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The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland

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Abstract

The diet of urban foxes and the availability of anthropogenic food were studied in the city of Zurich, Switzerland. A stomach analysis of 402 foxes, which were shot or found dead between January 1996 and March 1998, showed a broad variety in the diet of urban foxes, with a dominance of scavenged meat, other scavenge and cultivated fruit and crops. More than half of an average stomach content was anthropogenic. The proportion of anthropogenic food was increased in stomachs from the city centre – mainly due to the increasing proportion of scavenged meat – compared with stomachs from the periurban area. Significant seasonal variations in the diet were found for invertebrates, birds and for cultivated fruit and crops, which were all most frequently consumed in summer.

A written survey among the inhabitants of three municipal districts showed that 85% of the households provided anthropogenic food which was accessible to foxes. This food supply consisted of three quarters of rubbish and compost, completed by fruit and berries and, to a lesser extent, food provisions for pets, birds, and other wild animals. In contrast, the anthropogenic food supply of allotment gardens mainly consisted of berries, completed by fruit, compost and birdseed. The anthropogenic food supply in public areas was determined by transects. The overall food supply of households, allotment gardens and public areas would be sufficient to feed a much higher number of foxes than currently present. This overabundance of food resources could explain the continual increase of urban population densities. A possible further exploitation of anthropogenic food sources is discussed considering its specific characteristics and the necessary behavioural adaptations.

Key words: *Vulpes vulpes*, food supply, stomach analyses

Introduction

In the early 1980s, foxes were observed to have started breeding in Swiss cities and conurbations (GLOOR et al. 2001). Since then, the urban fox populations have increased continuously, corresponding to the general increase of fox abundance in Switzerland (BREITENMOSER et al. 2000) as well as in many other European countries

(Chautan et al. 2000). The severe rabies epizootic that spread throughout central Europe reached Switzerland in 1967 and caused a drastic decrease of fox populations, but due to successful oral vaccination campaigns, they started to recover from 1984 onwards. The current fox population densities are higher than before the outbreak of rabies (Breitenmoser et al. 2000). This development seems to be connected with the exploitation of new habitats. Indeed, all 30 Swiss cities with more than 20 000 inhabitants are colonised by foxes (Gloor et al. 2001; Gloor, unpubl. data). The current fox population of the city of Zurich, the largest Swiss conurbation, has reached densities of more than 10 adult foxes per km^2 (Gloor 2002), which is more than any studied rural fox population in Switzerland.

Foxes breeding in urban habitats are recorded in many European and North American cities (e.g. Harris and Rayner 1986; Schoeffel and Schein 1991; Adkins and Stott 1998). Considering the small home range sizes and the high population density of urban fox populations, human settlements generally seem to provide suitable habitats for foxes (Harris 1981b; Macdonald and Newdick 1982). Since rural foxes are known to be shy and avoid human encounters whenever possible, the colonisation of the free urban niches required behavioural ontogenetic adaptations. It therefore presumably needed a certain population pressure in the rural surroundings to initiate this development (Gloor et al. 2001).

Food is considered to influence the fox population size (Lloyd 1980; Lindström 1989) as well as their social organisation (Macdonald 1983). In urban habitats, its quality and abundance are strongly influenced by humans (Baker et al. 2000). Scavenge was the main component of the diet of urban foxes in London (GB; Harris 1981a), Oxford (GB; Doncaster et al. 1990), and Bristol (GB; Saunders et al. 1993; Baker et al. 2000). We therefore assume that a surplus supply of anthropogenic food is responsible for the high and still increasing fox population density in the city of Zurich. In order to test this hypothesis, the objectives of our study were (1) to analyse the composition of the diet of foxes inhabiting the city of Zurich with special reference to anthropogenic food, (2) to evaluate the availability of anthropogenic food supplied by households, in allotment gardens and public areas and (3) to estimate the potential population density supported by anthropogenic food.

Material and methods

Study areas

The study was conducted in Zurich, including its suburbs inhabited by about one million people. We defined two study areas in this project.

Study area A was used for the stomach analysis and consisted of the political community of Zurich. It covers 92 km^2, has a human population of 360 000 and is made up of 53% built-over area, 24% forest, 17% agricultural area and 6% water (Stat. Department of the City of Zurich 1998). We divided this area into an urban zone, a border zone and a periurban zone. The urban zone refers to the built-over area, whereas the periurban zone consists of the surrounding forests and agricultural areas, the 500 m wide border zone separating one from the other.

Study area B was selected to study the availability of anthropogenic food. It is situated in the western part of study area A covering 6.8 km^2. It consists of the urban and border zones of 4 neighbouring municipal districts, which are known to have a high fox population (Gloor 2002). Private properties cover 61% of the area, public areas 38% and allotment gardens 1%. 73% of the buildings are residential, 31% of them being detached houses. The population density is 9 700 inhabitants/km^2.

