The diet of Danish red foxes (Vulpes vulpes) in relation to a changing agricultural ecosystem. A historical perspective

Sussie Pagh, Rune Skjold Tjørnløv, Carsten Riis Olesen & Mariann Chriel

Mammal Research

ISSN 2199-2401

Mamm Res
DOI 10.1007/s13364-015-0244-y

Springer

Mamm Res
DOI 10.1007/s13364-015-0244-y

ORIGINAL PAPER

The diet of Danish red foxes (*Vulpes vulpes*) in relation to a changing agricultural ecosystem. A historical perspective

Sussie Pagh[1] · Rune Skjold Tjørnløv[2] · Carsten Riis Olesen[3] · Mariann Chriel[4]

Received: 21 October 2014 / Accepted: 24 August 2015

Abstract Rodents and especially voles (*Microtus agrestis* or *arvalis*) make up the basic diet of foxes (*Vulpes vulpes*) in Denmark. As the abundance of voles and mice may have decreased as a result of modern agricultural procedures, this study investigates potential changes in the diet of Danish red foxes over the past 4 decades in relation to a changing agricultural landscape. Our study compares the stomach contents of foxes collected in Jutland during the years 2012–2014 with a similar study from 1965 to 1970. The results show that small rodents occur in the stomachs of foxes with the same frequencies today (73 %) as 40–50 years ago (67 %), while the frequency of European brown hare (*Lepus europaeus*) has decreased from 7 to 3 % and the frequency of roe deer (*Capreolus capreolus*) has increased from 3 to 18 %. The changes in the occurrence of brown hare and roe deer in the diet of foxes during the past 40 years most probably reflect changes in the populations of the two species. By comparing digitised orthophotos of six agricultural areas (3.5×3.5 km) of the past 1974/1975 and present landscapes, it was revealed that the total area of crop fields, small natural habitats, hedgerows and grasslands have remained almost unchanged. However, mean field size has increased by 48 %, and the mean size of small natural habitats has increased by 15 %; meaning that the length of field boundaries and the number of small natural habitats have decreased by 65 and 33 %, respectively. The distance between natural habitats in the cultivated areas has become larger during the past 40 years. Overall, the areas of natural biotopes have remained the same in Denmark during the past 40 years. Field boundaries on the other hand which are known to be important vole habitats have become fewer in the cultivated areas. Despite this, small rodents still occur in high frequencies in the diet of nowadays foxes. As voles are sensitive to fragmentation, narrow stipes of permanent grass should be maintained or even re-established in the cultivated areas to improve life conditions for small rodents and other wildlife.

Keywords Food · Rodents · Vole · Microtus · Game species · Roe deer · *Capreolus capreolus* · European brown hare · *Lepus europaeus* · Partridge · *Perdix perdix* · Fragmentation

Communicated by: Matthew W. Hayward

✉ Sussie Pagh
sussiepagh@gmail.com

1 FO-Aarhus, Frederiksgade 78C, Aarhus, Denmark

2 Department of Bioscience, Aarhus University, Frederiksborgvej 399, Roskilde 4000, Denmark

3 Danish Hunters Association, Molsvej 34, 8410 Rønde, Denmark

4 Section for Diagnostics and Scientific Advice, National Veterinary Institute DTU, DK-1790 Copenhagen, Denmark

Introduction

Intensified farming methods have in a relatively short period of time altered the flora and fauna of the agricultural ecosystem, in favour of some species and to the disadvantage of others: European brown hare (*Lepus europaeus*) populations have declined throughout most of Europe since the1960s (Schmidt et al. 2004, 2005; Roedenbeck and Voser 2008; Reynolds et al. 2010), and populations of grey partridge (*Perdix perdix*) have decreased dramatically (Bro et al. 2000; Potts 1986; Potts et al. 2010; Kuijper et al. 2009; Aebischer and Ewald 2010; Topping et al. 2010). In contrast, populations of roe deer (*Capreolus capreolus*), mallard (*Anas platyrhynchos*) and greylag goose (*Anser anser*) have

Published online: 10 September 2015

increased (National Danish game bag records, University of Aarhus (NDGBR)).

The causes of the recent population decline in brown hare and grey partridge have been linked to anthropogenic changes of the rural landscape, e.g. loss of habitat diversity and the use of pesticides (e.g. Potts 1986; Huhta et al. 1996; Smith et al. 2005; Pita et al. 2009; Potts et al. 2010). However, predation, especially that of the red fox, has also been emphasised as a reason for the decline in the populations of small game species, e.g. grey partridge and brown hare (e.g. Newton 1993; Reynolds and Tapper 1996; Coté and Sutherland 1997; Schmidt et al. 2004; Fletcher et al. 2010).

In Europe, the basic diet of the red fox is rodents especially microtine rodents (Lloyd 1980; Jedrzejewski and Jedrzejewska 1992; Kauhala et al. 1998; Leckie et al. 1998; Gołdyn et al. 2003; O'Mahony et al. 1999), which has been confirmed by diet studies on Danish red foxes living in woodlands and rural areas. Bistrup (1890), Jensen and Sequeira (1978) and Nielsen (1990) found small rodents in 60–80 % of the scats or stomachs of foxes, mostly field vole (*Microtus agrestis*) and common vole (*Microtus arvalis*). In some habitats, however, e.g. in the Wadden sea, Toendermarsken, Southern Denmark, rodents occur in lower frequencies, and foxes there have specialised in waterfowl and sheep carrion (Meisner et al. 2014).

The density of rodents is generally low in arable crop fields (Jensen and Hansen 2003; Renwick and Lambin 2011). Rodents are numerous in natural biotopes such as hedgerows, narrow stripes of grass between crop fields, in pastures and meadows, and they are sensitive to landscape fragmentation (Jensen et al. 2014). Many of these natural habitats have disappeared in Denmark since the end of the nineteenth century and up until today (Levin and Normander 2008). Thus, populations of rodents on arable land may show a population decline similar to that of the brown hare and the grey partridge.

