = 1$, $p = 0.011$) and medium-large mammals ($\chi^2 = 2.223$, $df = 1$, $p = 0.136$), in particular roe deer ($\chi^2 = 3.940$, $df = 1$, $p = 0.047$), were consumed more frequently by cubs than by adult foxes. On the other hand, adult red foxes consumed invertebrates ($\chi^2 = 15.015$, $df = 1$, $p < 0.001$) and vegetable items ($\chi^2 = 20.058$, $df = 1$, $p < 0.001$) more frequently than cubs.

The relative contribution of the various food items to the overall diet of cubs at the dens differed in terms of volume ($\chi^2 = 22.174$, $df = 4$, $p < 0.001$) and of FO ($\chi^2 = 27.429$, $df = 4$, $p < 0.001$): vegetable items and insects were underrepresented, while larger prey such as mammals and birds accounted for most of the diet. The relative importance of the main food classes for adult red foxes (a) and for red fox cubs at the dens (b) is illustrated in Fig. 1.

Table 1 Whole scat equivalent (WSE, in percentage) and frequency of occurrence (FO) of all food items found in scats from adult red foxes and cubs during May–August 2003 and 2004 in southeastern Norway

	WSE (%)					FO				
	Adults			Cubs	Tot	Adults			Cubs	Tot
	Tot	Spr	Sum	Tot		Tot	Spr	Sum	Tot	
Small mammals	31.8	41.6	26.5	37.7	32.6	53.1	60.8	49.0	83.3	57.3
Clethrionomys glareolus	0.7	0.6	0.8	4.2	1.2	1.4	2.0	1.0	0.6	1.8
Clethrionomys rufocanus	0.2	0.0	0.3	0.0	0.2	0.7	0.0	1.0	0.0	0.6
Microtus agrestis	9.6	15.2	6.5	8.5	9.4	17.7	23.5	14.6	16.7	17.5
Arvicola terrestris	5.1	7.8	3.7	12.0	6.1	8.2	11.8	6.3	12.5	8.8
Myopus schisticolor	0.9	0.9	0.8	4.1	1.3	2.0	2.0	2.1	4.2	2.3
Apodemus sylvaticus	0.2	0.7	0.0	0.0	0.2	0.7	2.0	0.0	0.0	0.6
Rattus norvegicus	3.2	1.4	4.1	0.0	2.7	4.1	2.0	5.2	0.0	3.5
Unidentified	11.9	15.1	10.2	8.9	11.5	25.9	31.4	22.9	45.8	28.7
Medium-large mammals	22.9	32.5	17.8	39.5	25.2	32.0	45.1	25.0	50.0	34.5
Capreolus capreolus	6.7	10.1	4.9	20.2	8.6	8.8	11.8	7.3	25.0	11.1
Alces alces	0.7	2.0	0.0	0.0	0.6	1.4	3.9	0.0	0.0	1.2
Mustela vison	1.3	2.0	1.0	0.0	1.2	1.4	2.0	1.0	0.0	1.2
Mustela nivalis	0.7	0.0	1.0	0.0	0.6	0.7	0.0	1.0	0.0	0.6
Sciurus vulgaris	1.6	1.6	1.5	0.0	1.3	2.0	2.0	2.1	0.0	1.8
Lepus timidus	3.0	3.9	2.5	0.0	2.6	3.4	3.9	3.1	0.0	2.9
Erinaceus europeus	0.5	0.0	0.7	0.0	0.4	0.7	0.0	1.0	0.0	0.6
Bats	1.0	1.9	0.5	4.1	1.4	1.4	2.0	1.0	4.2	1.8
Cat	1.7	4.9	0.0	0.0	1.4	2.0	5.9	0.0	0.0	1.8
Sheep	1.5	2.0	1.3	0.0	1.3	2.0	2.0	2.1	0.0	1.8
Pig	0.8	0.4	1.0	11.9	2.4	1.4	2.0	1.0	16.7	3.5
Unidentified	3.5	3.9	3.3	3.3	3.5	6.8	9.8	5.2	4.2	6.4
