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SHORT COMMUNICATION

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Changes in red fox *Vulpes vulpes* diet due to colonisation by lynx *Lynx lynx*

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We studied the diet of red fox *Vulpes vulpes* in the presence of lynx *Lynx lynx* in the southern boreal forest of Sweden during 1999-2002 using scat analyses. Diet composition and food niche breadth was compared to an identical study conducted in the same area during 1974-1979 prior to the recolonisation by lynx. The consumption of roe deer *Capreolus capreolus* was higher in the presence of lynx, even compared to the particularly harsh winter in 1976/77 when roe deer suffered serious starvation related mortality. Scavenging on roe deer replaced feeding on presumably less profitable food such as fish and reptiles, invertebrates and vegetables. The winter food niche was narrowed. The frequent consumption of roe deer could have been a combined effect of a stable supply of deer carrion and a low abundance of other prey species. We thus conclude that presence of lynx feeding on roe deer creates an important, stable food supply for red foxes.

Key words: Diet, lynx, Lynx lynx, red fox, roe deer, scavenging, Vulpes vulpes

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Many carnivores and raptors scavenge more or less frequently, and the supply of carrion may thus be an important component of their feeding ecology (Jędrzejewska & Jędrzejewski 1998). Large carnivores such as wolf *Canis lupus* and lynx *Lynx lynx* often kill prey that is larger than they can consume in one feeding bout, and their presence may guarantee a fairly stable supply of carcasses for scavengers (Paquet 1992, Jędrzejewska & Jędrzejewski 1998, Buskirk 1999). Accordingly, the eradication of large predators worldwide has been suggested to affect scavengers in that carrion is produced in smaller or more variable amounts. For example, the present situation with small numbers of large predators leading to a deficiency of carrion, may be one reason for the rarity of arctic foxes *Alopex lagopus* and wolverines *Gulo gulo* in the Scandinavian mountains (Hersteinsson et al. 1989, Persson 2003, but see Linnell & Strand 2002). With the introduction of wolves in Yellowstone, USA, the amount of carrion tripled, to the benefit of the threatened grizzly bear *Ursus horribilis* for example (Crabtree & Sheldon 1999).

The feeding ecology of the red fox *Vulpes vulpes* in boreal Sweden has previously been studied at negligible abundances of large predators. Under these circumstances, foxes fed to a large extent on microtines (Lindström 1989), and their populations fluctuated in accordance with microtine abundance (Englund 1970, Lindström 1989). However, feeding on roe deer *Capreolus capreolus* that were dead or dying from late winter starvation was shown to be important for red fox survival in harsh winters when access to other prey was limited (Cederlund & Lindström 1983). With mainly starving adults and young fawns being accessible for foxes (Cederlund & Liberg 1995), consumption of roe deer varied greatly within and between years, and roe deer rarely dominated the diet (Lindström 1982, 1994).

During the last decade, the lynx population in boreal Sweden has increased in numbers and has expanded into new areas (Liberg 1998). Roe deer are at present a year-round staple for lynx in this region (Glöersen & Liberg 1998, Moshøj 2002). A roe deer makes up more food than a single individual or a family group of lynx can consume in one meal. Although lynx often return to their kills for additional feeding, substantial parts of the killed deer may be available to scavengers (Jędrzejewska & Jędrzejewski 1998, Moshøj 2002). Red foxes are common scavengers of lynx-killed prey (Jędrzejewska & Jędrzejewski 1998, Moshøj 2002), and often follow lynx trails in search of food remains (Haglund 1966). The increase in lynx numbers has therefore probably increased and stabilised the availability of roe deer carrion for foxes.

We studied diet composition and food niche breadth of the red fox in a southern boreal forest area, where an identical study had been conducted before the recolonisation by lynx, and where important prey species were continously monitored. We predicted that roe deer would constitute a larger proportion of the year-round fox diet, and that the fox food niche would be narrower due to a subsequent decrease in the consumption of presumably less preferred food.