Stomach analysis

Between January 1996 and March 1998, 402 foxes were collected by the 3 official game wardens of the city forest service and stored at –20 °C. Age determination of foxes was done by measuring the relative width of the pulp cavity of a lower canine tooth by X-rays (Kappeler 1991). Foxes were designated as juveniles when they were younger than 12 months, with the assumption that the cubs were born on April 1st (Wandeler

1976). We assigned the foxes to three seasons: spring (March–June), summer (July–October) and winter (November–February).
After removal and dissection of a stomach, its content was analysed as described by CAPT and STALDER (1988) and ROPER and LÜPS (1994). We defined 12 food categories, which we divided according to their origin into 5 natural, 5 anthropogenic and 2 intermediate food classes (Tab. 1). According to our definition, intermediate food has both natural and anthropogenic characteristics. Cultivated fruit and crops are, on the one hand, part of the traditional fox diet in rural areas and, on the other hand, grown by humans, and the origin of an indefinable item could be natural as well as anthropogenic.
For each fox the relative proportion of each category of the total stomach content was estimated according to its volume with an accuracy of 5%. If a food category was found in traces only, its relative proportion was noted as 1%. Soil materials, grass and fox hairs were not taken into consideration. Many of the foxes shot by game wardens were baited with meat. Therefore, meat was considered only if the fox died in an accident or for unknown reasons.
Birds and mammals were identified according to DAY (1966), NIETHAMMER and KRAPP (1982) and TEERINK (1991). For hair identification we (a) prepared prints of the medulla on transparent nail varnish that had been spread as a thin layer on a microscope slide, and (b) cut 10 µm cross-sections using a microtome.
To prevent underestimation of the presence of earthworms, we filtered the rinsing water in a sieve with mesh size 0.25 mm and transferred the filtrate portionwise in petri dishes. Chaetae were counted under a binocular, x50 magnification. According to WROOT (1985) and REYNOLDS and AEBISCHER (1991), one chaeta of *Lumbricus terrestris* corresponds to an average of 1.9 mg fresh weight, which allowed estimating the proportion of earthworms on the total stomach content.

Anthropogenic food supply

To estimate the availability of anthropogenic food in private properties, we distributed questionnaires to 3000 randomly selected households in study area B in March 1999. Questions regarded the weekly volume of rubbish and the people's

Table 1. Qualitative and quantitative analysis of the stomach contents of 212 urban foxes from the city of Zurich, Switzerland.

Food categories	Frequency of occurrence (%)	Mean proportion of total stomach content (% ± SE)	Mean volume when present (ml ± SE)	Number of stomachs containing the concerned category exclusively	Number of stomachs mainly containing the concerned category
Natural food					
(1) Rodents	25.9	11 (±1.8)	20.5 (±3.8)	7	16
(2) Birds	23.6	4.8 (±1.1)	8.6 (±2.3)	0	10
(3) Other vertebrates	5.7	2.1 (±0.8)	17.1 (±9.8)	1	3
(4) Invertebrates	31.6	4.4 (±1)	7.1 (±2)	3	3
(5) Wild fruit	22.6	5.2 (±1.2)	4.4 (±0.6)	3	7
Total	68.9	27.5 (±2.4)	16.6 (±2.1)	18	37
Anthropogenic food					
(6) Scavenged meat	47.6	21.1 (±2.2)	24.3 (±4.3)	9	30
(7) Other scavenge	60.8	22.2 (±2.1)	17.8 (±2.7)	6	39
(8) Pets and domestic stock	10.4	4.5 (±1.3)	29.8 (±23.8)	4	5
(9) Petfood	6.1	2.2 (±0.7)	36.3 (±10.8)	0	5
(10) Bird seed	9.4	3.7 (±1)	8.4 (±1.8)	3	3
Total	83.5	53.6 (±2.7)	34.2 (±4.7)	39	78
Intermediate food					
(11) Cultivated fruit and crops	49.1	18.2 (±2)	25.1 (±3.4)	4	35
(12) Indefinable items	4.2	0.7 (±0.4)	4.7 (±2)	0	1
Total	50.9	18.9 (±2)	24.5 (±3.3)	4	31

habits of composting, feeding pets, birds and other wild animals and growing fruit and berries. Vegetables were not considered, as their energetic value and their presence in fox stomachs was negligible. In apartment buildings the questionnaire was given to one randomly selected household, which we supposed to be representative of all the other households in the building.

Berries grown in gardens were considered to be freely accessible to foxes, whereas fruit was considered to be accessible to foxes as windfall only. The calculation of the annual energy content based on the growers' information about the number of plants, species, size, percentage of fruit picked, removal of windfall and energy content tables of Feucht (1982) and Elmadfa et al. (1987).

Concerning food offered to pets, birds and other animals, people had to specify the type, quantity and location of the food and if the food was left unattended and thus attainable for foxes. For birdseed we assumed that an average of 10% of the total amount of birdseed was accessible to foxes, even when located higher than 60 cm, as it would fall off bird tables and food nets.

Households either put their bin liners in solid skips, which are not accessible to foxes, or on the street border, where they get collected by municipal services once a week. The percentage of bin liners put out immediately before collection and therefore not accessible to foxes was estimated based on a sample of 470 bin liners. In order to estimate the average energy content of rubbish and compost we analysed samples of compost that were collected by 17 households during 7 days, and 18 bin liners, randomly collected in February 1999. Edible components were weighed and their energy content calculated according to Elmadfa et al. (1987) and Case et al. (1995). Considering all these evaluations, we estimated the energy content in megajoules per year (MJ/y) of the anthropogenic food supply from each household, which was accessible to foxes on the concerned private property. According to the statistics of the waste disposal authorities, there are no obvious seasonal differences in the amount of collected garbage.

In addition, we handed out questionnaires to 500 randomly selected leaseholders of allotment gardens in study area B, since allotment gardens were the second most selected habitat category as revealed by a radio-tracking study in this area (Gloor 2002). The questions were generally the same as with the households.

In order to evaluate the anthropogenic food supply in public areas, we randomly analysed streets, parks, cemeteries and play grounds using the transect method on 13 days from January to March 1999, collecting all the edible anthropogenic food. The searched area measured 67.5 ha and was representative for study area B, with respect to the proportions of these four habitat types. Contents of dustbins were considered if their upper edge was below 60 cm. Food items, which could be taken from bin liners without damaging them, were also collected.

To find out if foxes used bin liners as a food source, we checked on 6 days in February and March 1999 a total of 1 381 bin liners for animal damages. These bin liners had been accessible to foxes for at least one night.

Statistical analysis

Evaluating the proportional feeding on the 12 food categories, we had to consider the unit-sum constraint (Aebischer et al. 1993). The compositional analysis is a method testing seasonal and habitat effects on the intake of a food category, taking into account the utilisation of other food categories. We therefore transformed proportional values to log-ratios and substituted zero by 0.01% (Aebischer et al. 1993). Then we computed a multivariate analysis of variances ANOVA and Tamhane post-hoc tests. Critical significance levels were Bonferroni corrected according to Rice (1989) taking into account multiple tests on the same data.

To estimate the food supply of a whole apartment building, we multiplied the energy supply of rubbish and compost of the interviewed household with the number of flats. However, the energy supply of fruit and berries was kept as there was one garden per building only. The supply of animal food of the whole apartment building was calculated as follows: energy supply of the interviewed household + ($n_{households}$-1)*proportion (households in apartment buildings feeding animals)*median(energy supply of animal feeding households in apartment buildings).

To find out whether there were correlations between household size, the number of households in a building and the energy supply of households and buildings, we computed a multivariate analysis of variances ANOVA, followed by Scheffé post-hoc tests. Therefore, we defined 3 classes of household size (1–2, 3–4, 5 and more persons), 3 classes of building size (1–2, 3–8 and 9 and more households) and excluded extreme values, which were defined to be higher than 3.5 times the interquartile range above the median. In order to estimate the maximum number of foxes that could feed on anthropogenic food, we used median supplies distinguishing between detached/semi-detached houses and apartment buildings, because this was the most adequate obtainable land use information. According to SAUNDERS et al. (1993), we assumed a daily energy expenditure of 2.4 MJ per adult fox. 95% confidential intervals were calculated according to STAHEL (1995). All statistical tests were performed using SPSS 10.0 (NORUSIS 1986).

Results

Stomach contents analysis

In total, 190 (47%) of the 402 analysed stomachs were empty. Therefore, our analysis refers to a sample size of 212 stomachs with food content. The zonal and seasonal origin of the foxes as well as their age, sex and cause of death are presented in table 2. In spring, foxes were shot with special permission in the urban area only. This is why only 14% of the stomachs were collected in spring and originated of relatively fewer shot foxes.

The average proportions of the 12 food categories and their frequencies of occurrence showed a strong positive correlation (Spearman rang, $r_s = 0.93$, $p < 0.005$). In contrast, the mean proportion of a present component did not correlate with the other two parameters (Tab. 1).

Table 2. Origin and characteristics of the 212 foxes with food contained in stomachs, collected in the city of Zurich, Switzerland.

Zone			
Urban	Border	Periurban	Unknown
74 (35%)	86 (41%)	50 (24%)	2 (1%)
Season			
Spring	Summer	Winter	Unknown
29 (14%)	70 (33%)	112 (53%)	1 (0%)
Age			
Juveniles	Adults	Unknown	
117 (55%)	90 (43%)	5 (2%)	
Cause of death			
Shot	Accident	Unknown	
153 (72%)	47 (22%)	12 (6%)	
Sex			
Females	Males		
110 (52%)	102 (48%)		

Scavenged meat, other scavenge and cultivated fruit and crops were the staple diet, accounting for 61.5% of the mean stomach content (Fig. 1). Furthermore, these three categories were by far the most frequent main components, as 58% of all stomachs mainly or exclusively contained one of these three categories (Tab. 1). Ranking the number of stomachs in which the food category in question was the only component, scavenged meat, other scavenge and rodents were dominant (Tab. 1).

The following details facilitate comparisons with other studies:

Rodents: we identified 12 northern water voles (*Arvicola terrestris*), 10 common voles (*Microtus arvalis*), six bank voles (*Clethrionomys glareolus*), six yellow-necked mice (*Apodemus flavicollis*), five *Apodemus* spec., four house mice (*Mus domesticus*), three squirrels (*Sciurus vulgaris*), two wood mice (*Apodemus sylvaticus*), two field voles (*Microtus agrestis*) and one common rat (*Rattus norvegicus*). The genus of five rodents could not be determined.

Birds: 40 remains originated from Passeriformes, seven from Columbiformes and one from Falconiformes. Two feathers could not be assigned.

Other wild vertebrates: we found four small pieces of snake skin, hair of two roe deer (*Capreolus capreolus*), skin and flesh of one hedgehog (*Erinaceus europaeus*), one blindworm (*Anguis fragilis*) and one unidentified fish.

Invertebrates: 17.5% of the stomachs contained imagines and larvae of insects. Only larvae of Noctuidae and Syrphidae had been eaten in larger amounts. Earthworms were found in 20.9% of the stomachs, but they formed a mean proportion of only 2.6%.

Wild fruit: we identified yew (15×, *Taxus baccata*), hazelnut (13×, *Corylus avellana*), walnut (1×, *Juglans regia*) and rose hip (1×, *Rosa* spec.). 15 fragments could not be identified at the species level.

Scavenged meat: this category including all kinds of processed meat and bones (signs of processing: cooked, cut, without fur) was found in 48% of all stomachs.

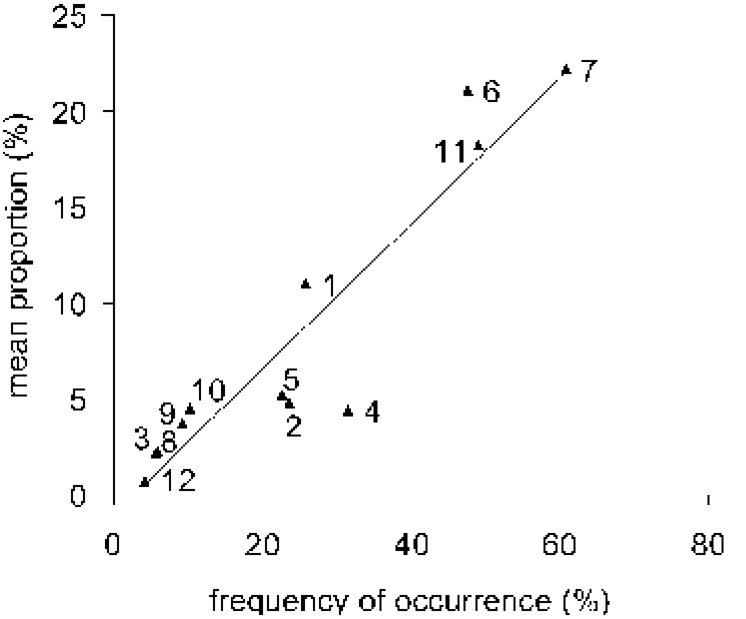

Fig. 1. Frequency of occurrence (%) and mean proportion of the total stomach content of 12 food categories. (1) rodents, (2) birds, (3) other wild vertebrates, (4) invertebrates, (5) wild fruit, (6) scavenged meat, (7) other scavenge, (8) pets and domestic stock, (9) pet food, (10) bird seed, (11) cultivated fruit and crops and (12) indefinable. Both variables refer to the 212 food-containing fox stomachs collected in the city of Zurich, Switzerland. $R^2 = 0.872$.

Other scavenge: 32.2% of the stomachs contained vegetable kitchen waste, 28.9% contained wrappers and other indigestible items and 27% contained remains of processed food such as bread, pasta or cheese.

Pets and domestic stock: we identified remains of 12 hens (*Gallus gallus*), five cats (*Felis sylvaticus* f. catus), four rabbits (*Oryctolagus cuniculus*), two dogs (*Canis lupus* f. familiaris) and a cattle (*Bos primigenius* f. taurus). Rabbits were all pets, because there are no wild populations in the area. The flesh of rabbits and hens could originate from animals killed by the fox itself. Since predation on the other species is unlikely, this flesh presumably originated from carcasses.

Petfood: commercial tinned or dried food for cats or dogs identified by its consistency and its smell had a low relative proportion, but its mean volume when present was the highest of all food categories (Tab. 1).

Birdseed: typical mixtures of cereals or grains as sold in shops for bird feeding was found in stomachs from January, February and March only.

Cultivated fruit and crops included cultivated fruit, berries, vegetables and cereals, which a fox could have found on a field, in an orchard or garden, according to the season and the local cultivation attitudes. Remains not fulfilling these conditions, remains cooked or showing traces of cutting were allocated to other scavenge. Fruit occurred in 38.4% of the stomachs. The most frequently identified fruit species were apples (*Pyrus malus*), plums and cherries (*Prunus* spec.). Vegetables were found in 4.2% of the stomachs, namely carrots (*Daucus carota*), potatoes (*Solanum tuberosum*), sugar beets (*Beta vulgaris*) and beans (*Phaseolus* spec.) with a mean proportion of 1.2%. Cereals like wheat (*Triticum* spec.) and corn (*Zea mays*) occurred in 13.7% of the stomachs.

Summarising, more than half of a mean stomach content was anthropogenic (Tab. 1). Furthermore, anthropogenic food was the sole element with zonal variation ($F = 11.7$, $df = 2$, $p < 0.001$), found in significantly higher mean proportions in urban than in periurban stomachs (Tamhane post-hoc test, $p < 0.001$; Fig. 2 a). A significant seasonal variation was observed for intermediate food ($F = 10.5$, $df = 2$, $p < 0.001$), the pro-

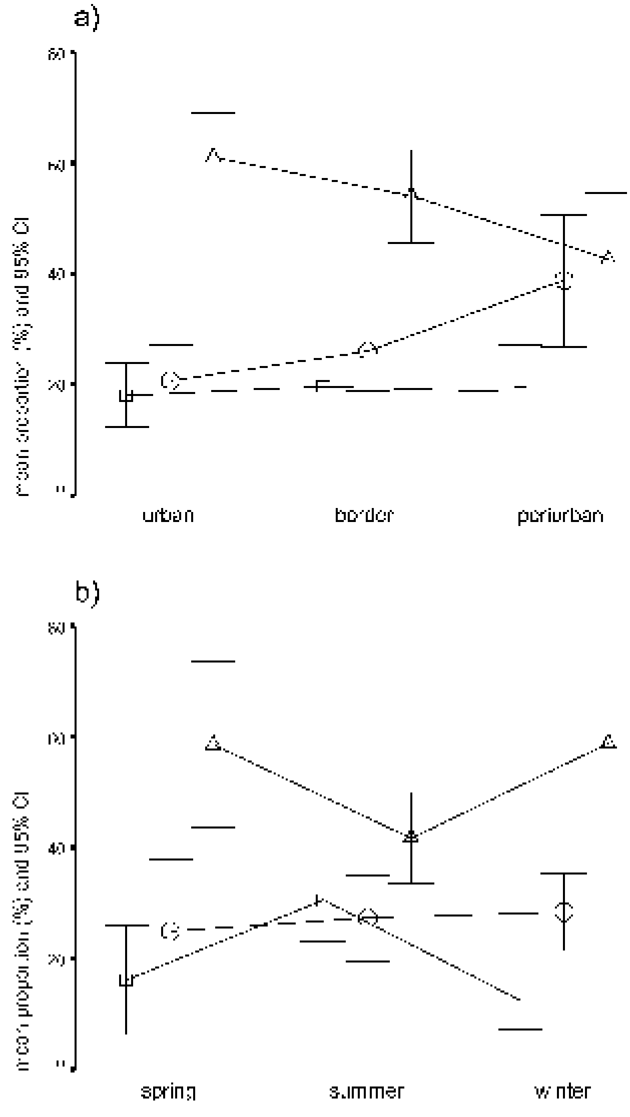

Fig. 2. Zonal (a) and seasonal variation (b) of the mean proportions of anthropogenic (triangles), natural (circles) and intermediate (squares) food in 212 fox stomachs from the city of Zurich, Switzerland. N(urban) = 74, N(border) = 86, N(periurban) = 50. N(spring) = 29, N(summer) = 70, N(winter) = 112. Anthropogenic food categories were: scavenged meat, other scavenge, pets and domestic stock, pet food and bird seed. Natural food categories were: rodents, birds, other vertebrates, invertebrates and wild fruit. Intermediate food categories were: cultivated fruit and crops and indefinable items. Differences are significant (for details see text).

portions of which were significantly higher in summer than in spring and winter (Tamhane, $p < 0.003$ resp. $p < 0.001$; Fig. 2 b).
Tests of all 12 food categories showed that the zonal variation of anthropogenic food was caused by scavenged meat, which was consumed in significantly highest proportions in the urban zone ($F = 71.3$, $df = 2$, $p < 0.001$; Tamhane $p < 0.002$ resp. $p < 0.014$; Fig. 3). Seasonal differences in the proportion of intermediate food were determined by cultivated fruit and crops, which contributed 30% of the summer diet, and significantly less of spring or winter diet ($F = 55.8$, $df = 2$, $p < 0.001$; Tamhane $p < 0.004$ resp. $p < 0.001$; Fig. 4 a).
Further seasonal differences were found for invertebrates ($F = 33.8$ $df = 2$, $p < 0.001$) and birds ($F = 12$, $df = 2$, $p < 0.018$). Proportions of invertebrates significantly decreased from summer to winter (Tamhane, $p < 0.001$; Fig. 4 b), corresponding to the proportions of birds (Tamhane, $p < 0.008$; Fig. 4 c).

Availability of anthropogenic food

Households

Of 3 000 distributed questionnaires, 573 were returned, 19 were not complete and thus 554 were considered in our evaluation. Anthropogenic food was provided by 468 households (84.5%). The average annual food supply from a household consisted of 77% digestible particles in bin liners and on compost heaps (Tab. 3). A further 18% consisted of windfall and berries. The proportion of food put out for birds, other wild animals and pets was 4%.
Bin liners were placed on curks by 248 households (44.8%). The average volume of a rubbish sack was about 35 l. The energy content of included edible items was 0.22 ± 0.08 MJ per litre of rubbish. 78% of 470 bin liners were accessible to foxes during at least one night. In our sample of 1 381 exposed bin liners, 1.3% had been damaged by foxes or other scavenging animals.
361 households (65.2%) habitually took compostable kitchen waste to a compost heap. Excluding the firmly covered ones as well as the compost heaps situated in public areas, this food source was available in 155 gardens only (28%). The daily average energy content of composted organic kitchen waste was 0.16 ± 0.04 MJ per person.
Berries were cultivated in 291 private gardens (52.5%), most frequently red currants

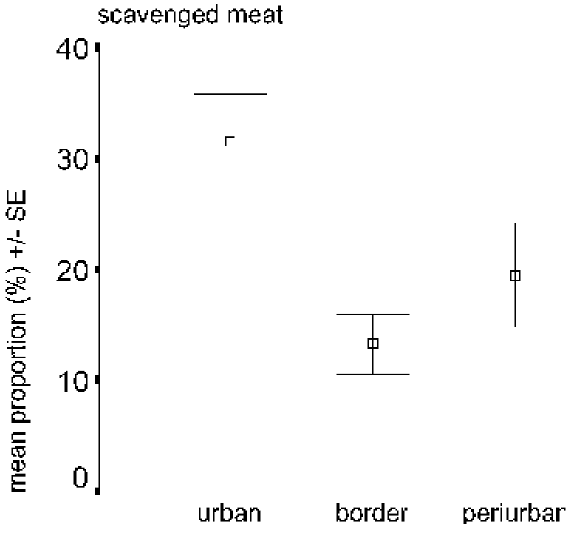

Fig. 3. Zonal variation of mean proportions (%) of scavenged meat in fox stomachs from the city of Zurich, Switzerland. N(urban) = 74, N(border) = 86, N(periurban) = 50. Differences are significant (for details see text).

(*Ribes rubrum*), raspberries (*Rubus idaeus*) and blackberries (*Ribes nigrum*).

Windfall was available on 175 private properties (31.6%). The most common fruit species were apples (*Pyrus malus*) and plums (*Prunus* spec.). A majority of householders estimated the proportion of windfall on the total yield to be less than 25%.

Birds were fed in the garden or on the balcony of 242 households (43.7%). Almost all householders restricted bird feeding to winter. Other wild animals were fed by 37 households (6.7%), 29 in the garden and eight elsewhere. The most regularly fed animals were hedgehogs (*Erinaceus europaeus*). Three householders (0.5%) fed foxes. Cats and dogs were fed outside by 46 households (8.3%).

The supply from households of the urban and the border zone did not significantly differ (df = 1, F = 0.09, p > 0.92). However, the number of households per building had a significant influence on the food supply from the interviewed household (df = 3, F = 6.45, p < 0.001), as well as on the summarised supply from the whole building (df = 2, F = 22.5, p < 0.001; Tab. 4). The significantly reduced supply from buildings with one or two households (Scheffé post-hoc test, p < 0.001) correlated with their reduced amount of rubbish (Scheffé, p < 0.001). On the other hand, these buildings offered significantly more berries than buildings with three or more households (Scheffé, p < 0.001) and more windfall than buildings with nine or more households (Scheffé, p < 0.017; Tab. 4). Food for wild animals was provided by significantly more buildings with three or more households (Scheffé, p < 0.04 resp. p < 0.001; Tab. 4).

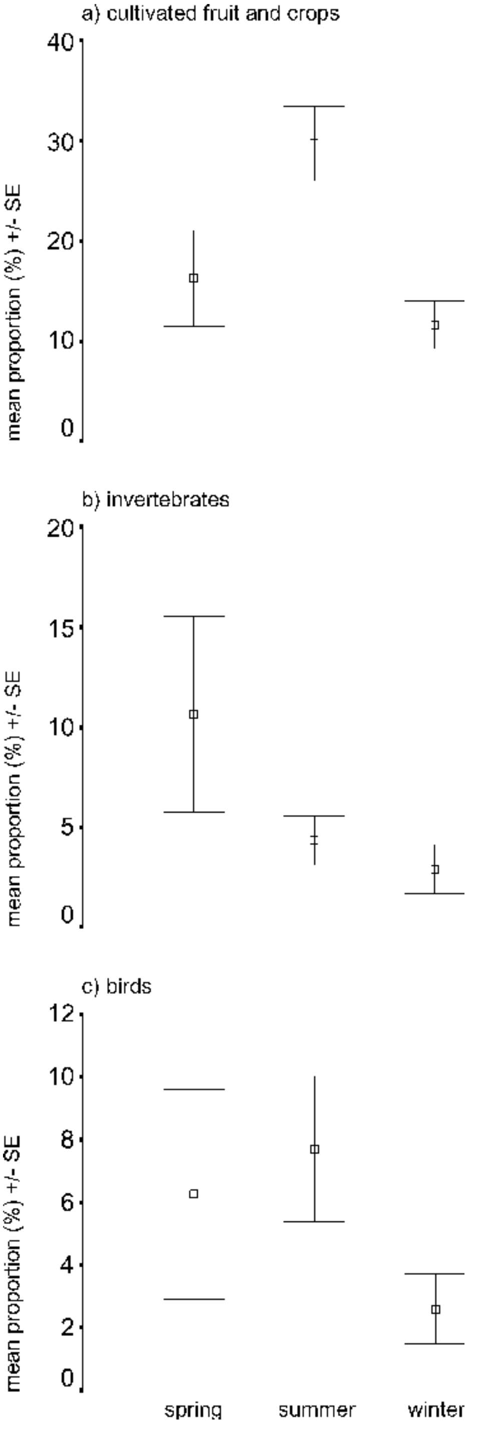

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Fig. 4. Seasonal variation of mean proportions of a) cultivated fruit and crops, b) invertebrates and c) birds in fox stomachs from the city of Zurich, Switzerland. N(spring) = 29, N(summer) = 69, N(winter) = 112. Differences are significant (for details see text).

Table 3. Average annual energy supply of anthropogenic food deriving from households, allotment gardens and public areas, which is accessible to foxes in the city of Zurich, Switzerland.

Food categories	Households (MJ/y*household ± SE) N = 554	Allotment gardens (MJ/y*garden ± SE) N = 147	Public areas (MJ/y*ha ± SE) N = 13
Rubbish	145.4 (±8.6)	–	79.1 (±20.2)
Compost	35.9 (±2.9)	11.9 (±2.6)	–
Berries	23.4 (±1.5)	67.6 (±3.4)	–
Windfall	18.3 (±2.1)	14.1 (±2.6)	–
Bird seed	6.7 (±0.9)	11.0 (±2.8)	8.9 (±4.5)
Pet food	1.5 (±0.5)	0.7(±0.4)	–
Food for wild animals	1.8 (±0.4)	0.4 (±0.4)	–
Mean	234.1 (±11.2)	106.8 (±5.7)	87.9 (±20.7)

Table 4. Statistical comparison of the annual anthropogenic food supply of residential buildings, depending on the number of households, which is accessible to foxes in the city of Zurich, Switzerland. n. s. = not significant

Food categories	1–2 households N = 277 (MJ/y ± SE)	3–8 households N = 186 (MJ/y ± SE)	9 and more households N = 91 (MJ/y ± SE)	F	p
Rubbish	196.2 (±15.3)	666 (±74.7)	788.3 (±156)	24.9	< 0.001
Compost	59.4 (±5.7)	107.2 (±17.3)	71.4 (±27.9)	3.7	< 0.025
Berries	35.7 (±2.3)	13.3 (±2.2)	10.7 (±3)	31.8	< 0.001
Windfall	32.9 (±4.7)	25 (±7.2)	4.9 (±3.7)	4.1	< 0.017
Bird seed	8.1 (±1.3)	21.4 (±10.9)	18.2 (±1.6)	1.4	n. s.
Pet food	5.5 (±3.9)	8.1 (±1.1)	17.2 (±1.3)	2.2	n. s.
Food for wild animals	4.8 (±1.4)	13.3 (±3.9)	22.8 (±1.7)	9.5	< 0.001
Total supply per house	342.4 (±18.9)	854.3 (±78.6)	933.5 (±156.4)	22.5	< 0.001

Allotment gardens

The returned questionnaires concerned 147 plots from 12 different allotment garden areas. Anthropogenic food was available in each plot. Bin liners were collected in skips and therefore not accessible to foxes. The mean anthropogenic food supply of allotment gardens was about half of the supply from a household (Tab. 3), and consisted of 63% berries, 13% fruit, 11% compost and 10% birdseed. Food for pets and wild animals was only occasionally available.

All gardeners, except one, cultivated berries. The most common species were the same as in the backgards. Fruit trees were cultivated by 97 gardeners (66%), among them 10.2% who collected windfall daily and therefore did not supply any fruit, and 73% whose proportion of windfall was less than 25% of the total yield. The most popular fruit species were plums and cherries (*Prunus* spec.), apples (*Pyrus malus*) and apricots (*Prunus armeniaca*). There was a compost heap in almost all allotment gardens, but only 64 (43.5%) of them were accessible to foxes. 34% of the gardeners brought less than 25% of their kitchen waste, 27% between 25 and 75% and 41% more than 75%. Birds were fed in 70 gardens (47.6%). Due to better accessibility, the average annual supply of bird seeds in allotment gardens exceeded the supply from households by 61%. Bird seed was available in winter only. Pet food was accessible to foxes in two gardens. Two gardeners put out food for foxes. One of them fed regularly, with an annual supply of 53.3 MJ. The other person occasionally fed foxes with unspecified quantities.

Public areas

The anthropogenic food supply in public areas consisted of 90% food waste such as bread, apples, remains of fast food and pasta and 10% birdseed. As most of the findings were found on rather concealed places, where there was no daily cleaning, we assumed an average age of three days for these particles. This leads to an average annual food supply in public areas of 87.9 ± 20.7 MJ/ha (Tab. 3).

Total anthropogenic food supply in study area B

We estimated that the total annual anthropogenic food supply from all households in study area B could cover the potential demand of 1 797 ± 942 foxes, and 207 ± 149 foxes, respectively, when neglecting bin liners (Tab. 5).
Accordingly, the total annual food supply of all 833 allotment gardens in study area B could cover the potential demand of 82 ± 13 foxes, and 24 ± 7 foxes in the 254 ha of public areas (Tab. 5). Combining these projections, the annual anthropogenic food supply in study area B corresponded to the potential demand of 1 902 ± 942 adult foxes or 141–418 foxes/km^2. A conservative approach which excluded bin liners leads to a maximum of 312 ± 149 foxes or 24–68 foxes/km^2.

Discussion

Anthropogenic food resources play an integral part in the diet of foxes living in the city of Zurich. Scavenged meat and other scavenge were by far the most frequent food categories consumed in largest proportions. This generally corresponds to the diet of urban foxes in Britain (Harris 1981a; Doncaster et al. 1990; Saunders et al. 1993). In contrast to the results of Lucherini and Crema (1994) and Ferrari and Weber (1995) for mountainous habitats, we did not find an increase of foraging on scavenge in winter, but considerable proportions of scavenge throughout the year. Besides scavenge, cultivated fruit was widely provided in our area. Correspondingly, cultivated fruit and crops were the third staple component in the diet of foxes. According to the seasonal variation in abundance (Doncaster et al. 1990; Ferrari and Weber 1995), its exploitation by foxes was characterised by a high seasonality.

Table 5. Mean anthropogenic food supply of households, allotment gardens and public areas, and the projection on study area B. This area is situated in the western part of the city of Zurich, Switzerland, and covers 6.8 km^2. The total includes rubbish in bin liners from households, whereas the conservative estimation excludes it.

	Mean		**Study area B**		
	Energy supply (MJ/y)	Number of supplied foxes	Number of unities	ΣMJ/y	Number of supplied foxes
Households including bin liners					
detached houses	272	0.31	1 690	$4.6*10^5$	524.7
buildings > 1 household	306	0.35	3 641	$11.1*10^5$	1 271.9
excluding bin liners					
detached houses	87.5	0.09	1 690	$1.5*10^5$	168.8
buildings > 1 household	9.1	0.01	3 641	$0.3*10^5$	37.8
Allotment gardens	86.6	0.10	833	$0.7*10^5$	82.3
Public areas	81.2	0.09	254	$0.2*10^5$	23.5
Total				$16.7*10^5$	1 902.4
Total, conservatively estimated				$2.7*10^5$	312.4

The large proportion of consumed anthropogenic food corresponds with its abundance and reflects the specific characteristics of anthropogenic food resources in human settlements, such as low seasonality, high predictability and a favourable cost-benefit ratio. Anthropogenic food, especially rubbish, is abundant throughout the year, and its ease of acquisition is constant, in contrast to many natural food categories, especially living prey (TSUKADA and NONAKA 1996). Due to the lack of limiting seasonal shortage, it should be completely exploitable.

Our results indicate that regular visits of sites with anthropogenic food resources such as compost heaps, fruit trees or feeding places are an efficient behaviour and can reduce time and energy that a fox has to exert in searching for food, as suggested by LOVARI et al. (1996) for vineyards. This allows a restriction of feeding activity to less disturbed times of day, thus facilitating the colonisation of a habitat with high rates of disturbances, as is the case for urban areas (GLOOR 2002). Since foxes are an intensely prosecuted species, the capability of avoiding humans has been a strong selective factor. For the exploitation of urban habitats, developing a certain tolerance towards disturbances would be advantageous. People who feed foxes often try to get in contact with the animals. Therefore, feeding places can contribute to the tolerance of foxes towards humans and enhance the behavioural ontogenetic adaptation of young foxes to disturbances in urban areas.

So far, we have not observed that foxes exploit bin liners regularly or even systematically, concurring to BAKER et al. (2000). As an explanation for the foxes restraint towards bin liners lined up along the pavements, where human disturbances are frequent, we suggest that the availability of less exposed food was so extensive that the behavioural adaptation, which is likely to be necessary for the exploitation of this food source has not yet been a selective factor. This corresponds to TSUKADA and NONAKA (1996), who found that the feeding of foxes on food provisions of tourists did not depend on the availability of such anthropogenic food, but was negatively correlated with the availability of natural food.

In Zurich, many inhabitants are concerned about the high prevalence of the small tapeworm *Echinococcus multilocularis* in the fox population and the high contamination of public areas with its eggs (HOFER et al. 2000; STIEGER et al. 2003), because this parasite can cause human alveolar echinococcosis (ECKERT and DEPLAZES 1999). The awareness of this health risk has probably influenced the population's attitudes towards foxes (BONTADINA 2001). These concerns as well as the success of the official information campaign INFOX could explain, why in Zurich the total average amount of food deliberately supplied to foxes was nine times lower than in Bristol (BAKER et al. 2000). Corresponding to ADKINS and STOTT (1998), we expect that with increasing annoyance with damaged bin liners, new infrastructures for the waste disposal would reduce the accessibility of rubbish. Therefore, the estimation of maximum population density including the current availability of rubbish in bin liners is probably hypothetical.

Natural food still contributed 20% of the foxes diet even in the urban zone, and therefore should also be considered. The seasonal variation of invertebrates and birds probably correlated with their abundance, according to DONCASTER et al. (1990) and TSUKADA (1997). The presence of areas of rural character, such as cemeteries and parks, has simplified the exploitation of city centres, since these rural-like habitats are generally preferred by urban foxes (GLOOR 2002).

Our finding of urban habitats being highly productive considering food resources is supported by many authors (e. g., DONCASTER et al. 1990; SAUNDERS et al. 1993). The high availability of food explains the high population density as well as the fact that urban home ranges are much smaller than rural home ranges, and that Zurich's fox families often consisted of more than two adults (GLOOR 2002). According to VON SCHANTZ (1984) and MACDONALD (1983), the breeding pair may share their territory with subordinate adults when food is abundant.

We suppose that the potential of anthropogenic food resources exceeds the needs of the current fox population by far, so that the adaptation to the use of secondary food resources has not yet become worthwhile.

Our most conservative estimation of a possible fox population density (26 adult foxes/km^2) is still far from being reached, as GLOOR (2002) estimated the current density in the area to be 11.5 adult foxes/km^2. However, we have to consider the competition of other animals exploiting anthropogenic food sources in urban habitats, such as cats (CALHOON and HASPEL 1989), stone martens (TESTER 1986) and badgers (HARRIS 1984). On the other hand, we neglected the potential of natural food resources in our estimates. We expect a further increase in the urban fox population density, especially if further ontogenetic adaptations, learned improvements in handling efficiencies and increased tolerance allow an even more intensive exploitation.

Regarding the availability of anthropogenic food, we suggest that other resources like secure day-time rest sites and breeding sites or social intolerance are more likely to have limiting effects on the density of urban fox populations. Concerning the management of fox populations in cities, only drastic changes in the availability of anthropogenic food resources can have regulative effects.

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Zusammenfassung

Die Nahrung von Rotfüchsen (*Vulpes vulpes*) und das Angebot anthropogener Nahrungsressourcen in der Stadt Zürich, Schweiz

Die Nahrungszusammensetzung von Füchsen der Stadt Zürich wurde untersucht und das verfügbare Angebot an anthropogener Nahrung geschätzt. Unsere Magenanalysen von 402 Füchsen, welche von Januar 1996 bis März 1998 erlegt oder tot aufgefunden worden waren, ergaben für die Stadtfüchse eine vielseitige Diät, wobei Fleischabfällen, anderen Abfällen, Obst und Feldfrüchten besondere Bedeutung zukam. Mehr als die Hälfte eines durchschnittlichen Mageninhaltes war anthropogen. In Mägen aus dem Stadtzentrum war der Anteil anthropogener Nahrung – insbesondere der Anteil von Fleischabfällen – im Vergleich zu Mägen vom Stadtrand deutlich erhöht. Signifikante saisonale Unterschiede zeigten sich bei der Nutzung von Invertebraten, Vögeln sowie Obst und Feldfrüchten, welche alle im Sommer am häufigsten gefressen wurden.

Gemäß einer schriftlichen Befragung der Bevölkerung eines Stadtquartiers bestand bei 85% der Haushalte ein für Füchse zugängliches anthropogenes Nahrungsangebot. Dieses Angebot setzte sich zu drei Vierteln aus Kehricht und Kompost zusammen, und wurde durch Obst, Beeren und in geringerem Maß auch Futter, das Haustieren, Vögeln und anderen Wildtieren angeboten wurde, ergänzt. In Schrebergärten umfaßte das anthropogene Nahrungsangebot vor allem Beeren, aber auch Obst, Kompost und Vogelfutter. Mittels Transekten bestimmten wir zusätzlich das anthropogene

Nahrungsangebot des öffentlichen Raums. Das anthropogene Nahrungsangebot von Haushalten, Schrebergärten und öffentlichem Raum zusammen könnte viel mehr Füchse ernähren, als gegenwärtig im Untersuchungsgebiet vorhanden sind. Dieses Überangebot an Nahrungsressourcen erklärt möglicherweise, warum die Populationsdichten von Füchsen im Siedlungsraum gegenwärtig weiter ansteigen.
Die spezifischen Eigenschaften anthropogener Nahrungsquellen und mögliche Verhaltensanpassungen werden im Hinblick auf die ansteigenden Fuchspopulationen diskutiert.

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