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Original article

Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey

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ABSTRACT

Diet composition of a generalist predator, the red fox (*Vulpes vulpes*) in relation to season (winter or summer) and abundance of multi-annually cyclic voles was studied in western Finland from 1983 to 1995. The proportion of scats (PS; a total of 58 scats) including each food category was calculated for each prey group. *Microtus* voles (the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*) were the main prey group of foxes (PS = 0.55) and they frequently occurred in the scats both in the winter and summer (PSs 0.50 and 0.62, respectively). There was a positive correlation between the PSs of *Microtus* voles in the winter diet of foxes and the density indices of these voles in the previous autumn. Other microtine rodents (the bank vole *Clethrionomys glareolus*, the water vole *Arvicola terrestris* and the muskrat *Ondatra zibethicus*) were consumed more in winter than in summer. The unusually high small mustelid predation by red foxes (PS = approx. 0.10) in our study area gives qualitative support for the hypothesis on the limiting impact of mammalian predators on least weasel and stoat populations. None of the important prey groups was preyed upon more at low than at high densities of main prey (*Microtus* voles). This is consistent with the notion that red foxes are generalist predators that tend to opportunistically subsist on many prey groups. Among these prey groups, particularly hares and birds (including grouse), were frequently used as food by foxes.

1. Introduction

Many empirical and theoretical studies have focussed on the influence of generalist predators on prey population dynamics (Erlinge et al., 1984; Korpimäki et al., 1990; Hanski et al., 1991, 2001; Korpimäki and Krebs, 1996; Lambin et al., 2000). Generalist predators are assumed to stabilize the small mammal population cycles driven by specialist predators due to their direct density-dependent impact on prey population densities (Hanski et al., 1991, 2001; Korpimäki and Krebs, 1996). Changes in the impact of stabilising generalists and destabilising specialists thus seem to play an essential role in variations of length and amplitude of population cycles of rodents (Hansson and Henttonen, 1988; Korpimäki and Norrdahl, 1989a,b; Hanski et al., 1991, 2001). These population cycles are a phenomenon well documented in northern Europe, where the length of the cycle is 3–4 years and predation has been shown to be the main factor driving the cycles

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(Norrdahl and Korpimäki, 1995; Korpimäki and Norrdahl, 1998; Korpimäki et al., 2002, 2005a). On the other hand, generalist predators can also vary the consumption of different prey species in response to fluctuations of their abundances and switch to alternative prey when the densities of their main prey decline (Erlinge, 1986; Korpimäki et al., 1990; Křivan and Sikder, 1999).

Larger generalist predators, such as birds of prey and red foxes (*Vulpes vulpes*), may feed on smaller specialist predators, such as small birds of prey and mustelids, when densities of their main prey, small rodents, decline (Korpimäki and Norrdahl, 1989a,b). Because the smaller specialist predators mainly feed on voles, they may suffer from inter-specific competition and intra-guild predation by larger generalist predators that subsist on small rodents only when these are at high density. In fact, small mustelids have frequently been found in the diet of birds of prey and large mammalian predators, averaging ca. 1% of the number of prey items identified (Latham, 1952; Rosenzweig, 1966; Erlinge, 1983; Liberg, 1984; Korpimäki and Norrdahl, 1989a). The proportion of small mustelids in the diet of birds of prey mainly subsisting on voles and other small mammals is higher in the decline than in the increase and low phases of the vole cycle (Korpimäki and Norrdahl, 1989a).

The red fox has a diverse diet, which apparently allows it to survive in variable habitats from arctic and sub-arctic barren regions to semi-arid deserts (e.g. Lindström, 1983; Macdonald, 1987; Calisti et al., 1990; Dobson, 1998; Dell'Arte and Leonardi, 2005). Small rodents, lagomorphs, birds, carrion, insects and fruits are the main food resources of red foxes, but the importance of these prey items varies largely in relation to habitat types and regional prey availability (Harris, 1981; Papageorgiou et al., 1988; Doncaster et al., 1990; Jędrzejewski and Jędrzejewska, 1992). Furthermore, field studies conducted in Northern Europe and Great Britain showed that diet composition of red foxes seems to track the population cycles of small rodents (Englund, 1965; Lindström, 1983, 1989; Kauhala et al., 1998; O'Mahoney et al., 1999). Although the food habits of red foxes in Northern Europe are quite well known, there is only scanty information on the variation of their diet composition between winter and summer, and in particular, as a response to small rodent abundance that varies in high-amplitude cycles in areas where snowy period lasts for several months.

