Foraging ecology of the red fox (*Vulpes vulpes*) in a Danish polder, Tøndermarsken

Specialeopgave (Cand. scient.)

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Foto: Katrine Meisner

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Indholdsfortegnelse:

Forord

Denne afhandling er mit specialeprojekt, som beskriver rævens diæt og home range i Tøndermarsken. Projektet er et led i en større undersøgelse af vadefuglenes ynglesuccces i Tøndermarsken, udført af Danmarks Miljøundersøgelser, Århus Universitet, Afdeling for Vildtbiologi og Biodiversitet. Trods fredningen af Tøndermarsken i 1988 er antallet af vadefugle gået drastisk tilbage. Bestanden af viber i det vigtigste yngleområde faldt fra 1.597 par i 1983 til kun 75 par i 2000. En mulig årsag til dette fald kan være, at bestanden af ræve har været stigende i området siden 1980erne. Der er flere gange observeret en stigning i bestandene af vadefugle umiddelbart efter år med få ræve på grund af udbrud af enten rabies eller skab.

Der blev derfor iværksat en omfattende undersøgelse af ræven i Tøndermarsken i 2007. Sammen med en anden specialestuderende, Katrine Meisner, drog jeg til Tøndermarsken, hvor formålet var at fange ræve og mærke dem med radiohalsbånd. Men rævene ville ikke, som vi ville og efter to måneder var det desværre kun lykkedes os at fange 2 ræve. Sideløbende med fangsterne havde vi samlet ræveekskrementer og talt pattedyr i området ved hjælp af natlysninger, så vi havde andet data at falde tilbage på. Vi delte data i mellem os, og jeg fortsatte undersøgelserne af rævens diæt.

Foto: Katrine Meisner

Denne specialeafhandling er udformet som et artikelmanuskript med henblik på senere indsendelse til diverse tidsskrifter.

God læselyst

Med Venlig Hilsen

Marie Skøt Hoelgaard

Tak

Denne afhandling var aldrig blevet en realitet havde det ikke været for alle de personer, der på den ene eller anden måde har hjulpet mig undervejs. Allerførst har mine 3 vejledere Peter Sunde og Preben Clausen fra DMU Kalø og Søren Toft, Århus Universitet fortjent en stor tak for råd og vejledning undervejs. Dernæst tak til DMU Kalø for at lade de specialestuderende være en del af arbejdspladsen. Der har altid været hjælp og inspiration at hente hos alle medarbejderne. Specielt tak til Morten Elmeros for hjælp med hår- og fjerbestemmelser i laboratoriet, tak til Aksel Bo Madsen for hjælp til artsbestemmelse af ekskrementer og til Anne-Mette Bindesbøl for gode råd og vejledning. Også en stor tak til de andre specialestuderende på DMU, Katrine, Linn, Anne, Kirsten, Heidi, Miriam, Kent og Rasmus for opbakning og hyggelige stunder. Specielt tak til Katrine for godt samarbejde og sparring undervejs i skrivefasen. Jeg skylder også en stor tak til Kevin og Casper, som indsamlede ekskrementer i vinterperioden og analyserede dem i laboratoriet. Sidst, men ikke mindst, en stor tak til min kæreste Michael for opbakning, støtte og overbærenhed under hele forløbet.

The foraging ecology of the red fox (*Vulpes vulpes)* in a Danish polder, Tøndermarsken

Abstract

Red foxes (*Vulpes vulpes*) potentially have a strong influence on the population dynamics of their prey, especially ground-nesting birds. We investigated the foraging ecology of the red fox in a Danish Polder, by scat analysis and radio tracking. The red foxes were not dependent on the influx of ground-nesting birds during the breeding season. Birds, however, proved to be the dominant food source during winter. In spring and summer sheep were the most important food resource for the foxes, whereas rodents and lagomorphs were of less importance. The relatively high density of foxes in Tøndermarsken, along with small home ranges and a non nomadic lifestyle, suggest that food sources are rich and stable year round. Furthermore, our results indicate that foxes in Tøndermarsken do not respond numerically to the influx of breeding ground-nesting birds.

Introduction

Predators potentially have a strong influence on the population dynamics of their prey, with effects on survival of both adults and young individuals. Especially for ground-nesting birds, the loss of eggs and chicks to predators is considered to be the most important cause of reproductive failure (Martin, 1993), and the ultimate cause of population decline in various species (Seymour et al., 2004).

By definition, generalist predators are opportunistic and vary the consumption of variable prey species in response to fluctuations in the abundance of these, i.e. they switch to alternative prey when availability of their primary prey decreases or availability of alternative prey increases (Erlinge et al., 1984; Kidd and Lewis, 1987; Erlinge et al., 1988). Therefore generalist predators are particularly significant predators for a wide variety of ground-nesting bird species, that during the breeding season provide an easily available prey (Lindström et al., 1994). Mammalian predators in particular are known to concentrate their search in nesting areas with high nest densities (Seymour et al., 2004), and thereby become periodically specialised predators.

The Red fox (*Vulpes vulpes)* is the most widely distributed generalist carnivore in temperate climate zones of the northern hemisphere because of its extreme adaptability (Jedrzejewski and Jedrzejewska, 1992). It lives in a range of different habitats and preys on a wide selection of food sources, including carrion. Lindström et al. (1994) proved it to be a crucial factor in the dynamics of the small game community in Scandinavia, primarily by keeping the densities of prey at low levels. Specifically, several studies have proven the red fox an important predator of ground-nesting birds (Johnson et al., 1988; Patterson et al., 1991; Lindström et al., 1994; Yanes and Suárez, 1996) and thereby lowering population numbers significantly. Hence, in the absence of larger predatory mammals in most managed landscapes, evidence is now accumulating for the red fox being a keystone predator in rural areas (Goszczynski, 1974; Goldyn et al., 2003; Webbon et al., 2006; Dell'Arte et al., 2007), woodland areas (Jedrzejewski and Jedrzejewska, 1992; Lindström et al., 1994; Sidorovich et al., 2006) as well as urban areas (Doncaster et al., 1990; Contesse et al., 2004). On this basis, red foxes are also suspected to have similar impact on a polder ecosystem. However, fox foraging ecology have not been systematically studied in these habitats.

This study investigates the foraging ecology of the red fox in a polder ecosystem in Denmark, Tøndermarsken, by use of scat analysis and radio tracking. In Tøndermarsken, the population of red fox has been increasing since 1980 (Rasmussen, 1999; Clausen et al., 2007), and the population sizes of several ground-nesting bird species have decreased accordingly (Clausen et al., 2005). The predation rate on lapwing (*Vanellus vanellus*) nests has also increased dramatically during that period. The predation on lapwing nests mainly occurs at night, suggesting nocturnal animals (mammals) as the main predators (Nielsen, 2008, in prep.). Since 1980, several outbreaks of Rabies and Sarcoptic Mange have resulted in periodically very low fox densities, as foxes died or were culled in high numbers. In the years following these events, an increase in the populations of ground-nesting birds was observed (Clausen et al., 2005).

The foraging ecology of the red fox has been investigated in a wide range of habitats, but never before in polders. Polders are important breeding sites for ground-nesting birds, and serve as an essential stop-over for migrating birds. The result is a high influx of birds most of the year. It is important to know the ecological dynamics and specifically the ecology of the main predators if management of polders are to benefit the vulnerable ground-nesting bird species.

We investigated the diet of the red fox before, during and after the breeding season of the ground-nesting birds, and in different parts of Tøndermarsken. Moreover, we determined the home range of 3 vixens. If the red fox is dependent on the influx of ground-nesting birds in the breeding season of these (April-May) we would expect foxes to have a dietary response and/or a numerical response during this season. If foxes have a dietary response, the proportion of birds and eggs in the diet should reach its seasonal maximum. Additionally, on a spatial level the proportion of birds in the diet should correlate positively with bird abundance. If foxes responded numerically (aggregatively) to the periodic availability of ground nesting birds, adult foxes should leave the area again with the departure of the breeding birds. On the other hand, if food sources are plentiful throughout the year we would expect a wide variety of prey species in the diet and consumed amounts of birds to be relatively constant in all seasons. Furthermore, the fox population in the area would be expected to be stable and to stay within the same home range throughout the year.

Materials and methods

Study area

Fox scats were collected in Tøndermarsken in the south-western most part of Denmark (57^{o}60'N, 8^{o}40'E) (Fig 3). Tøndermarsken consist of two minor areas, Margrethe Kog and Gl. Frederikskog. The areas lie mainly below sea level and are dammed by dikes along the shoreline as well as along a small river (Vidåen). The land consists mostly of grazed fields. The main grazers in the area are sheep and cattle.

Margrethe Kog is an area of 11.5 km^2 and is located along the Wadden Sea, and contains a man-made salt water lake with water levels controlled by a lock. This makes the area a very important breeding site for sea birds and wading birds, and an important stop-over for migrating birds. For this reason, Margrethe Kog was declared a natural reserve in 1985, and was thereby closed to the public most of the year.

Gl. Frederikskog is an area of 5.9 km^2 and is located around 3 km from the Wadden Sea and approximately 2 km from the salt water lake. The area consists mostly of grazed fields, but still houses many breeding seabirds and wading birds.

Collecting scats and identification and quantification of prey remains

Fox scats were collected Feb - Jul 2007 and Nov 2007 - Jan 2008. A specific collection route was used from May 2007, whereas before this, collection areas were chosen haphazardly. Yet the sampling of scats covered both Margrethe Kog and Gl. Frederikskog before and after May. The scats were collected mostly along roads and dikes. Date and UTM-coordinate was noted on site for each scat. The scats were kept deep-frozen until analysis. The exact date of deposit was known for only a small proportion of the scats. Deposit date for the rest was estimated subjectively according to date of collection and weather reports for the area.

The scats were analysed according to Reynolds and Aebischer (1991). Prior to examination, the scats were dried at 100 ^{o}C for 14 hours and weighed. Then each scat was soaked in water and gently washed through a fine sieve (0.5 mm).

Prey remains of mammals and birds were identified according to Teerink (1991), Debrot (1982), Day (1966) and Jensen (1993). Hair characteristics such as cuticle scale pattern, medulla patterns and cross sections of guard hairs were used to identify mammal remains. In most cases, mammals could be referred to species but some only to genus, including Lagomorpha spp (the majority were most likely hares, as these are more abundant in the area (Meisner, 2008 in prep.)), *Apodemus* spp. and *Microtus* spp. Teeth were also used for identification. The remains of birds were identified to taxonomic order from barbule nodes on feathers. Charadriiformes and Passeriformes were grouped together as they are very similar in appearance. Prey remains were dried at 100 ^{o}C for 14 hours and weighed separately.

Remains of birds' eggs and invertebrates were not identified further, due to small sample sizes. Fox hairs were ignored, as they were assumed to be from grooming. As the only plant material found was small parts of grass, it was assumed to be ingested by coincidence, and neglected in the analysis.

Data analysis of diet

When there was uncertainty as to which species a scat was from, or date or UTM-coordinate were uncertain, these samples were excluded from further analysis. The results are expressed both as frequency of occurrence and as proportion of estimated ingested biomass. Frequency of occurrence is defined as the number of times a specific prey item occurred, as a proportion of the total number of identifiable food items. Estimated biomass proportions ('biomasses' hereafter) is defined as estimated ingested biomass of a prey item divided by total estimated ingested biomass. Prey items were sorted into 4 prey groups: birds, rodents (including Insectivores), sheep and lagomorphs. Other prey groups (birds' eggs and invertebrates) occurred only sporadically and in small amounts, and were therefore excluded from further analysis. Correction factors: birds 35, rodents 23, lagomorphs 50 and roe deer 118 (Goszczynski, 1974), were used to estimate the ingested biomass of prey groups from egested biomass of prey remains. As there was no correction factor available for sheep, the correction factor for roe deer was used.

The study year was divided into 4 seasonal categories according to the breeding cycles of birds in the area: Feb - Mar (late winter, early spring and pre-breeding period), Apr (eggs available), May – Jul (broodlings available) and Nov – Jan (late autumn, early winter and non-breeding period). To analyse the diet for spatial effects, the area was divided into zones according to fox home ranges. Also, distances to salt water and distance to the Wadden Sea were calculated for all scats, using ArcGIS 9.1 (ESRI).

Statistical analysis of diet

Variation in overall diet composition based on frequency of occurrence in accordance to seasonal and temporal variation was tested by means of multinomial logistic regression: PROC GENMOD in SAS 9.1 (link function = GLOGIT). The diet was tested for any effect of time (seasonal categories and date) and space (zones, distance to salt water and distance to the Wadden Sea). The best model fit was found using Akaike's information criterion (AIC) (Burnham and Anderson, 1998) (appendix A).

Since the overall diet composition varied across time and spatial locations, post-hoc analyses for the 4 individual prey groups were carried out. The best fit model was also found for the individual prey groups using AIC. Post-hoc analyses of frequency of occurrence for each of the four individual prey groups were carried out with binary logistic regression: PROC GENMOD in SAS 9.1(link function = logit).

Analyses of biomasses were carried out using General Linear Models (GLM). Proportions of biomasses were Arcsine transformed prior to analysis. In this study, as is the case in most studies of diet composition in general (Reynolds and Aebischer, 1991), data were not normally distributed even after transformation and statistical assumptions thus violated. Therefore, parameter estimates were compared to Bootstrap estimates (Using the program Data Pilot 1.09) and a deviation of 4 percentage-points or less was found.

For all models a P-value < 0.05 counted as a significant result.

Trapping, radio tracking and litter size

Foxes were captured in baited tunnel box traps (manufactured at National Environmental Research Institute Denmark) in 2006 (as a pilot study) and 2007. Traps were placed along roads and dikes. In 2006 only one trap was activated for one night. In 2007 traps were monitored twice a day from March to May (468 trap-nights). Captured animals were sexed, weighed and ear tagged. In 2006 the captured fox was fitted with a GPS-collar (Televilt prototype Tellus Mini GPS collar) that remained functional for 1 month. In 2007 foxes were fitted with radio-collars transmitting on 151 MHz (Bio-track TW-3 large mammal tag with biothane collar) designed to remain functioning for 2 years.

Most tracking was carried out at night when the animals were active. Locations of the foxes in 2007 were fixed by triangulations, using a handheld receiver and antenna. There was a minimum of 1 hour between locations to ensure independence. Fox locations were recorded a minimum of 10 times per week. The open landscape allowed radio signals to be received at distances of 2-3 km. The foxes were located in almost all attempts. Home ranges were calculated as 95 % minimum convex polygons.

From 2005 – 2007 9 litters of fox cubs were observed outside fox dens in Tøndermarsken. As not all cubs are necessarily seen, the registered number of cubs is a minimum.

Results

The diet

In the total sample of 689 prey items originating from 389 scats (299 from Margrethe Kog, 90 from Gl. Frederikskog) the most frequent prey were birds (43 % of all items), followed by rodents (39 %), sheep (14 %) and lagomorphs (4 %).

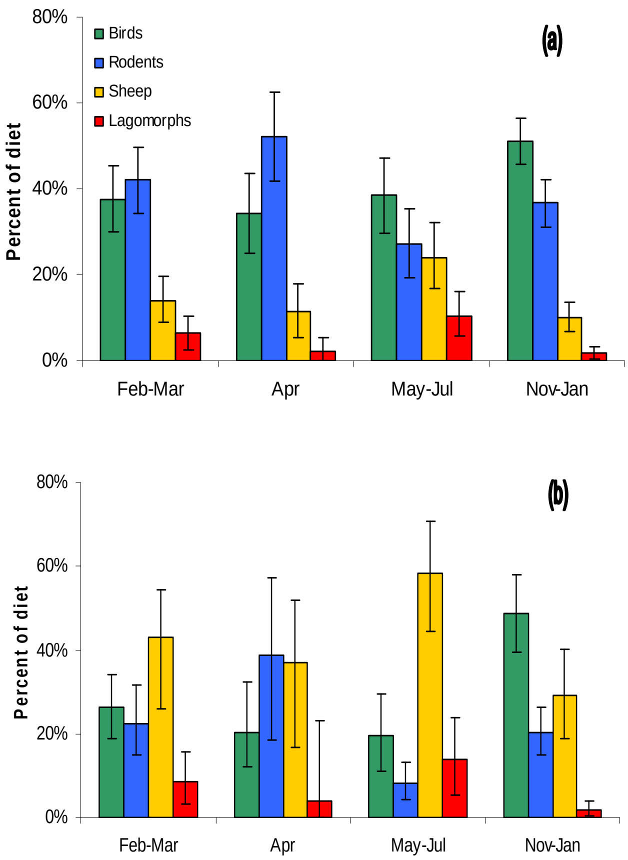
Prey remains of 14 different taxa of birds and mammals were found in the scats. The most frequently encountered birds were of Anseriformes, whereas the most frequently encountered rodent was *Microtus* spp. (Table 1).

The diet based on frequency of occurrence was dominated by birds and rodents in all 4 seasonal categories. Sheep and lagomorphs comprised a minor part (Fig. 1.a).

Model selection revealed significant effect of season and spatial location. According to AIC the best fit model included 4 seasonal categories and distance to salt water divided into 2 groups (Table 2). The difference in AIC value for distance to saltwater and distance to the Wadden Sea was less than 2, which means they are essentially indistinguishable (Burnham and Anderson, 1998). As distance to salt water had the lowest AIC value this was chosen for further analysis.

Post-hoc test revealed that both seasonal category and distance to salt water was significant for all 4 prey groups (Fig. 2). A strong correlation between distance to salt water and probability of occurrence in the diet was found only for birds (negative correlation) (Fig. 2.a) and rodents (positive correlation) (Fig. 2.c).

Fig. 1: Distribution of prey groups divided into seasonal categories for frequency of occurrence (a) and biomasses (b). Percentage of frequency of occurrence and percentage of biomasses calculated from 10.000 bootstrap estimates. Error bars represent 95 % confidence intervals after 10.000 bootstrapped estimates.



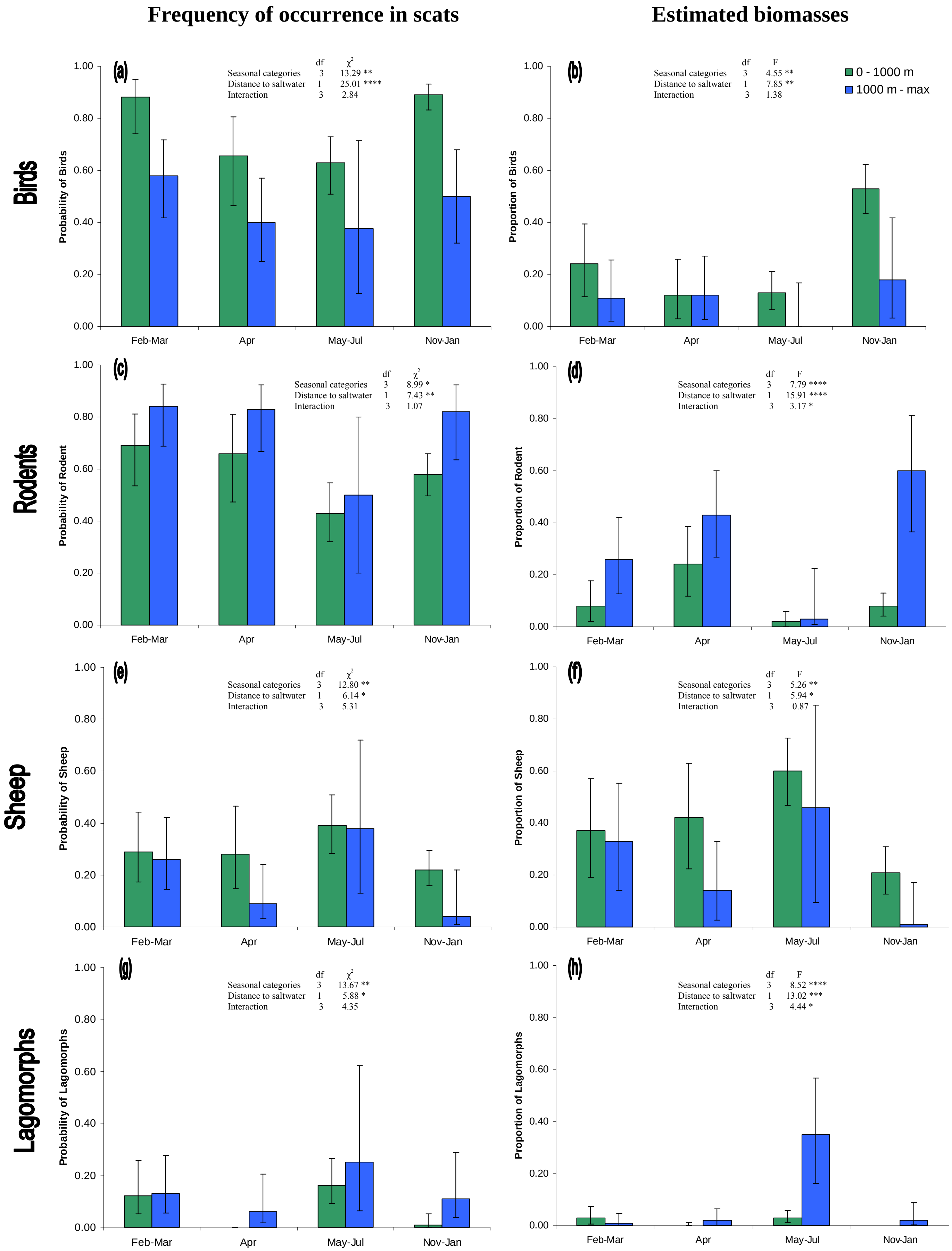
When data was corrected by use of available correction factors to estimate ingested biomasses, the main prey groups in the diet were sheep (41 %), birds (32%) and rodents (21 %) whereas lagomorphs (7 %) were less important. The diet was dominated by birds in Nov-Jan whereas sheep were dominating Feb-Mar and May-Jul. In Apr both rodents and sheep comprised the main prey (Fig. 1.b).

According to biomasses both seasonal categories and distance to salt water were significant for all 4 prey groups (Fig. 2). A strong correlation between distance to salt water and proportion of biomass in the diet was found for birds (Fig. 2.b), rodents (Fig. 2.d) and sheep (Fig. 2.f) but no obvious correlation was found for lagomorphs.

Table 1: Diet composition of foxes in 4 seasonal categories, based on frequency. Percentage and 95 % confidence intervals (CI) were calculated from 10.000 bootstrap estimates.

Taxa	February - March 2007			April 2007			May - July 2007			November 2007 - January 2008		
	n	%	95% CI	n	%	95% CI	n	%	95% CI	n	%	95% CI
Birds	59	37.58	29.94 - 45.22	33	34.38	25.00 - 43.75	48	38.40	29.60 - 47.20	159	51.13	45.66 - 56.59
Anseriformes	47	29.94	22.93 - 36.94	25	26.04	17.71 - 35.42	29	23.20	16.00 - 30.40	119	38.26	32.80 - 43.73
Charadriiformes+Passeriformes	5	3.18	0.64 - 6.37	5	5.21	1.04 - 10.42	8	6.40	2.40 - 11.20	36	11.58	8.04 - 15.11
Columbidae							1	0.80	0.00 - 2.40	1	0.32	0.00 - 0.96
Rallidae	1	0.64	0.00 - 1.91	2	2.08	0.00 - 5.21	4	3.20	0.80 - 6.40	1	0.32	0.00 - 0.96
Unidentified birds	6	3.82	1.27 - 7.01	1	1.04	0.00 - 3.13	6	4.80	1.60 - 8.80	2	0.64	0.00 - 1.61
Rodents	66	42.04	34.39 - 49.68	50	52.08	41.67 - 62.50	34	27.20	19.20 - 35.20	114	36.66	31.19 - 42.12
Apodemus spp.							1	0.80	0.00 - 2.40	3	0.96	0.00 - 2.25
Arvicola terrestris	2	1.27	0.00 - 3.18	6	6.25	2.08 - 11.46	1	0.80	0.00 - 2.40	3	0.96	0.00 - 2.25
Microtus spp.	52	33.12	26.11 - 40.76	39	40.63	31.25 - 50.00	27	21.60	14.40 - 28.80	82	26.37	21.54 - 31.19
Micromys minutus	2	1.27	0.00 - 3.18				1	0.80	0.00 - 2.40			
Ondatra Zibethicus	7	4.46	1.27 - 7.64	5	5.21	1.04 - 10.42	4	3.20	0.80 - 6.40	18	5.79	3.22 - 8.68
Rattus norvegicus	2	1.27	0.00 - 3.18							8	2.57	0.96 - 4.50
Unidentified rodent	1	0.64	0.00 - 1.91									
Insectivores										2	0.64	0.00 - 1.61
Erinaceus europaeus										1	0.32	0.00 - 0.96
Talpa europaea										1	0.32	0.00 - 0.96
Sheep	22	14.01	8.91 - 19.75	11	11.46	5.21 - 17.71	30	24.00	16.80 - 32.00	31	9.97	6.75 - 13.50
Lagomorphs	10	6.37	2.54 - 10.19	2	2.08	0.00 - 5.21	13	10.40	5.60 - 16.00	5	1.61	0.32 - 3.22
Total number of prey items	157			96			125			311		
Total number of examined scats	80			64			78			167		

Fig. 2: Variation in diet divided into prey groups: birds (a,b), rodents (c,d), sheep (e,f) and lagomorphs (g,h) according to distance to saltwater for the 4 seasonal categories. To show any effects of interactions these were included in the figures. Error bars represent the 95 % confidence intervals. * p<0.05, ** p<0.01, *** p<0.001, **** p<0.0001.



Home range and litter size

In 2006, one fox was caught in late April (Fox 3) and in 2007 one was caught in March (Fox 1) and one in May (Fox 2). All three foxes were vixens that were either pregnant or had cubs. Home ranges varied in area from 0.93 km^2 to 4.39 km^2 with a mean of 2.65 km^2. During winter Fox 1 was shot within the summer home range and fox 2 was located several times within the summer home range in the winter months (Fig.3).

Observations of fox cubs resulted in a mean litter size of minimum 4.44 ± 4.01 SE (n = 9) cubs.

Fig. 3: 95 % minimum convex polygons for 3 foxes. Fox 1 and 2 caught in 2007 and Fox 3 caught in 2006.

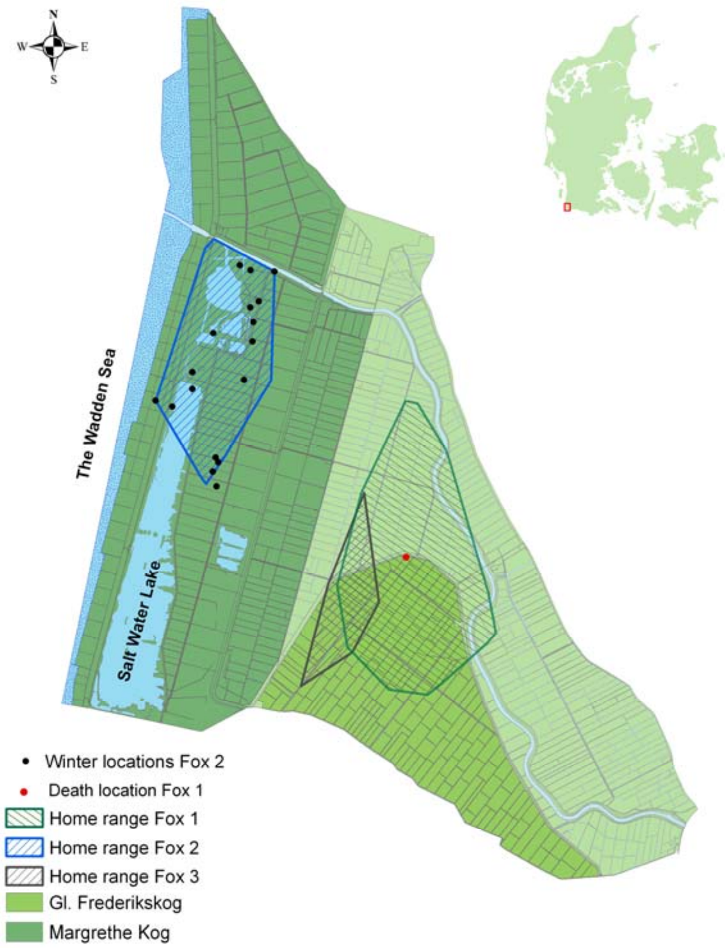


Table 2: Model selection by use of AIC. Not all models are included for illustrational reasons. Formulas for calculation of AIC weight can be found in Burnham and Anderson (1998).

Frequency of Occurrence of the overall diet	degrees of freedom	- 2 log likelihood	AIC	Difference in AIC	AIC weight
Distance to salt water 2 categories + 4 seasonal categories	15	1512.5	1542.5	0.0	97.02%
Distance to salt water 2 categories + 4 seasonal categories + cross	24	1501.5	1549.5	7.0	2.96%
4 seasonal categories	12	1536.0	1560.0	17.4	0.02%
Distance to salt water 2 categories	6	1550.7	1562.7	20.1	0.00%
Day + day*day	9	1547.9	1565.9	23.3	0.00%
Distance to salt water	6	1555.5	1567.5	24.9	0.00%
Distance to the Wadden sea	6	1556.2	1568.2	25.6	0.00%
3 seasonal categories	9	1556.8	1574.8	32.3	0.00%
4 zones	12	1551.7	1575.7	33.2	0.00%
Day	6	1564.6	1576.6	34.1	0.00%
Null hypothesis	3	1581.7	1587.7	45.1	0.00%
2 seasonal categories	6	1577.8	1589.8	47.3	0.00%

Discussion

This study suggests that the red fox in Tøndermarsken is not dependent on the influx of ground-nesting birds. If foxes were dependent on the influx of ground-nesting birds a dietary response in the breeding season would be expected. However, a significant increase of birds and eggs in the diet at this time, was not found. It is assumed that the digestion of broodlings is different compared to adults as down disintegrate faster in the stomach and intestines than feathers (Reynolds and Aebischer, 1991). Furthermore, broodlings are smaller than adults, and leave fewer remains. Also eggshells disintegrate fast, and were only found few times in the scats. As a result the ingestion of birds may be underestimated in May-July. However, there is no indication of an increased ingestion of birds in the breeding season at all, in fact May-July had the lowest proportion of ingested birds (Fig. 1.a, Fig. 2.b). A possible underestimation of birds is therefore not expected to change the overall result.

Birds dominate the diet during winter (Fig. 1.b, Fig 2.b). The main part of these consumed birds is assumed to be carrion, as adult birds are difficult prey for foxes. During winter, migrating birds arrive in huge numbers to rest and feed (Laursen et al., 2008) and it is assumed that some die from exhaustion. Also, along the shoreline bird carrion is washed in, and hunting activities by humans in the area may leave birds wounded or dead.
Sheep is the most dominant part of the diet during spring and summer (Fig. 1.b, Fig.2.f) when sheep are kept outside. During winter most sheep are kept in stables and the availability of sheep is therefore much lower. Some studies conclude that the main part of sheep eaten by foxes is carrion (Hewson, 1976, 1985; Greentree et al., 2000). This may also be the case in Tøndermarsken, as many dead sheep and lambs were observed year round. Especially in spring, when ewes die giving birth and lambs die during birth or shortly after. Lambs may however also be killed by the foxes. In England, predation on lambs were highly reduced if ewes gave birth inside stables, and were kept inside the first few days (Moberly et al., 2003).
Rodents comprise a considerable part of the diet (Fig. 1.b, Fig. 2.d). Compared to other studies however, rodents make up a smaller part of the diet than expected, whereas the high proportion of *Microtus* voles agree with many other studies (Goszczynski, 1974; Macdonald, 1977; Jensen and Sequeira, 1978; Jedrzejewski and Jedrzejewska, 1992; Goldyn et al., 2003; Lanszki, 2005; Sidorovich et al., 2006; Dell'Arte et al., 2007). This atypical low proportion of rodents may either be a result of high availability of alternative prey or low densities of rodents. Unfortunately, density data was not available. Lagomorphs comprised the smallest part of the diet, and are therefore not considered an essential food source for the foxes (Fig. 1.b, Fig. 2.h).

