Food selection by adult red foxes Vulpes vulpes during a water vole decline

Author: Weber, Jean-Marc

Source: Wildlife Biology, 2(4) : 283-288

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1996.032

SHORT COMMUNICATION

Short communication articles are short scientific entities often dealing with methodological problems or with byproducts of larger research projects. The style should be the same as in original articles.

Food selection by adult red foxes *Vulpes vulpes* during a water vole decline

Jean-Marc Weber

Weber, J.-M. 1996: Food selection by adult red foxes *Vulpes vulpes* during a water vole decline. - Wildl. Biol. 2: 283-288.

Food selection by adult red foxes *Vulpes vulpes* was studied in a mountainous environment characterised by fluctuating populations of water voles. According to optimal foraging theory, the diets of adults and cubs should be similar during vole highs, with voles as staple prey. On the other hand, a difference should occur when water voles become scarce. Adults should then bring larger alternative prey to their cubs, and consume smaller prey at the capture site. Adult and cub scats were collected around breeding dens during a 6-year period, from the peak to a near-extinction phase of the water vole population, and analysed. As predicted by the optimal foraging theory, no significant difference was found between the diets of cubs and adults when voles were abundant. Furthermore, cubs consumed a higher proportion of large alternative prey, i.e. lagomorphs, than adults in the first year of low vole density. Unexpectedly, this difference did not persist the following years despite the water vole scarcity. The consumption of large alternative prey at the den decreased significantly, whereas the consumption of small alternative prey, i.e. invertebrates, increased. Consequently, the composition of prey brought to the den was similar to that consumed at the capture site. Food selection was probably affected by the unpredictability of large prey availability and accessibility. It is suggested that if small alternative prey proves less profitable to the cubs than large prey, a long-lasting shortage of water voles could possibly become a factor regulating fox numbers in the area studied.

Key words: Arvicola terrestris scherman, food selection, population cycle, red fox, Vulpes vulpes, water vole

Jean-Marc Weber, Institut de Zoologie, Emile-Argand 11, 2007 Neuchâtel, Switzerland

Received 22 July 1996, accepted 30 January 1997

Associate Editor: Heikki Henttonen

Several studies on the diet of the red fox *Vulpes vulpes* have emphasised differences between the composition of prey consumed by adult foxes and that eaten by small cubs (see Artois 1989 for a review). A higher proportion of large prey, e.g. lagomorphs, is generally found in the diet of cubs than in the diet of adults. Lindström (1994) suggests that this difference reflects an optimal foraging behaviour by adult foxes. The optimal foraging theory predicts that a central place forager, i.e. an organism collecting food and carrying it to some central place, e.g. a den, should consume small prey at the capture site, and bring larger prey to its offspring (Orians & Pearson 1979). Furthermore, the theory also predicts that in a predator showing a functional response to a fluctuating prey, the difference between the composition of prey eaten at the capture site and prey brought to the central place would disappear as the abundance of the primary prey increases (Sonerud 1992). Lindström (1994) found that in a boreal forest fox cubs consumed a higher proportion of large alternative prey than adults during the first increase year of voles *Microtus agrestis* and *Clethrionomys glareolus*, their primary prey, but this difference disappeared when voles were abundant.

In this paper, I examine food selection by adult foxes during reproduction in a mountainous environment characterised by fluctuating populations (4-8 year population cycles: Saucy 1988) of the fossorial form of the water vole *Arvicola terrestris scherman*. The diets of cubs and adult foxes were investigated during a 6-year period, from the peak to the near-extinction phase of the water vole population. According to optimal foraging theory and Lindström's (1994) findings, the foraging behaviour of adult foxes should change as follows: 1) if there is a functional response of foxes to the number of water voles, the composition of prey brought to the central place and prey eaten at the capture site should be similar when water voles are abundant; 2) on the other hand, a difference should occur when water voles become scarce. Cubs should then consume a higher proportion of large alternative prey than adults.