Because red foxes are generally considered as generalist predators (e.g. Englund, 1965; Lindström, 1983, 1989; Doncaster et al., 1990; Jędrzejewski and Jędrzejewska, 1992; Kauhala et al., 1998; O'Mahoney et al., 1999), we would expect them to take a wide range of prey species so that the composition of their diet should reflect changes in abundance of main prey, with seasonal switches between food resources. Therefore, the first aim of this study was to investigate whether red foxes change their diet composition in response to large among-year variations in small rodent densities. Second, we assess the seasonal differences in their diet composition under the multi-annually cyclic food conditions. Third, we examine whether intra-guild predation could be important in this predator-prey system, i.e. whether red foxes eat smaller mammalian predators subsisting on small rodents and whether this depends on small rodent abundance.

2. Materials and methods

2.1. Study area

This study was conducted at Alajoki, in the vicinity of Kauhava and Lapua, western Finland (approx. 63°05′ N, 22°55′ E). The study area covered ca. 50 km^2 and mainly consisted of arable farmland (73%). Oats, barley and hay were the main cereal crops cultivated in the fields. The woodlands, especially spruce and pine forests, made up 19% of the landscape. Peat-land bogs and inhabited areas comprised only 8% of the total study area (for further details, see Korpimäki and Norrdahl, 1989a).

2.2. Collection and analysis of fox scats

Scats of foxes were collected during snow-tracking and other field work. All scats collected along a daily track of a fox, or collected from the same 3-km^2 area during one day, were regarded as one food sample. Later we took randomly one scat per bag for identification of food items. Each scat was examined carefully to find bone fragments, hair, feathers, parts of insects, or other remains of prey animals as well as remains of plant parts (seeds etc). The scale patterns, cross-sections and medulla types of hair remains were examined and these were identified according to Day (1966), Debrot et al. (1982), Teerink (1991), and using a reference collection of small mammals of known species trapped in the same general area. Feather remains were identified according to Day (1966) and reference material from the Zoological Museum, University of Turku.

A total of 58 scats of foxes were collected from 1983 to 1995. Thirty-four of them were gathered during winter (October to March) when snow usually covers the ground. The snow depth is at maximum usually in February to early March (mean long-term maximum snow depth approx. 30 cm). The remaining 24 scats were collected during summer (April to August). We classified the food items first in eight categories or groups: *Microtus* voles (field voles *Microtus agrestis* and sibling voles *M. rossiaemeridionalis*), ''other microtines'' (the water vole *Arvicola terrestris*, the muskrat *Ondatra zibethicus* and the bank vole *Clethrionomys glareolus*), murids (the harvest mouse *Micromys minutus* and the brown rat *Rattus norvegicus*), hares (*Lepus* spp.), mustelids (the stoat *Mustela erminea* and the least weasel *M. nivalis*), shrews (*Sorex* spp. and *Neomys fodiens*), birds and ''others'' (plants and insects).

Because each fox scat can contain more than one food category (range 1–5), we calculated the proportion of scats (PS) including each food category using the following method: PS = the frequency of each food category in scats/the total number of scats. This method is identical to the frequency of occurrence of food categories that has traditionally been used in dietary analyses of foxes and other mammalian predators (see Dell'Arte and Leonardi, 2005 and references therein). We first examined with a G-test whether there were any differences in the overall diet composition between low and high densities of the *Microtus* vole populations or between winter and summer seasons. Second, we performed Generalised Linear Models to test specific hypotheses on the occurrence of a prey group in the diet in relation to season (winter or summer) and the density of *Microtus* vole populations (high or low). The GLMs were conducted with GENMOD procedure (logit link, binomial distribution) in SAS statistical software version 8.2 (SAS 1989–96 Institute Inc., Cary, NC, USA). In these models, we assigned a binary code "1" or "0" according to whether a prey group occurred or did not occur in each scat, respectively (Zar, 1996). For this analysis we pooled "other microtines" and murids into a single group called "other rodents". Finally, we computed correlations between the PS of *Microtus* voles (main prey) in the winter diet of foxes and the abundance index of these voles in the field in the preceding autumn.

