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SHORT COMMUNICATION

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Breeding success of the red fox *Vulpes vulpes* in relation to fluctuating prey in central Europe

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The influence of water vole *Arvicola terrestris scherman* fluctuations on red fox *Vulpes vulpes* reproduction was investigated in a central European mountainous habitat. We also examined the relationship between annual variations in the mean body weight of the cubs and trophic changes. Water vole abundance was estimated by seasonal trappings, and fox families and cubs were counted every spring. The number of fox families differed little between years, and the differences were not related to water vole abundance. Mean litter size also varied from year to year, but independently of water vole densities. No relation was found between the weight of the cubs and water vole supply. The lack of any significant annual variations in fox breeding success means that despite the low availability of wild alternative prey, foxes found suitable trophic conditions in the absence of water voles. Moreover, as suggested by the increase in the consumption of food scraps by foxes during vole lows, man has certainly been instrumental in preventing a decrease in fox breeding success at the low stage of the water vole cycle.

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

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Red fox *Vulpes vulpes* reproduction has been extensively studied all over the range of the species (Artois 1989), but very few studies emphasised the relationship between fox breeding success and trophic conditions. Reproductive success is related to food availability in several north European regions (Englund 1970, Kolb & Hewson 1980, Lindström 1989). In these areas, foxes mainly feed on cyclic fluctuating prey and, as alternative prey often is scarce, they face drastic trophic conditions when their staple prey is in limited supply. One consequence of this is a variation in fox reproductive output between years. Indeed, different aspects of reproduction such as the number of active breeding dens, whelping frequency and mean litter size generally correlate with vole abundance (Englund 1970, Kolb & Hewson 1980, Lindström & Lindström 1991) or rabbit density (von Schantz 1984). In contrast, reproduction shows little variation between years in regions where different alternative food is available to foxes during vole lows (Lindström & Lindström 1991).

In the Swiss Jura Mountains, foxes feed to a large extent on the fossorial form of the water vole *Arvicola terrestris scherman* when the population of this cyclic fluctuating rodent is high (Weber & Aubry 1993). The scarcity, seasonality, unpredictability and limited accessibility of alternative prey in the study area greatly restrict prey choice during water vole decline and low. At these stages of the water vole cycle, only rubbish and invertebrates are available to foxes in reasonable quantities, and opportunistically, foxes mainly incorporate these items in their diet when water voles are scarce (Ferrari & Weber 1995, Weber 1996). However, this alternative food could be less profitable to foxes than their primary prey as suggested by a decrease in the mean body weight of the cubs recorded from year to year during the water vole decline (Meia 1994).

The aim of our study was to assess the influence of water vole population fluctuations on red fox reproduction in a central European region by posing the following question: would fox breeding success vary during a water vole cycle or would alternative food supply prevent any significant variations in fox breeding success? From 1989 to 1997, we investigated the reproduction of foxes and compared annual variations in fox breeding success with water vole abundance. In addition, we examined the relationship between annual variations in the mean body weight of the cubs and trophic changes.

Study area and methods

The study was carried out in a 30-km^2 rural area in the Swiss Jura Mountains, western Switzerland (47°09'N, 6°56'E), where the elevation ranges from approximately 995 m to 1,290 m a.s.l. The landscape has been shaped by human agricultural activities, and consequently pastures (22%) and meadows (30%) cover more than half the area. Wooded pastures (25%), forests (20%) and habitations (3%) constitute the other important habitats of the study area. A more complete description of the study area is presented in Weber & Meia (1996).

Every year from early March onwards, all known fox dens in the study area (ca 160) were systematically visited once a week to search for any signs of fox breeding activities (i.e. intensive scent marking). When evidence (i.e. prey remains, flattened vegetation) that a fox litter was present at a den was found, observations were initiated and the cubs were counted using 10 x 40 binoculars and a video camera. Then, the cubs were usually captured with footsnares, marked and weighed during the first two months (May-June) after their emergence from the den.