Study area

Our study was conducted in the Grimsö Wildlife Research Area (59°40'N, 15°30'E), covering 140 km^2 in the boreal forest of south-central Sweden. The area is relatively flat (50-150 m.a.s.l.), and characterised by coniferous forest, interspersed with bogs and lakes (ca 10-15% each) and small areas of agricultural land (3%). Modern forestry is practiced in most of the area, resulting in a mosaic landscape of even-aged forest. The ground is generally snow-covered from December through March, and mean snow depth is ca 20 cm, though some winters may be practically snow free (Dahlström 1995). The study area is described in more detail by Helldin (1999).

The density of red foxes in the study area is censused annually, primarily by den counts (Lindström et al. 1994). Winter densities of roe deer, hares *Lepus* spp. and Tetraonidae are censused by pellet counts (Pehrson 1997), and Microtinae by snap trapping (Lindström et al. 1994, Kjellander & Nordström 2003). The densities of these species have undergone major changes during the latest decades. The number of red foxes declined in the 1980s due to sarcoptic mange, and as a result, small game peaked simultanously (Lindström et al. 1994). The number of roe deer also increased during the 1980s and remained high until the mid-1990s, when roe deer numbers declined (Pehrson 1997). This decline concurred with the recolonisation by lynx in the area; the number of lynx increased in one or two years from virtually zero to a resident population of relatively high density (a regional measure of $>$ 1/100 km^2; Liberg & Glöersen 2000). Since the early 1990s, the number of voles have cycled on lower levels compared to the previous decades, with particularly spring numbers being low (Kjellander & Nordström 2003; Grimsö Wildlife Research Station, unpubl. data).

Methods

We collected scats from red fox from June 1999 through April 2002. Most scats were collected along forest roads (which were cleared from all old scats at the onset of the study). In the six summer months (May-October), the roads were searched for scats monthly. In the six winter months (November-April), snow cover made collection at regular intervals impractical, and instead the roads were searched once or twice when snow conditions were suitable, as well as at the end of the season, when the snow had melted. Some scats were also collected during snow tracking of foxes and in live traps for foxes.

A subsample of 60 scats/season was selected for analysis (except for the summer of 2000 when all 50 scats found were analysed). The subsample was designed to obtain scats with an even distribution within the study area and throughout the season.

Scats were dried at 110°C for > 5 hours, weighed and examined dry. Food remains were examined both macroscopically and microscopically, and compared with literature (Day 1966, Brunner & Coman 1974, Debrot et al. 1982) and a reference collection. It was not possible to determine whether roe deer remains came from an adult or a fawn. Food items were divided into eight categories (largely following Lindström 1982; Table 1). A food item was defined as an occurrence of a prey type in a scat. Accordingly, a food item could be constituted by several similar small prey or just part of a large prey. The biomass of food remains in a scat was calculated by estimating the proportion of each item by eye, and multiplying by the dry weight of the scat (Reynolds & Aebischer 1991). The biomass consumed was calculated by multiplying the biomass in scats with digestion factors ('corrections factors') as suggested by Lockie (1959, 1961).

Food niche breadth was calculated following Hurlbert (1978), and the variance of the food niche breadth was calculated using the 'delta' method (Smith 1982). In these calculations, the various food categories were arbitrarily assumed to be equally available.

The results were compared statistically with a similar study conducted in the same area during 1974-1979 (Lindström 1982). For this comparison, samples were pooled among winter and summer seasons, respectively. Diet composition was compared by contingency table analyses, using number of prey items in the respective category as indata. In comparisons of individual prey categories between studies, the prey items of the other seven categories were pooled, and Fisher's exact text was used. Niche breadths were compared using a Z-test (Zar 1996).

Results

During 1999-2002, roe deer constituted about half of the food consumed by foxes in winter, and on average 38% of the summer consumption (see Ta-

Table 1. Composition of food remains in red fox scats, and winter population indices of four important fox prey types, in the Grimsö Wildlife Research Area, Sweden. Red fox diet data are presented as percentages of food items and of the total biomass consumed (the latter in parentheses). Red fox diet data from 1974-1979 (Lindström 1982) are presented for comparison. N gives the number of prey item in the sample. Prey population indices from Pehrson (1997), Kjellander & Nordström (2003), Åke Pehrson (unpubl. data) and Grimsö Wildlife Research Station (unpubl. data), and are for roe deer expressed by number of pellet groups/10 m^2-plot, for hare by number of pellets/10 m^2-plot, for microtines by number caught/100 trap nights (average between autumn and winter indices) and for forest grouse by percent of 10 m^2-plots with pellets.

Season	Winter 1974/75	Summer 1975	Winter 1975/76	Summer 1976	Winter 1976/77	Summer 1977	Winter 1977/78	Summer 1978	Winter 1978/79	Summer 1999	Winter 1999/ 2000	Summer 2000	Winter 2000/01	Summer 2001	Winter 2001/02
Red fox diet															
N	33	86	94	85	103	45	100	52	96	123	92	80	85	113	77
Roe deer	9.1	2.3	7.4	5.9	12.6	6.7	11	5.8	5.2	17.9 (53.9)	27.2 (43.2)	7.5 (17.8)	37.6 (54.0)	16.8 (42.1)	26.0 (47.3)
Hare	3.0	4.6	3.2	2.4	3.9	2.2	1	3.8	12.5	0	7.6 (12.9)	7.5 (25.6)	8.2 (13.6)	2.6 (5.5)	5.2 (11.0)
Microtines	18.2	15.1	21.3	18.8	28.2	31.1	46	21.2	20.8	27.6 (20.5)	30.4 (17.3)	18.8 (10.1)	21.2 (5.5)	17.7 (13.5)	31.2 (11.2)
Other mammals	21.2	12.8	24.5	15.3	8.7	6.7	14	9.6	4.2	4.1 (1.8)	6.5 (13.2)	11.2 (6.5)	9.4 (7.1)	5.3 (5.9)	9.1 (7.2)
Birds	3.0	10.5	8.5	5.9	11.7	6.7	9	7.7	18.8	4.1 (5.7)	9.8 (8.1)	12.5 (16.3)	11.8 (17.1)	16.8 (20.7)	20.8 (22.5)
Fish and reptiles	3.0	4.6	9.6	4.7	6.8	6.7	2	1.9	6.2	0	1.1 (0.2)	2.5 (2.1)	1.2 (2.3)	1.8 (0.8)	0
Invertebrates	18.2	24.4	11.7	22.4	10.7	15.6	4	21.2	9.4	15.4 (0.3)	3.3 (0.1)	10.0 (1.7)	5.9 (0.1)	18.6 (1.7)	3.9 (0.0)
Vegetables	24.2	25.6	13.8	24.7	17.5	24.4	13	28.8	22.9	30.9 (17.7)	14.1 (5.0)	30.0 (19.9)	4.7 (0.2)	20.4 (9.8)	3.9 (0.7)
Prey indices															
Roe deer	-		-		0.14		0.22		0.23		0.11		0.11		0.13
Hare	-		-		0.89		2.84		1.85		0.75		0.48		0.72
Microtines	1.17		1.70		5.30		5.34		1.34		2.46		1.08		1.60
Forest grouse	-		-		9.14		6.91		4.55		4.28		4.22		4.63

ble 1). Other important prey, often making up about 10-20% of food consumed, were hares in winter, vegetables in summer, and microtines and birds in both seasons.

Both summer and winter diet of the red fox differed in 1999-2002 compared to 1974-1979 (contingency table analysis: summer: $\chi^2 = 26.2$, df = 7, P = 0.0005; winter: $\chi^2 = 74.1$, df = 7, P < 0.0001). In both seasons, the most pronounced difference was an increased proportion of roe deer in scats during 1999-2002 (Fisher's exact test: summer: $\chi^2 = 13.4$, P = 0.0001; winter: $\chi^2 = 48.9$, P < 0.0001).