A strong correlation between distance to salt water and both probability and proportion of prey groups were found for birds and rodents (Fig. 2.a-d). For sheep a strong correlation was only found according to proportion of biomasses (Fig. 2.f). Inside the Margrethe Kog reserve (< 1000 m from salt water) both the probability and proportion of birds in the diet was higher than outside the re-

serve (Fig 2.a.b). The availability of birds is higher inside the reserve year round, as more birds nest here and more migrating birds rest here (Clausen et al., 2007; Kent Olsen, pers.comm). Bird carrion is also available along the shoreline. Nature reserves, managed to promote breeding populations of ground-nesting birds, may benefit other prey species, and in some landscapes may provide relatively conspicuous and productive foraging patches for predators compared to surrounding habitats (Seymour et al., 2004).
The positive correlation between both probability and proportion of rodents and distance to salt water (Fig. 2.c.d) may be explained by higher population densities of voles with increasing distance from salt water. Other studies have found a clear correlation between voles in the diet and voles in the field (Dell'Arte et al., 2007). Also, a lower availability of both sheep and bird carrion further away from salt water, would lead to higher predation on rodents. The negative correlation for sheep (Fig. 2.f) may be explained by higher availability of sheep, and thereby sheep carrion, in the Margrethe Kog reserve (< 1000 m from salt water) than in Gl. Frederikskog.

The red fox is normally attached to a particular area, but the size of the areas varies with time. Specifically, foxes are known to wander out of their home range to exploit food resources. Our results indicate that breeding vixens are stable in the area and stay within their home-range throughout the year (Fig. 3), which indicates that food availability is high. The size of red fox home ranges can vary from a few hundred square meters to 10-20 km^2 (reviewed by Cavallini, 1996). According to the resource dispersion hypothesis the size of a red fox home range is determined by the availability of food sources i.e. a high availability of food sources lead to small home ranges (Macdonald, 1983). In Tøndermarsken the mean home range size of our three vixens in the breeding season was 2.65 km^2 which is relatively small compared to other studies (reviewed by Cavallini, 1996). This also indicates that food availability in Tøndermarsken is high.
A study of fox density in Tøndermarsken by spotlighting has revealed a density of 1.7 foxes/km^2 (Meisner, 2008 in prep.). Other studies have found quite similar but a slightly smaller density of 1.6 foxes/km^2 in farmland areas (Panek and Bresinski, 2002) and in woodland areas, both rich on food sources, whereas woodland areas, with lower food availability had a significantly lower density of 0,26 foxes/ km^2 (Sidorovich et al., 2006). This indicates that the population density of foxes in Tøndermarsken is relatively high.
An estimated mean litter size of minimum 4.44 cubs per female is higher than observations in both urban and rural areas in Denmark where a mean litter size of 3.7 cubs was found (Nielsen, 1989). The relatively high density of foxes in Tøndermarsken, along with small home ranges and a non nomadic lifestyle, suggest that food sources are rich and stable year round. Furthermore, our results indicate that foxes in Tøndermarsken do not respond numerically to the influx of breeding ground-nesting birds. Also, the relatively large litter size may indicate that food sources are not a limiting factor for the foxes in the area.

Even though the foxes in Tøndermarsken are not dependent on the populations of ground-nesting birds as a food source, the ground-nesting birds may suffer greatly from predation by foxes. When foxes are foraging for other prey it may lead to higher predation risk for ground-nesting birds i.e. incidental nest predation (Seymour et al., 2004). Furthermore Erlinge et al. (1988) concluded that high predation rates and high predator densities can be maintained by the presence of alternative prey species.

Predator removal is a possible action to manage the populations of ground-nesting birds in Tøndermarsken. Short term experiments with predator removal in Tøndermarsken have been successful in the past (Rasmussen, 1999) and more thorough removal programs may result in increased population sizes of ground-nesting birds.

Sheep proved to be the most essential food source for the foxes. The high availability of sheep carrion year round may sustain a large population of red foxes in Tøndermarsken which results in relative high predation rates on birds. Limiting food sources for the foxes outside the breeding season may also be a possible way to bring fox populations in Tøndermarsken down. It is not realistic to lower availability of rodents and birds, but it is possible to lower the availability of sheep carrion by actively removing carcasses, thereby lowering the carrying capacity for foxes. During the breeding season, however, it may be advisable to leave the sheep carcasses for the foxes, as studies have revealed that the rate of predation on ground-nesting birds is lower when alternative prey is relatively abundant (Beintema and Müslems, 1987; Bealey et al., 1999). A high availability of sheep carrion in the breeding season may therefore in fact reduce predation of nests and broodlings.

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