Birds	17.0	18.2	16.3	19.7	17.4	33.3	35.3	32.3	33.3	33.3
Passeriformes	4.2	6.5	3.0	4.1	4.2	6.8	11.8	4.2	4.2	6.4
Columbiformes	1.5	2.0	1.2	1.3	1.5	2.0	2.0	2.1	4.2	2.3
Galliformes	3.2	2.6	3.6	8.8	4.0	5.4	3.9	6.3	12.5	6.4
Charadriformes	0.4	0.0	0.6	0.0	0.4	0.7	0.0	1.0	0.0	0.6
Falconiformes	0.7	0.0	1.0	0.0	0.6	0.7	0.0	1.0	0.0	0.6
Birds unidentified	6.9	7.0	6.8	5.6	6.7	17.0	15.7	17.7	12.5	16.4
Eggs	0.0	0.1	0.0	0.0	0.0	0.7	2.0	0.0	0.0	0.6
Invertebrates	8.1	1.4	11.7	0.4	7.0	68.7	45.1	81.3	25.0	62.6
Carabus hortensis	0.7	0.2	1.0	0.0	0.6	12.9	5.9	16.7	0.0	11.1
Carabus coriaceus	0.3	0.0	0.4	0.0	0.2	4.1	0.0	6.3	0.0	3.5
Carabus nemoralis	0.2	0.0	0.3	0.0	0.2	1.4	0.0	2.1	0.0	1.2
Carabus violaceus	0.4	0.0	0.6	0.0	0.3	7.5	2.0	10.4	0.0	6.4
Pterosticus sp.	0.8	0.0	1.2	0.0	0.7	11.6	0.0	17.7	0.0	9.9
Geotrupes sp.	2.0	0.7	2.8	0.0	1.8	34.0	19.6	41.7	0.0	29.2
Nicrophorus sp.	0.0	0.0	0.0	0.0	0.0	2.0	2.0	2.1	0.0	1.8
Aphodius sp.	0.1	0.0	0.2	0.0	0.1	1.4	0.0	2.1	0.0	1.2
Coleoptera unidentified	2.2	0.2	3.3	0.1	1.9	32.7	19.6	39.6	16.7	30.4
Hymenoptera	1.2	0.1	1.7	0.0	1.0	8.8	3.9	11.5	0.0	7.6
Anellida	0.1	0.1	0.1	0.1	0.1	7.5	9.8	6.3	8.3	7.6
Others	0.2	0.1	0.2	0.2	0.2	5.4	3.9	6.3	4.2	5.3
Vegetable items	18.7	4.3	26.4	0.5	16.2	67.3	23.5	90.6	16.7	60.2
Berries	16.5	0.9	24.8	0.5	14.3	58.5	7.8	85.4	12.5	52.0
Fruits	0.0	0.0	0.0	0.0	0.0	1.4	2.0	1.0	0.0	1.2
Plants	2.2	3.4	1.6	0.0	1.9	15.0	13.7	15.6	4.2	13.5
Amphibians/reptiles	0.8	0.5	1.0	0.0	0.7	2.0	2.0	2.1	0.0	1.8
Others/unidentified	0.7	1.5	0.3	2.1	0.9	6.1	9.8	4.2	4.2	5.8
n	147	51	96	24	171	147	51	96	24	171

Development of the diet of adult red foxes from spring to summer

Figures 2 and 3 illustrate, respectively, the WSEs and the FO of the different food items in the diet of adult red foxes during spring and summer. In spring, the diet was essentially dominated by small and medium-large mammals, which, together, accounted for 74% of the WSE. Small mammals represented the most important food item from May to July, accounting for more than 40% of the volume of the total diet ($\chi^2 = 39.500$, df = 4, $p < 0.001$) and occurring in 61% of the scats ($\chi^2 = 15.877$, df = 4, $p = 0.003$). During the same period, medium-large mammals were the second most important food items

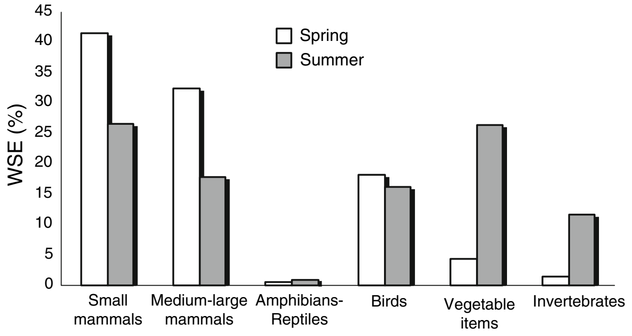

Fig. 2 WSE (%) of the main categories representing all food items composing the diet of adult red foxes during spring ($n=51$) and summer ($n=96$) 2003–2004