2.3. *Vole density estimates*

We estimated the relative abundances of small mammals at Alajoki by snap-trapping in May (spring trapping) and in September (autumn trapping). The number of trap nights totalled 10,834 in the whole study period. We used metal mouse snap traps set in sample plots on four main habitat types (a cultivated field, an abandoned field, a pine forest and a spruce forest). In each habitat type, 50–100 mouse snap traps were set at intervals of 10 m in small mammal runs for four nights and checked once a day (for further details see Korpimäki and Norrdahl, 1991). Mouse snap traps are useful to capture shrews, field voles, sibling voles, bank voles and mice. We used two density indices (spring and autumn trap index) for statistical analyses, calculated as the number of animals caught per 100 trap-nights. Because of the small sample size of scats, we did not analyse the seasonal variations of the diet composition during each phase of *Microtus* cycle (i.e. a possible interaction between season and phase of *Microtus* cycle). Instead, we examined the PSs including different food categories at low and high densities of these voles (number of trapped voles per 100 trap nights 0.00–7.74 vs. 7.75–28.30, respectively).

Assuming linear changes in the density indices of small mammals in two successive seasons, we considered that the density indices, calculated in autumn and spring, describe the field abundance of voles in the next winter and summer periods, respectively.

3. Results

We found a significant difference in the diet composition of red foxes between winter and summer seasons ($G = 18.01$, $df = 7$, $P = 0.012$; Fig. 1a) and a tendency for the diet composition to differ at low and high densities of *Microtus* voles ($G = 13.67$, $df = 7$, $P = 0.057$; Fig. 1b). *Microtus* voles emerged as main prey of foxes (PS = 0.56 in the total number of scats). They occurred in the scats equally in the winter and summer seasons (PS = 0.50 and 0.67, respectively), but more frequently when their densities in the field were high (GLM; season: $\chi^2 = 0.12$, $P = 0.73$, Fig. 1a; *Microtus* density: $\chi^2 = 7.17$, $P = 0.007$, Fig. 1b). There was a positive correlation between the PS containing *Microtus* voles in the winter diet of foxes and the density indices of these voles in the previous autumn during 1983 to 1995 (Fig. 2).

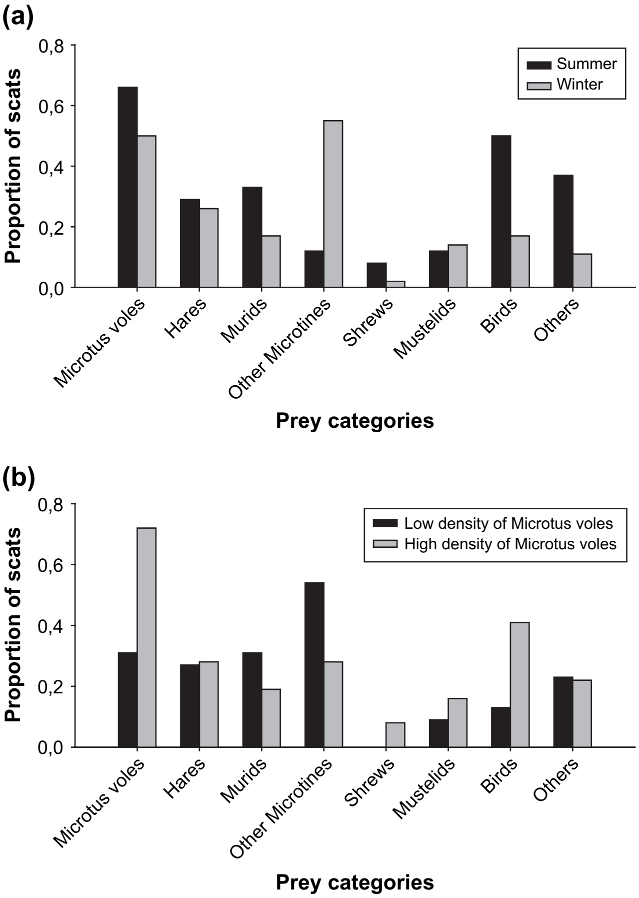

Fig. 1 – Diet composition of red foxes in summer (number of scat samples = 24 and number of occurrences of different prey categories = 60) and winter (*n* = 34 and 67; a) and at low (*n* = 22 and 42) and high (*n* = 36 and 85) densities of *Microtus* voles (b). Because each scat usually contains more than one prey category and because the proportion of scats including each prey category was used in the figure, the pooled proportion per season etc. ends > 1.00.