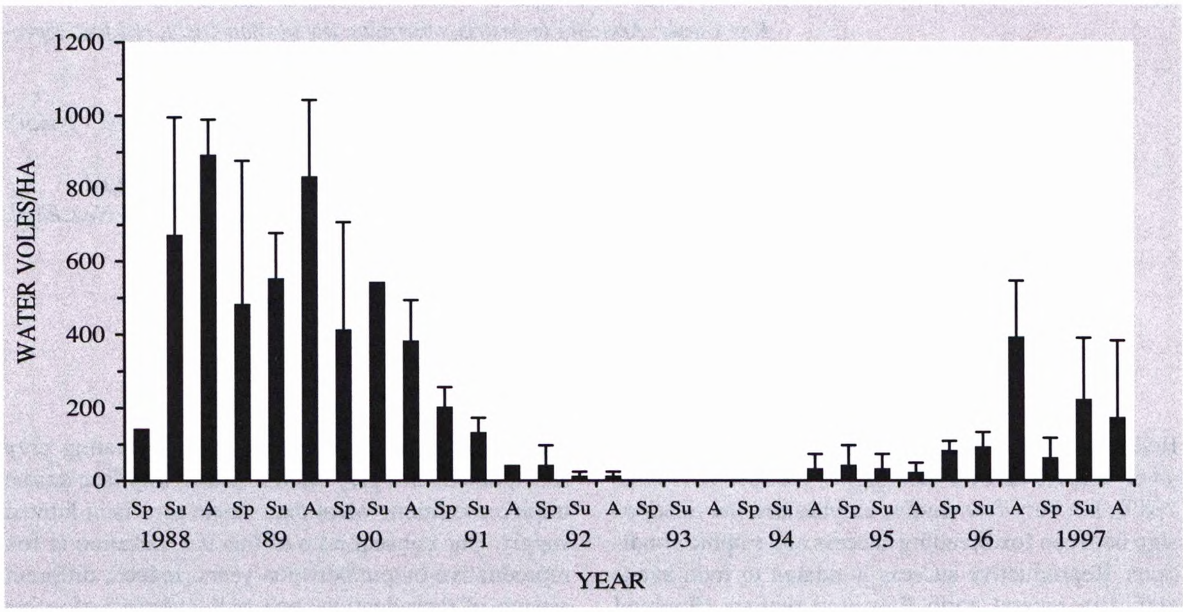

Figure 1. Mean seasonal (Sp = spring; Su = summer; A = autumn) densities of water voles in the study area during 1988-1997.

Table 1. Breeding performance by the red fox during 1989-1997.

Year	First observation	Number of litters	Litter/km²	Number of cubs	Number of cubs per litter			
					$\bar{x}$	Sd	Min	Max
1989	02.05	11	0.37	34	3.09	2.02	1	6
1990	17.04	10	0.33	46	4.60	1.50	2	7
1991	06.05	10	0.33	30	3.75	1.38	2	6
1992	29.04	12	0.40	43	3.58	1.38	2	7
1993	27.04	11	0.37	43	3.91	1.81	1	7
1994	03.05	10	0.33	38	3.80	1.32	2	6
1995	15.05	13	0.43	59	4.53	1.71	2	8
1996	03.05	13	0.43	52	4.00	0.91	2	5
1997	13.05	10	0.33	40	4.00	1.25	2	5

Water vole populations were sampled seasonally with Sherman traps in two areas representative of the entire study area. Trappings were made following Pascal & Meylan (1986). Snow cover and frozen ground prevented trapping during winter.

Results

Water vole populations peaked in autumn 1988 (mean ± sd; 890 ± 99 individuals/ha) and autumn 1989 (830 ± 212 individuals/ha). In 1990, densities declined markedly to reach 30 ± 42 individuals/ha in autumn 1991, and remained low until autumn 1995 (20 ± 30 individuals/ha). An increase in water vole abundance was observed in the following years (Fig. 1).