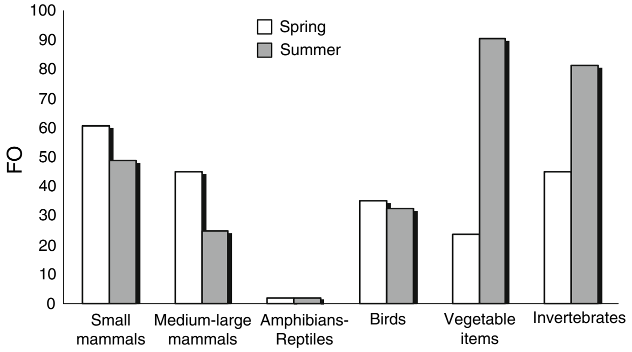

Fig. 3 FO of the seven categories representing the main food items composing the diet of adult red foxes during spring ($n=51$) and summer ($n=96$) 2003–2004

and, among these, roe deer dominated. Invertebrates and vegetable items were virtually irrelevant in terms of volume.

In summer, the available food items occurred more evenly in terms of volume, but more unevenly in terms of FO, when compared to spring. However, the overall occurrence of the various food items still differed in terms of volume ($\chi^2=10.221$, df = 4, $p=0.037$), with invertebrates, small mammals and vegetable items dominating the overall food spectrum (Fig. 2). The food items more frequently detected in the scats during summer were vegetable items and invertebrates ($\chi^2=132.561$, df = 4, $p<0.001$).

Factors affecting the occurrence of small mammals and roe deer in the diet of adult red foxes

Figure 4 illustrates the relationship between the index of abundance of roe deer and small mammals and the FO of roe deer and small mammals in the diet of adult red foxes from May to August. During this period, the availability of roe deer fawns reached a peak on the 19th of June and thereafter decreased (Panzacchi et al. 2007a), while the abundance of small mammals constantly increased according to the formula $y=30.849+2.138x/(1+0.003x)$ (see Panzacchi et al. 2007c). Contrary to our expectations, there was no positive relationship between the occurrence of small mammals in scats from adult red foxes and their index of abundance as the season progressed (GLM, $z=0.432$, df = 47, $p=0.666$). In addition, the occurrence of small mammals in the diet did not increase with time but, actually, decreased ($z=-2.141$, df = 145, $p=0.032$), and also when considering only those species for which we have density estimates (*Microtus*, *Clethrionomys* spp. and *Apodemus*; $z=-2.008$, df = 145, $p=0.045$). The occurrence of roe deer remains in the scats of adult red foxes decreased as summer progressed ($z=-2.443$, df = 145, $p=0.015$), but it was not affected by the index of abundance of roe deer fawns ($z=-0.619$, df = 145, $p=0.536$).