Proportions of other food categories were either similar or lower during 1999-2002, compared to 1974-1979. The proportion of invertebrates and vegetables was lower in the winter diet (Fisher's exact tests: χ^2 = 5.6-11.3, P = 0.0005-0.01), but did not differ in the summer diet (Fisher's exact tests: χ^2 = 0.0-1.36, P = 0.21-0.99). The food categories 'other mammals' and 'fish and reptiles' constituted lower proportions in both seasons (Fisher's exact tests: χ^2 = 3.61-9.48, P = 0.008-0.047), whereas the proportions of hares, microtines and birds did not differ between the two periods (Fisher's exact test: χ^2 = 0.0-1.0, P = 0.31-1.0). The winter food niche was narrower (0.60 ± 0.07; 95% C.I.) than the summer food niche (0.76 ± 0.07; 95% C.I.; Z-test: Z = 4.36, P < 0.0001), but the summer food niche did not differ between the two periods (0.69 in both cases; Z-test: Z = 0.03, P = 0.40).

Discussion

Roe deer made up the single most important food item all year round for red foxes during our study period of 1999-2002. The consumption of roe deer was high in all three winters, indicating that roe deer was a stable food source for red foxes in this energetically critical season. The consumption of roe deer in summer was too high to be explained only by predation on fawns, and roe deer remains were found in scats throughout the summer season, implying that foxes scavenged on roe deer also in summer.

Although all three winters during our study period were relatively mild and snow cover was shallow and short lasting (snow depth rarely exceeded 20 cm), the proportion of roe deer among fox food items was more than doubled compared to the particularly harsh winter of 1976/77 (snow depth >70 cm for four months), when roe deer mortality was high due to malnutrition, and fox consumption of roe deer was at a maximum for that study period (Lindström 1982, Cederlund & Lindström 1983).

The increased consumption of roe deer in our study could not be explained by a higher population density of roe deer as there was rather a decrease in the roe deer population estimates (see Table 1). Although the low roe deer density was at least in part due to the lynx recolonisation (H. Andrén & O. Liberg, unpubl. data), the lynx may still have made more deer carrion available all year round, by increasing the carrion production per deer, as suggested for Yellowstone wolves preying on elk *Cervus elaphus* (Wilmers & Getz 2004).

During the years of our study, the local roe deer population was monitored by radio-tracking in a parallel research project (O. Liberg & J. Nordström, unpubl. data). This project pointed at lynx predation as the dominating mortality cause for roe deer (except for young fawns, which were often taken by foxes), although some deaths were caused by hunting, road accidents, drowning, intra-specific strife and starvation. Of the latter causes, only starvation and drowning, and to some extent road mortality, may produce carcasses available to foxes in winter (hunting leaves few edible remains, road accidents are localised along major roads and often includes removal of carcasses, and intra-specific strife occurs mainly during the summer rut). These data indicate that the increase in roe deer consumption by foxes as compared to the previous study was mainly due to carcasses produced by lynx predation at least in winter.

Roe deer replaced food of presumed lower profitability for foxes (such as fish, reptiles, invertebrates and vegetables). In addition, the narrowed winter food niche indicated improved food availability for foxes (according to the optimal foraging theory; Pyke 1984). However, population indices of other prey previously known to be of importance to boreal red foxes (microtines in particular, but also hares and forest grouse; Lindström 1989) were generally lower in 1999-2002 as compared to 1974-1979 (see Table 1). Research on the red fox diet in the Białowieża Primeval Forest, Poland, showed that between-year variation in consumption of deer carrion was governed mainly by the densities of microtines and hares (a negative relationship), despite a frequent abundance of deer carcasses, dead from lynx or wolf predation or inanition (Jędrzejewski & Jędrzejewska 1992). Accordingly, the frequent consumption of roe deer in our study could have been a combined effect of a stable supply of deer carrion and a low abundance of other prey species.

We conclude that the presence of lynx feeding on roe deer results in a stable winter food supply for boreal red foxes, and that their summer diet is also supplemented. The total effect of lynx presence on red fox demography may, however, be two-fold. With an increased total food availability to foxes, or at least an additional buffer at low abundance of other prey, a subsequent increase in fox productivity and condition could be predicted. On the other hand, there are several examples of opposite population trends in sympatric carnivores, mainly due to interspecific predation or avoidance (reviews in Palomares & Caro 1999, Buskirk 1999, Linnell & Strand 2000). Lynx readily kill red foxes (e.g. Haglund 1966, Linnell et al. 1998). At present, fox population indices in the region rather describe a decline after the recolonisation by lynx (Helldin et al. 2006).

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