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Original investigation

The rise of urban fox populations in Switzerland

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Abstract

Since 1985 increasingly more foxes have been recorded from cities in Switzerland. The inquiry of town officials showed that foxes are observed in 28 out of the 30 largest Swiss cities today and breeding dens are known in 20 of these cities. Urban foxes are observed more often than one would expect in larger cities than in smaller towns. In Zürich, the largest city in Switzerland, urban foxes were very scarce until the early 1980s. According to the hunting statistics, from 1985 onwards, there was a drastic increase in the urban fox population. In the adjacent rural areas, there was also a clear but less extreme increase in the fox population from 1984 onwards due to successful vaccination campaigns against rabies. As an explanation for the presence of foxes in human settlements we suggest two alternative hypotheses, which focus either on the population pressure in the rural areas or on the behavioural adaptations of urban foxes. The presence of foxes in urban areas influences behaviour and attitudes of people towards urban wildlife and it has a consequences for the management of foxes and the treatment of zoonoses such as rabies and the alveolar echinococcosis.

Key words: *Vulpes vulpes*, urban habitat, invasion, adaptation

Introduction

Since 1985 fox populations have experienced a drastic increase in Switzerland (BREITENMOSER et al. 2000). Apart from this development in rural areas, increasingly more foxes have been recorded from large Swiss conurbations and cities such as Zurich and Geneva. Game wardens and wildlife biologists have observed foxes in urban areas; people having noticed foxes in their gardens turned to local officials for information; pictures and articles about foxes in the middle of residential areas have been published. Are these records just occasional observations or do they indicate the colonisation of a new habitat by the red fox?

Red foxes living in urban areas are known from Great Britain where urban foxes have been observed in cities such as London since the 1930s (TEAGLE 1967; BEAMES 1969, 1972; PAGE 1981). In the 1970s and 1980s, fox populations in British cities reached densities of up to five fox family groups per km^2 (representing 12 adults on average), densities which had never been

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observed so far (HARRIS 1981 a; HARRIS and RAYNER 1986 a). Similar fox population densities were nowhere recorded in urban areas outside of Great Britain, either on the European continent or in other parts of the distribution areas of the red fox. Therefore, urban foxes were thought to be a British phenomenon (HARRIS 1977; MACDONALD and NEWDICK 1982).

In the 1970s and 1980s, the fox population on the European continent experienced a heavy rabies epizootic, which reached Switzerland in 1967 (STECK et al. 1980; MÜLLER et al. 2000). Fox densities decreased drastically, and, as seen from the Swiss hunting record, reached a low in 1984 (BREITENMOSER et al. 2000). After the success of oral vaccination campaigns against rabies, started in Switzerland in 1978 (WANDELER et al. 1988), the fox population recovered again from 1985 onwards (KAPPELER 1991; BREITENMOSER et al. 2000). At that same time, foxes were increasingly observed in human settlements.

Our objectives in this study are to investigate the present situation in large Swiss settlements, to evaluate the recent development of the fox population in Zurich, the largest conurbation of Switzerland, and to compare it with the trend in surrounding rural areas.

Material and methods

Study area

Switzerland is a diverse and mountainous country. 24% of its total area of 40 000 km^2 (excluding lakes), are above 2 000 meters in elevation where fox population density is low. The remaining 76% of the country forms heterogeneous and mostly good quality habitat for the red fox.

In Switzerland there are 30 cities with more than 20 000 inhabitants, where 19% of the 6.9 million inhabitants live. The largest conurbation of Switzerland is the area of Zurich with some 1 000 000 inhabitants. However, only 352 200 of them live in the actual "city", the political community of Zurich. The political community of Zurich (92 km^2) – which we refer to when we are talking about the "city of Zurich" in the following report – consists of 53% urban area, 24% forest, 17% agricultural areas and 6% water (FEDERAL OFFICE OF STATISTICS 1998). Forest and agricultural areas surround the urban area and are referred to as the rural area of the city in the following. As far as hunting is concerned, the city of Zurich is organised as a game sanctuary. The city of Zurich belongs to the canton of Zurich, one of the most densely populated cantons of Switzerland (area 1 661 km^2, 683 inhabitants per km^2).

The present distribution of urban foxes in Switzerland

During a television series about urban foxes in spring 1997, the public was called to report fox sightings in Swiss cities. The sightings were recorded personally by collaborators of the Integrated Fox Project. Only fox sightings within human settlements were recorded. As the call on TV was biased towards the German speaking part of Switzerland, the scanty information from the French and Italian speaking regions of the country were excluded from further analyses. The program actus (ESTABROOK and ESTABROOK 1989) was used for the statistical test, which performs randomised contingency tables and gives probabilities for deviations from expected values.

In spring 1999 we carried out a phone inquiry with people or institutions in charge of wildlife management in all 30 Swiss cities (communities) with more than 20 000 inhabitants (FEDERAL OFFICE OF STATISTICS 1998). The experts were asked about occurrence and abundance of urban foxes, evidence of breeding dens in the urban area, the year of the first urban fox sightings and the current trend in the urban fox population. In cities with official game wardens (18 out of 30), they were interviewed, in all other cities we questioned non-professional hunters and the nature conservation officials. In the conurbation of Geneva (three communities with > 20 000 inhabitants) our contacts were wildlife biologists running an urban fox project; in Zurich we knew the situation from our own project.

Development of the urban fox population in the city and the canton of Zurich

There are no direct figures on the red fox population available. Therefore its development has to be shown indirectly through the hunting record and other recorded causes of death. Longtime figures for an urban area are available for the city of Zurich, because it has been a game sanctuary since 1929. All wildlife management tasks in the city are exclusively performed by official game wardens, therefore the hunting result is recorded and the locations of dead foxes (shot or found dead) are known.

For comparison of the data from the canton and the city of Zurich, we used the HIPD (hunting indicator of population density; BÖGEL et al. 1974). We defined the HIPD as the annual number of foxes hunted per km^2 excluding lakes and areas above 2 000 meters. We did not include data on foxes with other causes of death than hunting because generally these data have only been available since 1968.

To compare data from urban and adjacent rural areas within the city of Zurich, we used a total number of foxes shot or found dead (available from 1960 to 1997), and additionally numbers of the two mortality factors "shot" and "found dead" (mostly road casualties; for the whole city available since 1960, for urban and adjacent rural areas separately available since 1984). To analyse the development of the fox population in the city of Zurich we performed simple linear regressions because the fit of regression of the two mortality factors on the years 1984 to 1997 did not improve by exponential or logistic functions.

Results

The present occurrence of urban foxes in Switzerland

After the call for urban fox sightings on Swiss Television in spring 1997, 194 sightings from 78 different towns and villages of the German-speaking part of Switzerland were reported. 138 sightings came from towns with more than 10 000 inhabitants (Tab. 1). Of those, more sightings than expected concerned cities with more than 50 000 inhabitants (randomisation test, $p < 0.01$), and less sightings than expected from towns with 10 000 – 20 000 inhabitants ($p < 0.05$; Tab. 1).

According to our inquiry among institutions in charge of wildlife management in 8 out of 9 cities with > 50 000 inhabitants, and in 18 of the 19 cities with 20 000 – 50 000 inhabitants, foxes were occasionally found or common (Fig. 1, Tab. 2). Foxes seem not to

Table 1. Reported sightings of foxes in urban areas from the German-speaking part of Switzerland (randomisation test).

Size of township	Accumulated number of inhabitants	Number of fox reports	Expected number of fox reports according to numbers of inhabitants	Significance
> 50 000	958 746	97	60	higher ($p < 0.01$)
20 000–50 000	335 192	10	21	ns
10 000–20 000	897 430	31	57	lower ($p < 0.05$)
Total	2 191 368	138	138	

Table 2. Occurrence and trend of urban fox populations in 30 Swiss cities, according to an inquiry among people/institutions in charge of wildlife management. The two cities where no urban foxes were observed (Bern, Lugano) are excluded.

Questions	Answers	Cities with many urban foxes (n = 13)	Cities with few urban foxes (n = 15)
1. Where are the urban foxes observed?	(a) whole of the city	13	4
	(b) outskirts only	0	11
2. Are there any urban breeding dens?	(a) yes	13	7
	(b) no	0	8
3. Since when have urban foxes been present?	(a) 1985–1999	10	7
	(b) < 1985	3	3
	(c) not known	0	5
4. How do you judge the trend of the fox population?	(a) increasing	8	5
	(b) stable	2	10
	(c) decreasing	3	0

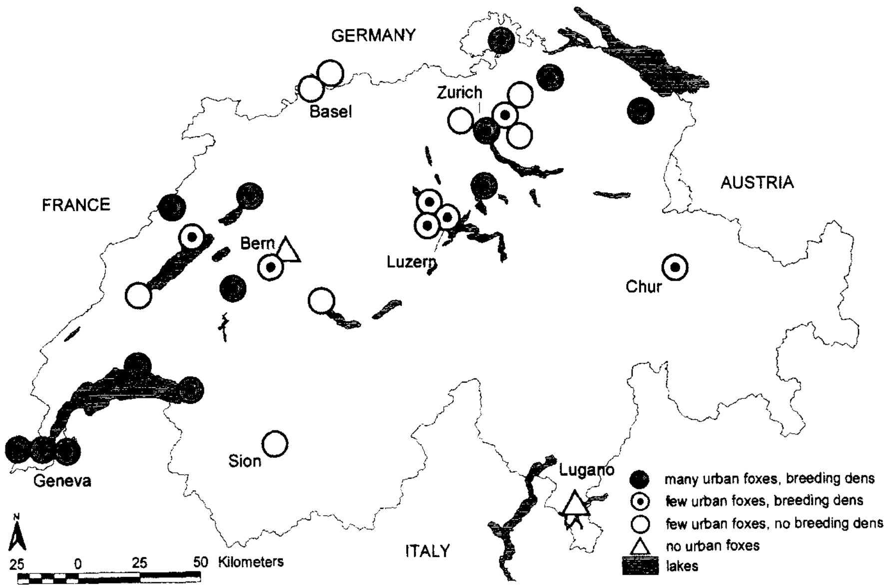

Fig. 1. Distribution of urban foxes in 30 cities with more than 20 000 inhabitants according to local wildlife management experts. Circles of adjacent cities are shifted to avoid overlapping.

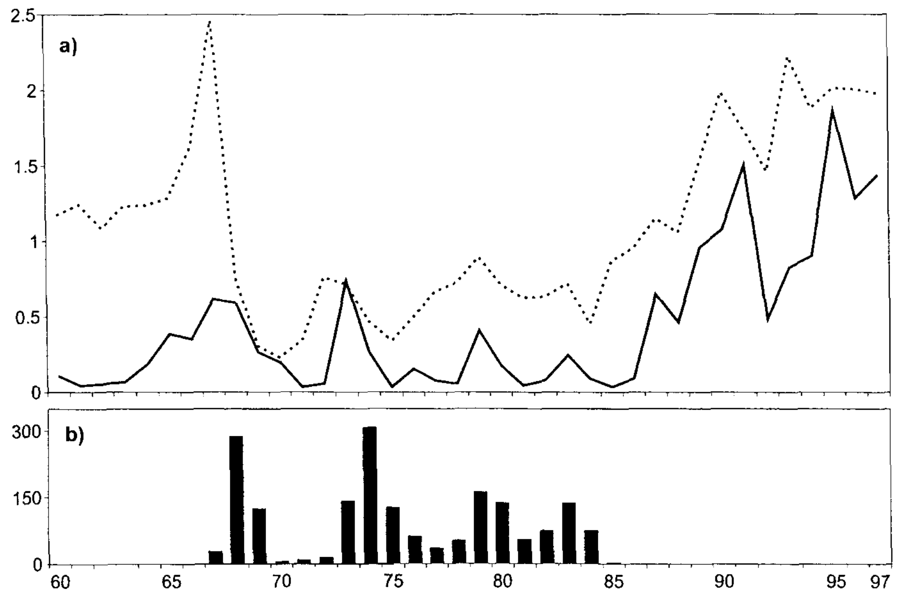

Fig. 2. a) Hunting indicator of population density (HIPD) for the city of Zurich (straight line) and the canton of Zurich (dotted line) from 1960 to 1997. **b)** Rabies cases in the canton of Zurich from 1960 to 1997.

be present in two towns only: in Bern, situated on the Swiss Plateau, and in Lugano, a city in the southern Alps.

In all 13 towns where foxes were reported to be common, they were observed throughout the urban area, (including the centre), and they were breeding in the urban area also (Tab. 2). In 4 cities with more than 50 000 inhabitants (Zurich, St. Gallen, Luzern, Biel), breeding dens are known even in the very city centre. In most cities (17 out of 28), urban foxes have been perceived as a recent phenomenon since 1985. No geographical trend can be recognised as far as the beginning of settlement in different cities is concerned.

Only in the conurbation of Geneva, with three cities (communities) with > 20 000 inhabitants (Geneva, Lancy, Vernier; Tab. 2) the population is said to decrease because of an outbreak of sarcoptic mange in 1996 (C. FISCHER, pers. comm.).

Development of the urban fox population in the city of Zurich

The HIPD of the canton of Zurich and the city of Zurich correlate significantly (Spearman, $r = 0.66$, $p < 0.001$; Fig. 2 a), the HIPD in the canton always being higher than in the city. Additionally, the HIPD of canton and city are strongly influenced by rabies trends between 1967, the year when rabies reached Switzerland, and 1985, the year with the last cases of rabies found on foxes in the canton of Zurich (Fig. 2 a, b).

According to the HIPD, the fox population in the city of Zurich and in the whole area of the canton of Zurich seems to have developed in parallel at least since the beginning of the 1970s. Both HIPDs are higher after the rabies epizootic than before. The average of the HIPD from 1993 to 1997 compared to the average of the HIPD from 1960 to 1964 is by 1.7 times higher (2.02 vs. 1.19) in the canton and 13.7 times higher (126 vs. 0.09) in the city of Zurich, indicating a stronger population increase in the city than in the canton. The increase of the HIPD started in the canton in 1984 and in the city in 1985, respectively.

However, the development of the fox population in the whole city of Zurich (with urban as well as adjacent rural areas) is not the same as the development of the population within the urban area. The first peak of the HIPD in 1967 (Fig. 2) only occurred in the records of foxes from the rural part of the city (Fig. 3), whereas in the urban part of the city fox numbers remained low during the 1960s and 1970s. The trend to an increasing urban fox population in fact just started from 1985 onwards.

Before 1985, most of the few foxes of the urban area were only recorded at the border of the city, apart from two foxes, one young fox near the city centre in August 1964 and one young fox in the fairly central railway station Enge in June 1967.

Rabies cases were recorded in and near the city of Zurich from 1967 to 1983 (Fig. 3). The prophylactic culling of foxes was carried out as intensively as possible from 1965 to 1995. The numbers of foxes found dead and shot, analysed separately for the whole city correlate significantly (Spearman, $r = 0.73$, $p < 0.001$). According to these numbers, the population remained low for almost 20 years after the rabies outbreak, and only in 1985, two years after the last rabies cases were recorded in the area, the fox population started to increase, both in the urban and in the adjacent rural part of the city. From 1985 to 1997 the number of foxes shot or found dead in the whole city increased by 20 times from 11 to 223. This trend is true for both mortality factors "shot" and "found dead" and examined separately for urban and adjacent rural areas (Tab. 3). Yet the increase in the number of foxes found dead was stronger in the urban than in the rural area (difference of coefficients, $t_{24} = 4.11$, $p < 0.001$).

Discussion

Today, urban foxes are recorded in almost all cities of Switzerland. The presence of breeding dens in urban areas up to the city centres indicates that foxes really live in the cities and are not just occasional roamers from the vicinity. We ascribe differences

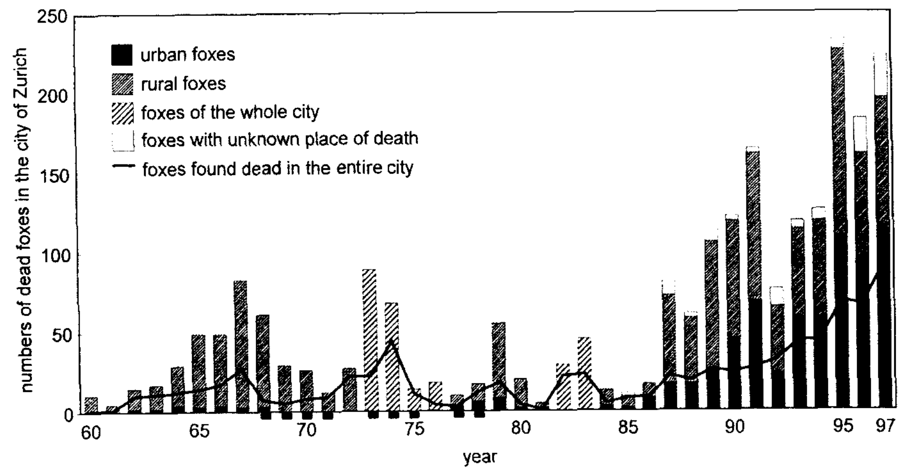

Fig. 3. Fox mortality (animals shot or found dead) in urban and rural areas in the city of Zurich from 1960 to 1997. From the years 1973–1976 and 1982–1983 there are only total numbers of dead city foxes available (widely hatched bars). No precise locations of death are available for some recorded foxes from 1984 onwards (white bars). The years with rabies cases within 5 km of the city centre (Kappeler 1991) are marked with black bars.

Table 3. The increase of numbers of recorded dead foxes within the city bordes of Zurich, described by the linear regression of the two mortality factors "shot" and "found dead" (mostly road casualties) from 1984 to 1997.

Foxes of urban areas			
Mortality factor	Coefficient	R^2	p <=
Shot	5.215	0.78	0.001
Found dead	3.310	0.85	0.001
Foxes of adjacent rural areas			
Mortality factor	Coefficient	R^2	p <=
Shot	4.842	0.46	0.01
Found dead	0.831	0.74	0.001

in fox population densities in Swiss cities of today mainly to the fact that urban foxes have been a recent phenomenon and the development is still going on.

Our call for fox sightings on Swiss television revealed that more foxes are recorded from larger towns than from smaller ones, a relation that was also observed by MACDONALD and NEWDICK (1982) in Great Britain. This could be because larger towns may have a higher proportion of suburban habitat, where the highest fox densities are found (HARRIS and RAYNER 1986 b).

Although red foxes generally avoid the direct presence of humans, some foxes have lived in the neighbourhood of humans settlements for a long time, shown, e. g., by the naturalist SCHINZ (in INEICHEN 1997), who noted in 1842, that red foxes had always lived in the moats surrounding the city of Zurich. The hunting statistics of the city of Zurich show that foxes have been present in the urban area since the early 1960s, but such observations remained isolated cases.

In 1985 the situation began to change. Due to successful oral vaccination campaigns against rabies, the fox population in Switzerland started to recover (BREITENMOSER et al. 2000), which is recorded in other European countries, as well (e. g. VOS 1993; ARTOIS et al. 1997). It was parallel to this general trend, when the urban fox population in the city of Zurich and in most other Swiss cities showed a drastic increase.

However, hunting statistics have to be interpreted cautiously, because they do not only correlate with the real fox populations but are also influenced by other factors such as the preferences of the hunters (MACDONALD and VOIGT 1985; GOSZCZYNSKI 1989) or outbreaks of zoonoses (KAPPELER and WANDELER 2000). A high hunting pressure most probably lasted during the whole period of rabies from 1967 until at least to the end of the 1980s. Therefore, the low HIPD during this period presumedly reflects low densities of fox populations. With the decrease of rabies the motivation to hunt foxes probably decreased drastically. The HIPD, on the other hand, was still increasing during the 1990s. We therefore suggest that the real trend of fox populations is underestimated by hunting statistics. The fox population in the canton of Zurich with its high degree of urbanisation must be even more underestimated by the HIPD, because foxes are hardly ever shot in most urban areas, where hunting generally is not permitted.

The game sanctuary of the city of Zurich is an exception, where a constant hunting regime is maintained by official game wardens. The significant correlation of the development of foxes "shot" and "found dead" within the city confirms, that the increasing numbers of dead foxes are not only the result of an increased shooting effort.

A similar development of urban foxes as in Switzerland recently took place in other parts of the distribution area of the red fox which is shown by reports, e. g., from Oslo, Norway (CHRISTENSEN 1985), Arhus, Denmark (MOLLER NIELSEN 1990), Stuttgart, Germany (T. ROMIG, pers. comm.), Toronto, Canada (ADKINS and STOTT 1998) and Sapporo, Japan (K. URAGUCHI, pers. comm.). The questions arises why the invasion of urban habitat started and which factors caused this new development.

According to HARRIS and RAYNER (1986 c), the colonisation of British towns already started in the 1930s. During these years there was a boom of private house construction resulting in large districts of middle-class suburbs with low-density housing, and medium-sized gardens. This is the type of habitat which HARRIS and RAYNER (1986 b) found to be favoured by foxes. Once established in these residential suburbs, foxes moved further into the city and also colonised less favoured habitats. HARRIS and RAYNER (1986 b) found urban foxes to be less common in areas consisting of council-rented housing, in city centres, and around industrial areas.

The colonisation of Swiss cities by foxes resulted in a similar phenomenon as known from Great Britain. However, the underlying cause for the rise of the urban fox populations seems to be different, because the development of Swiss cities in the past thirty years was unlike British cities in the 1930s. We propose two hypothetical explanations for the presence of urban foxes: The population pressure hypothesis (PPH) and, as an alternative, the urban island hypothesis (UIH).

The population pressure hypothesis PPH postulates that urban foxes are simply intruders from the adjacent rural areas. These foxes invade in human settlements because of a high population density in rural areas. According to the PPH, urban areas would provide suboptimal habitats for foxes, the dynamics of an urban fox population would closely correlate with the trend of the fox population in the adjacent rural areas, and the urban fox population would genetically not be different from the adjacent rural population (ROUSSET 1999).

The alternative urban island hypothesis UIH postulates that urban foxes have adapted to specific urban conditions such as high density of human population. Therefore, urban foxes would be able to use specific urban resources such as scavenged food items or special hiding places during daytime. The dynamics of such an urban fox population would be independent from the trend in the adjacent rural areas. The colonisation of urban areas could have been initiated by the behavioural adaptations of a few foxes that gave them access to exploit human settlements as a free niche. As only a few individuals founded the new urban population, we would expect it to be genetically isolated from the population in the rural surroundings.

The simultaneous emerging of urban foxes throughout Switzerland along with the increasing fox population indicates that the high population pressure has at least initiated the immigration of the founder individuals into the cities. MACDONALD and NEWDICK (1982) suggested that there was no strict division between rural and urban foxes in Oxford, because they had radio-tracked foxes which regularly commuted between urban and rural areas. Nevertheless, living in the city requires special adaptations, and many anecdotal observations reveal that foxes indeed have adapted to this exceptional environment. Further research on resource exploitation and genetic structure of the urban fox population will allow to compare the two hypotheses.

The presence of foxes in human settlements raises the question of the impact of human behaviour and human attitudes on the urban fox population (BONTADINA et al. 2000). HARRIS (1981 b) and DONCASTER et al. (1990) showed, that food directly or indirectly provided by humans can make up a major part of the diet of urban foxes. People feel ambivalent about urban foxes, being either fascinated by this wild carnivore in their neighbourhood or afraid of it because of zoonoses (Bontadina et al. 2000).

In fact, foxes in close vicinity to humans and pets could indicate new zoonotic risks (HOFER et al. 2000). The red fox is the main vector of rabies in Europe. Up to now urban areas were considered to be barriers to the spread of rabies (STECK et al. 1980), therefore the increase of urban fox populations calls for additional strategies in case of a new outbreak of rabies (MACDONALD and VOIGT 1985; HARRIS et al. 1988). Furthermore, the zoonosis alveolar echinococcosis (AE), caused by the small fox tapeworm *Echinococcus multilocularis*, could become more important through the increase of urban fox populations. In Switzerland, the incidence rate of human AE has not significantly changed over the past 36 years, suggesting a stable epidemiological situation (ECKERT and DEPLAZES 1999), but regarding the long incubation period of AE of 5–15 years, it would be advisable to study this zoonosis further, especially in urban areas. Results of such studies could have an important impact on the management of urban fox populations.

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Zusammenfassung

Die Entstehung urbaner Fuchspopulationen in der Schweiz

Seit Mitte der 1980er Jahre werden zunehmend Füchse inmitten von Schweizer Städten beobachtet. Die Befragung der zuständigen Behörden ergab, daß heute in 28 der 30 größten Schweizer Städte

Füchse registriert werden. In 20 dieser Städte sind Fuchsbaue mit Jungenaufzucht im Siedlungsraum bekannt. Dabei werden Stadtfüchse überproportional häufger in größeren Städten als in kleineren Ortschaften beobachtet. In Zürich, der größten Schweizer Stadt, waren gemäß der Jagdstatistik bis zu Beginn der 1980er Jahre Stadtfüchse sehr selten. Erst ab 1985 begann die städtische Fuchspopulation markant anzusteigen. Auch die umliegenden ländlichen Gebiete verzeichnen ab 1984 eine deutliche, allerdings weniger starke Zunahme der Fuchsbestände, die u.a. mit der erfolgreichen Tollwutbekämpfung zusammenhängt. Als Erklärung der Präsenz von Füchsen im Siedlungsraum, einem bisher vor allem aus Großbritannien bekannten Phänomen, schlagen wir zwei alternative Hypothesen vor, welche einerseits den Populationsdruck in ländlichen Gebieten, andererseits stadtspezifsche Verhaltensanpassungen der Füchse ins Zentrum stellen. Fuchspopulationen im Siedlungsraum beeinflussen das Verhalten und die Einstellung der Bevölkerung gegenüber Wildtieren und haben Konsequenzen für das Fuchsmanagement und den Umgang mit Zoonosen, wie Tollwut und alveoläre Echinokokkose.

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Original investigation

Feeding selectivity and food preference of *Ctenomys talarum* (tuco-tuco)

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Abstract

We tested feeding selectivity and food preference of *Ctenomys talarum* (tuco-tuco). To test feeding selectivity, above ground and below ground plant biomass from the field was determined and botanical composition of the diet was estimated in stomach contents using microhistological techniques. Feeding preferences were studied carrying out laboratory cafeteria experiments. *Ctenomys talarum* behave as generalist and opportunistic herbivores consuming the greater part of species present in the grassland. The above ground portion was preferred over the subterranean one. Grasses constituted 94% of the above ground vegetative fraction consumed and were generally selected. Preference trials also showed that *C. talarum* prefer above ground parts of grasses to other choices.

Key words: *Ctenomys talarum* diet, feeding selectivity, food preference

Introduction

Rodents of the genus *Ctenomys* (tuco-tucos) are subterranean herbivores whose populations are distributed in a discontinuous pattern throughout Argentina, Paraguay, Bolivia, Uruguay, Perú, Chile, and southern Brazil (WOODS 1984). Most herbivores inhabit a biotope in which the food plants are more or less continuously distributed in space and time, and whose accessibility is restricted by the structural and chemical properties of the vegetation (ILLIUS and GORDON 1993). They select food items according to their preference, and availability in the field. Preference is the predilection of a consumer for a particular class of food, and it is the result of how well the consumer "likes" this food relative to other ones, when all are equally available (NORBURY 1992). Diet selection in herbivores may be explained by models where the rate of intake is maximized with nutrient constraints, toxins are avoided or their intake is minimized (STEPHENS and KREBS 1986). A foraging herbivore maximizes its nutrient intake when greater nutrient intake converts directly into greater survival and reproduction (nutrient maximization; BELOVSKY and SCHMITZ 1994).

Food resources have been implicated as important to both burrow location and burrow

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