Study area and methods

The study was carried out from 1989 to 1994 in the Swiss Jura Mountains in western Switzerland (47° 09' N, 6° 56' E; altitude: 995 - 1,288 m a.s.l.). 'La Chaux d'Abel', the 30 km^2 study area mainly consists of grasslands interspersed with small patches of wooded pastures and forests. Human presence is an important factor, as the area holds ca 80 farms.

Scats of cubs and adults were collected at and in the proximity of breeding dens twice a month during the first two months after the emergence of the cubs from the dens (May-June), when scats could still be distinguished by size. Scat analyses were performed as described by Weber & Aubry (1993), and results were expressed as relative frequency of occurrence. Food items were categorised in four classes: (i) water voles, (ii) size-equivalent alternative prey (other rodents, passerines), (iii) larger alternative prey, e.g. lagomorphs, poultry, and (iv) smaller alternative prey, e.g. insects, earthworms *Lumbricus* spp. and rubbish, e.g. food scraps.

Fluctuations in the water vole populations were measured by seasonal trapping in two areas representative of the entire study area, but only the results of spring trappings were included in this paper. Trapping area A was surrounded by five potential breeding dens (200 - 1,500 m away), whereas trapping area B was in the vicinity (500 - 1,200 m) of three breeding dens. Trappings were carried out on a 100 × 5 m strip divided into 20 adjoining squares with no more than two Sherman live traps per square.

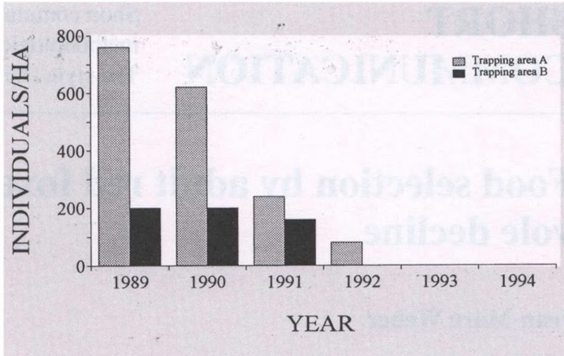

Figure 1. Spring densities of water voles in the two trapping areas in 1989-1994.

Traps were set for three days, and checked eight times (Pascal & Meylan 1986). Rodolphe & Pascal (1985) and Pascal & Meylan (1986) give details on how to transform trapping results into density estimates.

Results

Water vole populations peaked in late 1988 and early 1989, reaching 760 and 200 individuals/ha in trapping areas A and B, respectively (Fig. 1). A regular decrease was observed in the following years; in 1992, water vole density was below 100 individuals/ha in trapping area A, and the species was close to extinction in trapping area B. Eventually, no voles were caught in either of the trapping areas during spring 1993 and 1994.

A total of 504 cub scats and 95 adult scats were collected at breeding dens during 1989 - 1994 (Table 1). The consumption of water voles by both adult foxes and cubs was positively related to water vole availability (adults: $r_s = 1.00$; N = 6, P = 0.025; cubs: $r_s = 0.98$, N = 6, P = 0.044). Consequently, water voles were the most important prey to foxes during the peak and early population

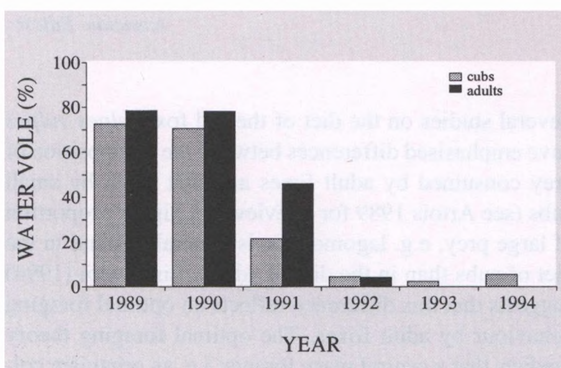

Figure 2. Water vole consumption (%) by adults and fox cubs during 1989 - 1994.