Foxes like other generalist predators switch to alternative prey when their preferred prey becomes scarce (Angelstam et al. 1984; Kjellander and Nordström 2003; Jedrzejewski and Jedrzejewska 1992; Small et al. 1993; Meisner et al. 2014). The study done by Goszczynski and Wasilewski (1992) showed that hares probably acted as an alternative prey for foxes, when voles were scarce, although this was not confirmed in the investigation by Panek (2009). Kjellander and Nordström (2003) found that the annual variation in the number of roe deer fawns in autumn was positively related to vole density. In years of high vole density, predation on roe deer fawns was relatively modest, but in years of low vole density, predation was more severe. Hence, if voles and mice populations have decreased on the Danish farmland due to fragmentation and loss of natural habitats, red foxes may have switched to alternative prey of human interest, e.g. game species such as roe deer, brown hare and grey partridge.

The aim of this study was to investigate whether the frequencies of rodents and game species in the diet of Danish red foxes have changed during the past 40–50 years and to relate potential differences in the diet to population changes in prey species and changes in the agricultural landscape.

Methods

Our investigation follows the methods described by Jensen and Sequeira (1978). Jensen and Sequeira (1978) analysed 285 fox stomachs mainly from the winter period and primarily collected on Djursland, and in Mid- and Southern Jutland. In this study, the frequency of prey was based on stomachs with content.

Material

In the present investigation, the contents of 344 stomachs were analysed, excluding 28 stomachs from foxes caught in traps, as these stomachs almost exclusively contained bait used for trapping. Most foxes were shot by hunters during the hunting season (n=251), others were road kills (n=33) and some had an unknown cause of death (n=32). Most foxes (n=278) were sampled during winter (October–February), and 34 foxes were sampled during summer (May–September) and four during spring (March–April). In total, 316 stomachs (of these 265 with content) from Djursland (n=131, n=100 with content), Mid Jutland (n=73, n=56 with content) and Southern Jutland (n=112, n=77 with content) were analysed.

Stomach analysis

The stomach analysis was carried out according to classical and known methods described by Day (1966). Prior to analysis, all stomachs were stored at −20 °C and by −80 °C for at least 1 week to eliminate the health risk of infection with zoonotic parasites. Prior to analysis, two samples were drawn from each stomach to find setae from dissolved earthworms according to methods described by Harris (1981) and Kruuk and Parish (1981). Mammal hairs were identified from microscopic characters of hair medulla, scales and cross sections with the aid of hair identification keys by Debrot et al. (1982) and Teerink (2004). Other items were identified with the use of a reference collection or by colleague experts.

Items found in the stomachs were pooled into 16 main categories as follows: ungulates, other large mammals, lagomorphs, rodents, small passerines (smaller or equal to the size of a blackbird), larger passerines (larger than a black bird), galliformes, anseriformes, other birds, insects, other invertebrates, antropogenetic food sources (e.g. from poultry, domestic pigs and mink farms, dog or cat food, and bird seed balls), fruit, other plant material, garbage and unidentified items. The volume of each category in each stomach was estimated by eye to the nearest 5 %. As the digestion degree of items in stomachs will be in different stages unlike that of scats, it is not possible to use correction factors to compensate for digestion. The amount of individual food items ingested is therefore given in weight calculated by multiplying the percent volume of the item by the total weight stomach content.

Data analysis

Differences between the two studies (the present study and that of Jensen and Sequeira 1978) were assessed using a chi-square test on frequency-of-occurrence data for each category separately. Frequency of occurrence is expressed as the number of stomachs containing a particular category. Stomachs from the winter period were most numerous in both studies, therefore, when presented for the winter period in the paper by Jensen and Sequeira (1978), frequencies of the winter period of both studies were used for comparison.

This study as well as the investigation by Jensen and Sequeira (1978) only included stomachs with content, offering the possibility of direct comparison of frequencies of prey; however, the analysis of seasonal and regional effects and the influence of cause of death on the diet in the present study also included empty stomachs.

Using NPMANOVA and PCA (PAST, Hammer et al. 2001), possible patterns in the diet composition (total weight of stomach content, weight of stomach content of roe deer, brown hare, rodents, passerine bird, wild galliformes and wildfowl) of different regions, years and with different causes of death were analysed. The NPANOVA was based on Bray-Curtis with Bonferruni-corrected *p* values. PCA was based on the covariance matrix. Tendencies revealed by NPMANOVA and PCA were further tested using univariate statistics using PAST (Hammer et al. 2001).

An index of difference, $D=(\sum|a-b|)/n$, where a is the frequency of occurrence of prey in a prey group of region a, b is the frequency of occurrence of prey in a group of region b, n is the number of prey groups (Frafjord 1993), was used to calculate the diet differences of foxes between the three regions (Djursland, Mid-Jutland and Southern Jutland) in the present study and to compare it with the D-index between the winter of the present investigation and the investigation by Jensen and Sequeira (1978).

Landscape changes from 1974 to 2010

To quantify major changes of the rural landscape over the past 4 decades, relevant landscape parameters focusing on natural habitats of rodents and small game species were digitised from orthophotos of the past (1974/1975) and present (2010) landscape using ArcGIS 10.2.1.

Historic and modern landscape parameters were digitised for six study areas (each 3.5 km×3.5 km) including four areas in Djursland (1974/2010) and two in Southern Jutland (1975/2010) with half of the study areas having a more intensified land use and the other half having a less intensified land use and more forestry.

The following parameters were digitised: (1) forest, (2) crop fields, (3) grass fields used for hay/livestock, (4) permanent grassland (grassland out of production, normally areas with high grass and scattered bushes and small trees), (5) meadows (wet), (6) buildings, (7) roads, (8) small habitat (non-cultivated areas in crop fields often moist patches with scrub), (9) hedgerows, (10) zones of non-cultivated land between fields and roads, (11) edge of woods and (12) field boundaries (narrow stripes of grass between fields). In the following, permanent grassland, meadows, small habitats, hedgerows, zones of non-cultivated land between fields and roads, edges of woods and field boundaries will be defined together as natural biotopes.