The "other microtines" group was the second most eaten prey, found in 0.37 of the scats. Their PS was significantly higher in winter than in summer (season: $\chi^2 = 7.64$, $P = 0.006$; Fig. 1a). The PS containing other microtines did not differ significantly between high and low *Microtus* densities even if they were present in 0.54 of scats collected in poor *Microtus* vole years (*Microtus* density: $\chi^2 = 0.01$, $P = 0.94$; Fig. 1b). Murids formed a considerable proportion of the diet, especially in winter (PS = 0.18) and at high *Microtus* densities (0.20; Fig. 1). When we pooled these two groups of rodents in our model, we did not find any obvious difference in the PS containing "other rodents" in relation to season or *Microtus* density (season: $\chi^2 = 0.85$, $P = 0.36$; *Microtus* density: $\chi^2 = 2.36$, $P = 0.13$).

Birds occurred frequently in the diet of red foxes (PS = 0.31 in the total number of scats). Thirty-nine percent of bird remains in the scats could be identified as grouse (*Galliformes*). There were no obvious differences in the PS containing birds

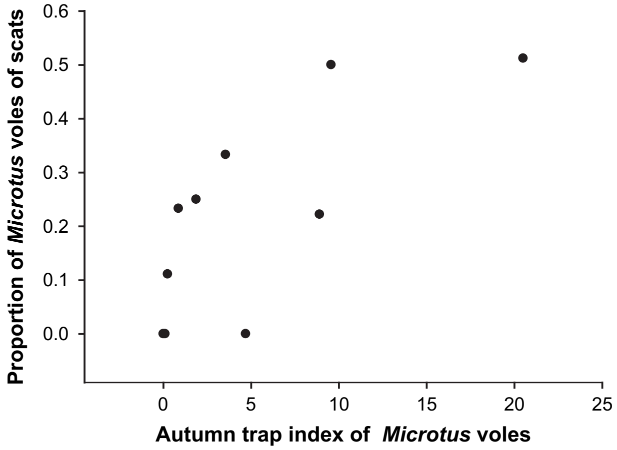

Fig. 2 – Yearly proportion of scats containing *Microtus* voles in the winter diet of red foxes against the trap index of *Microtus* voles (individuals trapped per 100 trap nights) in the previous autumn in 10 years during 1983 to 1995 ($r_s = 0.706$, $P = 0.023$). If the two data points from two winters with only one scat collected and no *Microtus* voles recorded in the diet of red foxes are removed, the correlation appears to be stronger ($r_s = 0.857$, $P = 0.007$).

in relation to season or *Microtus* density, although they tended to occur more frequently in the diet in the summer than in winter (season: $\chi^2 = 3.32$, $P = 0.069$; *Microtus* density: $\chi^2 = 1.85$, $P = 0.17$; Fig. 1). Hares were preyed by foxes similarly both in winter (PS = 0.26) and summer (PS = 0.29), and also at different *Microtus* densities (season: $\chi^2 = 0.05$, $P = 0.82$; *Microtus* density: $\chi^2 = 0.00$, $P = 0.95$; Fig. 1).

Foxes had eaten small mustelids quite frequently in both winter and summer (PS approx. 0.10; Fig. 1), and their PS did not differ according to *Microtus* vole densities (season: $\chi^2 = 0.42$, $P = 0.52$; *Microtus* density: $\chi^2 = 1.06$, $P = 0.30$). Shrews were present with low PSs in both seasons (PS = 0.05). They were also recorded with a low PS at high *Microtus* densities (Fig. 1b). The category "others", which mainly consists of plants and insects, was exploited during summer. Food items in this category were consumed both at high and low densities of *Microtus* voles (Fig. 1b).

4. Discussion

As found in previous studies made mainly in Northern Europe, the diet of the red fox consists mainly of small rodents, with *Microtus* voles as the main prey group (e.g. Englund, 1965; Lindström, 1989; Jędrzejewski and Jędrzejewska, 1992; Kauhala et al., 1998; Leckie et al., 1998; O'Mahoney et al., 1999). Our results show, however, that the proportion of *Microtus* voles in the diet of red foxes varied widely among years, at least in winter, and was closely related to their densities in the field (Fig. 2). These rodents were the staple food of red foxes in both seasons, their occurrence ranging on average from 0.50 to 0.66 of scats in winter and summer, respectively (Fig. 1a). Other microtine rodents were consumed more in winter than in summer. We suggest that the changes in the diet composition of the red fox reflected their large dependence on *Microtus* voles and other microtine rodents in the field, particularly during winter when there are few alternative prey types available in northern strongly seasonal environments.

The occurrence of *Microtus* voles in fox scats in winter varied widely among years and closely tracked the density indices of these voles in the field (Fig. 2). In other ecosystems with cyclic vole populations, like Swedish boreal forests, Scottish moorlands and British spruce forests (Leckie et al., 1998; Lindström, 1994; O'Mahoney et al., 1999), much less among-year variation in the occurrence of *Microtus* voles in the diet of foxes was found, but in these studies the diet composition of foxes was studied only in summer. The probable reason for wider variation in the occurrence of *Microtus* voles in the fox diet of our study area is that the amplitude of population fluctuations of voles is much higher in northern Europe than in western Europe (Hanski et al., 1991). In particular, in the low phase of the cycle, population densities of voles are order of magnitude lower in northern Europe than in western Europe (Korpimäki et al., 2003, 2005b). This induces a high need for foxes to find and use other food resources at low densities of voles.

The fact that none of the prey groups was preyed upon more at low than at high densities of main prey (*Microtus* voles) is consistent with the notion that red foxes are generalist predators that tend to opportunistically subsist on many prey groups. Among these prey groups, hares and birds, in particular grouse, were frequently used as food by foxes in our study area. In addition to hares and grouse killed by foxes, a part of these foods found in scats was probably included in the diet when found as carrion (remnants left by hunters and road kills). Therefore, they cannot be considered as alternative prey for foxes, but rather also as main prey groups.

Hares are more profitable prey in terms of biomass than microtine rodents, and other studies have found that they may compensate for the shortage of *Microtus* voles in poor vole years and in winters with deep snow cover (Marcström et al., 1989; Kauhala and Helle, 2000). In this study, the occurrence of hares in the diet of foxes varied only little between winter and summer and between high and low densities of *Microtus* voles (Fig. 1). It was also far less than in the early summer diet of red foxes in southern Finland (PS approx. 0.55, Kauhala et al., 1998).

Birds become more available in spring, during the breeding season, and foxes can catch birds especially from their roosting sites (Reig and Jędrzejewski, 1988) and nests. Accordingly, we found a tendency for birds to be preyed upon more in summer than in winter. Surprisingly, however, there was no difference in the occurrence of birds associated with the density of *Microtus* voles. A substantial proportion of birds eaten by foxes were grouse species, which suggests that foxes may be an important predator of these game species. Moreover, clear-cutting of forests may also increase densities of red foxes by creating wide areas of new grassy habitats for *Microtus* voles, the main food of foxes. Increased densities of red foxes might in turn be an important reason for declines in forest grouse populations in Finland and elsewhere in northern Europe (Kurki et al., 1997).

We found a high predation rate of small mustelids (least weasels and stoats) (approx. PS = 0.10 in the total number of scats) by red foxes as compared to low frequencies of occurrence recorded in central Europe (ca. 0.02; Jędrzejewski and Jędrzejewska, 1992) and in some other studies made in Northern Europe (Kauhala et al., 1998; Elmhagen et al., 2002). Small mustelids were present in the diet of foxes both at high and low densities of main prey (*Microtus* voles) and during winter and summer, although there was a tendency that mustelids were more preyed upon when densities of voles were high. In northern Europe, small mustelids use *Microtus* voles as their main food at high densities of these voles, in particular in winter, and they also show a delayed numerical response to widely fluctuating densities of voles (Korpimäki et al., 1991; Oksanen and Henttonen, 1996). When vole populations start to decline, the densities of small mustelids are high in the field and they probably move over long distances on the snow surface when searching for prey (Oksanen and Henttonen, 1996; Klemola et al., 1999; Aunapuu and Oksanen, 2003). Also, both stoats and least weasels in our study area prefer grassy farmland habitats typical for *Microtus* voles, especially at high densities (Klemola et al., 1999). These behaviours tend to increase the encounter rate of avian and mammalian predators resulting in a high predation risk for mustelids. Therefore, mortality due to red foxes might be important for the limitation of these mustelid populations (Latham, 1952; Rosenzweig, 1966; Erlinge, 1983; Korpimäki and Norrdahl, 1989a), although more specific studies using, for example, radio-telemetry are needed to confirm this idea.

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