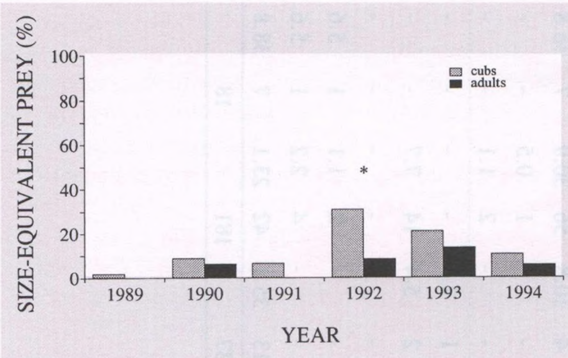

Figure 3. Relative consumption of size-equivalent alternative prey such as field and bank voles, murids, insectivores and passerines by adults and fox cubs during 1989 - 1994. * indicates significant differences (P < 0.05) between categories.

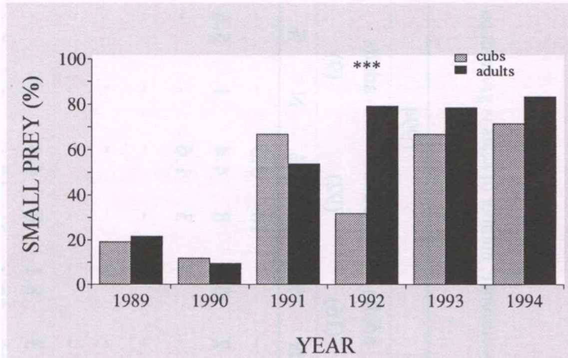

Figure 5. Relative consumption of small alternative prey such as insects, earthworms and rubbish by adults and fox cubs during 1989 - 1994. *** indicates significant differences (P < 0.001) between categories.

decline phases (Fig. 2). Furthermore, at these stages of the vole cycle, alternative prey were taken in various proportions (see Table 1), but no significant difference was recorded between adults and cubs (Fisher's exact probability test, P > 0.05; Figs. 3-5). As suggested by the ratio of large to small alternative prey (Fig. 6), the composition of prey brought to the den by adults was similar to that eaten at the capture site. In 1991, an increase of the consumption of small alternative prey and rubbish was observed in both adults and cubs (see Table 1 and Fig. 5). Nevertheless, as water voles were still available to foxes in reasonable numbers (240 and 160 individuals/ha), no difference between the composition of prey brought to the cubs and that eaten by adults was found.

In 1992, the first year of low water vole density, the ratio of large to small alternative prey became significantly higher in cub scats than in those of adults (see Fig. 6); the consumption of large alternative prey was higher at the den than on the spot (Fisher's exact probability test, P = 0.019; see Fig. 4). Size-equivalent prey were also preferentially given to the cubs (Fisher's exact probability test, P = 0.034; see Fig. 3). Conversely, adults, while bringing larger prey to the cubs, were predominantly feeding on small alternative prey (Fisher's exact probability test, P = 0.000; see Fig. 5). This difference could be expected to persist, since water vole density remained very low in 1993 and 1994. However, the consumption of large alternative prey at the den decreased significantly between 1992 and 1993, whereas that of small alternative prey increased (Fisher's exact probability test, P = 0.000). On the other hand, no change in the diet of adults was observed. In other words, the composition of prey brought to the den was similar to that consumed at the capture site in 1993 and 1994.

Discussion

Foxes clearly responded functionally to water voles in this mountainous habitat, resulting in intensive predation on water voles when these were abundant and easily available to foxes. As expected, at this stage of the vole cy-

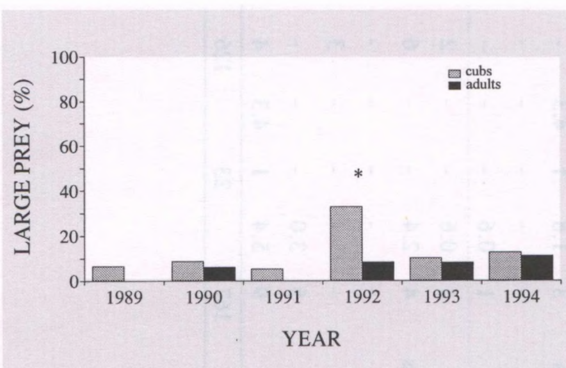

Figure 4. Relative consumption of large alternative prey such as hedgehog, fox, cat, lagomorphs, roe deer, cattle and poultry by adults and fox cubs during 1989 - 1994. * indicates significant differences (P < 0.05) between categories.