The very first signs of fox litters were generally found in late April or early May (Table 1). The number of fox families in the study area differed little between years, from 10 (0.33 litter/km²) to 13 (0.43 litter/km², see Table 1), and these differences were neither related to water vole abundance in the spring (r_s = - 0.1983, N = 9, P = 0.6090) nor to water vole abundance in the previous autumn (r_s = - 0.2735, N = 9, P = 0.4762). The number of cubs/litter/year during the study period averaged 3.09 (± 2.02) - 4.6 (± 1.5) according to the year, but these variations were not significantly different (one-way ANOVA, F = 1.0407, P = 0.4119). No relation was found between the mean litter size and spring respectively autumn densities of water voles (r_s = - 0.0506, N = 9, P = 0.8970; r_s = - 0.0836, N = 9, P = 0.8305, respectively).

A total of 88 fox cubs were captured and weighed. Their mean weight varied significantly from 1.63 kg (± 0.37) to 2.45 kg (± 0.35) according to the year (one-way ANOVA, F = 2.1326, P = 0.041; Table 2). However, cub weight did not correlate with water vole density in the spring (r_s = 0.2100, N = 9, P = 0.5874).

Table 2. Body weight (kg) of fox cubs during 1989-1997.

Year	Body weight (kg)		
	N	$\bar{x}$	Sd
1989	2	1.63	0.37
1990	12	2.45	0.35
1991	5	2.11	0.37
1992	18	1.91	0.48
1993	15	1.81	0.43
1994	8	1.93	0.60
1995	11	2.13	0.47
1996	7	2.04	0.35
1997	10	2.09	0.32

Discussion

Changes in water vole abundance had no apparent influence on red fox breeding success in our study area. Fox litter size did not decrease despite a severe vole decline followed by a 4-year low population phase, and the number of active breeding dens, though showing small between-year differences, did not vary according to vole fluctuations. In fact, fox reproduction remained rather stable during the study period.

Fluctuating food, i.e. rodents, may be an important limiting factor for red fox populations, particularly in northern Europe (Englund 1970, Lindström 1989). The low availability of alternative prey usually recorded in boreal regions makes foxes highly dependent on voles and, consequently, fox reproduction is generally quickly affected by decreasing vole supply. The numerical response of foxes to vole population changes occurs with a 1-year time lag (Lindström 1989). The trophic conditions faced by foxes in the Jura Mountains are also characterised by a fluctuating main prey, i.e. the water vole, and a low availability of wild alternative prey (Ferrari & Weber 1995). In this area, however, man greatly improves what could be at first glance precarious trophic conditions for foxes. Of about 80 farms evenly distributed over the study area, each supplied in average 0.96 kg of scavengeable items per night (Ferrari & Weber 1995). Dietary analyses showed how providential this permanent food production was for foxes when their main prey was scarce. During the phases of low vole density and compared with periods of vole highs, rubbish consumption, in terms of relative frequency of occurrence, by foxes increased 6 or 7-fold reaching ca 35% of the food items (Weber 1996). It is therefore assumed that anthropogenic food has been instrumental in preventing a decrease in fox breeding success in our study area. Actually, food scraps left daily on middens by local farmers likely played the role that additional food supply did in Lindström's (1989) feeding experiments, and positively influenced fox reproduction when natural trophic conditions were less favourable. The steady increase in fox numbers observed from year to year in the study area (Weber, Aubry, Ferrari, Fischer, Lachat Feller, Meia & Meyer 1997) and the maintenance by foxes of a stable group-living strategy (Meia & Weber 1996, S. Meyer, unpubl. data) clearly support this assumption.

Further to affecting fox breeding success, changes in vole abundance may also affect the growth of fox cubs under unfavourable trophic conditions (Lindström 1983). Preliminary data from the Jura Mountains also revealed a positive correlation between cub weight and vole supply during the water vole decline (Meia 1994), and consequently, it has been supposed that a long-lasting shortage of water voles could become a factor regulating fox numbers by affecting the growth of juvenile foxes (Weber 1996). However, as shown in our results, this relation did not persist after the analysis was carried out with a larger data set and over a complete water vole cycle. Moreover, as annual variations of juvenile fox weight were close to the limit of significance, the observed differences could be more likely assigned to some methodological bias (i.e. difficulty in capturing all cubs at the same developmental stage) rather than to between-year variation in cub growth. The lack of correlation between cub weight and vole supply could therefore confirm the suitability and profitability of alternative trophic resources to foxes in the absence of water voles.

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