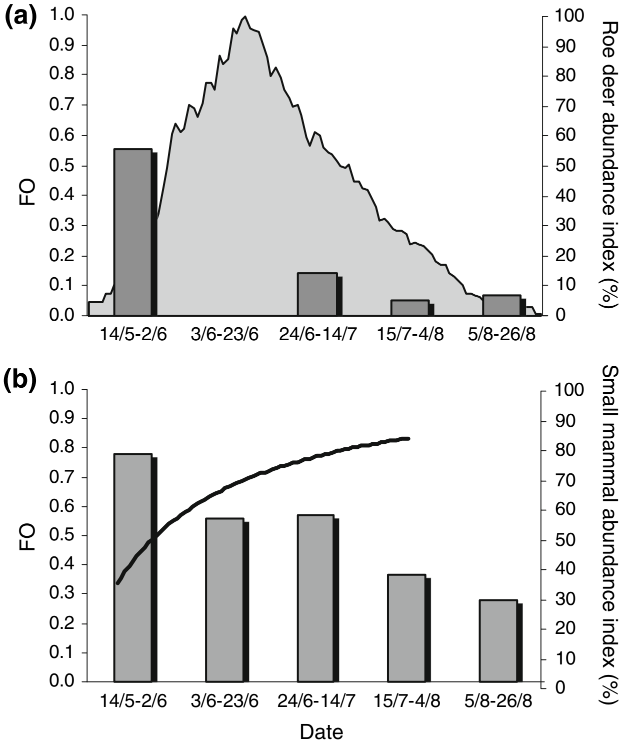

Fig. 4 **a** FO of roe deer fawns in scats of adult foxes (*bars*) compared to the index of abundance of roe deer fawns (*shaded area*) in the stage when they are vulnerable to red fox predation. **b** FO of small mammals in scats of adult foxes (*bars*) during May–August 2003–2004, compared to the index of abundance of small mammals (*curve*) calculated from the 21st May to the 2nd August 2003–2004. The indices of abundance are expressed as percentages with respect to the maximum values calculated during spring and summer. Both the index of abundance and the FO of small mammals refer to *Microtus* spp., *Chletrionomys* spp. and *Apodemus* spp. The indices of abundance of small mammals and of roe deer fawns refer to the same study area where the red fox scats collection has been carried out

Discussion

The overall picture of the red fox diet presented in this study conforms with the surprisingly little data that exists from the boreal forest (mainly Lindström's studies in south-central Sweden; Lindström 1989a, b). The diet was small mammal based (in particular, *M. agrestis*; see also Lindström 1982; O'Mahony et al. 1999), but surprisingly varied for such a northern environment. The results partially supported our predictions P1 and P2, since small mammals were the most important single food item and medium-large mammals, largely represented by roe deer, were the second most important food source in terms of volume. According to our prediction (P2), the rapid appearance of roe deer fawns in the diet of adult red foxes right at the start of the season supported previous studies (Panzacchi et al. 2007a), which indicated that, in our study area, the predators really do make an effort to actively hunt for them as they become available in early spring. Considering, that during, spring some important prey items, such as berries, are not yet available in the boreal forest, and that the vixens need to re-gain the energy lost during the pregnancy and the lactation period, roe deer fawns may actually be of some importance to red foxes during this critical period. However, during the summer, the FO of roe deer fawns in the diet of adult foxes markedly declined. Similarly, and partially contrary to our predictions (P1), the FO of small mammals in the diet of adult red foxes did not reflect their seasonal development in availability, but declined significantly as the season progressed. During the course of summer, adult red foxes replaced small mammals and roe deer fawns by large amounts of berries and invertebrates. Hence, P3 was rejected, as the summer feeding habits of red foxes were more reminiscent of a Mediterranean diet than one expected from the far north (Calisti et al. 1990; Lucherini and Crema 1994; Ciampalini and Lovari 1985). In fact, it would appear that the most homogenous diets occur at middle latitudes (Jedrzejewski and Jedrzejewska 1992).

The diet of cubs differed from that of adult foxes, as it was much less diverse and included a significantly higher proportion of large prey items, such as mammals and birds. Our study shows that, as the season progressed and cubs started eating solid food, the largest prey items were carried to the dens, while adult foxes relied upon smaller and more easily accessible food sources, such as berries and invertebrates.

Lindström (1994) achieved similar results and suggested that the higher FO of large prey items in the diet of cubs at dens reflects the optimal behaviour of a central-place forager (Stephens and Krebs 1986). One implication of the optimal foraging theory (Schoener 1979) is that red foxes are single-prey loaders, which minimise the net energy loss associated with the return to the den by maximising the size of the prey transported.

In addition, Lindström (1994), who studied fox diet in a boreal ecosystem with markedly fluctuating vole densities, showed that the diet of adults and cubs diverged only in years of low vole density, while it converged otherwise. He argued that the availability of large prey items during the years of low vole density might determine the size of the home ranges and, in turn, red fox population density. On the contrary, in our study area, red foxes' main prey do not exhibit multi-annual cycles and, thus, the size of red fox home ranges is likely to be less strictly dependent on the availability of larger prey items compared to areas where small mammals are a periodically limited resource. However, the observed marked divergence between the diet of adults and cubs highlights the importance of large prey items for vixen raising cubs, which is in agreement with the central-place foraging theory. Furthermore, it suggests that either the availability of mammals and birds per predator is limited in our study area or that the vixens' energetic cost of hunting for her own sustenance during the summer exceeds the energy gain of feeding upon larger prey items compared to more easily accessible items, such as insects and berries.

Roe deer remains occurred more frequently in scats found at dens (25%) compared to those from adult foxes (9%), indicating that vixens were using fawns to feed their cubs, and that fawns constituted a profitable food source in our study area. A long-term study in southern Sweden showed that, when the population density of voles, which was subjected to marked multi-annual fluctuations, was higher, the mortality of roe deer fawns was minimal and vice versa (Kjellander and Nordström 2003). This suggests that roe deer fawns represent a key resource for red foxes only when their net profitability exceeds that of the main prey item—as can happen in areas where small mammal populations are cyclic—and that of other alternative large prey items (i.e. birds, hares and domestic animals). In our study area, the medium-high density of roe deer enhanced the profitability of fawns (Panzacchi et al. 2007a, b) and induced the predator to use roe deer fawns as a relevant prey item for raising cubs. However, considering the constant inter-annual availability of red foxes' main prey, and their great trophic plasticity, we suggest that roe deer fawns are an important, but not an irreplaceable, food item for red foxes. Hence, it appears unlikely that the importance of fawns to the diet of foxes, and, hence, to their population dynamics, could be as great as the impact that the predator has on roe deer populations. Thus, in our study area, the newborn ungulates are unlikely to activate any feedback mechanism that could stabilise the predator–prey relationship.

Future studies should further investigate the importance of roe deer fawns for the growth and survival of red fox cubs, and on the overall social regulation of red fox populations in different ecological settings.

Acknowledgements The various stages of this study have been funded by the Norwegian Research Council (three consecutive project grants covering the period 1996–2007 and an individual cultural exchange scholarship to the lead author), the Norwegian Directorate for Nature Management, the Norwegian Institute for Nature Research, the Norwegian Ministry of Defence, the Offices for Environmental Affairs in the counties of Buskerud, Oppland, Hedmark, Akershus, Østfold, and a Marie Curie scholarship to the lead author. The authors are grateful to their colleagues within Scandlynx for their fruitful discussions.

References

Aanes R, Andersen R (1996) The effects of sex, time of birth, and habitat on the vulnerability of roedeer fawns to red fox predation. Can J Zool 74:1857–1865

Andersen R, Linnell JDC (1998) Ecological correlates of mortality of roe deer fawns in a predator-free environment. Can J Zool 76:1217–1225

Angerbjörn A, Tannerfeldt M, Erlinge S (1999) Predator–prey relationships: arctic foxes and lemmings. J Anim Ecol 68:34–49

Calisti M, Ciampalini B, Lovari S, Lucherini M (1990) Food habits and trophic niche variation of the red fox *Vulpes vulpes* (L., 1758) in a Mediterranean coastal area. Rev Ecol 45:309–320

Ciampalini B, Lovari S (1985) Food habits and trophic niche overlap of the badger (*Meles meles* L.) and the red fox (*Vulpes vulpes* L.) in a Mediterranean coastal area. Z Säugetierkunde 50:226–234

Dalgaard P (2002) Introductory statistics with R. Springer, New York. ISBN 0-387-95475-9

Degiorgis MP, Segerstad CH, Christensson B, Mörner T (2001) *Otodectic otoacariasis* in free-ranging Eurasian lynx in Sweden. J Wildl Dis 37(3):626–629

Hanski I, Hansson L, Henttonen H (1991) Specialist predators, generalist predators, and the microtine rodent cycle. J Anim Ecol 60:353–367

Jarnemo A, Liberg O (2005) Red fox removal and roe deer fawn survival—a 14-year study. J Wildl Manage 69(3):1090–1098

Jarnemo A, Liberg O, Lockowandt S, Olsson A, Wahlström K (2004) Predation by red fox on European roe deer fawns in relation to age, sex, and birth date. Can J Zool 82:416–422

Jedrzejewski W, Jedrzejewska B (1992) Foraging and diet of the red fox Vulpes vulpes in relation to variable food resources in Bialowieza National Park, Poland. Ecography 15:212–220

Kjellander P, Nordström J (2003) Cyclic voles, prey switching in red fox, and roe deer dynamics—a test of the alternative prey hypothesis. Oikos 101:338–344

Kruuk H, Parish T (1981) Feeding specialization of the European badger *Meles meles* in Scotland. J Anim Ecol 50(3):773–788

Leckie FM, Thirgood SJ, May R, Redpath SM (1998) Variation in the diet of red foxes on Scottish moorland in relation to prey abundance. Ecography 21:599–604

Lindström ER (1982) Population ecology of the red fox (*Vulpes vulpes* L.) in relation to food supply. PhD thesis, University of Stockholm, Sweden

Lindström ER (1989a) The role of medium-sized carnivores in the Nordic boreal forest. Finn Game Res 46:53–63

Lindström ER (1989b) Food limitation and social regulation in a red fox population. Hol Ecol 12:70–79

Lindström ER (1994) Large prey for small cubs—on crucial resources of a boreal red fox population. Ecography 17(1):17–22

Lindström ER, Andrén H, Angelstam P, Cederlund G, Hörnfeldt B, Jöderberg L, Lemnell P-A, Martinsson B, Sköld K, Swenson JE (1994) Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology 75(4):1042–1049

Lindström ER, Brainerd SM, Helldin JO, Overskaug K (1995) Pine marten—red fox interactions: a case of intraguild predation. Ann Zool Fenn 32:123–130

Linnell JDC, Strand O (2000) Conservation implications of aggressive intra-guild interactions among mammalian carnivores. Div Distrib 6:169–176

Linnell JDC, Strand O (2002) Do arctic foxes Alopex lagopus depend on kills made by large predators? Wildl Biol 8(1):69–75

Linnell JDC, Odden J, Pedersen V, Andersen R (1998) Records of intra-guild predation by Eurasian lynx, *Lynx lynx*. Can Field-Nat 112(4):707–708

Lockie JD (1959) The estimation of the food of foxes. J Wildl Manage 23:224–227

Lucherini M, Crema G (1994) Seasonal variation in diet and trophic niche of the red fox in an Alpine habitat. Z Säugetierkunde 59:1–8

Macdonald DW (1977) On food preference in the red fox. Mamm Rev 7(1):7–23

Mayfield HF (1975) Suggestions for calculating nesting success. Wilson Bull 87:456–466

Meteorologisk Institutt (2006) Home page at http://met.no/index.shtml

O'Mahony D, Lambin X, MacKinnon J, Coles C (1999) Fox predation on cyclic field vole populations in Britain. Ecography 22:575–581

Panzacchi M, Linnell JDC, Odden J, Odden M, Andersen R (2007a) When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. PhD thesis, University of Bologna, Italy; University of Trondheim, Norway

Panzacchi M, Linnell JDC, Odden M, Odden J, Andersen R (2007b) Effect of family and landscape composition on roe deer fawns' predation risk to red foxes. PhD thesis, University of Bologna, Italy; University of Trondheim, Norway

Panzacchi M, Linnell JDC, Melis C, Odden M, Odden J, Andersen R (2007c) Effect of land-use on small mammal abundance and diversity in a forest–farmland mosaic landscape in south eastern Norway. PhD thesis, University of Bologna, Italy; University of Trondheim, Norway

Panzacchi M, Herfindal I, Linnell JDC, Odden M, Odden J, Andersen R (2007d) Predation risk, habitat use and distribution of alternative prey: the case of red fox, roe deer fawns, and small mammals. PhD thesis, University of Bologna, Italy; University of Trondheim, Norway

Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153(5):492–508

R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Home page at http://www.R-project.org

Reynolds JC, Aebischer NJ (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mamm Rev 21(3):97–112

Schoener TW (1979) Generality of the size–distance relation in models of optimal feeding. Am Nat 114:902–914

Selva N, Jedrzejewska B, Jedrzejewski W, Wajrak A (2005) Factors affecting carcass use by a guild of scavengers in European temperate woodland. Can J Zool 83:1590–1601

Smedshaug CA, Selås V, Lund SE, Sonerud GA (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. Wildl Biol 5(3):157–166

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, 247 pp

Teerink BJ (1991) Hair of West-European mammals. Cambridge University Press, Cambridge, 224 pp