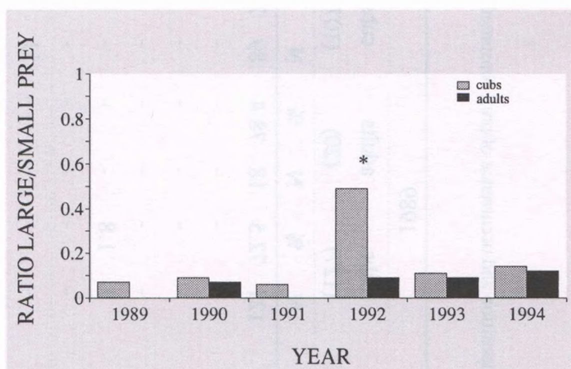

Figure 6. Ratio of large to small alternative prey in the diets of cubs and adult foxes during 1989-1994. * indicates significant differences (P < 0.05).

Table 1: Composition and occurrence of prey consumed by adults and fox cubs during 1989 - 1994. N: number of prey items; %: relative frequency of occurrence; number of scats is given in parentheses.

	1989				1990				1991				1992				1993				1994			
	cubs (127)		adults (20)		cubs (107)		adults (27)		cubs (62)		adults (10)		cubs (57)		adults (13)		cubs (59)		adults (16)		cubs (92)		adults (9)	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Water vole	121	72.5	18	78.4	89	70.6	25	78.1	20	21.5	6	46.2	4	4.4	1	4.2	3	2.3	-	-	10	5.5	-	-
Field vole	-	-	-	-	-	-	1	3.1	-	-	-	-	10	11.0	-	-	7	5.4	2	5.4	8	4.4	1	5.6
Bank vole	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1.6	-	-
Murids	-	-	-	-	-	-	-	-	-	-	-	-	5	5.5	-	-	6	4.6	-	-	-	-	-	-
Mole	3	1.8	-	-	-	-	-	-	-	-	-	-	8	8.8	2	8.4	4	3.1	-	-	-	-	-	-
Shrews	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	3.1	-	-	-	-	-	-
Passerines	-	-	-	-	11	8.7	1	3.1	6	6.5	-	-	5	5.5	-	-	6	4.6	3	8.1	8	4.4	-	-
Insects	20	12.0	3	13.0	11	8.7	1	3.1	24	25.8	3	23.1	7	7.7	6	25.0	34	26.3	12	32.4	31	17.1	1	5.6
Earthworms	3	1.8	1	4.3	-	-	-	-	5	5.4	-	-	6	6.7	5	20.8	12	9.3	4	10.8	56	30.9	7	38.8
Hedgehog	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.5	-	-
Red fox	1	0.6	-	-	--	-	-	-	-	-	-	-	-	-	-	-	2	1.6	-	-	2	1.1	-	-
Cat	1	0.6	-	-	2	1.6	1	3.1	3	3.2	-	-	6	6.7	-	-	3	2.3	1	2.7	-	-	-	-
Lagomorphs	4	2.4	-	-	6	4.8	1	3.1	2	2.1	-	-	13	14.3	-	-	2	1.6	2	5.4	14	7.7	-	-
Roe deer	-	-	-	-	-	-	-	-	-	-	-	-	2	2.2	1	4.2	1	0.8	-	-	-	-	-	-
Cattle	-	-	-	-	3	2.4	-	-	-	-	-	-	4	4.4	1	4.2	2	1.6	-	-	2	1.1	1	5.6
Poultry	5	3.0	-	-	-	-	-	-	-	-	-	-	5	5.5	-	-	3	2.3	-	-	4	2.2	1	5.6
Rubbish	9	5.4	1	4.3	4	3.2	2	6.3	33	35.5	4	30.7	16	17.6	8	33.3	40	31.0	13	35.1	42	23.1	7	38.8
Total	167		23		126		32		93		13		91		24		129		37		181		18	