For the calculation of the total area (parameters 1–10) or length (parameters 10–12) occupied by each landscape parameter, the digitised parameters were clipped using the circumference of the areas thereby constraining the total area of all parameters to $3.5\times3.5\ km^2$. To obtain a measurement of the mean size of each parameter, we only used elements having their centroid inside the study area.

Results

The mean weight of stomachs was 104 g±105 (±SD). The mean weight of stomachs with content (excluding empty stomachs) was 123 g±104 (±SD). The stomachs were from 163 adult females, 149 adult males, five cubs (four females and one male) and four foxes of unknown sex. The mean weight of the 80 females was 5.8 kg±1.2 (±SD), and the mean weight of the 77 males was 6.6 kg±1.1 (±SD).

Mammals

Remains of mammals were found in 238 (89 %) stomachs with content. Ungulates (roe deer) were found in 46 stomachs (17 %). Since most stomachs were from the winter period, roe deer was eaten as carrion most probably from road kills or as offal left from hunters. Domestic pigs were found in 18 (7 %) stomachs. Lagomorphs were found in 17 (6 %) stomachs. We were unable to distinguish between the hairs of rabbits (*Oryctolagus cuniculus*) and brown hares, but we considered all lagomorph hairs to originate from the latter species since rabbits only occur in small populations in some parts of Southern Denmark. Small rodents were found in 194 (73 %) stomachs. Remains from other larger mammals that were found in 37 (14 %) stomachs of these 6 sheep (*Ovis aries*), 4 mink (*Neovison vison*), 2 martes sp, 1 badger (*Meles meles*), 1 fox and 6 cats (*Felis catus*), could be identified.

In total, 341 rodents were identified; hence, stomachs with rodents contained 1.76 rodent per stomach. Most stomachs contained between one and three rodents, four stomachs contained more than 15 rodents and up to 32 rodents were found in a single stomach. Most rodents were identified as microtidae (n=273, 80 % of the rodents). Of these 210 were identified as field (*Microtus agrestis*) or common vole (*Microtus arvalis*), 5 as European water vole (*Arvicola amphibious*) and 11 as bank voles (*Myodes glareolus*). Only 14 % were identified as muridae: 5 rats (*Rattus norvegicus*), 30 harvest mouse (*Micromys minutus*) and 7 *Apodemus* sp.

Insectivora

No insectivores were found in the stomachs of foxes in this study.

Birds

Birds were found in 96 (36 %) stomachs with content. Of these, 35 (13 %) were galliformes, at least 15 (6 %) were poultry, hence considered as an "anthropogenic" food source, leaving 20 (7 %) as wild galliformes. Passerine birds were the most frequent group of bird species found in the stomachs, occurring in 30 (11 %) of stomachs with content. Of these, 8 % were smaller and 3 % larger passerine birds. Anseriformes (including one domestic duck) were found in 16 (10 %) stomachs. Other birds were assigned to the groups columbiformes (n=3) and seagulls (n=2).

Wild bird species identified from feathers or other remains, e.g. from bills or legs, were pheasant (*Phasianus colchicus*) (n=12), mallard (*Anas platyrhynchos*) (n=3), teal (*Anas crecca*) (n=1), corvidae (n=6) of these one hooded crow (*Corvus cornix*) and one eurasian jay (*Garrulus glandarius*), common blackbird (*Turdus merula*) (n=6), fieldfare (*Turdus pilaris*), Redwing (*Turdus iliacus*), song thrush (*Turdus philomelos*), house- or/ eurasian tree sparrow (*Passer domesticus/ P. Montanus*), one blue tit (*Parus caeruleus*), common chaffinch (*Fringilla coelebs*) and brambling (*F. monti fringilla*). Remains of eggshells were found in four stomachs.

Reptiles, amphibians and fish

No remains of reptiles or amphibians were identified in this study. Remains of fish were found in eight stomachs (3 %). In one case, the remains of fish were found in the same stomach as the remains of a mink; hence, the fish remains in this case may be remains from the stomach of the mink.

Insects and other invertebrates

In total, 35 (13 %) stomachs contained invertebrates, most invertebrates were insects, and especially dung beetles and ground beetles were common, occurring in 14 stomachs (5 %).

Insects and especially large beetles were found: dung beetles (12 stomachs), *Geótrupes vernalis* (one stomach with 1 individual), *Anoplotrupes stercorosus* (6 stomachs, approx. 50 individuals) and *Geotrupes spiniger* (4 stomachs approx. 10 individuals); and ground beetles, *Carabus hortensis* (2 stomachs with 2 individuals), *Carabus granulatus*, (2 stomachs with 2 individuals), *Carabus nemoralis* (1 stomach with 1 individual.), *Pterostichus sp* (3 stomachs with 3 individuals), *Pterostichus vericicoler* (1 stomach with 1 individual.), *Pterostichus niger or P. melanarius* (2 stomachs with 2 individuals). Also, larvae of diptera, *Noctuidae* sp., *Dytiscidae* sp., *Silphidae* sp. and *Nicrophorus* sp., were found in few numbers. Earthworms or remains of earthworms were found in five stomachs, remains of a crab in one stomach, parasites *Toxocara canis* in five stomachs and *Sarcoptic scabei* from auto-grooming in one stomach.

Plant material

Plant material, e.g. leaves from herbs and trees, twigs, hay, seeds or remains of fruit, was found in most stomachs (n=202, 76 % of stomachs with content). In most cases, the plant material appeared to have been swallowed incidentally along with prey. Grass as well as fruits may, however, have been eaten deliberately. Seeds and/or skin and flesh of cherries (*Prunus avium*), mirabells (*Prunus cerasifera*), apples (*Mallus* sp) and raspberry (*Rubus* sp) were found in 51 stomachs.

Anthropogenic food

Remains of food produced by humans were found in 28 stomachs (including 15 domestic hens and one duck). Also at least one domestic rabbit with an ear tag was found. Bird seed balls were found in four stomachs and what was considered to be leftovers from meals in three stomachs and cat or dog feed in two stomachs. Domestic pigs and sheep have been included in the section "Mammals."

Other remains

Unidentified remains and garbage were found in 50 stomachs but made up less than 5 % of the total weight. This could, for instance, be pieces of plastic, cloth, lumps of fat, gristle and fragments of bones.

The diet of foxes in 1965–1970 compared to that of 2012–2013

Significant differences between the diet of foxes in the two time periods 1965–1970 and 2012–2013 were found in almost half of the main food categories. The difference in the occurrence of ungulates, domestic pig, poultry and insects was found to be highly significant (Table 1). Ungulates were found in higher frequencies, and domestic pig and poultry in lower frequencies in the present study compared to the study conducted 40 years ago. Lagomorphs also occurred in lower frequencies in the present study compared to the reference study. The overall frequency of rodents did not vary significantly.

Variation in diet between region and research year

Principal component analysis (PCA) showed significance on the first vector explaining 73 % of the variance. Highest loading values were 0.93 for stomach content, 0.33 for roe deer and 0.13 for small rodent.

NPMANOVA (one way) showed no significant differences in relation to region and sex, but significance was found in relation to research year and death causes (Table 2). Univariate analysis showed no significance for death cause (Table 2). Univariate analysis showed that the mean weight of roe deer was significantly higher in the stomachs of foxes in the winter 2012/2013 than in the winter 2013/2014. Also, rodents occurred in higher numbers in the winter 2012/2013 than in the winter 2013/2014 (Table 2).

No other tendencies in the amount of main food categories could be revealed in relation to research year, region and cause of death or sex.

The D-index within the three regions (Djursland, Mid Jutland and Southern Jutland) (D=5.7) was lower than the historical D-index (D=12.40) between the winter diet of the present investigation and the investigation by Jensen and Sequeira (1978) (Table 3). The historical D-index was significantly higher (t test, p<0.02), than the D-index between regions.

Comparison of landscape parameters from 1974/1975 to 2010

The result of the landscape analysis of the six agricultural areas showed that crop fields, buildings and roads covered around 70 % of the areas, woodlands around 20 % and only 10 % of the present agricultural landscape are left for natural habitats such as small natural biotopes, hedgerows, grasslands, field boundaries and uncultivated areas between crop fields and roads (Table 4). Surprisingly, this had not changed markedly during the past 40 years. However, the mean area of crop fields had increased by approx. 48 %, and as a consequence, the extent (m) of field boundaries had been reduced by 65 % (Fig. 1). Also, the mean size of small natural habitats had increased by 15 %; hence, their number had decreased by 33 % (Table 4).

Discussion

The study confirms the opportunistic food habits of the red fox. Microtine rodents, especially field vole and common vole, are the most frequent prey found in the stomachs of Danish red foxes. Yet, roe deer carrion, birds, insects, fruit

Table 1 The frequency (in percent of stomachs with content) of main food groups found in the present study and the study by Jensen and Sequeira (1978)

Prey group	Present study 2012–2013			Study 1965–1970 (Jensen and Sequeira 1978)			Comparison (chi-square)	
	Summer	Winter	Total	Summer	Winter	Total	p value	Sample
Rodentia	57	76	73	68	67	67	0.05	Winter
Lagomorphs	0	7	6	19	14	15	0.03	Winter
Ungulata	11	18	17	0	3	2	0.0001	Winter
Domestic pig	11	6	7	10	31	27	0.0001	Winter
Poultry	0	7	6	15	28	15	0.0001	Winter
Wild birds	29	31	30	37	37	37	0.18	Winter
Galliformes	4	8	8	–	–	6	0.8	Total
Anseriformes	7	6	6	–	–	3	0.43	Total
Passeriformes	18	11	11	–	–	17	1	Total
Insects	21	4	6	34	19	22	0.0001	Winter
Fruit	18	20	19	10	19	16	0.92	Winter
No. of stomachs	28	233	265	59	226	285		

The frequencies of the main food groups of the two studies are compared with chi-square test

Table 2 Results of NPMANOVA and univariate analyses on the weight (g) of prey items in stomachs in relation to region, research year, sex and cause of death

Variable	NPMANOVA	Stomach content	Roe deer	Small rodent
Region (n=3)	$p \leq 0.08$; F=1.766 NS	–	–	–
Year (n=2)	$p \leq 0.002$; F=4.769	$p \leq 0.06$ NS	Mean weight winter 12/13=22.48 g±SD 6.58 Mean weight winter 13/14=11.39 g±SD 3.57 $p \leq 0.001$ (Mann-Whitney)	Mean weight winter 12/13=35.96 g±SD 4.28 Mean weight winter 13/14=27.86 g±SD 3.63 $p \leq 0.04$ (Mann-Whitney)
Sex	$p \leq 0.67$; F=0,6163 NS	–	–	–
Death cause	$p \leq 0.003$; F=2.605	$p \leq 0.16$ NS	$p \leq 0.62$ NS	$p \leq 0.11$ NS

NS non-significant

and anthropogenic food also make up an important part of the diet of Danish foxes.

The diet of foxes is known to vary both between local habitats and between seasons (e.g. Nielsen 1990; Meisner et al. 2014). Multivariate analysis (NPMANOVA), however, showed no significant differences between the regions of this investigation, and the D-index (Frafjord 1993) showed that the differences found between the two time periods in this study were significantly larger than those found between the three regions. Thus, the differences found between the two studies are likely to be caused by changes in availability of prey during the past 40 years. Collecting foxes from larger regions of Denmark will represent foxes from different habitats. Therefore, on this larger regional scale, data on fox diet are not likely to be sensitive to bias caused by feeding habits of local foxes. A comparison of the data from the present study with that of the reference study is based on frequencies of food items. Therefore, there has been no attempt to neither calculate nor discuss the actual food intake in biomass by the foxes (Lokie 1959; Putman 1984; Reynolds and Aebischer 1991; Klare et al. 2011).

The result of the present landscape analysis is comparable to earlier and larger analyses of the Danish landscape by Levin and Normander (2008). Around the year 2000, agricultural areas accounted for approx. 60 % of Denmark, forest approx. 11 %, open natural and semi-natural habitats (dry/mesic, wet and open grasslands, coastal meadows, scrub heathlands, mires and dunes) for 10 % and built-up areas approx. 10 %. In comparison, open areas of natural habitats covered more than 25 % of Denmark in 1888 (Levin and Normander 2008).

Density-dependent consumption of roe deer

The content of roe deer remains in the stomachs of the foxes has increased significantly compared to the earlier study by Jensen and Sequeira 1978. This increase is undoubtedly due to the increased abundance of roe deer. In Denmark, the National game bag records of roe deer was 35,000 in 1970 (NDGBR), and in 2012 around 122,000 (Asferg 2014). The overall increase in the number of roe deer in Europe is associated with the general increase in woodland areas in the recent decades, more extensively grown winter cereals and lack of competition with former more abundant livestock husbandry feeding

Table 3 Comparison of food frequencies in stomachs from foxes sampled in the three regions

Prey group	Frequency of preygroup in the present study			Difference	
	Djursland	Mid-Jutland	South Jutland	Between regions	Historically
Rodentia	80	71	74	6.00	9.00
Lagomorphs	4	9	11	4.67	7.00
Ungulata	24	11	17	8.67	15.00
Domestic pig	5	4	8	2.67	25.00
Poultry	7	2	9	4.67	21.00
Wild birds	46	34	30	10.67	6.00
Insects	5	2	3	2.00	15.00
Fruit	21	12	14	6.00	1.00
No. of stomachs	100	56	77		
D-index				5.67	12.40

Historically (Jensen and Sequeira 1978)

Table 4 Mean and standard deviation (SD) of parameters of the six agricultural areas of Denmark (each 3.5 × 3.5 km^2) digitised from orthophotos from 1974/1975 to 2010

Digitised parameter	Mean 1974	Mean 2010	% difference in relation to 2010	SD 1974	SD 2010	% of total areal 1974	% of total areal 2010
Forest (m^2)	2,415,845	2,756,433	12	2,142,718	2,474,165	20	23
Crop fields (m^2)	8,340,846	7,848,793	−6	1,929,182	2,190,127	68	64
Grassfields used for hay/lifestock (m^2)	522,430	473,755	−10	141,488	267,993	4	4
Permanent grassland (m^2)	113,509	228,002	50	73,768	137,176	1	2
Meadows (wet) (m^2)	69,354	73,262	5	0	0	1	1
Buildings (m^2)	317,884	401,868	21	131,122	216,239	3	3
Roads (m^2)	89,720	93,378	4	21,391	20,530	1	1
Small natural habitats (m^2)	30,243	30,579	1	30,243	6523	0	0
Zones of non-cultivated land (m^2)	179,581	160,828	−12	68,274	59,156	1	1
Hedgerows (m^2)	138,950	152,661	9	36,490	152,661	1	1
Edge of woods (m)	44,167	53,399	17	44,167	35,261		
Mean field size (m^2)	25,345	48,290	48	6296	9004		
Mean size of small natural biotope (m^2)	1285	1517	15	456	508		
Field boundaries (m)	99,160	59,931	−65	31,045	19,741		
No of hedgerows	78	76	−2	15	76		
No of small natural habitats	29	22	−33	18	8		

on understory vegetation (Fuller and Gill 2001; Olesen and Asferg 2006). In addition, a milder climate and less snowy winters may play an important role in the success and northern boundaries of the roe deer population (Mysterud and Østerby 2006).

It should be stated that remains of roe deer found in the stomachs in this study mainly derive from adult individuals, as most of the stomachs analysed were from foxes killed during the winter time, and therefore presumably from carcases. Most of the roe deer carcases probably derived from fallen roe deer, road kills or offal from hunters, all likely to be more abundant nowadays than in 1974. Fox predation on fawns has previously been found to be related to the density of roe deer (Panzacchi et al. (2008), it is therefore expected that fox

Fig. 1 Cultivated landscape (3.5 km × 3.5 km) from Mid-Jutland. The digitised parameters show the fragmentation of the landscape, especially due to the reduction in field boundaries from 1974 to 2010

predation on fawns has increased, too. However, there should be no need for concern for roe deer population in relation to fox predation as the roe deer population has nearly quadrupled during the past 40 years, despite of predation by foxes.

Fox predation on European brown hare

The frequency of brown hare remains in the stomachs of foxes in the present study is 50 % below the frequency found by Jensen and Sequeira (1978). This drop is most probably associated with the marked drop in the population of brown hare in Denmark. The game bag records of brown hare in Denmark have dropped from around 300,000 hares in 1970 according to the NDGBR to around 50,000 in 2012/2013 (Asferg 2014). Game bags are assumed to correlate to the abundance of hares, although hunters in recent years may have reduced the hunting pressure on hares to protect the population (Jensen 2009). Long-term studies of game bag records of foxes in Denmark and Germany showed negative correlations between the game bags of hares and foxes (Schmidt et al. 2004; Jensen 2009; Knauer et al. 2010). In some studies, fox control has shown to increase the abundance of hares (Panek et al. 2006; Reynolds et al. 2010).

In a recent investigation by Panek (2013), fox predation on hares in western Poland showed a type III functional predator response to long-term changes in hare abundance, i.e. the graphical relationship between of number of prey consumed and the density of the prey population is sigmoidal. This means that foxes at low prey densities will drop hunting efforts on the prey- in this case hares -, preventing the extinction of hares. With increasing prey density, foxes will according to the model accelerate their hunting efforts by more than a linear relationship; hence, a moderate reduction of the fox population may only result in the remaining foxes catching more hares (Panek 2013). The significant increase in the frequency of hare remains found in the fox stomachs from 2012 to 2013 may support a type III functional predator response by the foxes, as game bag records of foxes have dropped by 26 % from the hunting season 2012/2013 to 2013/2014 (Asferg 2014). The sudden drop in the hunting season 2012/2013 compared to 2013/14 may be due to a widespread outbreak of canine distemper in Jutland in the summer of 2012 (Asferg 2014; Trebbien et al. 2014). However, more data on the frequency of hare remains in fox stomachs or scats related to the proportion between abundance of foxes and hares is needed to reveal if it is a general trend.

The influence of habitat factors on the hare population

Especially crop field size has increased from 1974/1975 to 2010 in the Danish agricultural areas; hence, length of field boundaries has decreased. In most studies, field size was found to be negatively correlated with hare abundance, and the presence of pasture positively correlated with hare abundance (Smith et al 2005). In a Danish investigation (Schmidt et al. 2004), winter cereals were found to have a significant negative association with brown hare abundance, whereas root crop areas were positively related to hare numbers. Fox predation on hares decreased with increasing habitat diversity, especially in areas with low hare density (Panek 2009). Also, Smith et al. (2005) conclude, on the basis of 77 research papers from 12 European countries, that habitat changes caused by agricultural intensification are the ultimate cause of the decline in the hare population. The influence of predators is reinforced due to loss of high-quality year-round forage and cover (Smith et al 2005). Parameters such as habitat diversity, fallow land, vegetation cover and small woodlands are positively correlated with hare density (Smith et al 2005). The reduction of the hare population and the following drop of hares in the diet of foxes are most probably initiated by increasing field size and loss of habitat diversity in the cultivated areas of Denmark.

Rodents in the diet of foxes

It is not clear from the landscape analysis whether the overall population of voles may have changed during the past 40 years due to loss of natural habitats. On one hand, the area of rodent habitats such as permanent grasslands, meadows and small natural habitats has not been reduced significantly during the past 40 years; on the other, fields have become larger, and therefore, many narrow stripes of grass between adjacent fields have disappeared (Table 4, Fig. 1). Therefore, populations of voles in the cultivated areas have most probably decreased.

Vole populations are known to exhibit three to four yearly cyclic population dynamics not only in northern Fennoscandia but also in Central, Western and Southern Europe (Lambin et al. 2006; Dell'Arte et al. 2007). Also, it is known that the occurrence of voles in the diet of foxes is related to the density of voles (Leckie et al. 1998; Sidorovich et al. 2006; Dell'Arte et al. 2007). Therefore, the occurrence of rodents in the stomachs of foxes in the present study and that of Jensen and Sequeira (1978) could reflect only the instantaneous vole numbers at the time when the study was carried out. However, the data from the study by Jensen and Sequeira (1978) are not expected to be sensitive to yearly cyclic oscillation in vole abundance, as the study was conducted over a 5-year time period. Regarding the present study, it is known, from a monitoring study of mice and voles on Djursland carried out by the Natural History Museum of Aarhus during 14 years, that the number of field vole in 2012 and 2013 at this locality was below the maximum voles numbers found in 2005, with 26 and 76 %, respectively (personal communication, Christina Vedel-Smith, Natural History Museum). The number of voles on Djursland is expected to mirror vole cycles in other parts of the country in vole habitats the same year, meaning that the number of field voles was above average in October 2012, while that of October 2013 was below average. The relatively high frequency of voles found in the diet of foxes in this study does therefore not seem to reflect exceptionally high numbers of field voles in the research years. The significantly higher mean weight of small rodents in the fox stomachs in winter 2012/2013 than in the winter 2013/2014 (Table 2) may reflect that voles numbers were higher in October 2012 than in October 2013.

The fox population may have been below usual. There has been a long-term drop in the game bags of foxes in Denmark during the past 40 years. The National game bag record of foxes in Denmark reports a reduction in the number of hunted foxes from around 55,000 in 1974 to just below 40,000 foxes in 2011 to less than 28,000 foxes in 2013/2014 ((NDGBR), Asferg 2014). The significant drop in the hunting bags in 2013–2014 is most likely a result of severe outbreak for canine distemper resulting in marked decrease of foxes in Jutland (Trebbien et al. 2014). It is not known if the long-term drop in the game bag of foxes is due to chance in hunting pressure on foxes or if the fox population has decreased in number. It is expected that the number of foxes to share rodents in an area may affect the intake of rodents per fox. Although vole numbers most probably have decreased in the cultivated areas of Denmark, this study show that foxes are still able to maintain high frequencies of rodents in the diet in years with moderate to high number of voles. A study of the dietary structure of foxes in Belarus showed that foxes will prefer voles rather than other prey, if voles are present in high numbers even if other prey is available (Sidorovich et al. 2006).

Wild galliformes in the diet of foxes

The frequency of wild galliformes in the current diet of foxes was not different from that found by Jensen and Sequeira (1978). While the National game bag records of common pheasant (*Phasianus colchicus*) was almost the same in 1974 (NDGBR) as in 2013/2014, around 700,000 birds, the game bag records of grey partridge have decreased markedly from around 200,000 birds in 1974 to 28,000 birds in 2013/2014 (NDGBR, Asferg 2014). No remains of partridges were found in the present study. However, it is not always possible to distinguish between other galliformes and partridges; therefore, few partridge may have been among the food items.

Fewer insects in the diet of foxes

Significantly fewer insects were found in the diet of today's foxes than that of foxes 40 years ago (Table 1). In both investigations, insects eaten by the foxes were mostly dung beetles and larger ground beetles. Although ground beetle populations may have declined in the Danish agricultural landscape, the major cause for the drop in insect remains should undoubtedly be addressed to fewer dung beetles as a consequence of fewer pastures with livestock. In Denmark in 1974, there were approx. 1 million dairy cows all on pasture in the summer period, and in 2013, this has been reduced to 500,000 dairy cows and less than 25 % of the dairy cattle are on pastures in the summer (according to Statistics on agriculture, gardening and forestry 1974; Knowledge Centre for Agriculture, UHL). Thus, the areas of traditional cattle-grazed pastures with dung have declined significantly.

Major switch in anthropogenic food items

From 1974 until today, there has been a major switch in diet of foxes caused by human activities (Table 1). The reduced occurrence of domestic pigs and poultry is due to changed husbandry and stricter regulation on carcase disposal. In 1974, it was still common to discard dead piglets and hens on the dunghills behind the farm. Today, it is mandatory to leave dead piglets and poultry in closed containers to be collected for rendering by a special collection service. This has reduced the possibility for foxes to scavenge on offal from animal production.

Urban areas have become of growing importance for foxes. Bird seed balls and food for cats, dogs or hedgehogs like, e.g. leftovers from meals and pet food in the stomachs of foxes in the present study, indicate that nowadays foxes search for food around houses.

Concluding remarks

In spite of the reduction in field boundaries in the cultivated areas, the frequency of rodents was found to be high in the diet of foxes today as well as in the study 40 years ago. The study also confirms that consumption on hares and roe deer is density-dependent. Natural biotopes should be re-established in the intensively managed agricultural ecosystem to serve as a refuge for voles and other wildlife. As foxes seem to prefer voles to other prey, restoring vole habitats may reduce fox predation on other wildlife.

Acknowledgments We thank The 15th Juni Foundation and the Danish Hunters' Nature Foundation for supporting our project. We are grateful to the many hunters and employees at the Falck rescure stations for collecting foxes for us and special thanks go to Jesper Kjær Illemand and Klaus Berg for laboratory assistance. We would also like to thank a number of people for their assistance in the identification of food items: Jørgen Terp Laursen for identification of teeth of small rodents, Stefan Pihl for identification of feathers, Søren Tolsgaard for identification of insects and Mohammad Nafi Solaiman Al-Sabi for identifying parasites found in the stomach contents, and Else-Marie Nielsen and Karin Coles for English corrections and to Cino Pertoldi for statistical advises.

Ethical standards The study complies with the current Danish laws. No animals were sacrificed for the purposes of this study. Therefore, a formal approval by an Institutional Animal Care and Use Committee was not necessary.

Conflict of interest The authors declare that they have no conflicts of interest.

References

Aebischer NJ, Ewald JA (2010) Grey partridge *Perdix perdix* in the UK: recovery status, set-aside and shooting. Ibis 152:530–542

Angelstam P, Lindström E, Widén P (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia 62:199–208

Asferg T (2014) Vildtudbyttestatistik for jagtsæsonen 2013/14. Notat fra DCE – Nationalt Center for Miljø og Energi. Aarhus Universitet

Bistrup E (1890) Ræven og musene. Tidsskrift Skovvæsen 2A:37–43

Bro E, Sarrazin F, Clobert J, Reitz F (2000) Demography and the decline of the Grey partridge *Perdix perdix* in France. J Appl Ecol 37:432–448

Coté IM, Sutherland V (1997) The effectiveness of removing predators to protect bird populations. Conserv Biol 11:395–405

Day MG (1966) Identification of hair and feather remains in the guts and faeces of stoats and weasels. J Zool (Lond) 148:201–217

Debrot S, Fivaz G, Mermod C, Weber JM (1982) Atlas des poils de mammifères d'Europe. (Atlas of the hair of European mammals.). University of Neuchâtel, Neuchâtel

Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimäki E (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecol 31:276–281

Fletcher K, Aebischer NJ, Baines D, Foster R, Hoodless AN (2010) Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. J Appl Ecol 47:263–272

Frafjord K (1993) Food habits of Arctic foxes (*Alopex lagopus*) on the western coast of Svalbard. Arctic 46:49–54

Fuller RJ, Gill RMA (2001) Ecological impacts of deer in woodland. Forestry 74:189–192

Gołdyn B, Hromada M, Surmacki A, Tryjanowski P (2003) Habitat use and diet of the Red fox *Vulpes vulpes* in an agricultural landscape in Poland. Z Jagdwiss 49:191–200

Goszczynski J, Wasilewski M (1992) Predation of foxes on a hare population in central Poland. Acta Theriol 37:329–338

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4(1):9pp. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Harris S (1981) The food of suburban foxes (V*ulpes vulpes*), with special reference to London. Mam Rev 11:151–168

Huhta E, Mappes T, Jokimäki J (1996) Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. Ecography 19:85–86

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

Jensen TL (2009) Identifying causes for population decline of the brown hare (*Lepus europaeus*) in agricultural landscapes in Denmark. PhD-Thesis. National Environmental Research Institute (Aarhus University). 193pp

Jensen TS, Hansen TS (2003) Biodiversitet og biotopfordeling hos småpattedyr i det åbne land. Flora Fauna 109:9–21

Jensen B, Sequeira DM (1978) The Diet of the Red Fox (*Vulpes vulpes* L.) in Denmark. Danish Rev Game Biol 10(8):1–16

Jensen TS, Olsen K, Hansen TS (2014) Fungerer økologisk jordbrug som refugium for småpattedyr? Flora Fauna 119:142–149

Kauhala K, Laukkanen P, Von Rége I (1998) Summer food composition and food niche overlap of the Raccoon dog, Red fox and badger in Finland. Ecography 21:457–463

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

Klare U, Kamler JF, Macdonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. Mammal Rev 41(4):294–312

Knauer F, Küchenhoff H, Pilz S (2010) A statistical analysis of the relationship between Red fox *Vulpes vulpes* and its prey species (Grey partridge *Perdix perdix*, Brown hare *Lepus europaeus* and rabbit *Oryctolagus cuniculus*) in western germany from 1958 to 1998. Wildl Biol 16:56–65

Knowledge Centre for Agriculture, UHL: http://www.vfl.dk/Afdelinger/Kvaeg/FaktaOmKvaegproduktion/Dyrevelfaerd/Faktaomkoerpaagraes/hvor_mange_paa_graes.htm#.VEYSjE2KDIU

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

Kuijper DPJ, Oosterveld E, Wymenga E (2009) Decline and potential recovery of the European Grey partridge (*Perdix perdix*) population-a review. Eur J Wildl Res 1–9

Lambin X, Bretagnolle V, Yoccoz NG (2006) Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? J Anim Ecol 75:340–349

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

Levin G, Normander B (2008) Land-use in Denmark from the end of the nineteenth century up until today. Faglig rapport fra DMU no. 682. University of Aarhus, Denmark

Lloyd HG (1980) The red fox. Harper Collins Distribution Services

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

Meisner K, Sunde P, Clausen KK, Clausen P, Fælled C, Hoelgaard M (2014) Foraging ecology and spatial behavior of the Red fox (*Vulpes vulpes*) in a wet grassland ecosystem. Acta Theriol 59(3):377–389

Mysterud A, Østerby E (2006) Effect on climate and density on individual and population growth of Roe deer (*Capreolus capreolus*) at northern latitudes: the Lier Valley, Norway. Wildl Biol 12:321–329

Newton I (1993) Predation and limitation of bird numbers. Curr Ornithol 11:143–198

Nielsen SM (1990) The food of rural and suburban woodland foxes (*Vulpes vulpes*) in Denmark. Nat Jutlandica 23:25–32

Olesen CR, Asferg T (2006) Assessing potential causes for the population decline of European brown hare in the agricultural landscape of Europe - a review of the current knowledge, National Environmental Research Institute (NERI Technical Report). http://www2.dmu.dk/pub/fr600.pdf

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

Panek M (2009) Factors affecting predation of Red foxes *Vulpes vulpes* on Brown hares *Lepus europaeus* during the breeding season in Poland. Wildl Biol 15:345–349

Panek M (2013) Long-term changes in the feeding pattern of red foxes *Vulpes vulpes* and their predation on brown hares *Lepus europaeus* in western Poland. Eur J Wildl Res 59:581–586

Panek M, Kamieniarz R, Bresiñski W (2006) The effect of experimental removal of red foxes *Vulpes vulpes* on spring density of brown hares *Lepus europaeus* in western Poland. Marek Acta Theriol 51(2):187–193

Panzacchi M, Linnell JDC, Odden J, Odden M, Andersen R (2008) When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions. Can J Zool 86:116–126

Pita R, Mira A, Moreira F, Morgado R, Beja P (2009) Influence of landscape characteristics on carnivore diversity and abundance in mediterranean farmland. Agric Ecosyst Environ 132:57–65

Potts GR (1986) The partridge: pesticides, predation and conservation

Potts GR, Ewald JA, Aebischer NJ (2010) Long-term changes in the flora of the cereal ecosystem on the Sussex Downs, England, focusing on the years 1968-2005. J Appl Ecol 47:215–226

Putman RJ (1984) Facts from faeces. Mammal Rev 14:79–97

Renwick AR, Lambin X (2011) Abundance thresholds and the underlying ecological processes: field voles *Microtus agrestis* in a fragmented landscape. Agric Ecosyst Environ 144:364–369

Reynolds CR, 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*. Mammal Rev 21:97–122

Reynolds JC, Tapper SC (1996) Control of mammalian predators in game management and conservation. Mam Rev 26:127–155. doi:10.1111/j.1365-2907.1996.tb00150.x

Reynolds JC, Stoate C, Brockless MH, Aebischer NJ, Tapper SC (2010) The consequences of predator control of Brown hares (*Lepus europaeus*) pn UK farmland. Eur J Wildl Res 56:541–549

Roedenbeck IA, Voser P (2008) Effects of roads on spatial distribution, abundance and mortality of Brown hare (*Lepus europaeus*) in Switzerland. Eur J Wildl Res 54:425–437

Schmidt NM, Asferg T, Forchhammer MC (2004) Long-term patterns in European brown hare population dynamics in Denmark: effects of agriculture, predation and climate. BMC Ecol 4

Sidorovich VE, Sidorovich AA, Izotova IV (2006) Variations in the diet and population density of the red fox *Vulpes vulpes* in the mixed woodlands of northern Belarus. Mam Bioliol 71(2):74–89

Small RJ, Marcstrim V, Willebrand T (1993) Syncronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. Ecography 16:360–364

Smith RK, Jennings NV, Harris S (2005) A quantitative analysis of the abundance and demography of European hares in relation to habitate type, intencity of agriculture and climate. Mammal Rev 35:1–24

Statistics on agriculture, gardening and forestry, 1974 (1975) Report from the National Danish Statistics. 312pp

Teerink BJ (2004) Hairs of Westeuropean mammals. Atlas and identification key. BAS Printers Limited Over Wallop, Hampshire

Topping CJ, Høye TT, Odderskær P, Aebischer N (2010) A pattern-oriented modelling approach to simulating populations of Grey partridge. Ecol Model 221:729–737

Trebbien R, Chriel M, Struve T, Hjulsager CK, Larsen G, Larsen LE (2014) Wildlife reservoirs of canine distemper virus resulted in a major outbreak in Danish farmed mink (*Neovison vison*). PLoS One 9(1):e85598. doi:10.1371/journal.pone.0085598