Number and activities of farm cat (Felis catus) in the Swiss Jura). - Zeitschrift für Säugetierkunde 58: 84-91.
Lindström, E. 1983: Condition and growth of red foxes (Vulpes vulpes) in relation to food supply. - Journal of Zoology 199: 117-122.
Lindström, E. 1994: Large prey for small cubs - on crucial resources of a boreal red fox population. - Ecography 17: 17-22.
Meia, J.-S. 1994: Organisation sociale d'une population de renards (Vulpes vulpes) en milieu montagnard. (In French with English summary: Social organization of a red fox population in a mountainous habitat). - Ph.D. thesis, University of Neuchâtel, 208 pp.
Meia, J.-S., Aubry, S., Ferrari, N., Lachat, N., Mermod, C. & Weber, J.-M. 1993: Observations nocturnes au phare dans le Jura bernois entre septembre 1988 et août 1991. (In French with English summary: Nightlighting in the Bernese Jura from September 1988 to August 1991). - Mitteilungen der Naturforschenden Gesellschaft in Bern 50: 193-202.
Meia, J.-S. & Weber, J.-M. 1996: Social organization of red foxes (Vulpes vulpes) in the Swiss Jura Mountains. - Zeitschrift für Säugetierkunde 61: 257-268.
Orians, G.H. & Pearson, N.E. 1979: On the theory of central place foraging. - In: Horn, D.J. & Mitchell, R.D. (Eds.); Analysis of ecological systems. Ohio State University Press, pp. 155-177.
Pascal, M. & Meylan, A. 1986: L'échantillonnage linéaire des populations de la forme fouisseuse du campagnol terrestre (Arvicola terrestris scherman (Shaw)): description des techniques. - Défense des Végétaux 237: 3-12. (In French).
Rodolphe, F. & Pascal, M. 1985: Méthode d'échantillonnage de la forme fouisseuse du campagnol terrestre (Arvicola terrestris scherman). Recherche d'un estimateur sans biais de la densité pour un piègeage en bande. - Acta Oecologica Oecologia Applicata 6: 143-163. (In French).
Saucy, F. 1988: Dynamique de population, dispersion et organisation sociale de la forme fouisseuse du campagnol terrestre (Arvicola terrestris scherman (Shaw), Mammalia, Rodentia). (In French with English summary: Population dynamics, dispersal and social organization in the fossorial from of the water vole, Arvicola terrestris scherman (SHAW) (Mammalia, Rodentia)). - Ph.D. thesis, University of Neuchâtel, 366 pp.
Sonerud, G.A. 1992: Functional responses of birds of prey: bias due to the load-size effect in central place foragers. - Oikos 63: 223-232.
Weber, J.-M. & Aubry, S. 1993: Predation by foxes, Vulpes vulpes, on the fossorial form of the water vole, Arvicola terrestris scherman, in western Switzerland. - Journal of Zoology 229: 553-559.

cle, the composition of prey eaten by adult foxes was not different from that eaten by the cubs. In optimal foraging behaviour of adult foxes, the similarity between adult and cub diet could to some extent have been strengthened by the multiple-prey loading behaviour - more than one prey item carried per trip to the central place (Orians & Pearson 1979) - sometimes adopted by adult foxes during vole highs (Lindström 1994). The results of the present study do not contradict Lindström's suggestion. Foxes, although usually considered single-prey loaders, i.e. only one prey item is carried to the central place per trip, (see Artois 1989 for a review), were regularly observed carrying up to eight water voles at a time to their offspring during the peak and early decline phases of the water vole population.

The near disappearance of water voles constrained foxes to concentrate their hunting effort on alternative prey, of which the largest should then predominantly be given to the cubs according to central place foraging theory (Orians & Pearson 1979). Adult foxes behaved in accordance with the theory during the first year of low water vole density, as a higher proportion of large prey was recorded in the diet of cubs than in the diet of adults. However, unexpectedly, this difference disappeared in the following years. Although water voles were still rare in the area, diets of adults and cubs became similar, with invertebrates and rubbish as staple prey. The availability and accessibility of large alternative prey probably influenced the foraging behaviour of adult foxes. Most prey that could favourably - in term of size - replace water vole in fox diet had a seasonal character or a limited availability in the study area (Meia et al. 1993, Ferrari & Weber 1995). Thus, small rodents such as *Microtus* spp., and brown hares *Lepus europaeus* were scarce, and gamebirds, i.e. partridge *Perdrix perdrix* and pheasant *Phasianus colchicus*, and wild rabbits *Oryctolagus cuniculus* did not occur in the area. Actually, the galliformes and rabbits identified in fox scats were exclusively domestic, and their accessibility to foxes depended on farmers' personal habits and was highly limited, sometimes completely restricted (Ferrari & Weber 1995). Free-ranging domestic cats *Felis catus* were numerous in the area (Lachat et al. 1993), and could therefore constitute a more accessible prey to foxes. However, my observations showed that in frequent dyadic encounters between foxes and cats, they usually ignored each other, and in all but one of the few agonistic interactions, the cat dominated and chased the fox (unpubl. data). This suggests that foxes would find cats a costly prey to hunt. The low frequency of occurrence of cats in fox diet throughout the study reinforced this hypothesis.

As an opportunist predator, the red fox takes what is readily available (Doncaster et al. 1990, Cavallini & Lovari 1991, Ferrari & Weber 1995). The unpredictability of large prey availability and accessibility probably affected the foraging behaviour of foxes, which had to feed their offspring with less unpredictable food resources. Invertebrates and rubbish were known to be abundant and quickly renewable items in the study area (Ferrari & Weber 1995). In these circumstances, the most abundant item could be the most profitable one in terms of energy intake per time unit spent searching and handling prey, at least to adult foxes. But how about to the cubs? Earthworms are considered a profitable prey to badger cubs (D.W. Macdonald, pers. comm.).

The absence of any significant variation in fox reproductive output, and the maintenance of spatial groups despite these drastic trophic changes (Meia & Weber 1996) suggest that even in the absence of their main prey, the area could provide enough food for foxes to breed successfully. In this regard, through his food scraps man could be an essential factor in the persistence of foxes in the study area during the low phase of water vole density. On the other hand, a significant decrease in the mean body weight of the cubs was recorded from year to year during the water vole decline (Meia 1994). Was this decrease related to the trophic changes? Lindström (1983) also found a positive correlation between juvenile fox growth and vole abundance, which could indicate that alternative prey given to the cubs were less profitable to them than their primary prey. Therefore, a long-lasting shortage of water voles, with an unpredictable supply of large alternative prey, could possibly become a factor regulating fox numbers by affecting adult foraging behaviour, hence cub growth and survival.

Acknowledgements - I thank S. Aubry for field assistance, and Drs R. Hewson, H. Henttonen and two anonymous referees for useful comments on the manuscript. Financial support was provided by the Swiss National Science Foundation (grant 31-27766.89) and by the Federal Office of Environment, Forests and Landscape.

References

Artois, M. 1989: Le renard roux (Vulpes vulpes Linnaeus, 1758). - Encyclopédie des carnivores de France No 3. Société française pour l'étude et la protection des Mammifères, Paris, 90 pp. (In French).

Cavallini, P. & Lovari, S. 1991: Environmental factors influencing the use of habitat in the red fox Vulpes vulpes (L. 1758). - Journal of Zoology 223: 323-339.

Doncaster, C.P., Dickman, C.R. & Macdonald, D.W. 1990: Feeding ecology of red foxes Vulpes vulpes in the city of Oxford, England. - Journal of Mammalogy 71: 188-194.

Ferrari, N. & Weber, J.-M. 1995: Influence of the abundance of food resources on the feeding habits of the red fox, Vulpes vulpes, in western Switzerland. - Journal of Zoology 236: 117-129.

Lachat, N., Aubry, S., Ferrari, N., Meia, J.-S., Mermod, C. & Weber, J.-M. 1993: Effectifs et activités du chat domestique (Felis catus) dans le Jura suisse. (In French with English summary: