The Rise of Urban Foxes (*Vulpes vulpes*) in Switzerland and Ecological and Parasitological Aspects of a Fox Population in the Recently Colonised City of Zurich

Dissertation

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Summary

Over the last 15 years of the 20th century, the Swiss red fox *Vulpes vulpes* (Linneaus, 1758) population increased about fourfold, as can be derived from the statistics of known fox mortality. The increase was strong in rural areas, but most prominent in cities and conurbations. This astonishing population dynamic of one of the larger carnivores of Europe was the reason for the start of the Integrated Fox Project IFP in 1995, a research and communication project about the development of fox populations in Switzerland. The aim of this study, which took place in the frame of the IFP, was an overview on status and development of urban foxes in Swiss cities and the investigation of ecological and parasitological aspects of the urban fox population in Zurich.
In the year 2000, foxes lived in 28 of 30 Swiss cities with more than 20'000 inhabitants and breeding dens were known in 20 of these cities. In Zurich, the largest conurbation of Switzerland, urban foxes were very scarce until the early 1980s, but from 1985 onwards, there was a drastic increase of the urban fox population. In the adjacent rural areas, there also was a clear but significantly less extreme increase of the fox population from 1984 onwards.

Spatial and social organisation and habitat association of 22 foxes (13 females and 9 males) were studied by means of tracking radio-tagged adult foxes in an urban and peri-urban area of Zurich between December 1996 and June 1999. According to their spatial use foxes were separated in resident female and male foxes and non-resident floating male foxes. There were no significant differences in home range size neither between resident females and males, nor between seasonal home range sizes, the home range size of females being 28.8 ± 22.7 ha, of males 30.8 ± 11.0 ha. The three floaters had 3 to 11.2 times larger home ranges. The tracked foxes were classified into “urban” or “rural” according to the amount of urban area within their home ranges. There was an obvious separation between rural and urban foxes: although the urban border was within reach of all tracked foxes, it was only rarely crossed. Most foxes lived in family groups of more than two adult foxes and the fox density in the study area was estimated to be about 11 adult foxes per km^2.

Habitat association was studied of 17 resident foxes, for rural and urban foxes separately, based on habitat categories of vegetation cover and human utilisation types. Rural as well as urban foxes showed a significant overall difference in habitat selection compared to habitat availability within their home ranges. Of rural foxes, the mostly selected habitat categories for nightly activity were “grassland”, “forest” and "public parks and cemeteries". Rural foxes had most of their day-time rest sites in forest. Urban foxes used for nightly activity mostly "public parks and cemeteries" and "allotment gardens", whereas "residential areas with medium or high density housing" and "streets and places" were least selected. Urban foxes used "public parks and cemeteries" more in the first half of the night and residential areas more in the second half of the night. We conclude that urban foxes, in order to avoid contact with people, used closed areas such as parks in the early night, when humans are still active, and changed to "residential areas with low density housing" mainly when human presence in these areas was low. Contrary to rural foxes, urban foxes selected several different habitat categories for day-time rest sites. As "areas with medium density housing" correlated positively with home range size, we conclude that they did not supply suitable habitat for foxes because their surroundings - mostly plain lawn – provide little cover and poor food resources.

As an explanation for the presence of foxes in human settlements we discuss two alternative hypotheses, which focus either on the population pressure in the rural areas (Population Pressure Hypothesis, PPH) or on the specific ontogenetic behavioural adaptations of urban foxes (Urban Island Hypothesis, UIH). The results of our studies show, that urban foxes in Zurich are not out-competed rural foxes which dispersed to a suboptimal habitat, as predicted by the PPH. Urban foxes have rather adapted to urban habitat, are able to explore urban resources and reach higher densities than rural populations. Our results therefore support the Urban Island Hypothesis.

The presence of foxes in urban areas in close vicinity to people and their pets has implications for zoonoses such as the alveolar echinococcosis caused by the small fox tapeworm (*Echinococcus multilocularis*). To estimate the prevalence of this helminthic parasite in urban foxes, over a period of 26 months from January 1996 to February 1998, 388 foxes were sampled from the city of Zurich, and examined for intestinal infections with this parasite. The prevalence of *E. multilocularis* in urban foxes was 47% and significantly smaller than in foxes of adjacent rural areas where 67% of the foxes were infected. Rodents trapped in areas at the border of the city were examined with respect to *E. multilocularis* metacestodes. The prevalence in 781 *Arvicola terrestris*, an important intermediate host, was 9.2% with fully developed protoscolices (14-240,000) occurring in 24 *A. terrestris*. Thus, an urban parasite cycle has been established and a potential infection risk exists not only for urban residents but also for domestic dogs and cats. Because of this new epidemiological situation and the emerging public awareness concerning zoonoses we re-

commend further research on *E. multilocularis* in urban areas and the evaluation of local intervention in the cycle of this parasite.

The results of these studies are summarised and discussed in five manuscripts. They have been published or are prepared for submission in international journals.

Zusammenfassung

Im Verlaufe der letzten 15 Jahre des 20. Jahrhunderts nahmen die Populationen des Rotfuchses *Vulpes vulpes* (Linneaus, 1758) in der Schweiz um etwa das Vierfache zu, wie aus der statistisch erfassten Mortalität ersichtlich ist. Die Zunahme war markant in ländlichen Gebieten, besonders ausgeprägt jedoch in Siedlungsräumen. Diese erstaunliche Populationsdynamik eines der grössten Karnivoren Europas war 1995 der Anlass das Integrierte Fuchsprojekt IFP ins Leben zu rufen, ein Forschungs- und Kommunikationsprojekt über die Entwicklung der Fuchsbestände in der Schweiz. Ziel der vorliegenden Untersuchungen, welche im Rahmen des IFP durchgeführt wurden, war, einen Überblick über die Situation in Schweizer Städten zu erhalten und wildbiologische und parasitologische Aspekte urbaner Fuchspopulationen am Beispiel der Stadtfüchse von Zürich zu untersuchen.
Im Jahr 2000 lebten Füchse in 28 von 30 Schweizer Städten mit mehr als 20'000 EinwohnerInnen und Aufzuchtsorte von Jungfüchsen waren in 20 dieser Städte bekannt. In Zürich, der grössten Agglomeration der Schweiz, waren Füchse im Siedlungsraum bis in die frühen 1980er-Jahre selten. Erst ab 1985 begannen die städtischen Fuchsbestände stark anzusteigen. In angrenzenden ländlichen Gebieten war die Zunahme ebenfalls deutlich, jedoch weniger ausgeprägt.

Von Dezember 1996 bis Juni 1999 wurden die räumliche und soziale Organisation und die Habitatassoziation von 22 adulten Füchsen (13 Fähen und 9 Rüden) in einem Gebiet der Stadt Zürich mittels Radiotelemetrie untersucht. Anhand der Raumnutzung wurden diese Füchse in residente Fähen und Rüden und nicht-residente Rüden unterteilt. Bei den Aktivitätsgebietsgrössen residenter Füchse konnten keine signifikanten Unterschiede, weder saisonale noch geschlechtliche, festgestellt werden. Die Aktivitätsgebiete von Fähen betrugen 28.8 ± 22.7 ha, diejenigen von Rüden 30.8 ± 11.0 ha. Die drei nicht-residenten Füchse hatten 3 bis 11.2 mal grössere Aktivitätsgebiete. Aufgrund des Anteils an urbanen Habitaten in ihren Aktivitätsgebieten wurden die Füchse einer „urbanen“ bzw. einer „ländlichen“ Gruppe zugewiesen. Dabei war eine offensichtliche Aufteilung zwischen urbanen

und ländlichen Füchsen zu beobachten: obwohl die Stadtgrenze in Reichweite aller untersuchten Füchse lag, wurde sie kaum je überquert. Die meisten Füchse lebten in Familiengruppen mit mehr als zwei adulten Tieren. Die Fuchsdichte im Untersuchungsgebiet wurde auf etwa 11 Füchse/km^2 geschätzt.

Die Habitatassoziation wurde von 17 residenten Füchsen - nach städtischen und ländlichen Füchsen getrennt - analysiert. Das Habitatangebot wurde auf Grund der Vegetations- und Nutzungskartierung der Stadt Zürich erhoben. Urbane und ländliche Füchse zeigten eine signifikant unterschiedliche Habitatnutzung im Vergleich zum Habitatangebot innerhalb ihrer Aktivitätsgebiete. Bei ländlichen Füchsen waren die am häufigsten genutzten Habitatkategorien „Wiese, Weide" und „Wald". Die meisten Tagesruheplätze von ländlichen Füchsen lagen im Wald. Urbane Füchse nutzten während ihrer nächtlichen Aktivitätszeit am häufigsten „öffentliche Grünanlagen und Friedhofareale" und „Schrebergärten", während „Wohngebiete mit mittlerer bis hoher Besiedlungsdichte" und „Strassen und Plätze" am seltensten genutzt wurden. Urban Füchse nutzten „öffentliche Grünanlagen und Friedhofareale" häufiger in der ersten Nachthälfte, während „Wohngebiete mit niedriger Bebauungsdichte" häufiger in der zweiten Nachthälfte aufgesucht wurden. Wir schliessen daraus, dass Füchse dem direkten Kontakt mit Menschen ausweichen, indem sie zu Beginn der Nacht, wenn noch viele Menschen im Freien unterwegs sind, abgeschlossene Areale wie Parkanlagen nutzten. In Wohngebiete hingegen hielten sich Füchse dann häufiger auf, wenn die Präsenz von Menschen im Freien sehr gering war. Im Gegensatz zu ländlichen Füchsen nutzten urbane Füchse verschiedene Habitate für ihre Tagesruheplätze. „Gebiete mit mittlerer Besiedlungsdichte" korrelierten positiv mit der Aktivitätsgebietsgrösse der Füchse, was darauf hindeutet, dass diese Gebiete keine geeigneten Habitate für Füchse bieten. Die Aussenräume in solchen Wohnquartieren bestehen meist aus weitläufigen Rasenflächen mit wenig Versteckmöglichkeiten und einem geringen Futterangebot.
Als Erklärung der Präsenz von Füchsen im Siedlungsraum schlagen wir zwei alternative Hypothesen vor, welche einerseits den Populationsdruck in ländlichen Gebieten (Population Pressure Hypothese, PPH), andererseits stadtspezifische ontogenetische Verhaltensanpassungen der Füchse (Urban Island Hypothese, UIH) ins Zentrum stellen. Die vorliegenden Resultate zeigen, dass Füchse in der Stadt nicht einfach aus ländlichen Gebieten in diesen suboptimalen Lebensraum verdrängt wurden, wie dies die PPH voraussagen würde. Vielmehr haben sich Füchse an den Siedlungsraum angepasst, können spezifisch städtische Ressourcen nutzen und erreichen höhere Dichten als in ländlichen Gebieten. Unsere Resultate unterstützen somit eher die Urban Island Hypothese.

Die Präsenz von Füchsen in städtischen Gebieten in direkter Nachbarschaft zur Bevölkerung und zu Haustieren könnte von Bedeutung sein für Zoonosen wie die alveoläre Echinokokkose, einer Infektionskrankheit des Menschen, hervorgerufen durch den kleinen Fuchsbandwurm (*Echinococcus multilocularis*). Um die Prävalenz dieses Parasiten bei urbanen Füchsen zu schätzen, wurden von Januar 1996 bis Februar 1998 388 Füchse aus dem Gebiet der Stadt Zürich gesammelt und bezüglich einer Dünndarminfektion mit *E. multilocularis* untersucht. Die Prävalenz bei urbanen Stadtfüchsen war mit 47% signifikant kleiner als bei Füchsen aus angrenzenden ländlichen Gebieten, wo sie 67% betrug. Nagetiere aus einem Stadtrandgebiet wurden bezüglich eines Vorhandenseins von *E. multilocularis*-Metazestoden untersucht. Die Prävalenz bei 781 *Arvicola terrestris*, einem wichtigen Zwischenwirt, betrug 9.2%, wobei in 24 *A. terrestris* vollständig entwickelte Protoscolices (14-240,000) festgestellt wurden. Daraus kann geschlossen werden, dass sich ein urbaner Lebenszyklus des Kleinen Fuchsbandwurms etabliert hat und dass damit ein potentielles Infektionsrisiko nicht nur für die städtische Bevölkerung, sondern auch für Hunde und Katzen besteht. Auf Grund dieser neuen epidemiologischen Situation und der zunehmenden Sensibilisierung der Bevölkerung für Themen rund um Zoonosen empfehlen wir weitere Forschungsarbeiten zu *E. multilocularis* in städtischen Gebieten und die Evaluation von lokalen Interventionen in den Zyklus dieses Parasiten.

Die Resultate der vorliegenden Untersuchungen sind in fünf Publikationen dargestellt, welche bereits publiziert oder für eine Einreichung in internationalen Zeitschriften bereit sind.

Einleitung

Die Entwicklung der Fuchspopulationen der Schweiz seit den 1960er-Jahren

In den letzten 15 Jahren stieg die Population des Rotfuchses (*Vulpes vulpes*) in der Schweiz rasch an; die statistisch erfasste Mortalität der Füchse in der Schweiz (Eidg. Jagdstatistik, BUWAL 1997) vervierfachte sich von 1984 – 96 (Breitenmoser et al. 2000). Füchse sind heute nicht nur in ländlichen Gegenden allgegenwärtig, sondern vermehrt auch in Dörfern und Städten zu beobachten (Wandeler & Lüps 1993). Den markantesten Anstieg der Fuchspopulation - gemessen an der bekannten Mortalität - zeigten denn auch städtische Agglomerationen wie die Stadt Zürich oder der Kanton Genf (Stauffer pers. Mitteilung; C. Fischer, pers. Mitteilung). Es scheint eine eigentliche Invasion des Fuchses in den Siedlungsraum stattgefunden zu haben.

Vorkommen und Häufigkeit des Fuchses liegen heute deutlich höher als vor dem Auftreten der Tollwut ab 1967 und die Zunahme erfolgte auch in Gebieten, die nicht oder lange nicht mehr von der Seuche betroffen waren (Breitenmoser & Müller, eingereicht). Wir gehen deshalb davon aus, dass das ausserordentliche Wachstum der Fuchspopulation zwar erst möglich wurde, nachdem die Tollwut mittels Impfkampagnen ab 1978 (Steck 1980) als wichtigster Mortalitätsfaktor weitgehend ausgeschaltet wurde, dass dafür aber grundsätzliche Veränderungen in der Kulturlandschaft verantwortlich sind (Chautan et al. 2000; Breitenmoser & Müller, eingereicht). Der Fuchs ist eine sehr anpassungsfähige Art und kann deshalb Veränderungen in seiner Umwelt optimal ausnutzen, was zu einer Erhöhung der Tragfähigkeit (Carrying Capacity) des Fuchslebensraumes geführt haben könnte.

Das “Britische Phänomen”

Der Begriff des „Stadtfuchses“ wurde in Grossbritannien geprägt. Das Vorkommen von Füchsen in Städten und hohe Populationsdichten in urbanen Gebieten sind aus Grossbritannien seit den 1930er-Jahren bekannt und verschiedene ökologische Aspekte der „urban foxes“ wurden in Städten wie London, Bristol, Oxford und Edinburgh intensiv erforscht (z.B. Harris 1977, Harris 1981, Macdonald & Newdick 1982, Kolb 1984 und 1985, Harris & Rayner 1986a, b, Doncaster & Macdonald 1991, White et al. 1996, Saunders et al. 1997, Baker et al 2000). Das Vorkommen von Füchsen im urbanen Siedlungsraum Grossbritanniens war eng korreliert mit der sozialen und städtebaulichen Entwicklung während der 1930er-Jahre (Teagle 1967, Beames 1969, 1972, Page 1981). Tiefe Bodenpreise und eine erhöhte Mobilität der städtischen Bevölkerung führten damals in vielen britischen Städten dazu, dass innert weniger Jahre grosse Mittelklasse-Vorstadtgebiete mit einem hohen Anteil an privatem Wohneigentum, niedriger Bebauungsdichte, geringer Anzahl Personen pro Haushalt, mittelgrossen Gärten und ruhigen Quartierstrassen entstanden (Harris & Rayner 1986a, b). Dies sind genau jene Gebiete, die Füchse in Grossbritannien als städtischen Lebensraum bevorzugen (Harris & Rayner 1986a, Harris & Smith 1997, White et al. 1996, Baker et al. 2000). Erstmals wurden zudem in suburbanen Gebieten beobachtet, dass Füchse, die bis dahin als Einzelgänger gegolten haben, sich unter bestimmten Bedingungen zu Familiengruppen zusammenschliessen können (Macdonald 1979, 1981, 1984). In den 1970er- und 1980er-Jahren wurden zudem in britischen Städten nie zuvor beobachtete Fuchsdichten von bis zu 5 Fuchsfamiliengruppen/km^2 und von 10 und mehr Altfüchsen/km^2 festgestellt (Harris & Smith 1987, Voigt & Macdonald 1984). Zur gleichen Zeit wurde auf dem europäischen Festland in ländlichen Gebieten durchschnittliche Dichten von 0.4 bis 1.8 Altfüchsen angegeben (Wandeler & Lüps 1993). Da nirgendwo sonst im Verbreitungsgebiet des Fuchses nur annähernd hohe Populationsdichten wie in britischen Städten beobachtet wurden, galten Stadtfüchse bis in die 1980er-Jahre als "unique British phenomenon" (Harris 1977, Macdonald & Newdick 1982).

"Population Pressure Hypothese" versus "Urban Island Hypothese"

Seit Mitte der 1980er-Jahren wurden jedoch auch Füchse in Städten auf dem europäischen Festland, in Kanada und Japan beobachtet. Füchse scheinen überall in ihrem Verbreitungsgebiet des Fuchses mehr und mehr in menschliche Siedlungsgebiete vorzudringen: z.B. in Oslo, Norwegen (Christensen 1985), Arhus, Dänemark (Moller Nielsen 1990), Brüssel, Belgien (B. Brochier, pers. Mitteilung), Stuttgart, Deutschland (T. Romig, pers. Mitteilung), Toronto, Kanada (Adkins & Stott 1998) und Sapporo, Japan (K. Uraguchi, pers. Mitteilung).

Es stellt sich nun die Frage, weshalb diese Entwicklung einsetzte und weshalb mit einer mehr als 60-jährigen Verzögerung im Vergleich zu Grossbritannien. Handelt es sich auf dem Kontinent Europas um eine eigene Entwicklung mit anderen Ursachen als in Grossbritannien? Oder wurde die Entwicklung durch die Tollwut verzögert, von welcher Grossbritannien bisher verschont geblieben ist?

Um das Phänomen der Stadtfüchse zu erklären, formulierten wir zwei Hypothesen:
Die **Population Pressure Hypothese PPH** geht davon aus, dass Städte für Füchse suboptimale Habitate bieten und erst dann besiedelt werden, wenn ein genügend grosser Populationsdruck besteht, d.h. wenn auf dem Land die Fuchsdichten zunehmen. Die PPH postuliert, dass Städten tiefere Populationsdichten aufweisen und Füchse innerhalb der Städte vermehrt ländliche Ressourcen nutzen. Zwischen ländlichen und städtischen Gebieten findet nach der PPH ein steter Austausch statt, womit sich „Stadtfüchse“ und „Landfüchse“ weder im Verhalten noch im Erbgut unterscheiden (Rousset 1999).

Die **Urban Island Hypothese UIH** geht davon aus, dass Stadtpopulationen von einzelnen, an den städtischen Lebensraum angepassten Individuen gegründet worden sind, welche durch ihre Verhaltensanpassung Zugang zu spezifisch städtischen Ressourcen wie etwa Abfall von Komposthaufen oder Kehrichtsäcken erhielten. Die Zunahme der Stadtfuchspopulationen wäre gemäss der UIH eine stadtinterne Zunahme, die von der ländlichen Entwicklung weitgehend unabhängig verläuft. Die UIH postuliert, dass Städte für die angepassten Füchse ein optimaler Lebensraum sind und diese Füchse die spezifisch städtischen Ressourcen gezielt nutzen können. Nach der UIH findet wenig Austausch zwischen städtischen und ländlichen Gebieten statt, da „Stadtfüchse“ dank ihrer Anpassungen gegenüber ihren ländlichen Artgenossen konkurrenzfähiger sind.

Existiert ein Lebenszyklus des Kleinen Fuchsbandwurms *Echinococcus multilocularis* im städtischen Gebiet?

Der Kleine Fuchsbandwurm *Echinococcus multilocularis* ist ein Parasit und gehört zur Familie der *Taeniidae*, welche komplexe Entwicklungszyklen durchlaufen, die geschlechtsreife Stadien in sogenannten Endwirten, eine freilebende Phase als Ei sowie Larvalstadien (Finnen, Metazestoden) in Zwischenwirten umfassen. Hauptsächlicher Endwirt von *E. multilocularis* in Mitteleuropa ist der Rotfuchs (Eckert 2000), wo der Parasit im Dünndarm lebt, weniger häufig Hund und Katze. Als Zwischenwirte sind v.a. Kleinsäuger wie Schermäuse *Arvicola terrestris* und Feldmäuse *Microtus arvalis* bekannt, wo die Metazestoden in der Leber leben. Zur Entwicklung der Metazestoden kommt es in Zwischenwirten und selten auch im Menschen (Fehlwirt) durch die orale Aufnahme der Eier von *E. multilocularis* (Deplazes 1997).
Die alveoläre Echinokokkose beim Menschen, verursacht durch die Metazestoden von *E. multilocularis*, ist eine sehr seltene, jedoch gefürchtete Zoonose, da sie ohne Behandlung meist zum Tode führt (Stössel 1989). Die mittlere jährliche Inzidenz-

rate pro 100'000 Einwohner in der Schweiz liegt bei 0.11 (0.04-0.75) Neuerkrankungen pro Jahr (Eckert et al. 1995) und ist in den letzten rund 40 Jahren weitgehend konstant geblieben (Eckert & Deplazes 1999). Es stellt sich jedoch die Frage einer möglicherweise veränderten epidemiologischen Situation durch das Vordringen der Füchse in den Siedlungsraum und die dadurch entstehenden nahen Kontaktmöglichkeiten zwischen Fuchs und Mensch und im Fall eines etablierten Lebenszyklus von *E. multilocularis* im urbanen Gebiet ein potentiell erhöhtes Infektionsrisiko für Hunde und Katzen.

Management der Fuchspopulation im städtischen Siedlungsraum

Die Eingriffe in die Fuchspopulation im Siedlungsraum erfolgen heute unspezifisch, da davon ausgegangen wird, dass es sich bei diesen Füchsen weitgehend um solche handle, die aus umliegenden Gebieten in die Städte eindringen oder dass zumindest ein steter Austausch zwischen Füchsen aus städtischen und umliegenden ländlichen Gebieten stattfindet. Ohne spezifische Kenntnisse über Raumnutzung, Ökologie, Dynamik der Füchse im Siedlungsgebiet und deren Austausch mit den umliegenden ländlichen Population sind die Auswirkungen der Kontrollmassnahmen in den Städten ungewiss. Die heute durchgeführten Kontrollmassnahmen könnten im Hinblick auf die Bekämpfung von Tollwut und anderen Zoonosen wie der Alveolären Echinokokkose möglicherweise sogar kontraproduktiv sein. Für die Planung des weiteren Vorgehens ist ein fundiertes Wissen sowohl über ökologische und parasitologische Aspekte der Fuchspopulation sowie über das Verhalten und die Einstellung der städtischen Bevölkerung gegenüber diesem mittelgrossen Karnivoren Voraussetzung.

Methoden

Eine Übersicht über die Situation bezüglich der Füchse im Siedlungsraum in der Schweiz erhob ich mit der mündlichen Befragung der offiziellen Wildtierverantwortlichen in Städten mit mehr als 20'000 EinwohnerInnen. Eine ähnliche Vorgehensweise wurde in einem ersten Schritt auch in Grossbritannien gewählt und hat sich unter Vorbehalt einer vorsichtigen Interpretation als zuverlässig erwiesen (Harris et al. 1986b, Wilkinson & Smith 2001).
Die Entwicklung der Fuchspopulationen seit Anfang der 1960er-Jahre wurde anhand der Jagd- und ab 1968 auch anhand der Fallwildstatistik aus dem Kanton Zürich erhoben (BUWAL, Eidgenössische Jagdstatistik). Die entsprechenden Zahlen aus der Stadt Zürich standen in Form der Abschuss- und Fallwildstatistik des Wildschonreviers der Stadt Zürich zur Verfügung.

Populationsschätzungen aufgrund von Jagdstatistiken werden kritisiert, da sie nicht nur die Entwicklung der Fuchspopulationen wiedergeben, sondern auch von anderen Faktoren wie Trends in der Jagdpolitik, Fellpreisen, Vorlieben von Jägern oder deren Meldezuverlässigkeit (Macdonald & Voigt 1985, Goszczynski 1989), dem Ausbruch von Zoonosen (Kappeler & Wandeler 2000) und von den Wetterbedingungen abhängen können. Zur Interpretation der Daten sollten deshalb weitere Angaben wie etwa die Tollwutfälle in einem Gebiet einbezogen werden. Im Wildschonrevier der Stadt Zürich waren und sind immer und ausschliesslich von der Stadt angestellte Wildhüter für die Abschuss- und Fallwildstatistik zuständig und der Abschuss von Füchsen wurde in den vergangenen 40 Jahren immer intensiv betrieben. Diese Zahlen dürften demnach ein zuverlässigeres Bild von der Fuchspopulationsentwicklung bieten als die gängigen Jagdstatistiken.

Daten zur Raum- und Habitatnutzung und zur sozialen Organisation der Füchse wurden mit der Beobachtung von sendermarkierten Tieren erhoben. Dabei wurden in einem Untersuchungsgebiet in Zürich Wiedikon (Fläche 11 km^2) von Dezember 1996 bis Mai 1999 24 adulte Füchse gefangen und mit einem Halsbandsender ausgerüstet. Mittels dieser Methode wurde die Raumnutzung und die Aktivität von 22 Füchsen während der Nacht, sowie die Tagesschlafplätze festgehalten. Die Daten zum nächtlichen Raumverhalten wurden mit der Fokustier-Methode erhoben, indem jeweils einem Tier während einer Nacht gefolgt wurde und in Intervallen von 15 Min. dessen Aufenthaltsort bestimmt wurde (White & Garrott 1990). Die Grösse der Homeranges von sendermarkierten Füchsen wurden mit der Methode des Minimum Konvex Polygons (Harris et al. 1990) und aufgrund der Nutzungsdichte mit Kernel-Schätzungen (Worton 1989) bestimmt. Die Daten wurden dazu in das geografische Informationssystem ArcView (ESRI, Version 3.1) übernommen und mit Hilfe der Extensionen Spatial Analyst und Animal Movement Analyst (Hooge & Eichenlaub 1997) berechnet.
Die Habitatauswertungen wurden ebenfalls mit Hilfe von ArcView in der Extension Spatial Analyst ausgeführt. Grundlage für die Habitatauswertung bildete dabei die Vegetations- und Nutzungskartierung der Stadt Zürich (Bernowitz & Leutert 1988) und eigene Kartierungen. Habitatassoziationen wurden anschliessend mittels einer Compositional Analysis (Aebischer & Robertson 1992, Aebischer et al. 1993, Saunders et al. 1998) analysiert.

Für die parasitologischen Untersuchungen und die Erfassung weiterer Populationsparameter wie Geschlecht, Alter und Reproduktionsstatus der Füchse der Stadt Zürich wurden ab Januar 1996 alle geschossenen oder tot aufgefundenen Füchse innerhalb des Wildschonreviers gesammelt, bei -20°C gelagert und zu einem späteren Zeitpunkt seziert. Diese Füchse wurden in bezug auf Dünndarminfektionen mit *Echinococcus multilocularis* und anderen Helminthen untersucht. Um die Kontamination der städtischen Gebiete durch Eier von *E. multilocularis* zu schätzen, wurden zudem Kotproben von Füchsen gesammelt und mit einem Koproantigen-ELISA getestet. Ausserdem wurde die Prävalenz von *E. multilocularis* bei Nagetieren im Grüngürtel um den Siedlungsraum der Stadt Zürich ermittelt, indem in diesen ländlich geprägten Gebieten Nagetiere gefangen und anschliessend bezüglich eines Befalls durch *E. multilocularis* untersucht wurden.

Manuskript A: Die Entstehung urbaner Fuchspopulationen in der Schweiz

Seit Mitte der 1980er-Jahren 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 häufiger 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 stadtspezifische 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.

Manuskript B: Die räumliche Organisation von Füchsen in der kürzlich besiedelten Stadt Zürich, Schweiz

Rotfüchse *Vulpes vulpes* (Linneaus, 1758) haben urbane Gebiete der Schweiz seit den 1980er-Jahren besiedelt. In der Stadt Zürich, der grössten Schweizer Agglomeration, wurden zwischen Dezember 1996 und Juni 1999 13 weibliche und 9 männliche Füchse mit Halsbandsendern markiert und in ihrem räumlichen Verhalten beobachtet. Es ergaben sich keine signifikanten Unterschiede in den Homerange-Grössen, weder zwischen residenten Fähen und Rüden noch zwischen den Saisons. Die mittlere Aktivitätsgebiets-Grösse von Fähen (Minimum Convex Polygon) betrug 28.8 ± 22.7 ha, von Rüden 30.8 ± 11.0 ha. Drei Rüden, sogenannte "Floater", hatten 3 bis 11.2 mal grössere Aktivitätsgebiete und die mittlere Distanz, welche sie in 15 Min. zurücklegten (162 m ± 19.4), war ebenfalls grösser als diejenigen von residenten Füchsen (101 m ± 20.2). Wir klassifizierten die sendermarkierten Füchse in die beiden Gruppen "urban" und "rural" nach dem Anteil an urbanem Gebiet in ihrem Aktivitätsgebiet. Zwischen urbanen und ruralen Füchsen ergab sich eine deutliche Auftrennung bezüglich ihres räumlichen Verhaltens: obwohl sich die Stadtgrenze theoretisch in Reichweite aller sendermarkierten Füchse befand, wurde sie nur selten überquert. Es gab klare Hinweise für die Existenz von Familiengruppen im Untersuchungsgebiet: (1) die Sektionsdaten von den geschossenen und tot aufgefundenen Füchsen aus Zürich wiesen 40.6 % nicht-reproduzierende Fähen auf, (2) die Aktivitätsgebiete von residenten Füchsen zeigten z.T. grosse Überlappungen und (3) Beobachtungen an Reproduktionsorten wiesen die Anwesenheit von meist mehr als 2 Altfüchsen an diesen Bauen nach. Basierend auf der Anzahl Reproduktionsorten im Untersuchungsgebiet, der Anzahl beobachteter Füchse an diesen Jungenaufzuchtsorten und den Sektionsdaten schätzen wie die Fuchspopulationsdichte im Untersuchungsgebiet auf etwa 11 adulte Füchse pro km^2. Als eine Erklärung der Anwesenheit von Füchsen im Siedlungsraum diskutieren wir die beiden alternativen Hypothesen, welche einerseits den Populationsdruck in ländlichen Gebieten (Population Pressure Hypothese), andererseits stadtspezifische Verhaltensanpassungen der Füchse im Siedlungsraum (Urban Island Hypothese) ins Zentrum stellen. Die Resultate unserer Untersuchungen unterstützen die Urban Island Hypothese.

Manuskript C: Anpassungen an den urbanen Lebensraum bezüglich der Habitatassoziation von Rotfüchsen

Die Besiedlung von urbanen Gebieten durch Füchse setzte in der Schweiz Mitte der 1980er-Jahre ein. Obwohl es sich um ein relativ neues Phänomen handelt, sind in der Stadt Zürich bereits hohe Populationsdichten von mehr als 10 adulten Füchsen / km^2 zu verzeichnen. Von Dezember 1996 bis Juni 1999 wurde in einem Untersuchungsgebiet in der Stadt Zürich die Habitatnutzung der nächtlichen Aktivität und der Tagesschlafplätze von 17 adulten, residenten Füchsen mit Hilfe von Halsbandsendern untersucht. Die Aktivitätsgebiete von 11 Füchsen lagen mehrheitlich innerhalb der Stadtgrenze ("Stadtfüchse"), während die Aktivitätsgebiete von 6 Füchsen am Stadtrand mehrheitlich ausserhalb der Stadtgrenze lagen ("Landfüchse"). Für die Aufnahme des Habitatangebotes wurden 11 Kategorien unterschieden, die sich auf Vegetationstypen und die Nutzung durch den Menschen beziehen. Habitatnutzungs-Analysen wurden für Stadt- und Landfüchse separat mit der Methode der Compositional Analysis durchgeführt.

Stadt- und Landfüchse zeigten eine signifikant unterschiedliche Habitatnutzung im Vergleich zum Habitatangebot innerhalb ihrer Aktivitätsgebiete. Die am häufigsten gewählte Habitatkategorie von Landfüchsen bei Nacht waren "Wiesen", "öffentliche Grünanlagen, Friedhofareale" und "Schrebergärten" am Stadtrand. Die 214 Tagesschlafplätze von Landfüchsen lagen mehrheitlich im Wald. Stadtfüchse wählten während der Nacht über erwarten häufig "Schrebergärten", "öffentliche Grünanlagen, Friedhofareale", während "Wohngebiete mit mittlerer bis hoher Besiedlungsdichte" und "Strassen und Plätze" am wenigsten genutzt wurden. Stadtfüchse waren in öffentlichen Grünanlagen mehr in der ersten und in Wohngebiete mit niedriger Bebauungsdichte mehr in der zweiten Nachthälfte aktiv. Wir schliessen daraus, dass Stadtfüchse dem direkten Kontakt zu Menschen ausweichen, indem sie zu Beginn der Nacht, wenn die Stadtbevölkerung im Freien noch aktiv war, häufiger Areale nutzten, die des Nachts abgeschlossen werden. In der zweiten Nachthälfte hielten sie sich dann häufiger in Wohngebieten auf, wenn die Störung durch Menschen nur noch sehr gering war. Stadtfüchse wählten ihre 615 Tagesschlafplätze in verschiedenen Habitatkategorien, wiederum wurden "Wohngebiete mit mittlerer bis hoher Bevölkerungsdichte" am wenigsten gewählt. Da "Wohngebiete mit mittlerer Bevölkerungsdichte" signifikant positiv mit der Aktivitätsgebietsgrösse korrelierten, schliessen wir, dass diese keine geeigneten Lebensraum für Füchse darstellen. Dies dürfte daran liegen, dass die Grünbereiche um diese Wohnsiedlungen – meist ausgedehnte Rasenflächen mit wenig Bäumen und Büschen – kaum Schutz und Deckung und nur beschränkte Nahrungsressourcen bieten. Wir diskutieren die Resultate in Bezug auf potentielle Empfehlungen für Gegenmassnahmen gegen die Bekämpfung von Zoonosen in städtischen Gebieten.

Manuskript D: Hohe Prävalenz von *Echinococcus multilocularis* bei urbanen Rotfüchsen (*Vulpes vulpes*) und Schermäusen (*Arvicola terrestris*) in der Stadt Zürich, Schweiz

In der Stadt Zürich wurden während einer Zeitspanne von 26 Monaten von Januar 1996 bis Februar 1998 388 Füchse gesammelt. Diese Füchse wurden in bezug auf Dünndarminfektionen mit *Echinococcus multilocularis* und anderen Helminthen untersucht. Die Prävalenz von *E. multilocularis* bei Füchsen, welche während des Winters gesammelt wurden, wies eine signifikante Zunahme von 47% in städtischen Gebieten zu 67% in angrenzenden ländlichen Gebieten auf, während die Prävalenz von anderen Helminthen für beide Gebiete gleich gross war. Saisonale Unterschiede der Prävalenz von *E. multilocularis* wurde nur bei urbanen subadulten männlichen Füchsen gefunden, welche signifikant seltener im Sommer im Vergleich zum Winter infiziert waren. Die Verteilung der Biomasse von *E. multilocularis*, erfasst in Anzahl Wurmindividuen pro Fuchs, wurde bei 133 infizierten Füchsen untersucht, welche zufällig aus den im Winter gesammelten Füchsen ausgewählt wurden. 10 dieser Füchse (8%) waren mit mehr als 10’000 Individuen infiziert und enthielten 72% der gesamten erfassten Wurm-Biomasse von *E. multilocularis* (398'653 Individuen). Bezüglich des Alters und des Geschlechts konnte bei diesen Füchsen kein signifikanter Unterschied gefunden werden, die Wurmbürden waren jedoch signifikant höher bei subadulten im Vergleich zu adulten Füchsen. *E. multilocularis*-Metazestoden wurden bei Schermäusen *Arvicola terrestris*, welche in einem Stadtpark von Zürich gefangen wurden, aufgrund morphologischer Merkmale und mit PCR identifiziert. Die Prävalenz bei den 60 Schermäusen, welche 1997 gefangen wurden, betrug 20%, bei den 75 Schermäusen, welche 1998 gefangen wurden, 9%. Protoscolices traten in zwei Fällen von Fängen aus 1997 auf. Wir diskutieren das mögliche Risiko für Infektionen beim Menschen in bezug auf einen in der Stadt etablierten *E. multilocularis*-Zyklus.

Manuskript E: Urbane Übertragung von *Echinococcus multilocularis*

In verschiedenen Europäischen Ländern wurde in den vergangenen 15 Jahren einen deutliche Zunahme der Populationen des Rotfuchses (*Vulpes vulpes*) verzeichnet, die in städtischen Gebieten besonders ausgeprägt war. Die Anzahl geschossener oder tot aufgefundener Füchse in der Stadt Zürich nahm zwischen 1985 und 1997 um das 20-fache zu. Diese Tatsachen waren Anlass für ein interdisziplinäres Projekt, in welchem ökologische und parasitologische Aspekte der Fuchspopulationen in urbanen Gebieten untersucht wurden.
Vorläufige ökologische Resultate zeigen, dass die Populationsdichten hoch und die Aktivitätsgebiete der Füchse klein sind in städtischen Gebieten. Die Prävalenz des Kleinen Fuchsbandwurms *Echinococcus multilocularis* nahm ab von 67% in den Naherholungsgebieten unmittelbar um das Siedlungsgebiet auf 47% im Gebiet innerhalb der Stadtgrenzen.

Um die Kontamination der städtischen Gebiete durch Eier von *E. multilocularis* zu schätzen, wurden Kotproben von Füchsen gesammelt und mit einem Koproantigen-ELISA untersucht. Die räumliche Verteilung der koproantigen-positiven Kotproben stimmte mit der Prävalenz, welche bei sezierten Füchsen gefunden wurde, überein. Bei Nagetieren, welche in den an den Siedlungsraum angrenzenden ländlichen Gebieten gefangen wurden, wurden *E. multilocularis*-Metazestoden mittels morphologischen Untersuchungen, EmG11-antigen ELISA und PCR festgestellt. Die Prävalenz bei 781 Schermäusen *Arvicola terrestris* war 9.2%. Bei 24 *A. terrestris* (3.1%) wurden vollständig entwickelten Protoscolices (14-240’000) nachgewiesen. Somit konnte ein urbanere Parasitenzyklus von *E. multilocularis* nachgewiesen werden. Dies bedeutet eine potentielles Risiko nicht nur für die städtische Bevölkerung sondern auch für Heimtiere wie Hunde und Katzen. Aufgrund dieser neuen epidemiologischen Situation und der damit zusammenhängenden wachsenden öffentlichen Sensibilisierung betreffend dieser Zoonose empfiehlt sich eine Evaluation lokaler Interventionen in den Lebenszyklus von *E. multilocularis*.

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The rise of urban fox populations in Switzerland

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Abstract

Since 1985 more and 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 of the urban fox population. In the adjacent rural areas, there also was a clear but less extreme increase of 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 consequences for the fox management and the treatment of zoonoses such as rabies and the alveolar echinococcosis.

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

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Introduction

Since 1985 fox populations have experienced a drastic increase in Switzerland (Breitenmoser et al. 2000). Apart from this development in rural areas, more and more foxes have been recorded from large Swiss conurbations and cities such as Zurich or Geneva. Game wardens and wildlife biologists 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 were 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 like 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 observed so far (Harris 1981a, Harris and Rayner 1986a). Similar fox population densities were nowhere recorded in urban areas outside of Great Britain, neither on the European continent nor in other parts of the distribution area 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 bag, 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 where fox population density is low.

The remaining 76% of the country form a 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 pages - 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 pages.

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 1661 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 few 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 bag 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 bag is recorded and the locations of dead foxes (shot or found dead) are known.
For the 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 death causes 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 towns with 10 000 – 5 0000 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 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 ur-

ban area, too (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 es 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. 2a), 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. 2a, 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 (1.26 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 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 in population densities in Swiss cities of today mainly to the fact that urban foxes have been a recent phenomenon and the development still goes 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 1986b).

Although red foxes generally avoid the direct presence of humans, some foxes have lived in the neighbourhood of people's 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 according to hunting statistics.

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 till 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 raise why the invasion of urban habitat started and which factors caused this new development.
According to Harris and Rayner (1986c), the colonisation of British towns already started in the 1930s. In 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 (1986b) 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 (1986b) 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 through foxes results in a similar phenomenon as it is 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 are 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 (1981b) 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 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 epidemio-

logical 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.

Acknowledgements

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Zusammenfassung

Die Entstehung urbaner Fuchspopulationen in der Schweiz

Seit Mitte der 1980iger Jahren 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 häufiger 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 stadtspezifische 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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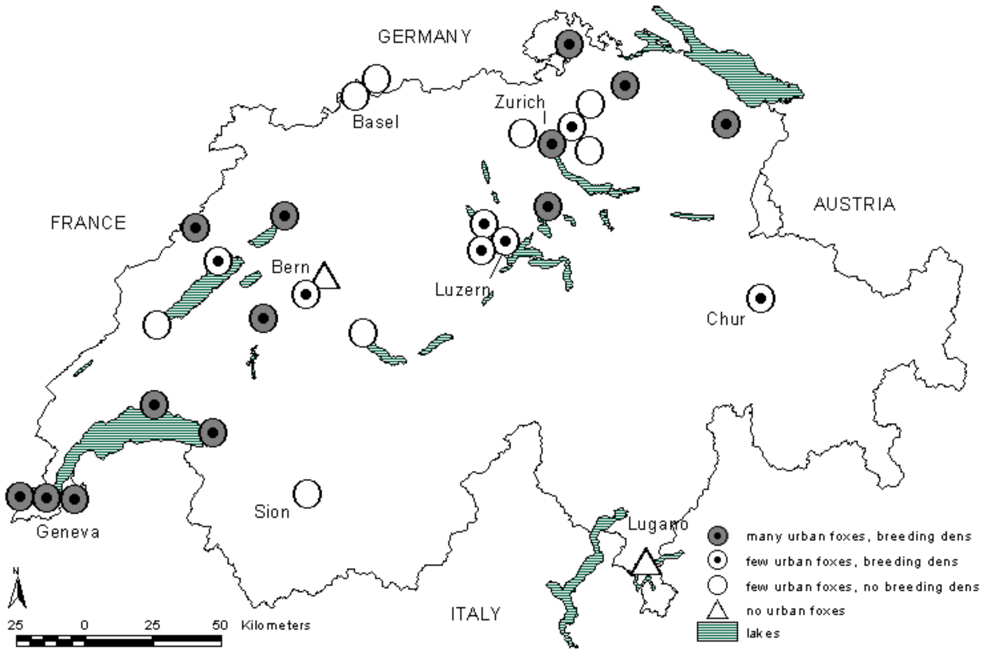

Fig. 1: Distribution of urban foxes in 30 cities with more than 20'000 inhabitants according to local wildlife management experts. Circles of adjacent cities are shifted to avoid overlapping.

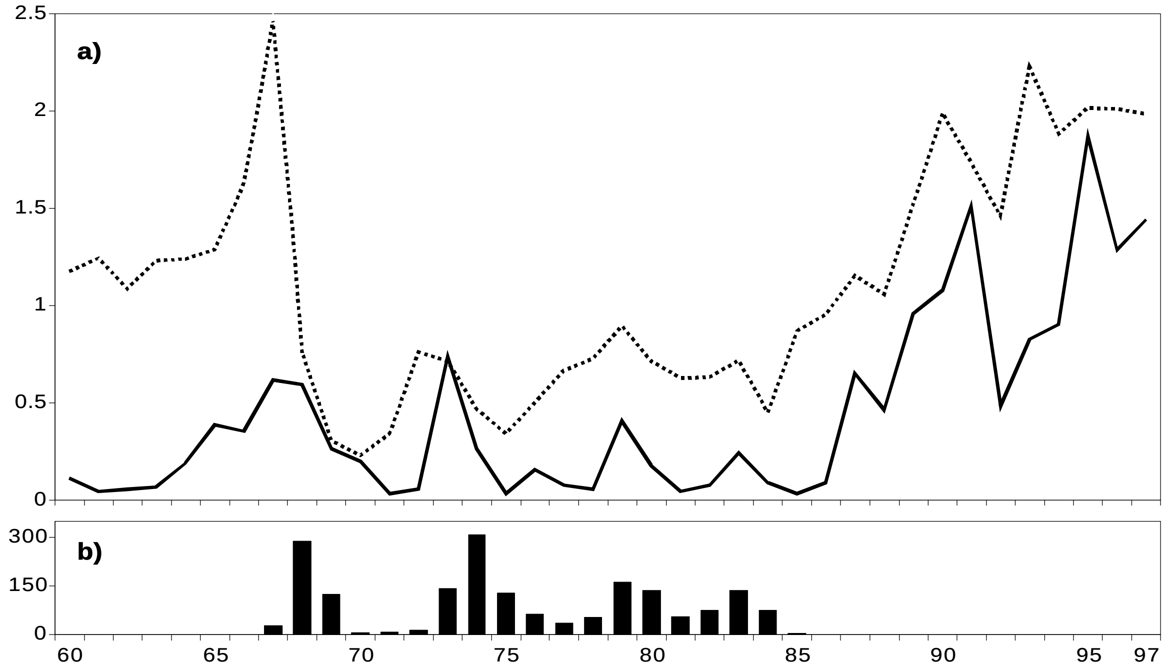

Fig. 2: a) Hunting indicator of population density (HIPD) for the city of Zurich (straight line) and the canton of Zurich (dotted line) from 1960 to 1997. b) Rabies cases in the canton of Zurich from 1960 to 1997.

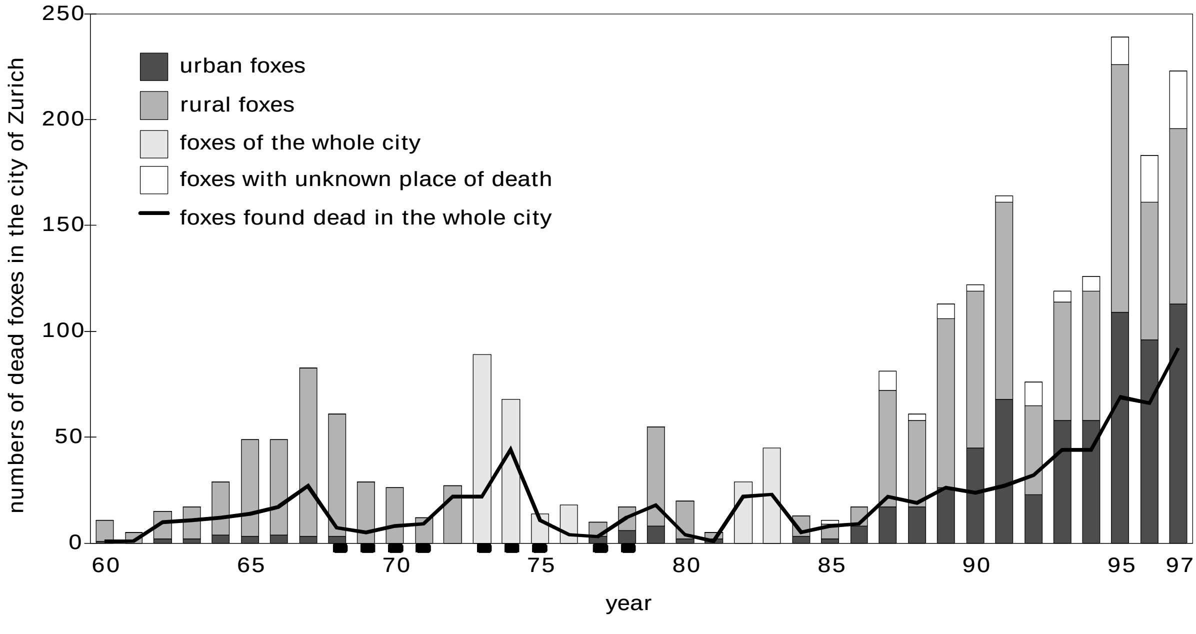

Fig. 3: Fox mortality (animals shot or found dead) in urban and rural areas in the city of Zurich from 1960 to 1997. Of the years 1973 – 1976 and 1982 - 1983 there are only total numbers of dead city foxes available (light grey bars). No precise locations of death are available of some recorded foxes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

Tab. 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	

Tab. 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)
Where are the urban foxes observed?	whole of the city	13	4
	outskirts only	0	11
Are there any urban breeding dens?	yes	13	7
	no	0	8
Since when have urban foxes been present?	1985-1999	10	7
	< 1985	3	3
	not known	0	5
How do you judge the trend of the urban fox population?	increasing	8	5
	stable	2	10
	decreasing	3	0

Tab. 3: The increase of numbers of recorded dead foxes within the city border 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	Coefficiant	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	Coefficiant	R^2	p<=
Shot	4.842	0.46	0.01
Found dead	0.831	0.74	0.001

Spatial organisation of foxes in the recently colonised city of Zurich, Switzerland

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Abstract

In Switzerland red foxes *Vulpes vulpes* (Linneaus, 1758) have colonised urban areas since the 1980s. In the city of Zurich, 13 female and 9 male foxes were radio-tracked between December 1996 and June 1999. During the same period, breeding dens were documented in an area of 6.7 km^2. From January 1996 to December 1999, 716 foxes shot or found dead were collected within the city area and 661 of them were dissected and age, sex and reproductive status was recorded.

There were no significant differences in home range size neither between resident females and males, nor between seasonal home range sizes, the home range size of females being 28.8 ± 22.7 ha, of males 30.8 ± 11.0 ha. Three male foxes, so-called floaters, had 3 to 11.2 times larger home ranges and larger mean travel distances in 15 min. (162 m ± 19.4) than the other males (101 m ± 20.2). The tracked foxes were classified into “urban” or “rural” according to the amount of urban area within their home ranges. There was an obvious separation between rural and urban foxes: although the urban border was within theoretical reach of all tracked foxes, it was only rarely crossed. There was clear evidence for the existence of family groups: post-mortem data with 29 % non-reproducing females, largely overlapping home ranges in resident foxes, and direct observations at breeding dens. According to the number of breeding dens in the study area, the number of foxes observed at breeding dens and the post-mortem data we estimated the fox density in the study area to be 9.8 – 11.2 adult foxes per km^2. As an explanation for the presence of foxes in human settlements we discuss two alternative hypotheses, which focus either on the population pressure in the rural areas or on the specific behavioural adaptations of urban foxes. The results of our study rather support the latter, the Urban Island Hypothesis.

Key words: family group, invasion, population density, *Vulpes vulpes*, urban habitat.

Introduction

Fox populations in Continental Europe have undergone extreme changes in densities in the second half of the 20th century (Goszczynski 1989, Vos 1993, Chautan, Pontier & Artois 2000), by a severe rabies epizootic starting at the eastern border of Poland at the end of the 1930s and spreading through Central and Western Europe in the following decades (e.g. Bögel, Moegle, Knorpp, Arata, Dietz & Diethelm 1976, Steck & Wandeler 1980). The rabies epizootic reached Switzerland in 1967 and resulted in a drastic decrease of the fox populations, as can be seen in the Swiss hunting records (Zanoni, Kappeler, Müller, Müller, Wandeler, & Breitenmoser 2000). Due to successful oral vaccination campaigns against rabies in foxes, the fox population has begun to recover again since 1984 (Breitenmoser, Müller, Kappeler & Zanoni 2000). Today, Switzerland is officially "rabies free" and the fox abundance is considerably higher than before the outbreak of rabies (Breitenmoser et al. 2000, Breitenmoser & Müller, submitted). A similar development was recorded for the whole of Western Europe (Chautan et al. 2000).

Parallel to the re-increase of the population in "traditional" rural fox habitat, a new phenomenon was observed in large Swiss cities: foxes living in urban areas (Gloor, Bontadina, Hegglin, Deplazes & Breitenmoser 2001). In Zürich, the largest conurbation in Switzerland, the actual colonisation of urban areas by foxes started around 1985 and the urban fox population has since increased. Today foxes live in all 30 Swiss cities with more than 20'000 inhabitants (Gloor et al. 2001; pers. obs.).
Until the 1970s and early 1980s, urban foxes were mainly known from Great Britain (Teagle 1967, Beames 1969, 1972, Page 1981) and thought to be a British phenomenon (Harris 1977, Macdonald & Newdick 1982). Foxes in British cities reached high population densities nowhere else observed (Harris & Smith 1987) indicating that cities can provide most suitable habitat to foxes.

The colonisation of urban areas by foxes includes the possibility of an introduction of diseases (e.g. zoonoses) in the urban area and it raises questions concerning new potential public health risks (Hofer, Gloor, Müller, Mathis, Hegglin & Deplazes 2000), principally with respect to two zoonoses with the fox as main host and vector: alveolar echinococcosis caused by the small fox tapeworm *Echinococcus multilocularis* (Stieger, Hegglin, Schwarzenbach, Mathis & Deplazes 2002, Hegglin in prep.) and sylvatic rabies (Trewhella, Harris, Smith & Nadian 1991, Saunders, White & Harris 1997, Wilkinson & Smith 2001). Consequently, the increased observation of foxes in Zurich has lead to a growing number of people who feel ambivalent about urban foxes. Some are fascinated by this wild carnivore in their

neighbourhood, others or afraid of them because of zoonoses (Bontadina, Contesse & Gloor 2001). Many people believe that the foxes intrude from the rural vicinities and are not able to live within the urban area.
In fact, the simultaneous emerging of urban foxes throughout Switzerland along with the increasing fox population in rural areas could indicate that the rural development resulted in an increasing population pressure for foxes to colonise new, less profitable habitats and therefore initiated the immigration of foxes into the cities (Population Pressure Hypothesis PPH, Gloor et al. 2001).
On the other hand, the British phenomenon shows that cities can provide a highly suitable fox habitat (Doncaster, Dickman & Macdonald 1990, Smith & Harris 1991). Therefore we postulate the alternative Urban Island Hypothesis UIH (Gloor et al. 2001). According to the UIH, urban foxes have adapted to specific urban conditions and consequently 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.
In order to find out whether foxes in urban areas are just out-competed rural foxes or whether there exists an independent fox population in the urban area, we tested the following predictions:
a) Spatial organisation: There is no strict division between rural and urban foxes, and foxes commute between rural and urban areas (PPH) or there is a segregation between foxes adapted to urban areas and foxes living in adjacent rural areas (UIH).
b) Social organisation: Foxes in Swiss cities live solitary or in pairs (PPH) as they do in less profitable habitat or they are organised in family groups (UIH) as they are in suitable habitat.
c) Population density: The population densities of foxes in Swiss cities are lower than in rural areas (PPH) or higher because of the access to profitable resources (UIH).

The objectives of the study were (1) to find out the distribution of foxes in an urban district of Zurich, (2) to analyse the spatial and social organisation of the urban foxes by means of radio-tracking and (3) to estimate the density of the local fox population by breeding den counts and post-mortem data.

Methods

The study area was situated in the conurbation of Zürich, where about one million inhabitants live. The political community of Zurich (360 000 inhabitants) covers an area of 92 km^2 consisting of 53 % urban area, 24 % forest, 17 % agricultural areas and 6 % water. We refer to forest and agricultural areas as rural or peri-urban. Zürich is a game sanctuary where three game wardens are exclusively responsible for wildlife management.

The study area was the roaming area of the radio-tagged foxes of about 11 km^2 and was situated in the western part of Zürich, on 410 to 871 m above sea level, with 6 km^2 of urban zone below and 4 km^2 of woodland above 490 m (Fig. 1). About 1 km^2 were pastures and allotment gardens at the urban border. The urban part of the study area was a typical urban zone with 47 % built over areas (streets, houses etc.), 53 % "green", open areas (gardens, parks etc.), 62 % residential areas and a human population density of 97 persons/ha (all information from the statistical year book of the City of Zurich 2000).

We defined the city border as the line following properties with buildings in daily use not more than 100 m apart from each other.

Foxes were captured in box-traps at 9 sites (3 places outside the city in a distance of 220 to 336 m to the city border, 6 places within the city in a distance of 546 to 1568 m to the city border) near fox tracks. We used traps of two sizes (1.8 x 0.5 x 0.5 m and 1.5 x 0.4 m x 0.4 m x 1.5 m). The traps were baited and permanently monitored by means of trap transmitters (Karl Wagener, Telemetrie-Material, Köln 1, Germany).

Captured foxes were anaesthetised by an intra-muscular injection of 1.0 ml Medetomidin (Domitor) and 0.3 ml Ketasol-100. The foxes were measured, fitted with radio collars (Wagener, BRD; Biotrack, GB; AVM, USA), and tagged with numbered plastic ear tags (Rototag; Dalton Supplies Ltd., Hauptner, Wallisellen, Switzerland). The age of the foxes was estimated in year classes by their tooth wear (Harris 1978). Before the release of the foxes, we injected 1.0 ml Atipamezol (Antisedan).

We radio-tracked the foxes using TRX-1000 (Wildlife Materials, Inc., Illinois, USA), and modified YEASU FT-290 receivers (adapted by Karl Wagener, Germany) with hand-held H-aerials. We tracked foxes either continuously from 21:00 to 5:00 (MEZ), or divided the night in two periods from 21:00 to 1:00 and 1:15 to 5:00 and tracked individual foxes in two different nights. Locations were taken every 15 min. and the following data were tape-recorded: activity (fox active or passive), displacement since last location (yes or no), location of the fox or two bearings and location of the observer („homing in", White & Garrott 1990). Because of the abundance of streets and paths in the study area, the distance to the observed animal was always less than 200 m. Therefore it was possible to estimate the foxes locations at a high level of accuracy.

Daytime rest sites were weekly located by radio-tracking during day light.

Home ranges were calculated on a seasonal basis, as they may change in size (White, Saunders & Harris 1996) or drift in time (Doncaster & Macdonald 1991). We divided the year into three seasons which were defined as follows: spring, March – June, to coincide with birth and lactation; summer/autumn, July – October, to coincide with growth and independence of cubs; winter, November – February, to coincide with the main dispersal period and mating.
All active fixes, but only the first passive fix after a displacement were used for home range calculations, because inactive fixes during the nightly resting periods have an undue influence on measures of internal range use (White et al. 1996). Only data from at least three nights and 60 active fixes per season and at a minimum of four hours of radio-tracking per night were considered to compute seasonal individual home ranges.

We used the minimum convex polygon method (MCP) to determine home range size to assure comparability to other studies (Harris, Cresswell, Forde, Trewhella, Woollard & Wray 1990). Additionally, we estimated mutual home range overlap and overlap with the city border by means of 90 % Kernel analysis (90 % KERNEL) calculated by the ArcView AnimalMovementExtension (Hooge & Eichenlaub 1997, 1999), using a smoothing parameter (h) of 50 m. The home range overlap of two foxes (dyad) was expressed as the percentage of the total combined home range area (MCP and 90% KERNEL respectively) of these two foxes (e.g. total combined home range = home range of fox A $\cup$ home range home range of fox B; home range overlap = A's home range $\cap$ B's home range) (White et al. 1996).
In all analyses, individual foxes were considered as independent units. In ANOVA design, foxes were calculated as blocks. If data of several seasons of a fox were available, we computed arithmetic means, except in the case of M02, which changed his status from floater to resident. In this case he behaved so differently in two seasons compared to the third season, that he was treated as two independent units (M02f=M02 as floater, M02r=M02 as resident).
The mean distance between two consecutive fixes was calculated for each fox to estimate the mean distance travelled in 15 minutes.

From 1997 to 1999 we recorded all breeding dens in the total area (MCP) of the resident foxes (11 females, 6 males) of 6.7 km^2 (Fig. 1). Dens were found by radio-tracking, reported by resident people or discovered by the local game warden. We also consulted managers of parks, swimming pool areas and cemeteries and searched forest areas for evidence of litters of cubs by transect walks in May and June each year. We assumed the number of active breeding dens in the study area to be equal to the number of family groups. A family group consisted of one pair of reproducing foxes and, according to observations at breeding dens, additional non-breeding individuals.

As a control we estimated the adult fox density in the study area based upon the data from the known mortality, again using the number of breeding dens of 1999 as a calibration value. From 1996 to 1999, all foxes shot or found dead were collected by the local game wardens and subsequently dissected. Based on placental scar counts (Harris 1979, Lindström 1994) we decided whether a female was barren or had bred in the previous spring. The number of placental scars is difficult to count under certain circumstances. This is true mainly at the end of the reproductive year, since the scars are fading out. We therefore excluded females shot or found dead in February and March from analysis with respect to placental scars. We calculated the population density by adding the proportion of barren vixens for the study area to the minimum population density estimation (one reproducing pair per breeding den), and including additional males according to the ratio of females:males found in the total record of dead foxes.

Results

21 adult foxes were captured and radio-tagged (Tab. 1). The data of 11 females and 8 males were used for home range analyses. Two foxes (F08, M09) were excluded from these analyses as their number of active fixes was too small.

Home ranges of resident foxes

Mean seasonal home ranges (MCPs) of females varied from 5.8 ha to 82.6 ha and of males from 17.1 ha to 191.4 ha (Tab. 2). There were no significant differences in home range sizes (MCP and 90 % KERNEL calculations) neither between resident females and resident males, nor between seasonal home range sizes (two way ANOVA, with foxes as blocks, F(sex) = 0.000, d.f. = 1, p = 0.998, F(season) = 0.299, d.f. = 2, p=0.746) (Tab. 3), the mean home range size of females being 28.8 ± 22.7 ha (n=18, data averaged per fox) and the mean home range size of males being 30.8 ± 11.0 ha (n=10, data averaged per fox).

Home ranges of floating foxes

Three male foxes had 3.0 to 11.2 times larger home ranges (averaged MCPs) than the other male foxes. Additionally, their mean travel distance in 15 min. was larger

(162 m ± 19.4, n=3) than the travel distances of resident male foxes (101 m ± 20.2, n=6) (Fig. 2). They crossed the home ranges of many resident foxes. According to their spatial behaviour and in accordance with descriptions in other studies (Macdonald 1983, Zimen 1984, Meia & Weber 1995) we called these three foxes floaters. Two of these floaters were one year old when tagged, the third one (M02) however, was already 2 years old. He was a floater for two seasons (winter 1996/97, summer/autumn 1997), but he changed his spatial behaviour in the third season (spring 1998), when he established himself next to the home range of M03 and became a resident fox.

Evidence for family groups

Resident foxes caught at the same trap sites were during the field work also occasionally observed at the same breeding den sites and obviously belonged to the same family group. Such individuals also showed a larger home range overlap among themselves (14.4 to 55 %) than with foxes of neighbouring family groups (1.5 to 5.8 %) (Tab. 4). According to their home range overlap and observations at breeding dens we assigned the 17 radio-tracked resident foxes to 8 family groups (Tab. 5) with 3 to 4 individuals. We had no evidence, that there was more than one resident male fox per family group.

Urban foxes and rural foxes at the urban border

We classified the radio-tracked foxes in two groups according to the amount of urban area within their MCP home ranges. Foxes with more than 50 % of urban area are “urban foxes” (70.5 – 100 %), all others “rural foxes” (0 – 31.7 %). 12 of 22 radio-tracked foxes stayed either totally within the urban area (n=10) or totally outside the urban area (n=2). The other 10 foxes (5 females and 5 males) showed home range overlap with the urban border (Tab. 6), however only to a small extend: 4 foxes stayed mainly within the urban area, 6 foxes stayed mainly within the rural area (Fig. 1b-d). The urban foxes had 38 of 40 daytime rest sites within the urban area, whereas the rural foxes mostly used daytime rest sites in the peri-urban area (86 of 89; Tab. 6).

Fox population density in the study area

The total area (MCP) of the resident foxes (11 females, 6 males) measured 6.7 km^2 (Fig. 1). This area contained 30 dens used for breeding between 1997 and 1999. 23 of these breeding dens were occupied in 1999. In that year, we had no evidence for more than one breeding den per family group. The density of fox family groups consequently was 3.43 groups per km^2.

From the fieldwork, we estimated a minimum of 3.13 adult foxes per family group (Tab. 5). This number contained one breeding male, one breeding female and additional non-breeding females. If we add the three known floaters to the estimated number of foxes in the study area, the average density of adult foxes would have been 11.17 per km^2 in 1999.

As a control we estimated the adult fox density in the study area based upon the data from the known mortality, again using the number of breeding dens of 1999 as a calibration value. Between January 1996 and December 1999, there were 758 foxes (367 females, 379 males, 12 of unknown sex) shot or found dead. These foxes were collected and dissected. 131 of the 302 female foxes of known age were of breeding age. From these foxes 29 females from February and March were excluded for placental scar analysis and of 30 females placental scar counts were not able to be carried out. Based on placental scar counts, 21 vixens (29.2 %) were barren, 51 females (70.8 %) had placental scars. Therefore, the ratio of breeding to non-breeding females was 1:0.41. If we assume the data for the whole city to be representative for the study area, the adult fox population in the study area consisted of 23 breeding males, 23 breeding females and an additional 9.4 non-breeding vixens. If we take floating males into account and assume, that the ratio of females:males was 1:1.03 (as the post-mortem data indicated), we estimate 32.4 females and 33.4 males living in the study area, which corresponded to 9.8 adult foxes per km^2.

Discussion

Foxes are a recent addition to the urban fauna in Switzerland. The development begun in the middle of the 1980s after the decline of rabies in Switzerland (Gloor et al. 2001). Despite this, from a biological point of view, new development of the past 15 years, foxes not only used the outskirts of the city but also intruded into overbuilt areas far from the urban border. Many of the radio-tagged foxes lived completely within the urban area. Most foxes observed in the city were not only roamers from adjacent rural areas, but real urban foxes.

Until the 1970s and early 1980s, urban foxes were mainly known from Great Britain. They colonised urban areas during the interwar times in the 1930s (Teagle 1967; Beames 1969, 1972; Page 1981) when land prizes were low and therefore new residential suburbs were built consisting of privately owned, low density housing with gardens and quiet streets. It was in those urban areas that the highest fox densities ever were found in the 1970s, 1980s and 1990s (Harris 1981a, Harris & Rayner 1986, Baker, Funk, Harris & White 2000). Because similar urban fox population densities were nowhere else recorded outside of Great Britain, urban foxes

were thought to be a British phenomenon (Harris 1977; Macdonald & Newdick 1982).
However, since the 1980s urban foxes have been recorded not only from Switzerland but also from other parts of the distribution area of the fox, e.g. from Oslo, Norway (Christensen 1985), Arhus, Denmark (Moller Nielsen 1990), Brussels, Belgium (B. Brochier, pers. comm.), Stuttgart, Germany (T. Romig, pers. comm.), Toronto, Canada (Adkins & Stott 1998) and Sapporo, Japan (K. Uraguchi, pers. comm.), indicating that foxes started to colonise cities in other parts of the world as well.

In Zurich, mean home range sizes of 29 - 31 ha were small compared to home ranges in rural areas which tend to be much larger, and range up to 500 to 2000 ha in farmland in Ontario, Canada (Voigt & Macdonald 1984; see overview in Cavallini 1996 and Adkins & Stott 1998). The numbers found in Zurich were comparable with figures reported from British cities: 40 ha (Macdonald 1981) and 45 ha (Doncaster & Macdonald 1991) in Oxford, 45 ha (Harris 1980) and 25 - 30 ha (White et al. 1996) in Bristol, and 42 - 460 ha in Edinburgh (Kolb 1984). The home range sizes of foxes reported from Toronto, Canada, were between 49 and 63 ha (Adkins & Stott 1998), so comparable to home ranges from the British and Swiss studies.

According to Artois (1989), home range size of foxes mainly depends on food availability and according to Macdonald (1983) of resource dispersion (mainly of food resources). As we found no significant difference of home range size of resident foxes between sexes or between seasons, we hypothesise that the food availability in our study area was either stable or abundant. In fact, a survey about potential anthropogenic prey in Zurich such as scavenged items from compost heaps and garbage bags or berries and fruit not harvested by people, indicated, that urban areas can provide rich food resources (Contesse, Hegglin, Gloor, Bontadina & Deplazes submitted). This was in accordance with studies in England (Harris 1981b, Doncaster et al. 1990, Saunders et al. 1993, Baker 2000), which showed, that a diverse and abundant food base for foxes was supported in urban ecosystems and Smith & Harris (1991) stated that urban environments may be both stable and highly productive in terms of fox population density.

In Bristol however, male foxes had significantly larger home ranges than females (males in spring/summer/autumn: 30.1 ± 4.2 ha, females: 25.1 ± 1.9 ha) and males used larger home ranges during winter (65 ± 18.4 ha), when they made excursions to have the possibility to mate with different females (White et al. 1996), indicating, that home range size can also be influenced by social factors. We assign the lack of

a significant difference between females and males in Zurich to the wide extend of variation of individual home ranges (females: 28.8 ± 22.7 ha, males: 30.8 ± 11.0), which could be the result of an uneven distribution of food resources (Macdonald 1981). Analyses of habitat availability and habitat associations of the foxes in the study area might clarify this assumption.
An alternative explanation would be that Zurich is still in the status of being colonised. Baker et al. (2000) showed in a study about the spatial organisation before and during an outbreak of sarcoptic mange, that home ranges of foxes increased after the neighbouring fox groups disappeared and these increases of range were not associated with a decline in the availability of food in the original home range. They conclude, that resource dispersion and availability are not the only factors affecting home range size, when a population has not yet reached its carrying capacity.

A stable seasonal situation as far as home range size was concerned despite environmental changes was found by Meia & Weber (1995) in their study area in the Jura Mountains, what they assigned to abundant food resources. They furthermore did not find different home range sizes for females and males. The home ranges in this area were small and comparable with figures of Zurich, although they obviously came from very different habitats.

According to the resource dispersion hypothesis (Macdonald 1983, Carr & Macdonald 1986), animals choose a minimum territory size for periods of food scarcity and share it with conspecifics when food is abundant. Von Schantz (1984) suggested that the evolution of kinship-groups in the red fox was induced by temporary resource surplus within the territories. Therefore, small home ranges and fox family groups both point to abundant food resources.
In Zurich we not only found small home ranges but also clear evidence for the existence of family groups, consisting of a pair of reproducing foxes and additional barren females. Besides there were a number of floating, probably non-reproducing males present in the study area. Only few authors gave detailed information about such animals, so-called floaters, itinerants or nomadic foxes (Zimen 1984, Zabel & Taggart 1989, Lovari, Valier & Ricci Lucchi 1994, Meia & Weber 1995, Cavallini 1996), and often they were excluded from further analyses (e.g. Harris 1980, von Schanz 1981, Goszczynski 1989, Doncaster & Macdonald 1991). However the neglect of floating individuals can lead to an underestimation of fox density.

The fox population density in our study area was estimated to be relatively high with 3.43 family groups per km2 and 7.4 to 11.2 adult foxes per km2. The first estimation method based on observations only and therefore the number of floaters

was probably underestimated as the female:male ratio was near to 1 in the post-mortem data. On the other hand, the second estimation was based mainly on the post-mortem data of the whole city. The percentage of non-reproducing females observed at the eight studied breeding dens was 56.5 %, for the whole city 33 %. This points to a especially high fox density in the study area. However our density estimation, although cautious, was similarly high compared to density estimations of other urban areas.
In the rural suburbia on the outskirts of Oxford, Great Britain, fox density was recorded to be as many as 10 adult foxes per km2 (Voigt & Macdonald 1984). Harris (1981a) and Harris & Rayner (1986) published fox densities from nine English cities, ranging from 0.19 to 2.06 fox family groups per km2. In Bristol mean number of adult foxes per family group was 3.39, and mean density was 6.2 adult foxes per km2 with local densities of up to 5 family groups per km2 (Harris & Smith 1987). In 1994 the observed minimum group size in an area in Bristol was 6.57 adult foxes per group or 32.85 adults per km2 (Baker et al. 2000), the highest fox population density recorded so far. The comparison of these figures with the findings from Zurich indicates that the density in our study area in Zurich was similar to the higher densities reported from British cities in the 1970s and 1980s and exceeds today the densities of most rural areas by far. Nevertheless, the exceptionally high densities of some areas in Bristol with 5 family groups per km2 are not yet reached in Zurich.

However, looking at the trend of fox populations in the city and in the canton of Zurich, the country surrounding the city of Zurich, (Gloor et al. 2001), we anticipate a further increase. The number of foxes found dead in the Canton of Zurich has increased by almost 10 times from 204 in 1984 to 1137 in 2000 (numbers without those of the city of Zurich, AEFL 2001). But the development of the fox population in the city and in the rural surroundings must not follow the same trend, as the populations seem to be clearly separated according to a genetic survey of foxes of the city of Zurich and foxes from close-by rural areas from the region of Zurich (Wandeler, Funk, Largiadèr, Gloor & Breitenmoser, submitted). The results indicated that the urban area was settled by a small number of individuals from adjacent rural areas and that there has been little immigration or little genetic input from immigrants since. Moreover there was a clear segregation between radio-tracked foxes in urban and adjacent rural areas in Zurich. Although the urban border was within theoretical reach of all radio-tracked foxes because they can travel several kilometres each night (Goszczynski 1989, Adkins & Stott 1998), the radio-tracked resident urban foxes remained in urban areas and only floaters and one yearling female made occasional excursions into rural, forested areas. Foxes on the rural side of the

city border stayed in the rural part and did not intrude to a large extent into residential areas.
A similar situation as far as the rural foxes in Zurich were concerned was found in Toronto, Canada (Adkins & Stott 1998) where the foxes studied were primarily found in a bushy ravine crossing a golf courses and park land. Foxes intruded in low-density housing areas near the border of the urban area, but avoided adjacent medium–density housing areas. This indicates that these animals may not have been as habituated to urban habitat as described from Great Britain and Switzerland. The results of Zurich however are in contrast to findings of Macdonald & Newdick (1982), who suggested that there was no strict division between rural and urban foxes, because they had radio-tracked foxes which regularly commuted between urban and rural areas.

We conclude that most of our predictions derived from the Population Pressure Hypothesis can be rejected by the results of the study. Our findings rather support the Urban Island Hypothesis UIH.

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Tab. 1: Data of 12 female and 9 male foxes radio-tracked in the study area.

st. = status: r = resident foxes, f = floaters (non-resident); cp = capture place: u = within urban border, pu = peri-urban, outside the urban border; t. = tracked; RP = day-time rest site.

Fox	st.	cp	age [y]	period tracked	nights t.	seasons t.	active fixes	RP
F01	r	pu	2-3	30/6/98 – 24/6/99	8	1	204	27
F04	r	u	2	15/6/97 – 24/6/99	19	2	296	22
F06	r	u	1	17/1/97 – 26/6/99	21	4	353	31
F08[1]	r	u	2	2/4/98 – 27/7/98	(2)	(1)	(44)	(2)
F10	r	pu	1	30/6/98 – 29/10/98	4	1	113	9
F12	r	pu	2	28/6/98 – 6/2/99	8	1	196	12
F15	r	pu	4	9/7/98 – 1/4/99	6	1	116	28
F18	r	pu	1-2	4/1/99 –22/6/99	8	2	149	8
F20	r	u	2-3	27/10/98 – 14/6/99	9	2	180	14
F41	r	u	<1	2/1/99 – 19/3/99	9	1	202	2
F51	r	u	<1	29/12/98 – 1/7/99	9	2	188	6
F61	r	u	1-2	18/5/99 – 24/6/99	8	1	186	5
M01	r	u	>3	11/12/96 – 3/2/97	5	1	91	17
M02	f/r	u	>2	16/1/97 – 1/7/98	12	3	189	13
M03	r	u	>3	13/1/97 – 25/5/98	8	1	101	15
M05	f	u	1	6/4/98 – 11/1/99	10	2	206	18
M09[1]		u	>3	16 – 30/10/98	(1)	(1)	(27)	(2)
M11	r	u	1.5	10/3/98 – 21/12/98	9	2	203	22
M19	f	u	<1	7/12/98 – 26/6/98	20	2	344	11
M22	r	pu	3	21/12/98 – 24/6/99	8	1	197	9
M31	r	pu	2	20/7/98 – 3/6/99	13	2	319	36
data of all tracked foxes					199	34	3904	309
data of 19 analysed foxes				11/12/96 – 1/7/99	194	32	3833	305

[1] Data of foxes F08 and M09 were not used for further home range analyses as the number of active fixes was too small.

Tab. 2: Seasonal home range estimates and total home ranges for 11 resident female, 6 resident male, and 3 floating male foxes.

spring = March – June; sum/aut = summer/autumn = July – October; winter = November – February. total hr = home ranges of the whole radio-tracking season. M02r = M02 as a resident fox (spring 1998), M02f = M02 as a floater (summer/autum 1997; winter 1997/98).

		MCP (ha)				90% KERNEL (ha)			
	Fox	**spring**	**sum/aut**	**winter**	**total hr**	**spring**	**sum/aut**	**winter**	**total hr**
Females	F04		5.9[a]		9.3		6.3[a]		5.7
	F61	7.0			7.0	4.7			4.7
	F20	5.0		10.3	10.3	4.7		10.0	8.3
	F10		17.4		17.4		13.1		13.1
	F15		20.7		20.8		9.7		11.2
	F41			27.1	27.1			5.4	5.4
	F18	28.1		27.1	40.1	9.2		4.1	11.3
	F12		28.5		33.6		17.4		6.5
	F01		42.5		42.5		12.3		14.9
	F06		48.1[b]	51.6[c]	95.1		14.9[b]	10.6[c]	23.5
	F51	73.5		91.7	123.6	18.1		5.3	8.4
Males	M11		22.8	11.3	25.0		9.1	13.3	13.1
	M03			20.6	25.4			18.6	14.8
	M02r	28.1			28.1	12.3			12.3
	M01			34.6	34.6			13.9	13.9
	M22	40.4		36.7	50.7	7.7		15.5	11.0
	M31	50.3	68.2	19.5	83.1	19.7	6.3	14.4	14.5
Floaters	M19	85.0		189.5	222.8	12.2		10.8	8.4
	M05		264.2	111.5	281.6		42.1	24.4	32.6
	M02f		231.7	151.0	508.3		11.4	16.5	17.7

[a] F04: 1997 mcp= 6.9 ha, 90% Kernel= 7.4 ha; 1998: mcp= 4.8 ha, 90% Kernel=5.2 ha
[b] F06: 1997 mcp= 46.9 ha, 90% Kernel= 7.7 ha; 1998: mcp= 49.3 ha, 90% Kernel=22.1 ha
[c] F06: 1997/98 mcp= 24.2 ha, 90% Kernel= 14.2 ha; 1998/99: mcp= 78.3 ha, 90% Kernel=6.9 ha

Tab. 3: Home range estimates for resident female and male foxes and floating male foxes radio-tracked per season.

Values are given as the mean ± SD. Individual foxes are averaged per each season. Numbers in brackets are numbers of individuals.

		seasonal home ranges (ha)		
		spring March - June	summer/autumn July - September	winter October - February
females	MCP	28.4 ± 31.8 (4)	27.2 ± 15.9 (6)	41.5 ± 31.6 (5)
	90% KERNEL	9.2 ± 6.3 (4)	12.3 ± 3.0 (6)	7.1 ± 3.0 (5)
males	MCP	39.6 ± 11.1 (3)	45.5 ± 32.0 (2)	24.5 ± 10.8 (5)
	90% KERNEL	13.2 ± 6.1 (3)	7.7 ± 2.0 (2)	15.1 ± 2.1 (5)
floaters	MCP	85.0 (1)	142.0 ± 22.9 (2)	150.7 ± 39.0 (3)
	90% KERNEL	12.2 (1)	26.8 ± 21.7 (2)	17.2 ± 6.8 (3)

Tab. 4: Overlap of home ranges of resident foxes.

fg= family group. Same breeding den = foxes were observed at the same breeding den. The overlap is calculated as percentage of total combined home range area of each dyad (home range overlap of fox A and fox B = A's home range $\cap$ B's home range). sp. = spring; s./a. = summer/autumn; w. = winter.

					overlap of	
	dyads	same place of capture	same breeding den	season	MCP [%]	90% K. [%]
same fg	F06-M11	x	x	w. 98/99	14.4	20.9
	F10-F12	x	x	s/a 98	22.1	22.0
	F01-M31	x	x	s/a 98	23.7	0.0
	F06-F51	-	x	w. 98/99	31.0	0.9
	F06-M11	x	x	s/a 98	31.6	17.8
	M22-F18	x	?	sp. 99	55.0	38.5
adjacent fg	M22-F51			sp. 99	1.5	0.0
	F18-F51			sp. 99	5.1	0.0
	M31-M22			w. 98/99	5.8	0.0

Tab. 5: 8 family groups as revealed by radio-tracking and observations at breeding dens from July 1998 to June 1999.

family group	tracked foxes	additionally observed foxes at breeding den	Least number of adult family members
1	F10, F12	breeding female, 1	4
2	F15, F20	1	3
3	F01, M31	F99	3
4	F61, F08	M09	3
5	F41	breeding female, 1	3
6	F04	1	2
7	F06, F51, M11	1	4
8	F18, M22	1	3
	mean number of adult family members		3.13

Tab. 6: Use of urban and peri-urban areas by radio-tracked foxes.

10 of 22 radio-tracked foxes had both, urban and peri-urban areas within their MCPs. 12 of 22 radio-tracked foxes stayed either totally within the urban area (n=10) or totally outside the urban area (n=2). RP = daytime rest sites.

			overlap with urban area [%]		
		n season	MCP	90% KERNEL	total RP/urban RP
urban foxes	F51	1	99.6	100.0	5/5
	M19	1	97.9	100.0	6/6
	M05	1	95.2	99.9	10/10
	M02f	2	70.5	93.5	13/11
rural foxes	F18	2	31.7	12.2	9/3
	M22	2	20.8	19.8	9/1
	M31	3	4.1	11.0	39/0
	F12	1	14.0	6.9	6/0
	F01	1	5.2	0.0	17/0
	F10	1	0.0	0.0	9/0

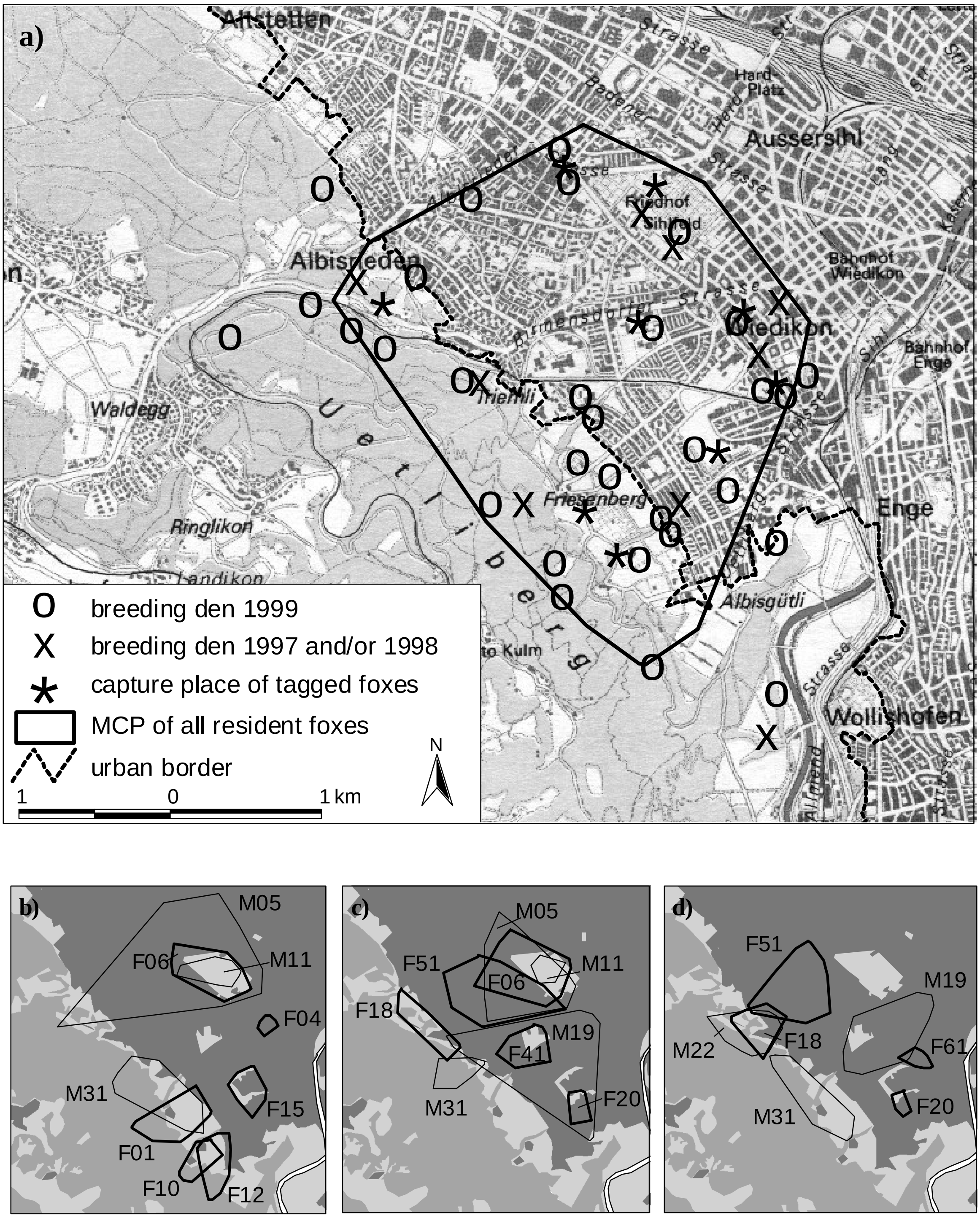

Figure 1a: Breeding dens from 1997 to 1999 in the study area.

The minimum convex polygons (MCP) of 12 radio-tracked foxes are marked with black lines. Breeding dens used only in 1997 and/or 1998 are marked with a black circle. 23 breeding dens were used in 1999 (marked with a white circle with black point). 17 of these breeding dens were also used in previous years. 1b) Home ranges (MCP) of 9 radio-tracked foxes in summer/autumn 1998. 1c) Home ranges (MCP) of 10 radio-tracked foxes in winter 1998/99. 1d) Home ranges (MCP) of 7 radio-tracked foxes in spring 1999. 1b) – 1d) light grey = rural area; middle grey = forest; dark grey = urban area.

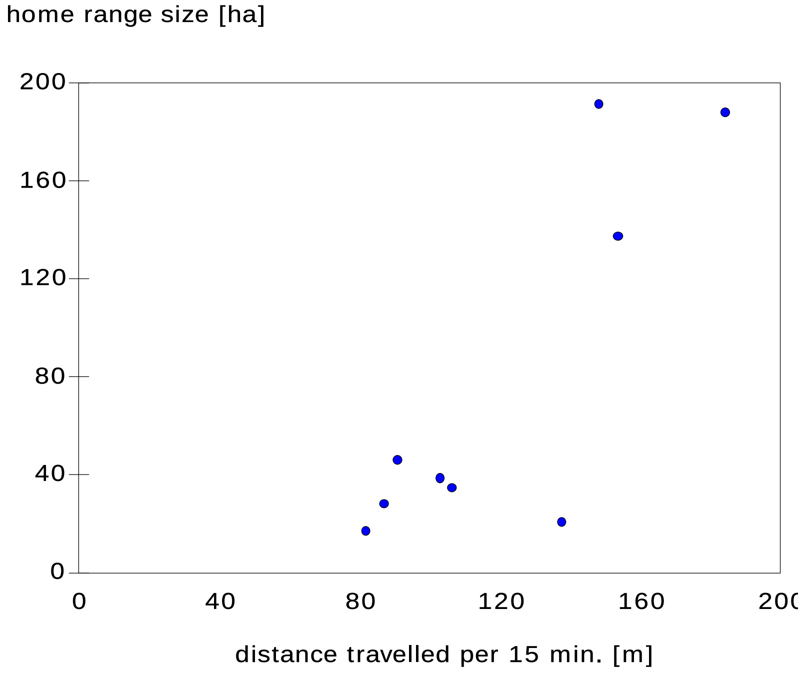

Figure 2: Mean seasonal home range size and mean travel distance in 15 min. for male foxes. Three male foxes, so-called floaters (on top right), had larger home ranges and travelled larger distances per 15 min. than resident male foxes.

Adaptations to urban environment in habitat association of foxes (*Vulpes vulpes*)

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Summary

The colonisation of urban areas by foxes started in Switzerland in the mid-1980s. Although a new phenomenon, foxes have reached high population densities of more than 10 adult foxes per km^2 in the city of Zurich. From December 1996 to June 1999, habitat selection for nightly activity and day-time rest sites of 17 adult resident foxes were studied in the area of Zurich by means of radio-tracking. 11 foxes had their home range mostly within the city border (“urban foxes”), the home ranges of 6 foxes were situated near, but mostly outside the city border (“rural foxes”). 11 habitat categories of vegetation cover and human utilisation types were distinguished for habitat availability calculations. Habitat selection analyses were done by compositional analysis, for rural and urban foxes, separately. Rural as well as urban foxes showed an overall difference in habitat use at night and day compared to habitat availability within their home ranges. The mostly selected habitat categories for nightly activity of rural foxes were “rural areas”, “forest” and “allotment gardens” at the urban border. Rural foxes had most of their day-time rest sites in forest. Urban foxes used for nightly activity mostly “parks and cemeteries” and „allotment gardens“, whereas “residential areas with medium and high density housing” and “streets and places” were least selected. Urban foxes used public parks more in the first half of the night and residential areas more in the second half of the night. We therefore conclude that urban foxes, to avoid contact with people, used closed areas such as parks in the early night, when humans are still active in other areas, and changed to residential areas only when human presence in these areas was low. Urban foxes selected several habitat categories for rest sites, MRes+HRes were least selected. As areas with medium density housing correlated positively with home range size, we conclude that they did not supply suitable habitat for foxes because their surroundings - mostly plain lawn – provide little cover and poor food resources. We discuss the results with reference to their potential implications for countermeasures against zoonoses in urban areas.

Key words: Red fox, habitat use, compositional analysis, urban area, zoonoses control

Introduction

Urban foxes have emerged in Switzerland over the past 15 years (Gloor et al. 2001). Despite the novelty of this development, foxes live already in all Swiss cities with more than 20,000 inhabitants. In addition, a markedly large population with more than 10 adult foxes per km2, fox family groups with several adult foxes, and relatively small individual home ranges (Gloor et al., submitted) indicate that suitable habitat and other necessary resources are availability in the city of Zurich.
Urban foxes were mainly reported from Great Britain where they started to colonise urban areas in the 1930s (Teagle 1967, Harris 1977, Macdonald and Newdick 1982). However, since the 1980s, urban foxes have been recorded not only from Switzerland but also from other parts of Europe and North America, e.g. from Oslo, Norway (Christensen 1985), Brussels, Belgium (Brochier 1989), or Toronto, Canada (Adkins and Stott 1998), indicating that foxes started to colonise cities in other parts of the world as well. This raises the question about the underlying reasons for this new colonisation of urban areas and about the suitability of cities as living space for red foxes.
Fox populations on the European continent have undergone dramatic changes in the 20th century due to a heavy rabies epizootic spreading amongst foxes from the 1930s onwards (Goszczynski 1989, Vos 1993, Chautan et al. 2000). The consequence of this epizootic was a drastic depression of fox populations, starting in Switzerland in 1967, when the first rabies case was recorded (Steck et al. 1980; Müller et al. 2000).
After successful vaccination campaigns, fox populations began to recover in the late 1980s and the early 1990s (Breitenmoser et al. 2000), and started to show up in urban areas with an increasing frequency. Are urban fox populations therefore the result of an increasing population pressure and the expansion of rural fox populations, and, consequently, urban areas marginal habitat only? However, high population densities and small home ranges contrarily indicate that the city is a well suited living space for this omnivorous carnivore. The high population pressure may have initiated the immigration of founder individuals, but a swift adaptation to living in the city must have made this colonisation so successful.

The objectives of this study were to investigate the habitat association of urban foxes during their active time at night and the choice of day-time rest sites. In order to understand the specific life of urban foxes and their adaptations to this new environment, we examined their use of human made, “urban” habitat types such as residential areas and industrial places and “rural” habitat types such as parks or cemeteries within the city and compared it to the habitat preferences of conspecifics living at the border of the city.

This examination has an immediate practical importance. The increasing presence of foxes in cities is of great concern to the public with respect zoonoses like rabies or Alveolar Echinococcosis caused by the small fox tape worm Echinococcus multilocularis (Hofer et al. 2000). Medical treatment of urban fox populations were suggested at several occasions (e.g. Schelling et al. 1997). In order to plan effective countermeasures in urban areas such as vaccination campaigns, a precise knowledge of habitat association of foxes in this new environment is necessary (Macdonald et al. 1981, Saunders et al. 1997).

Methods

Study area

The political community of Zurich (360,000 inhabitants), part of the conurbation of Zurich (around 1 million people), covers an area of 92 km2 consisting of 53 % urban area, 24 % forest, 17 % agricultural area and 6 % water. We refer to forest and agricultural area as rural or peri-urban.

The study area was defined as the roaming area of 17 resident radio-tagged foxes and measured 6.7 km2 (minimum convex polygon of all home ranges). It was situated in the western part of Zurich, on 410 to 871 m above sea level, with 4.3 km2 of urban zone below and 2.3 km2 of rural zone above 490 m. We defined the city border as the line following properties with buildings in daily use not more than 100 m apart from each other. The average human population density in the urban zone was 9,700 ind./km2.

Trapping, radio-tracking procedures and home range calculations

Foxes were captured in baited box-traps permanently monitored by means of transmitters (Karl Wagener, Telemetrie-Material, Köln, Germany). A trapped fox was sedated and fitted with a radio-collar (for details see Gloor et al, submitted).

We radio-tracked the foxes by cross-triangulation using TRX-1000 (Wildlife Materials, Inc., Illinois, USA) and modified YEASU FT-290 receivers (adapted by Karl Wagener, Köln, Germany) with hand-held H-aerials. We tracked foxes on foot or by bicycle either continuously from 21:00 to 5:00 (MEZ), or divided the night in two periods from 21:00 to 1:00 and 1:15 to 5:00 and tracked individual foxes in two different nights. Locations were taken every 15 min. and simultaneously direct sightings, movements, and bouts of inactivity were tape-recorded. Because of the abundance of streets and paths in the study area, the distance to the observed animal was always less than 200 m, allowing to estimate the foxes' locations at a high level of accuracy. Day-time rest sites were generally located once every week, but daily in July 1997, September 1998, and January 1999.

Seasonal home ranges of radio-tracked foxes were calculated as 100% minimum convex polygons (MCP) (Harris et al. 1990). Only data from at least three nights and 60 active fixes per season and a minimum of four hours of radio-tracking per night were considered to compute seasonal individual home ranges (for details see Gloor et al., submitted).

We classified the radio-tracked foxes into two groups according to the amount of area within the urban border in their MCP home ranges. Foxes with more than 50 % of urban zone were called "urban foxes", all others "rural foxes" (Gloor et al. submitted). For these two groups the analyses were carried out separately.

Habitat availability

The habitat availability was assessed through recording of vegetation cover and human utilisation categories in the city of Zurich (Bernowitz & Leutert 1988). The habitat map of a scale of 1:5,000 was a mosaic of polygons of different size, each belonging to one of the habitat categories. The habitat map was scanned into the geographic information system ArcView (ESRI, Version 3.1), georeferenced by means of the ArcView extension Image Warp 2.0 (McVay, 1999, unpublished program), and digitised on the screen. The 78 habitat categories of the recording were compiled into 11 habitat categories (Tab. 1). Percentage of land occupied by buildings and ground covered e.g. by asphalt or concrete was estimated by a sample of 500 locations randomly distributed in each habitat category. In the following, we refer to "ground covered" e.g. by asphalt or concrete as "sealed ground". Land occupied by buildings was excluded for further analysis. The relationship between home range size and habitat availability was examined by multiple regression analysis in SPSS 10.

Compositional analysis

A problem in habitat selection analysis is that the area of a specific habitat class is inversely correlated with the area of the other classes (Otis & White 1999). We therefore used compositional analysis to avoid this constraint (Aebischer & Robertson 1992, Aebischer et al. 1993, Saunders et al. 1998). The advantage of this non-parametric technique in comparison with other methods (e.g. Neu et al. 1974, Alldredge & Ratti 1986, White & Garrott 1990) is the use of single animals (or seasonal home ranges, respectively) instead of the locations as sample unit, and that all habitats are considered simultaneously. We computed the statistics with an Excel macro (P. Smith, Department of Zoology, University of Aberdeen, 1, Bettws Cottage, Bettws, Abergavenny, Monmouthshire, NP7 7LG, Wales, UK, pgsmith@aber1.fsnet.co.uk, beta version of an unpublished program), which also carried out the randomisation procedure recommended by Aebischer et al. (1993).

Based on the 11 habitat categories, the habitat composition (proportion of each habitat category) of the home ranges (MCP) of individual foxes were determined using the ArcView extension Spatial Analyst. Likewise, for each home range of each fox the proportion of the habitat categories of the radio-locations were calculated. Habitat utilisation during nightly activity was examined by taking the habitat composition within each MCP home range as available habitat, and comparing it to habitat utilisation as described by the composition of habitat categories of the radio-locations. Log ratios (yi) of the proportional use (xi) of each habitat by each fox compared with the proportional availability (xj) of that habitat in the fox' home range (yi = ln(xi/xj)) were calculated as the basis for subsequent analysis (Aebischer et al. 1993).
Seasonal home ranges of the same fox were handled as independent units if they showed less than 50 % overlap in their total combined home range. If seasonal home ranges of one fox overlapped to more than 50 %, they were combined in order to avoid auto-correlation and this combined home range was considered as independent unit.

Habitat utilisation in day-time rest sites was examined by taking the habitat composition within each total MCP home range of the whole radio-tracking period of each fox as available habitat, and then comparing it to habitat utilisation of all day-time rest sites used by each fox.

Habitat use in the course of the night

The night was divided into four parts of 2 hours each, from 21:00 to 5:00 (MEZ). For each part the proportion of used habitat was calculated for individual foxes on the bases of the radio-locations. Data of each 2 hour-interval was averaged for both rural and urban foxes, respectively, on the bases of foxes as units. A possible change of habitat use in the course of the night was examined by comparing habitat use in the first and the second half of the night and tested by Wilcoxon Sign Ranked Test in SPSS 10, corrected for multiple tests.

Results

Available habitat categories in the study area

The study area consisted of 35 % residential areas (LRes, MRes, HRes), 24 % open green space like public parks, swimming pool areas and cemeteries (Par), allotment gardens (All), fallow land (Fal), 2 % industrial areas (Ind) and areas with large buildings with no open green space (LBuil), 8 % streets and places (StPl), 5 % grassland (Rur) at the urban border and 21 % forest (For) (Tab. 1).

Classification of foxes based on spatial segregation

23 tracking periods of 17 adult resident foxes were studied in regard to their habitat selection (Tab. 2). The foxes studied represented two clusters, if the mean distance of all locations of a fox to the urban border was plotted in relation to the proportion of sealed ground in the seasonal home range (Fig. 1). The group called „rural“ was represented by 8 tracking periods and was situated outside of the urban border with always more than 80 % of open (not sealed) ground (examples see Fig. 2a). In the urban area, the proportion of open ground within home ranges varied largely mainly because of the existence of large parks, cemeteries and swimming pool areas (Fig. 2a,b). Two urban foxes, M11 and F06 (4 tracking periods), had very little sealed area within their home ranges (8.5 % – 27.7 %) (Fig. 2b), similar to some of the rural foxes (2.1 % – 17.0 %), because large parts of their home ranges were situated within a cemetery and adjacent allotment gardens. The range of sealed ground of the other urban foxes varied from 29.8 to 64.7 %.

Correlation of habitat composition with home range size

We tested the eleven habitats for having an influence on home range size. In rural area no difference was detected, but sample size was small and several missing values occurred. In urban area MRes (residential areas with blocks of 3 – 6 floors and public green areas around them) was the only habitat category which was found to have a significant positive effect ($R2 = 0.70$, $B = 2.05$, $p = 0.043$). On average an increase of 1% of the proportion of MRes area led to an increase of home range size of about 0.31 ha.

Habitat selection

Habitat selection was investigated separately for rural and urban foxes. Both rural as well as urban foxes mainly moved in cover and usually remained invisible for humans, because in only 4.7 % of all radio-locations (in 3.0 % of rural fox locations and in 5.7 % of urban fox locations) we actually saw the fox.

Log ratios of the proportional use of each habitat by each fox compared with the proportional availability of that habitat in the fox's home range (MCP) were calculated. These log-ratios relate independently to the proportional use of the habitats and are the base in compositional analysis (Aebischer et al. 1993). They are given for each fox-period in Tab. 3. A positive log-ratio indicates usage more than expected by availability, and vice versa. To examine overall pattern of habitat use for the two groups of animals, the log-ratios of each habitat category were averaged over all individuals. Multivariate analysis of variance showed an overall difference in habitat use within both groups, rural and urban foxes, respectively (for rural foxes: $Chi2 = 39.76$, $df = 5$, randomised $p = 0.010$; for urban foxes: $Chi2 = 18.74$, $df = 5$, randomised $p = 0.012$).

In the rural fox group, the analysis revealed the following ranking with 5 as the most and 0 as the least preferred habitat category: (5) Rur, (4) For, (3) Par+Fal, (2) LRes, (1) All, (0) REST (StPl+LBuil+Ind+HRes+MRes). Rural foxes selected grassland (Rur) and forest (For) significantly over REST, which represented all habitat categories with urban character (Tab. 4a). The three mostly selected categories, representing the habitat categories of 82 % of all radio-locations, had all a rural character with almost no houses (0 – 10 % of the area) and 92 – 100 % open (not sealed) ground and no people living there.

Urban foxes selected habitat categories in the following sequence (most to least selected): (5) Par+Fal, (4) All, (3) LRes, (2) Ind (1) MRes+HRes, (0) StPl+LBuil. All categories except residential areas with medium to high density housing (MRes+HRes, Fig. 3a) were significantly selected over streets and places (StPl+LBuil). Parks, cemeteries and fallow land (Par+Fal) and allotment gardens (All) and were significantly selected over residential areas with medium to high density housing (MRes+HRes) (Tab. 4b). The two mostly selected categories, which represented the habitat categories of 65 % of all radio-locations, had a rural character with 0 – 20 % land occupied by buildings and 88 – 100 % of the free area open (not sealed) and no people living there. However, the third category were residential areas with low density housing (LRes), which represented 16 % of all radio-locations and had a clear urban character with 30 % of the land occupied by houses, 27 % sealed ground and people living there. Additionally, habitat selection differed between individuals. 7 urban foxes showed an over-proportional use of residential areas with low density housing and one of the smallest home ranges was the one of vixen F61 which lived in an area of about 7 ha mostly within an industrial place.

Habitat use in the course of the night

Rural foxes tended to use forest areas more at the beginning and at the end of the night, and less in between. From 21:00 to 23:00 and from 03:00 to 05:00 49 % and 51 % of the radio-locations were situated in the forest (n=295 and 251 locations), whereas from 23:00 to 03.00 only 38 % of the radio-locations were situated in the forest (n=621 locations). This trend could be explained by the locations of their day beds which were mostly situated in the forest. However, as there were only 6 rural foxes, the change was not significant.

Urban foxes showed a significant change in the use of Par+Fal (parks, cemeteries, fallow land) and in LRes (residential areas with low density housing), if the first half of the night was compared to the second half. The changes were in inverse direction. Par+Fal were more used from 21:00 to 01:00 (57 % of the 1128 radio-locations in this period, 102 ± 51 locations per fox) than from 01:00 to 05:00 (45 % of the 810 radio-locations in this period, 74 ± 35 locations per fox) (Wilcoxon Sign Ranked Test, $p = 0.048$, corrected for multiple tests). The category “residential areas with low density housing” was significantly less used from 21.00 to 01:00 (14 % of radio-locations in this period) than from 01:00 to 05:00 (32 %; Wilcoxon Sign Ranked Test, $p = 0.048$, corrected for multiple tests).

The habitat categories Par+Fal comprised areas which were closed for people during the whole night and provided to a large extend areas with little or no human disturbance for foxes. In residential areas on the other hand, human activity was generally high at the beginning of the night and decreased afterwards. Therefore, after 01:00 residential areas with low density housing provided almost undisturbed area for foxes when they were preferably used.

Habitat selection in day-time rest sites

From December 1996 of June 1999, 815 day-time rest sites were located, 615 sites of urban foxes and 214 sites of rural foxes (Tab. 5). Compositional analysis of day-time rest sites was carried out on the basis of the frequency of habitat categories used for day-time rest sites averaged per fox and compared to the proportion of habitat categories in the total home ranges (MCP) of each fox (Tab. 6).

Multivariate analysis of variance showed an overall difference in habitat use within both groups, rural and urban foxes, respectively (for rural foxes: Chi2 = 27.15, df = 4, $p < 0.001$; for urban foxes: Chi2 = 19.65, df = 5, $p < 0.001$).

129 or 60 % of all day-time rest sites of rural foxes were situated in forest, and 3 rural foxes (F01, M22, M33) had all their day-time rest sites in forest. The ranked variable sequence (most to least used) for rural foxes was as follows: (3) For, (2) Par+Fal+Rur+All, (1) LRes, (not used) MRes+HRes, (not used) LBuil+StPl+Ind.

Ranked variable sequence (most to least used) for urban foxes were as follows: (5) Par+Fal, (4) All, (3) Ind (2) LRes, (1) MRes+HRes, (0) LBuil+StPl. All habitat categories were significantly selected over LBuil+StPl (areas with large buildings, streets and places and without open, not sealed ground). Day-time rest sites of urban foxes were distributed in more different habitat categories than those of rural foxes which were clearly concentrated in the habitat category “forest”. Indeed, some of the urban day-time rest sites radio-tracked revealed a clear adaptation of foxes to urban habitat and human activity (Fig 3).

Discussion

We used the focus animal sampling method (Harris et al. 1990) to assess habitat association of radio-tracked foxes and assumed that this correlated with foraging. However, as direct observations of the foxes during the tracking at night were rare, it was often not possible to know whether a fox stayed in an certain area because it was foraging or for social reasons or comfort behaviour. It is therefore more appropriate to call our results “habitat association” rather than “habitat use” (Adkins & Stott 1998). However habitat association of foxes often correlates with food availability and distribution (Cavallini & Lovari 1991), and therefore may reflect the direct, representative importance for foxes.
The foxes in this study were clearly divided into two groups in regard to their spatial behaviour and habitat association: (1) peri-urban, rural foxes at the border of the city, and (2) urban foxes, living completely inside the city border. Unlike the foxes in Oxford (Macdonald & Newdick 1982), which moved readily between rural and urban habitats, foxes at the urban border in Zurich were mainly active in habitat with rural character and did not intrude much into urban area. Urban foxes selected mostly rural-like habitats, but were also active in quiet residential areas with low density housing and small private gardens. In these areas as well as in allotment gardens they were able to profit from abundant food resources: human refuse from compost heaps, fruit and berries from gardens, general rubbish from streets and even food deliberately offered to foxes or other wild animals and pets. These were the typical food categories found in stomachs of foxes shot or found dead in Zurich (Contesse 1999), in accordance with studies from urban populations in Great Britain (Harris 1981, Doncaster et al. 1990, Baker et al. 2000). On the other hand, in Toronto, Canada, there was no evidence that suburban foxes were scavenging on human refuse as garbage was generally well packed away and thus inaccessible for foxes (Adkins & Stott 1998). The Toronto foxes did not intrude very far into the city, thus behaved similar to the rural foxes in Zurich.

Urban foxes are only able to benefit from urban resources because they adapted to the presence of people. This can be seen from the choice of day-time rest sites: where rural foxes mostly selected day-time rest sites in the forest with little or no disturbance, urban foxes used habitat categories of both rural and urban character. Some of the day-time rest sites discovered were at astonishing places very near to human activity. Nevertheless, human activity still strongly influenced urban foxes in their habitat association and their activity pattern. More frequently they used cemeteries, public parks and swimming pool areas in the first half of the night, when such places were already abandoned by humans. In the second half of the night,

when human activity decreased to a very low level, the foxes visited the residential areas with low density housing. However residential areas with medium to high density housing and surrounding common green areas were less frequently used. The positive correlation of the share of such areas within a home range with home range size stresses that these areas provide less suitable habitat, likely due to the specific management of the green areas: they consist mainly of plain lawn with only few trees or bushes. There is no cover and probably not much food. Additionally there may be more people because human population density in such areas is higher than in areas with low density housing.
Cover seems to play an important role in habitat selection of foxes in rural and urban areas for both, activity and day-time rest sites (Kolb 1985, Cavallini & Lovari 1991, Cavallini & Lovari 1994, Lucherini et al. 1995, Saunders et al. 1997, Weber & Meia 1996). Urban foxes in Zurich seemed to avoid direct contact to humans. During the field work, we rarely saw the tracked foxes, although we generally were at a close distance to them. Most people living in the "fox areas" of Zurich only occasionally see a fox despite the high fox population density. A similar situation was described by Adkins & Stott (1998) for suburban foxes in Toronto, Canada. These experiences are in contrast to the situation in Bristol, GB, where the foxes were often seen by the researchers and the public (Harris Saunders et al. 1997).

Our results differed from those of studies from Great Britain, as far as the relative importance of residential areas with low density housing was concerned. In Bristol, GB, urban foxes showed a selection for these residential areas (Harris 1977, Harris & Rayner 1986, Macdonald 1981), whereas in Zurich these areas only ranked at third place. However, in Bristol, relatively undisturbed habitats such as back gardens, woodland, rough ground, allotment gardens and cemeteries were preferred, too (Saunders et al. 1997), similar to the habitat selection of urban foxes in Zurich. According to Harris (1977), foxes in Bristol avoided parks and public open space, whereas in Zurich, public parks were mostly selected for day-time rest sites and also frequently used in the first half of the night. We assign this difference to the fact, that maybe unlike parks in British cities, all parks in Zurich provide a lot of cover. Additionally, dogs are banned from most such areas, and Zurich has very few stray dogs which are known to have a negative influence on the presence of foxes (Harris 1981, Adkins & Stott 1998).

The comparison of the urban foxes of Zurich to those of Britain on the one hand and of Toronto, Canada on the other hand, indicate, that Zurich's foxes are in an in-between position as far as the adaptations to urban areas is concerned. They live inside the urban border and are to some degree active in residential areas, unlike foxes in

Toronto which stay outside the actual city. On the other hand the foxes in Zurich mostly selected habitat categories with rural character, unlike urban foxes in Great Britain. We assume that foxes in British cities are already better adapted to the co-existence with people after 60 years of colonisation of cities. However, the habitat selection of some fox individuals in Zurich reveal the use of clearly urban areas and anecdotal observations e.g. of tame foxes playing with children in swimming pool areas and foxes roaming around during day-time point to the same direction: urban foxes in this city will most probably adapt further to urban conditions in the future and therefore they will be able to live even closer to people than they do already today.

The results of the habitat analysis have some important implications for counter-measures against zoonoses such as rabies or alveolar echinococcosis (Macdonald et al. 1981, Saunders 1997, Deplazes & Eckert 2001, Deplazes et al. 2001). During the vaccination campaigns against the past rabies epizootic in Switzerland from 1978 to 1999, it was assumed that foxes move around and not through or within human settlements (Steck et al. 1980) which is obviously no longer true, today. Future vaccination campaigns have to be adjusted to this new situation (Hegglin et al. in prep). In order to reach as many urban foxes as possible, it is advisable to distribute vaccine baits in those areas which were mostly selected by the foxes: in allotment gardens and public green areas such as parks and cemeteries. The distribution of baits in residential areas with medium and high density housing is less important.
However, urban foxes are not only a matter of concern with regard to zoonoses control, but also a challenge for people living in cities who have to reconsider their attitudes towards this medium-sized carnivore and new resident in their neighbour-hood.

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Tab. 1: Habitat categories in the study area in Zurich.

Habitat in study area (%) = proportion of habitat categories in the study area. Land occ. by build. = Land occupied by buildings (excluded for further analysis). Sealed ground is ground covered e.g. by asphalt or concrete and with no vegetation. The proportion of sealed ground is without land occupied by buildings. Combination in rural/urban area = Combined categories for compositional analysis in rural/urban area. n.a. = habitat category not available.

Habitat	Combination in rural area	Combination in urban area	Description of habitat category	Habitat in study area (%)		Land occ. by build. (%)	Sealed gr. (%)
				rural	urban		
Rur		n.a.	Rural areas, grassland, meadows. Mostly at the urban border, in peri-urban areas.	13	n.a.	0	0
For		n.a.	Forest.	62	n.a.	0	0
All			Allotment gardens. Closed during night.	10	3	20	13
Par	↑	↑	Public parks, cemeteries, public swimming pool areas, sports grounds. Closed during night.	11	22	10	8
Fal	↓	↓	Fallow land, nature reserve. Mostly not accessible for humans.	1	2	0	0
LRes	↑		Residential areas built before 1950, houses with one to six flats, detached, semi-detached and terraced houses, private gardens, low density housing.	1	15	30	27
MRes	|	↑	Residential areas, mostly built in the 1950s, but also earlier, large buildings with 3 to 6 floors, common gardens (mostly lawn) around the buildings, medium density housing.	0	34	24	30
HRes	|	↓	Blocks and large buildings along streets with an inner courtyard, accessible from the street, with at least 1/3 of common green area, high density housing.	0	3	58	31
Ind	|		Industrial areas, factories.	0	6	50	100
LBuil	|	↑	Areas with large buildings like shopping centres, office buildings. Little housing space.	0	3	48	100
StPl	↓	↓	Streets and places covered by asphalt or concrete.	3	11	0	100
				100	100		

Tab. 2: Data of 23 tracking periods of 17 resident adult foxes in the study area, radio-tracked from December 1996 to June 1999.

Rural foxes: 4 female and 2 male foxes. Urban foxes: 7 female and 4 male foxes. MCP = 100 % minimum convex polygon (ha), sp = spring, sa = summer/autumn, w = winter. Total hr = total home range (ha).

fox code	Tracking period	total hr (MCP)	total active fixes	season-year	MCP (ha)
Rural foxes					
F01	30/6/98 – 24/6/99	43.2	204	sa98	42.5
F10	30/6/98 – 29/10/98	19.7	113	sa98	17.4
F12	28/6/98 – 6/2/99	33.7	196	sa98	28.5
F18	4/1/99 –22/6/99	28.1	149	w98/99	27.1
				sp99	28.1
M22	21/12/98 – 24/6/99	50.7	197	w98sp99	49.3
M31	20/7/98 – 3/6/99	83.1	319	sa98sp99	76.8
				w98/99	19.5
Urban foxes					
F04	15/6/97 – 24/6/99	9.2	296	sa97sa98	7.5
F06	17/1/97 – 26/6/99	95.2	350	sa98w98/99	82.3
				w96/97	24.2
F15	9/7/98 – 1/4/99	20.8	116	sa98	20.7
F20	27/10/98 – 14/6/99	10.4	180	w98/99	10.3
				sp99	5.0
F41	2/1/99 – 19/3/99	28.3	202	w98/99	27.1
F51	29/12/98 – 1/7/99	123.7	187	w98/99	73.5
				sp99	91.7
F61	18/5/99 – 24/6/99	7.6	182	sp99	7.0
M01	11/12/96 – 3/2/97	37.9	114	w96/97	34.6
M02	16/1/97 – 1/7/98	28.2	66	sp98	28.1
M03	13/1/97 – 25/5/98	25.3	100	w96/97	20.6
M11	10/3/98 – 21/12/98	24.9	203	sa98	22.8
				w98/99	11.3

Tab. 3: Log-ratios of utilisation of the different habitat categories compared to habitat availability for all individual foxes.

The log-ratios ln(xi/xj) (xi = used, xj = available) reveal the habitat selection of individual foxes. A positive value indicates over-proportional use, compared to availability, and vice versa. Seasons: w = winter (November to February), sp = spring (March to June), sa = summer/autumn (July to October). / = habitat category not available. LBuil = areas with large buildings, HRes = residential areas with high density housing, LRes = residential areas, low density housing, MRes = residential areas, medium density housing, Ind = industry, StPl = streets and places, Par = parks and cemeteries, All = allotment gardens, Rur = rural areas, Fal = fallow land, For = forest. REST = StPl+LBuil+Ind+HRes+MRes (used less than 2 % on average).

			habitat categories							
		Rural foxes	For	Rur	Par+Fal	All	LRes	REST		
		Urban fox						Ind	HRes+ MRes	StPl+ LBuil
	MCP (ha)	season								
Rural foxes										
F01	14.4	sa98	-0.66	0.63	0.81	-1.70	1.21		-0.98	
F10	42.5	sa98	-0.57	0.36	0.67	-0.19	-4.11		-1.04	
F12	28.5	sa98	-0.72	0.54	0.03	0.79	-0.48		-1.50	
F18	28.1	sp99	-0.16	0.37	1.16	0.96	-1.05		-1.15	
F18	27.1	w9899	0.50	-1.16	-5.90	-0.04	-0.56		-1.74	
M22	19.5	w9899sp99	-0.11	0.28	0.06	0.99	-0.07		-1.12	
M31	49.3	sa98sp99	0.19	-0.14	-0.17	-1.15	1.15		-0.81	
M31	76.8	w9899	-0.06	-0.04	1.13	-3.63	0.69		0.00	
		average	-0.20	0.11	-0.28	-0.50	-0.40		-1.04	
Urban foxes										
F04	7.50	sa97sa98	/	/	-0.03	0.00	0.64	0.00	-0.83	-2.78
F06	24.20	w9697	/	/	-0.19	0.85	5.22	3.84	-0.63	-5.51
F06	82.30	sa98w98	/	/	0.46	0.96	-5.52	-4.62	-2.29	-2.10
F15	20.70	sa98	/	/	0.82	0.37	-6.12	-7.91	-7.16	-6.89
F20	5.00	sp99	/	/	0.31	0.52	0.08	1.09	-0.89	-2.62
F20	10.30	w9899	/	/	-0.13	2.05	-0.09	-6.43	-2.43	-2.11
F41	27.10	w9899	/	/	0.64	0.33	-2.70	0.00	-1.38	-7.38
F51	73.50	w9899	/	/	-1.17	-6.29	2.17	7.20	-0.55	-0.61
F51	91.70	sp99	/	/	0.77	1.66	0.12	-1.25	-0.26	-7.23
F61	7.00	sp99	/	/	-1.33	0.61	-2.05	0.55	0.07	-7.07
M01	34.60	w9697	/	/	0.06	2.60	1.15	-1.46	-0.96	-1.18
M02	28.10	sp98	/	/	0.18	-0.75	0.46	-2.44	-0.07	-1.43
M03	20.60	w9697	/	/	0.43	0.16	-0.86	0.02	-1.30	-1.01
M11	22.80	sa98	/	/	0.23	-1.62	0.00	0.00	-5.78	-6.06
M11	11.30	w9899	/	/	0.07	-1.06	0.00	0.00	-5.09	-0.69
		average			0.07	0.02	-0.50	-0.76	-1.97	-3.65

Tab. 4: Magnitude of log-ratio differences between utilised (columns) and available habitat (rows) in nightly activity of rural and urban foxes.

A positive sign indicates an over-proportional use compared to availability, a double sign represents statistically significant deviation from random at $P < 0.05$.

REST = StPl+LBui+Ind+MRes +MRes (used less than 2 % on average). LBuil = areas with large buildings, HRes = residential areas with high density housing, LRes = residential areas, low density housing, MRes = residential areas, medium density housing, Ind = industry, StPl = streets and places, Par = parks and cemeteries, All = allotment gardens, Rur = rural areas, Fal = fallow land, For = forest.

a) Rural foxes	Habitat categories available						
Habitat categories used	Par+Fal	All	LRes	Rur	For	REST	Rank
Par+Fal		+	+	-	-	+	**3**
All	-		-	-	-	+	**1**
LRes	-	+		-	-	+	**2**
Rur	+	+	+		+	++	**5**
For	+	+	+	-		++	**4**
REST	-	-	-	--	--		**0**

b) Urban foxes	Habitat categories available						
Habitat categories used	Par+Fal	All	LRes	Ind	MRes+ HRes	StPl+ LBuil	Rank
Par+Fal		+	+	+	++	++	**5**
All	-		+	+	++	++	**4**
LRes	-	-		+	+	++	**3**
Ind	-	-	-		+	++	**2**
MRes+ HRes	--	--	-	-		+	**1**
StPl+LBuil	---	--	--	--	-		**0**

Tab. 5: Number of day-time rest sites of rural and urban foxes in relation to their habitat categories.

LBuil = areas with large buildings, HRes = residential areas with high density housing, MRes = residential areas, medium density housing, LRes = residential areas, low density housing, Ind = industry, StPl = streets and places, Par = parks and cemeteries, All = allotment gardens, Rur = rural areas, Fal = fallow land, For = forest. total RP = total number of daytime rest sites.

Fox	Habitat categories											
	LRes	Fal	MRes	LBuil	Ind	MRes	Par	All	Rur	For	StPl	total RP
Rural foxes												
F01										60		60
F10							7			7		14
F12							66		1	2		69
F18	7							1	3	4		15
M22										10		10
M31										46		46
total	**7**	**-**	**-**	**-**	**-**	**-**	**73**	**1**	**4**	**129**	**-**	**214**
(%)	**(3)**						**(34)**	**(1)**	**(2)**	**(60)**		**(100)**
Urban foxes												
F04	138	2					9					149
F06	15			7	1	14	30	54				121
F15		48			21			3				72
F20		15						17				32
F41							28					28
F51	19					13						32
F61					8							8
M01	26	1	1		1	1	4					34
M02						12	3					15
M03		45				1						46
M11							64					64
total	**198**	**111**	**1**	**7**	**31**	**41**	**138**	**74**	**-**	**-**	**-**	**601**
(%)	**(33)**	**(19)**	**(0)**	**(1)**	**(5)**	**(7)**	**(23)**	**(12)**				**(100)**

Tab. 6: Log-ratios of utilisation of the different habitat categories for day-time rest sites compared to habitat availability in the total home ranges (MCP) for all radio-tracked foxes.

The log-ratios ln(xi/xj) (xi = used, xj = available) reveal the habitat selection of individual foxes. A positive value indicates over-proportional use compared to availability and vice versa. / = not used. n.a. = not available. LBuil = areas with large buildings, HRes = residential areas with high density housing, LRes = residential areas, low density housing, MRes = residential areas, medium density housing, Ind = industry, StPl = streets and places, Par = parks and cemeteries, All = allotment gardens, Rur = rural areas, Fal = fallow land, For = forest. total RP = total number of rest sites.

	habitat categories						
rural foxes urban foxes	For	Par+Fal +Rur Par+Fal	All	LRes	HRes+MRes	LBuil+StPl	Ind
a) rural foxes							
F01	0.85	/	/	/	/	/	n.a.
F10	0.03	0.21	/	/	/	/	n.a.
F12	-2.44	0.71	/	/	/	/	n.a.
F18	-0.29	0.36	-6.72	0.76	/	/	n.a.
M22	0.43	/	/	/	/	/	/
M31	0.63	/	/	/	/	/	/
b) urban foxes							
F04	n.a.	-1.59	n.a.	1.16	/	/	n.a.
F06	n.a.	-0.54	1.69	1.17	-0.96	-0.76	-1.18
F15	n.a.	0.43	0.46	/	/	/	-0.08
F20	n.a.	0.36	1.84	/	/	/	/
F41	n.a.	0.72	/	/	/	/	/
F51	n.a.	/	/	1.93	-0.20	/	/
F61	n.a.	/	/	/	/	/	0.52
M01	n.a.	-0.30	/	1.57	-1.76	/	-0.25
M02	n.a.	-0.24	/	/	1.05	/	n.a.
M03	n.a.	0.91	/	/	-1.85	/	/
M11	n.a.	0.27	/	/	/	/	n.a.

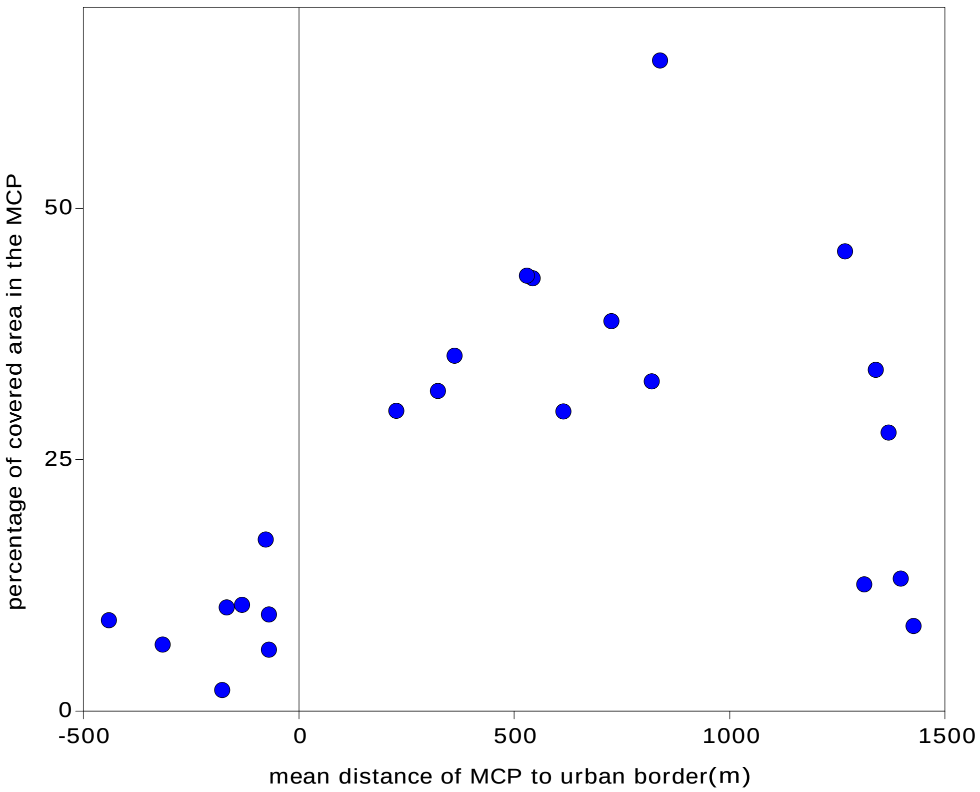


Fig. 1: Percentage of covered (sealed) area in home ranges and mean distance of all locations to the urban border.

23 tracking periods of 17 foxes were taken into account. The foxes with home ranges on the left hand side of the urban border (zero line) were “rural”, those with home ranges on the right hand side were “urban” foxes. A group of urban foxes had low proportion of covered (sealed) area in their MCPs (on bottom right) comparable to rural foxes. “Covered areas” represent areas with ground covered by asphalt or concrete.

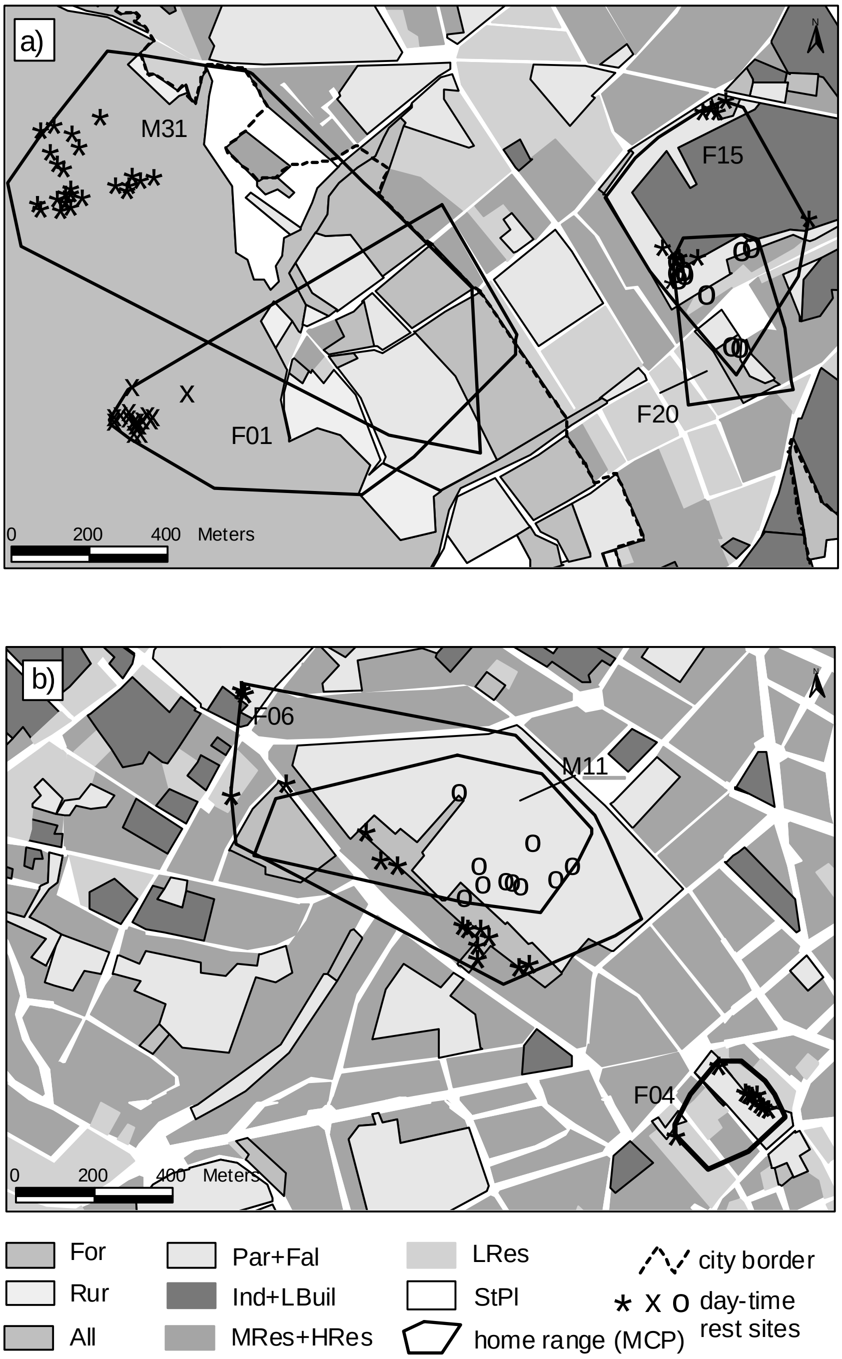
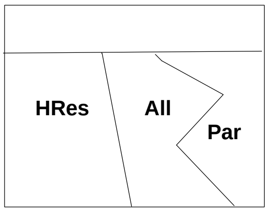


Fig. 2: Exemplary home range areas (100 % MCP) of rural and urban foxes and their day-time rest sites in summer/autumn 1998 and winter 1998/99, respectively.

For = forest; Rur = rural area; All = allotment gardens; Par+Fal = parks, fallow land, cemeteries, sports fields; Ind+LBuil = industry, area with large buildings; MRes+HRes = residential areas with medium to high density housing; LRes = residential areas with low density housing; StPl = streets and places.

a) F01 and M31 were rural foxes radio-tracked in summer/autumn 1998. All of their day-time rest sites were situated in the forest (For). F15 and F20 were urban foxes tracked in summer/autumn 1998 and winter 1998/99, respectively. **b)** F06 and M11 were urban foxes with a high amount of parks and allotment gardens within their home range, tracked in summer/autumn 1998. F04 was an urban female fox tracked in summer/autumn 1998.

a)



b)

Fig. 3: The habitat categories “Parks and cemeteries (Par)”, “Allotment gardens” (All) and “Residential areas with medium density housing” (LRes) (from right to left) and female F61 at a day-time rest site in an industrial area.

a) The habitat categories “Par+Fal” (parks, cemeteries, fallow land) like the cemetery on the right-hand side were mostly used during the first half of the night and significantly more used than MRes+HRes (residential areas with medium to high density housing like the blocks on the left hand side). MRes+HRes correlated positively with home range size (R2 = 0.74, B = 1.38, p = 0.018). Allotment gardens (All, in-between) were the mostly selected habitat category by urban foxes. **b)** The female fox F61 had 112 of 182 day-time rest sites in an industrial area.

High prevalence of *Echinococcus multilocularis* in urban red foxes (*Vulpes vulpes*) and voles (*Arvicola terrestris*) in the city of Zurich, Switzerland

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Summary

Over a period of 26 months from January 1996 to February 1998, 388 foxes were sampled from the city of Zurich, Switzerland, and examined for intestinal infections with *Echinococcus multilocularis* and other helminths. The prevalence of *E. multilocularis* in foxes sampled during winter increased significantly from 47% in the urban to 67% in the adjacent recreational area, whereas prevalence rates of other helminths were similar in both areas. Seasonal differences in the prevalence of *E. multilocularis* were only found in urban subadult male foxes which were significantly less frequently infected in summer than in winter. The distribution of the *Echinococcus* biomass, as expressed by worm numbers per fox was investigated in 133 infected foxes randomly sampled in winter. Ten of these foxes (8%) were infected with more than 10,000 specimens and carried 72% of the total biomass of *E. multilocularis* (398'653 worms). Prevalences did not differ significantly in these foxes in regard to age and sex but worm burdens were significantly higher in subadult foxes as compared with adult foxes. In voles (*Arvicola terrestris*) trapped in a city park of Zurich, *E. multilocularis*-metacestodes were identified by morphological examination and by PCR. The prevalence was 20% among 60 rodents in 1997 and 9% among 75 rodents in 1998. Protoscolices occurred in two of the cases from 1997. The possible risk for human infection is discussed with respect to the established urban *E. multilocularis* cycle.

Key words: Echinococcosis, *Echinococcus multilocularis, Vulpes vulpes, Arvicola terrestris*, urban, zoonosis.

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Introduction

Human alveolar echinococcosis (AE), caused by larval stages of *Echinococcus multilocularis,* is one of the most lethal helminthic zoonoses (Amman & Eckert, 1995). In Europe, the natural cycle of *E. multilocularis* predominantly involves red foxes (*Vulpes vulpes*) as definitive hosts and several rodents species as intermediate hosts. Domestic dogs and cats have also been identified as definitive hosts, but their significance for zoonotic transmission needs further elucidation (Eckert & Deplazes, 1999).

In recent years, *E. multilocularis* prevalences in foxes of up to 60% have been reported from Central Europe, and this tapeworm was also reported from areas where it had not been described previously (Lucius & Bilger, 1995; Eckert & Deplazes, 1999). Furthermore, increasing fox densities were registered in several European countries (Chautan, Pontier & Artois, 1999) with this population increase being most noticeable in suburban and urban areas.

Although urban and suburban foxes had been a well known phenomenon in the UK since the 1940s (Macdonald & Newdick, 1982; Harris, 1977), it is only in approximately the last 15 years that high fox densities have been reported from cities also on the continent e.g. from Berlin (Schöffel *et al*., 1991) and from Århus and Copenhagen (Møller Nielsen, 1990; Willingham *et al.*, 1996). In Switzerland, a considerable increase of the fox population was observed over the past ten years (Breitenmoser *et al.,* 1995), and foxes are now commonly seen in urban areas with cubs being bred in public parks and private gardens. The fox population in the city of Zürich is estimated to consist of 300-400 adult animals (Gloor, unpubl. data).

The most important intermediate host species of *E. multilocularis* in Europe are *Microtus arvalis* and *Arvicola terrestris*. Few data are available about parasite prevalences in rodents, but in general they are low (<1%–6%) as compared to those in foxes from the same area (20–60%). However, studies in France and Switzerland indicated that high-endemic areas of rodent *E. multilocularis* infections do exist focally where prevalences of up to 39% were observed (Eckert *et al.*, 2000a).

The epidemiological situation of alveolar echinococcosis in humans in Switzerland was stable over the last 36 years (Eckert & Deplazes, 1999). However, the invasion of urban areas by foxes raised new questions concerning the potential public health risks caused by them with regard to zoonotic parasitic infections. The city of Zurich is surrounded by an endemic area where *E. multilocularis* was detected in 40% of foxes (Ewald *et al*., 1992). In order to investigate the potential contamination of public areas with *E. multilocularis* eggs and to assess whether an urban cycle of the parasite occurs, a survey of the intestinal helminths in foxes and metacestodes of *E. multilocularis* in voles was conducted in the city of Zurich.

Materials and methods

Study area

The city of Zurich (92 km², 360 000 inhabitants) was divided into an urban and an adjacent rural area consisting mainly of wood, parks, farm land and allotment gardens. By our definition, the urban area extends 250 m from the built-up area into the rural zone (Fig. 1).

Foxes

Sampling. A total of 388 red foxes (*Vulpes vulpes*) were collected by 3 game wardens of the city forest service between January 1996 and February 1998. In 297 cases (76·5%) the foxes were shot in the course of the official local population control programme. Deaths of another 91 foxes (23·5%) resulted from road or rail traffic accidents or from unknown causes. Carcasses were wrapped up in plastic bags and stored at –20°C until necropsy. In winter (November to February) 123 foxes were sampled in the urban area and 129 foxes in the rural area. In the close season (spring, March 1st until June 15th) shooting of foxes was performed with special allowance in the urban area only. Therefore, 39 foxes (19 shot and 20 killed in accidents) were sampled in spring, all originating from the urban area. In summer (July to October) 93 urban and 4 rural foxes were collected.

Parasitological examination. Necropsy and examination of the intestines was carried out following strict safety precautions as described by Deplazes & Eckert (1996) and Eckert *et al.* (2000b) (e.g. separated laboratory, protective clothes, deep-freezing of intestines at –80^{o}C for at least 4 days). Two techniques were performed. The intestinal scraping technique (IST) was done as described by Deplazes & Eckert (1996) using 15 deep mucosal scrapings which were taken from equally distributed sites of the small intestine. The intestinal sedimentation and counting technique (SCT) was performed as described by Rausch, Fay & Williamson (1990) with modifications. Briefly, the small intestine was incised longitudinally and cut into 5 pieces of approximately the same length. These pieces were transferred to a glass bottle containing 1 litre of 0.9% NaCl-solution. After shaking the bottle vigorously for a few seconds, the pieces of intestine were removed and the superficial mucosal layer stripped by means of pressure between thumb and forefinger to dislodge any attached helminths. After a sedimentation time of 15 min the supernatant was decanted and the bottle refilled with physiological saline solution. This procedure was repeated 2–6 times until the supernatant was clear. The sediment fraction was examined in small portions of about 5-10 ml in square Petri dishes (9 x 9 cm,

Falcon®, Lincoln Park, NJ, USA) in transmission light under a stereomicroscope at a magnification of 120x. The whole sediment was checked if up to 100 worms were found; if higher numbers were present the total worm burden was calculated from the count of 1 subsample.
The SCT was performed with 310 intestines, of which 170 had previously been examined with the IST. Seventy-eight intestines were examined with the IST only.

Identification of helminths. *E. multilocularis* was identified based on typical morphological characteristics (Thompson, 1995). In cases where only juvenile stages were present, in particular scolices, *E. multilocularis* was confirmed by PCR (Bretagne *et al.*, 1993). The identification of *Taenia* spp. was based on length and shape of rostellar hooks (Verster, 1969). Specimens lacking hooks but with typical *Taenia* proglottids bearing taeniid eggs were recorded as *Taenia* sp.

Age determination of foxes. In line with the study of Wandeler (1976), cubs were assumed to be born on 1 April. Age determination of foxes collected after 1 July was done by measuring the relative width of the pulpar cavity of a lower canine tooth by X-rays (Kappeler, 1985), allowing to discriminate adults (older than 12 months) from subadults. In addition the age of 93 adult foxes randomly collected in winter was determined by counting annual incremental lines in tooth cementum (Grue & Jensen, 1979).

Rodents

From October to December 1997 and from July to October 1998, 60 and 75, respectively, Arvicola terrestris were trapped with tong traps in an urban public park („Irchelpark“) in the city of Zurich (Fig. 1). At necropsy, the liver in particular was examined for lesions. Metacestodes of E. multilocularis were identified directly on squashed metacestode material using the immunofluorescent labelled monoclonal antibody G 11 (Deplazes & Gottstein, 1991) and by histological identification of typical structures in HE-and PAS-stain. Specimens giving doubtful results were confirmed by PCR (Bretagne et al., 1993) after proteinase K digestion of the cut-up material. Species determination of metacestodes of other cestodes was evaluated by gross morphology and by comparing hook morphology and length.

Statistics

Calculation of 95% confidence intervals (CI) was performed as described by Lorenz (1988). Prevalence differences were compared by the χ^2 test and differences in infection intensity were compared by the Mann-Whitney U-test. Differences were considered significant at P < 0·05.

Results

Helminths recovered

A total of 344 of the 388 foxes examined (88·7%) carried intestinal helminths (Table 1). The highest prevalence (66·8%) was recorded for Uncinaria stenocephala followed by Toxocara canis (47·4%) and E. multilocularis (44·3%). In 64 foxes (16·5%) infections with Taenia spp. were recorded but in approximately half of the cases the species could not be determined due to inappropriate conservation of the worms. T. crassiceps and T. polyacantha were found in 7·6% and 0·5% of the foxes, respectively.

E. multilocularis infections

Comparison of 2 parasitological methods. In 170 cases small intestines were investigated with both the intestinal scraping technique (IST) and the intestinal sedimentation and counting technique (SCT). E. multilocularis infections were detected in 87 cases (51·2%) with the SCT and in 68 cases (40·0%) with the IST. The sensitivity of the IST was 78% as compared with the results obtained with the SCT. None of the foxes diagnosed negative by the SCT turned out positive with the IST. In 12 of the 19 cases detected with the SCT only, less than 10 and in 5 cases 10-100 worms per fox were recovered. In 2 remaining cases, infections with juvenile E. multilocularis stages were detected and confirmed by PCR (worm numbers of 432 and 11 640, respectively).

Prevalences in urban and rural foxes. Sampled foxes were not distributed homogeneously within the study area (Fig. 1). Statistical comparison of rural and urban foxes could be performed with animals originating from winter (November to February) only. The E. multilocularis prevalences in urban foxes (47·3%) and rural (66·7%) were significantly different as assessed by the χ^2 test (P < 0·01) (Table 2). On the other hand, the prevalences of infections with the other helminths investigated did not differ significantly among these 2 fox populations (P > 0·1, χ^2 test; data not shown).

Relation to fox sex and age. Within both areas investigated no significant differences in the prevalences of E. multilocularis were found related to sex or to the age groups „subadult“ and „adult“ (Table 2). Furthermore, no significant differences in the E. multilocularis prevalences were found between subadult and 93 adult foxes whose age was determined more precisely. Hence, the prevalence was 63% in 117 subadult foxes, 58% in 62 foxes aged 12-35 months, and 48% in 31 animals aged 36-70 months ($P > 0{\cdot}1$, χ^2 test; data not shown).

Annual and seasonal differences. Prevalences in rural and urban foxes sampled during 2 subsequent winters showed no significant differences within both habitats ($P > 0{\cdot}1$, χ^2 test; data not shown). Seasonal variations in the prevalence of E. multilocularis were investigated in the urban area only. Urban foxes collected in winter were significantly more frequently infected (47·3%) than those from summer (20·4%) ($P < 0{\cdot}0001$; χ^2 test) (Table 2). Interestingly, this significant difference was found in subadult male foxes only ($P < 0{\cdot}001$; χ^2 test). Statistical analyses of 19 cubs (5% infected with E. multilocularis) and 20 adult foxes (30% infected with E. multilocularis) collected in spring revealed no significant differences considering age and sex ($P > 0{\cdot}05$; χ^2 test; data not shown). This small group of animals was not used for further comparative analyses.

Distribution of the E. multilocularis biomass. The total Echinococcus biomass in 57 urban and 76 rural infected foxes randomly sampled during 2 winters was 398 653 E. multilocularis specimens. No significant difference in the worm burden was found between these urban foxes, carrying 42%, and rural foxes, carrying 58% of the total biomass, respectively ($P > 0{\cdot}1$, Mann-Whitney U-test). Therefore, further quantitative evaluations of the worm burden in foxes of both areas were not independently analysed. Figure 2 shows the distribution of the biomass of E. multilocularis in the foxes investigated. In 92 (69%) of the foxes infections with less than 1000 E. multilocularis worms were found representing 3% of the total biomass. Infections with more than 1000 worms occurred in 41 foxes (31%) carrying 97% of the total biomass. As few as 10 foxes (8%) which were infected with more than 10 000 specimens harboured 72% of the total biomass of E. multilocularis. The two heaviest infections (56 970 and 45 020 worms; 26% of the biomass) were detected in 2 subadult male foxes collected in February in the urban area. The worm burden revealed no significant differences related to sex but subadult infected foxes carried significantly higher worm burdens than adults (Table 3). Furthermore, the median number of E. multilocularis worms was more than twice as high in subadult as compared with adult foxes.

Prevalence of metacestode infections in *Arvicola terrestris*

Metacestodes of E. multilocularis were found in 19 (14%) of 135 A. terrestris trapped in the Irchelpark in the city of Zurich (Fig. 1). The prevalence was 20% in 60 animals examined in 1997 and 9% in 75 animals examined in 1998. Protoscoleces occurred in 2 A. terrestris from 1997 only. In 27 animals (20%) an infection with the metacestodes of T. taeniaeformis (*Strobilocercus fasciolaris*) was found. Metacestodes of T. crassiceps were detected on 2 occasions in subcutaneous cysts and once in the pleural cavity.

Discussion

The prevalence of 67% in foxes from recreational areas in the city of Zurich is comparable to the prevalences found in a previous study from adjacent rural areas (Ewald et al., 1992). Also, a high percentage of the urban dwelling foxes in the city of Zürich was infected with E. multilocularis (prevalence 47%). This decline in the E. multilocularis prevalences from the recreational to the urban area is significant and may be caused by a lower predation on rodents by urban foxes. Indeed, stomach content analyses of 229 foxes investigated in this study revealed a lower number of rodent items in the stomachs of urban foxes as compared with those from rural areas (Gloor, unpublished data).
The prevalence of Taenia spp., however, which also are dependant on rodents as intermediate hosts did not differ significantly between these 2 fox populations most probably reflecting the higher biotic potential of Taeniid-species as compared with Echinococcus.

Schelling et al. (1991) found significantly higher prevalences of E. multilocularis in foxes (age not determined) collected in winter than in those collected in summer. This overall difference could also be observed in our study in urban foxes but closer examination revealed that only young urban male foxes contributed to this fact. This might be explained by the findings of Tackmann and colleagues (1998) that the diet of young foxes contains a lower proportion of rodents in June and July when they become less dependent on adults.
The influence of the foxes' age on the prevalence of E. multilocularis, however, is not yet fully understood. Juvenile foxes were found to be significantly more frequently infected than adults (Ewald, 1993; Vos & Schneider, 1994) whereas in other studies no significant age dependent differences were detected (for references see Tackmann et al., 1998). Interestingly, young foxes were significantly more frequently infected with E. multilocularis than adults under high-endemic conditions,

whereas under low-endemic conditions adult foxes tended to be more frequently infected (Tackmann et al., 1998).
However, in our study which was conducted in a high-endemic area, the prevalence rates of subadult and adult foxes collected in winter did not differ significantly as determined with the highly sensitive intestinal sedimentation and counting technique which even allows detection with very low worm numbers. On the other hand, subadult foxes carried significantly higher worm burdens than adult foxes. This might be an indication for the acquisition of a partial immunity after repeated infections as had been shown in dogs experimentally infected with E. granulosus (Gemmell, Lawson & Roberts, 1986). erlauben

The high variation in the worm burdens of the individual foxes indicates that the parameter “prevalence” might not be the most adequate one to characterize the epidemiological situation of E. multilocularis. A few highly infected foxes carrying thousands of fertile E. multilocularis worms can be responsible for most of the egg contamination in a distinct area. A similar distribution of parasites has been observed in dingoes infected with E. granulosus in south-eastern Australia (Jenkins & Morris, 1991). Furthermore, subadult male foxes which carried the major part of the E. multilocularis biomass in our study could have a special role for spreading the parasite in the environment because they usually migrate further away than the age-matched females (Storm, 1976).

The spectrum of the rodent fauna in the study area is not yet investigated. When analysing the stomachs of the foxes, the water vole Arvicola terrestris was the most frequently found potential intermediate host besides others that also were present (Microtus arvalis, Clethrionomys glareolus and Mus domesticus; Gloor, unpublished data). According to many authors (reviewed by Weber & Aubrey, 1993) predation of foxes on A. terrestris occurs, but is generally considered to be light. However, Weber & Aubrey (1993) found, that A. terrestris, when highly abundant, was the most frequent prey of foxes in a rural area of western Switzerland. Furthermore, in an endemic alveolar echinococcosis area in France, A. terrestris was the most abundant and the only infected rodent species (Laforge et al., 1992).
Low prevalences below 1% were found in geographically extensive studies (Eckert et al., 2000a) but E. multilocularis infections are not randomly distributed in A. terrestris populations in endemic areas. High-endemic foci were described with prevalences in A. terrestris up to 39% (Pétavy & Deblock, 1983; Gottstein et al., 1996). Furthermore, seasonal differences were observed in France where the highest prevalence of 17·6% was found in January (74 animals examined), while no infections were found in October (167 animals examined) (Pétavy & Deblock, 1983). Contrary to the previously mentioned study we found high prevalences in late summer and

autumn when the vole density was high with the prevalence rates being highest in October 1997 (one third of the 30 animals examined infected). Therefore, we suspect that even higher prevalences could be higher in the park investigated at an earlier time of the year with more animals harbouring metacestodes that contain protoscolices.

The discovery of *E. multilocularis* infections in urban foxes and *A. terrestris* originating from a high-endemic focus in a public park provides evidence for the existence of a parasite cycle within the urban area. Furthermore, a synanthropic cycle including rodent-catching domestic carnivores, as described in a village in France (Pétavy, Deblock & Walbaum, 1991), seems to be possible in the area investigated. We detected urban *A. terrestris* that were infected with metacestodes of *T. taeniaeformis*, a cestode that is common in domestic cats, but was not found in our study in foxes. This indicates that an infection cycle between domestic cats and wild rodents indeed does exist. Although experimental studies with cats had shown that development of *E. multilocularis* was retarded and lower worm burden were found as compared to dogs which were highly susceptible (Thompson & Eckert, 1983), cat ownership was identified as a risk factor for alveolar echinococcosis (AE) in a recently published retrospective case-control study of patients in Austria (Kreidl *et al*., 1998). Low prevalences of *E. multilocularis* of 0·3% and 0·4%, respectively, were found in Switzerland (Deplazes *et al*., 1999) when investigating 660 randomly selected dogs and 263 cats, but higher prevalences of up to 12% have been reported in farm dogs with free access to rodents (Gottstein *et al*., 1997). Considering the high number of domestic dogs and cats in Central Europe the urbanisation of the *E. multilocularis* cycle could increase the infection risk for domestic carnivores and consequently also for humans.

E. multilocularis-infected foxes in urban areas pose novel epidemiological and infectiological questions. Recreational areas (e.g. public parks and outdoor swimming pool areas) within or adjacent to the city are frequently and intensively used by city-dwellers. However, it is not proven that an increased infection pressure results in a higher number of AE cases in humans. At present we have no evidence of an increase in the incidence of human AE in the study area. A major difficulty to unravel such epidemiological relations is the long incubation period (5-15 years) of AE (Amman & Eckert, 1995).

Acknowledgements

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Table 1. Small intestinal helminths discovered in 388 foxes collected from January 1996 to February 1998 in the city of Zurich (rural and urban area).

	No. of infected foxes	P (%)	CI (%)
Echinococcus multilocularis	172	44·3	39·3 – 49·4
Taenia spp.*	64	16·7	13·0 – 20·7
Mesocestoides sp.**	17	4·4	2·7 – 7·1
Dipylidium sp.**	2	0·5	0·1 – 2·1
Uncinaria stenocephala	259	66·8	61·8 – 71·4
Toxocara canis	184	47·4	42·4 – 52·5
Alaria sp.**	8	2·1	1·0 – 4·2

* *Taenia crassiceps*: 7·6%; *T. polyacantha*: 0·5%; *Taenia* sp.: 8·4%.

** No further species differentiation performed.

P, Prevalence; CI, Upper and lower 95% confidence interval.

Table 2. Seasonal differences in the prevalences of *Echinococcus multilocularis* in urban and rural foxes collected from January 1996 to February 1998 in the city of Zurich.
(Statistical comparisons were done (a) between age and sex groups, (b) between rural and urban foxes in winter (c) between urban foxes in winter and summer. Statistically significant differences are indicated with a letter.)

Season	Foxes	Urban foxes No. investigated / No. infected*	Rural foxes No. investigated / No. infected*
Winter (Nov.–Feb.)	adult females	39 / 16 (41%)	34 / 21 (62%)
	subadult** females	22 / 8 (36%)	20 / 14 (70%)
	adult males	29 / 13 (45%)	33 / 19 (58%)
	subadult males	39 / 24 (62%)[d]	36 / 28 (78%)
	Total	129 / 61 (47.3%)[a]	123 / 82 (66.7%)[b]
Summer (July–Oct.)	adult females	22 / 5 (23%)	1 / 1 (n.a.)
	subadult females	31 / 5 (16%)	1 / 1 (n.a.)
	adult males	12 / 4 (33%)	1 / 1 (n.a.)
	subadult males	28 / 5 (18%)[e]	1 / 0 (n.a.)
	Total	93 / 19 (20.4%)[c]	4 / 3 (n.a.)

* Chi-squared test: **a b** $P < 0{\cdot}01$; **a c** $P < 0{\cdot}0001$; **d e** $P < 0{\cdot}001$.
** Less than 12 months of age.
n.a.=not applicable

Table 3. Biomass of *Echinococcus multilocularis* (E. m.) expressed as percentage of the total worm numbers (398,653 worms) in 133 infected foxes collected in the city of Zurich in winter (November to February) in relation to sex and age.

	No. of infected foxes	E. m. biomass (%)	Median no. of E. m. specimens	∅ Worm number per fox	Worm number range	Mann-Whitney *U*-Test*
Female adult foxes	36	10%	60	1 050	1 – 19,344	n.s.
Female subadult foxes	20	22%	119.5	4 334	1 – 27,030	
Total female foxes	56	32%	56	2 223	1 – 27,030	
Male adult foxes	29	5%	120	730	1 – 5,720	n.s.
Male subadult foxes	48	63%	162.5	5 271	1 – 56,970	
Total male foxes	77	68%	150	3 561	1 – 56,970	
Total adult foxes	65	15%	63	907	1 – 19,344	$P < 0.05$
Total subadult foxes	68	85%	147	4 995	1 – 56,970	
Total foxes	133	100%	108	2 997	1 – 56,970	

* Significance of differences in the worm numbers

n.s. not significant

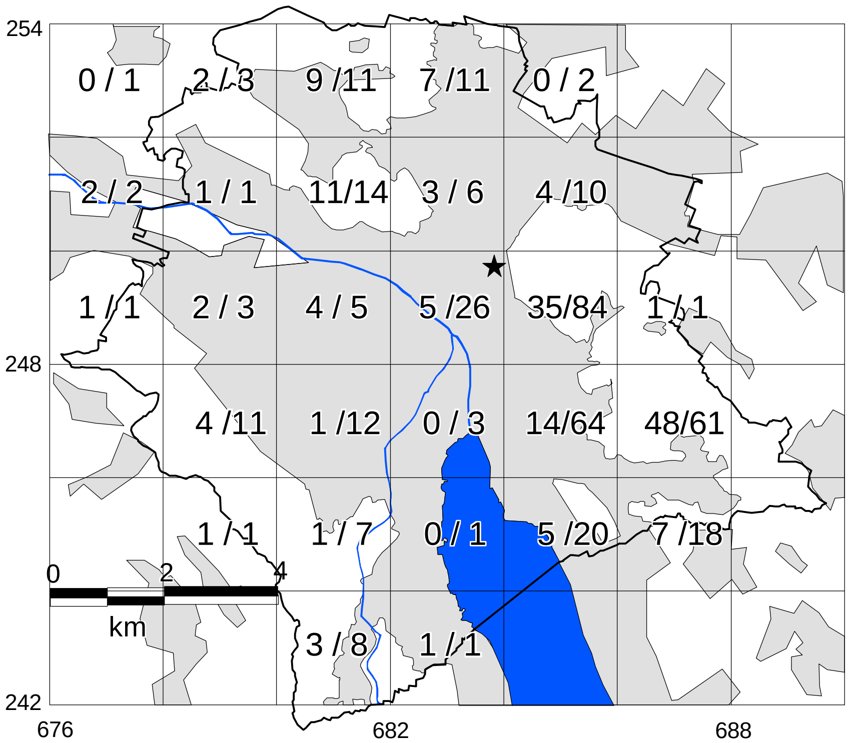

Fig. 1. Distribution of the 388 foxes investigated in the municipality of Zurich. Foxes originating from a grid of 4 km^2 were taken together (no. of foxes infected with *E. multilocularis* / no. of examined).White: rural area; light grey: urban area; dark grey : lake and rivers; black line: border of municipality; asterisk: Irchelpark (sampling site of *Arvicola terrestris*).

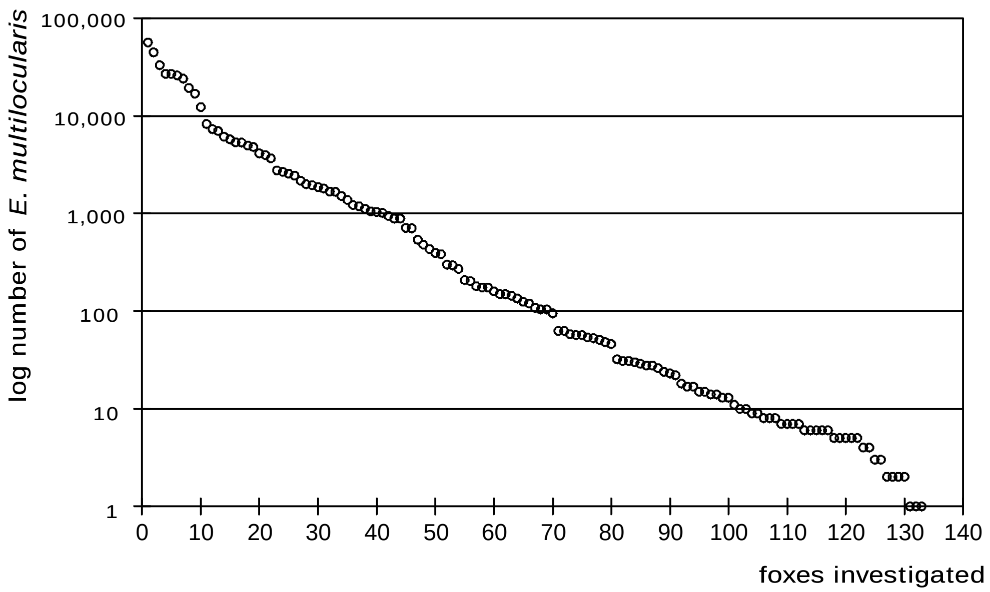

Fig. 2. Distribution of *Echinococcus multilocularis* biomass in 133 infected foxes (total worm burden 398,653) sampled in the city of Zurich (rural and urban area) in winter (November to February).

Urban transmission of *Echinococcus multilocularis*

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Abstract

In several European countries a distinct increase of the red fox (*Vulpes vulpes*) population was observed in recent years, particularly in urban areas. The number of foxes shot or found dead in the city of Zürich increased 20 times between 1985 and 1997. Therefore, an interdisciplinary project was initiated to study ecological and parasitological aspects of the urban fox population.

Preliminary ecological results show that the population density of foxes in the urban area is high and the animals have small homeranges. Within the city border, the prevalence of *Echinococcus multilocularis* in foxes increased significantly from the urban (47%) to the adjacent recreational area (67%).

To estimate the contamination of city areas with eggs of *E. multilocularis*, faecal samples of foxes were collected and investigated by a coproantigen ELISA. The spatial distribution of coproantigen positive samples was in accordance with the different prevalences found in necropsied foxes. In rodents trapped in recreational areas of the city, *E. multilocularis* metacestodes were identified by morphological examination, by EmG11-antigen detection with ELISA and by PCR. The prevalence in 781 *Arvicola terrestris* was 9.2% with fully developed protoscolices (14-240,000) occurring in 24 *A. terrestris*. Thus, an urban parasite cycle is established and a potential infection risk exists not only for urban residents but also for domestic dogs and cats. This new epidemiological situation and the emerging public awareness concerning zoonoses justify the evaluation of local intervention in the cycle of *E. multilocularis*.

Cestode Zoonoses: Echinococcosis and Cysticercosis

P. Craig and Z. Pawlowski (Eds.)

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1. Introduction

Echinococcus multilocularis is typically perpetuated in a wild-life (= silvatic) cycle including foxes (genera *Vulpes* and *Alopex*) as definitive hosts and different rodent species, mainly *Arvicolidae*, as intermediate hosts [1]. In some endemic areas, other species of wild carnivores, such as coyote, wolf, and raccoon dog, are involved as definitive hosts. In addition, a synanthropic cycle exists in some rural communities with domestic dogs as definitive hosts, which acquire the infection from wild rodents [2, 3, 4].

In the central European endemic area, red foxes (*Vulpes vulpes*) are likely to be responsible for most of the environmental contamination with *E. multilocularis* eggs. This was concluded from a study in which the prevalences of *E. multilocularis* in foxes, dogs and cats were related to the estimated population sizes of these definitive hosts [1]. Recent studies have shown that *E. multilocularis* has a wider geographic range than previously anticipated but prevalences of *E. multilocularis* in red foxes differ widely within and between endemic areas from about 1% to over 60% [5, 6, 7, 8]. Furthermore, there are reports on increasing *E. multilocularis* prevalences in some regions [7].

From retrospective studies, there is no direct correlation between fox population densities and human alveolar echinococcosis (AE). In Switzerland, the country-wide average annual incidences of human AE did not vary (0.10–0.18) during 36 years (1956-1992) suggesting a stable epidemiological situation despite high variations of the fox densities during this time [1]. In Europe**,** there is now evidence for growing populations of red foxes in some areas, for an increasing invasion of cities by foxes in the last 15 years [chapter 2] and also for the establishment of the parasite cycle in urban areas [9]. However, a retrospective analysis (1975-1999) comparing cases of AE in humans living in urban and rural communities in Switzerland revealed no significant changes in the incidence rates [E.C. Renner-Schneiter and R.W. Ammann, personal communication]. Whether these data reflect a continuing stable and low infection risk in urban areas or whether the increased infection pressure in highly populated areas will lead to a delayed increase in the incidence of AE cases in the future, remains to be seen. In certain regions, e.g. China, ecological changes have been reported to have influenced the epidemiological situation of AE in the past [3, 4].

In this review, we focus on the *E. multilocularis* transmission in urban settings in respect of the changing fox ecology in such highly populated areas.

2. Ecological changes in urban areas: the urban fox phenomenon

2.1. Historical overview

Red foxes living in urban areas are known from Great Britain since the inter-war period in the 1930s [10]. In these years there was a boom of private house construction because of cheap land prices, resulting in large districts of middle-class suburbs with low-density housing and medium-sized gardens. This is the type of habitat which was found to be favoured by foxes [11]. Once established in these residential suburbs, foxes moved further into the city and also colonised less prefered habitats.

In the 1970s and 1980s, fox populations in British cities reached densities of up to five fox family groups per km2 (representing 12 adults on average, in some cases more than 30 adult foxes per km2), densities which had never been observed so far [12]. As these observations were unique world-wide, urban foxes were initially thought to be an isolated British phenomenon [13, 14].

On the European continent fox populations experienced in the 1970s and 1980s a heavy rabies epizootic, a zoonosis not present on the British Isles. Subsequently, fox populations decreased drastically on the continent. Rabies hit Switzerland in 1967 [15] and fox densities reached a low in 1984, as can be seen from the Swiss hunting bag [16]. However, fox populations recovered again from 1985 onwards (e.g. [17]) because of successful oral vaccination campaigns against rabies, which started in Switzerland in 1978 [18] and which were extended into the whole European epizootic area in the following years (e.g. [19]).

Apart from this development in rural areas, more and more foxes have been recorded from large Swiss conurbations and cities such as Zürich or Geneva. An inquiry of town officials and persons responsible for wildlife management revealed that foxes are present in 28 of the 30 largest Swiss cities [20]. Similar observations were recorded from other parts of the distribution area of the red fox, e.g. from Oslo, Norway [21], Arhus, Denmark [22], Stuttgart, Germany [7], Toronto, Canada [23] and Sapporo, Japan [24].

The presence of urban fox populations raises the question of the impact of human behaviour and attitudes towards these wild animals [25]. Food provided by humans represents a major part of the diet of urban foxes in Great Britain [26, 27]. Additionally, the presence of foxes in close neighbourhood of people influence the management of fox populations and prevention strategies of zoonoses (e.g. rabies and alveolar echinococcosis).

2.2. Ecological aspects of an increasing red fox population in the city of Zürich: preliminary results

The largest conurbation of Switzerland is the area of Zürich with some 1,000,000 inhabitants. However, only 360,000 of this population live in the political community of Zürich, which we refer to when we use the term "the city of Zürich". The city (92km^2) consists of 53% urban area, 24% forest, 17% agricultural areas and 6% water surface [28]. Forest and agricultural areas surround the urban area and are referred to as the recreational area of the city in the following pages (Fig. 4). Correspondingly we distinguish between foxes found in urban area (urban foxes) and foxes found in adjacent recreational area (rural foxes).

As far as hunting is concerned, the city of Zürich is a game sanctuary. Official game wardens have maintained a constant hunting regime and a reporting system since 1926. Urban foxes have been present in the city of Zürich since the 1960s, but at low numbers until the mid 1980s (Fig. 1). From then onwards the number of foxes shot or found dead in the whole city increased drastically, i.e. 20 times between 1985 and 1997, notably in the urban area [20].

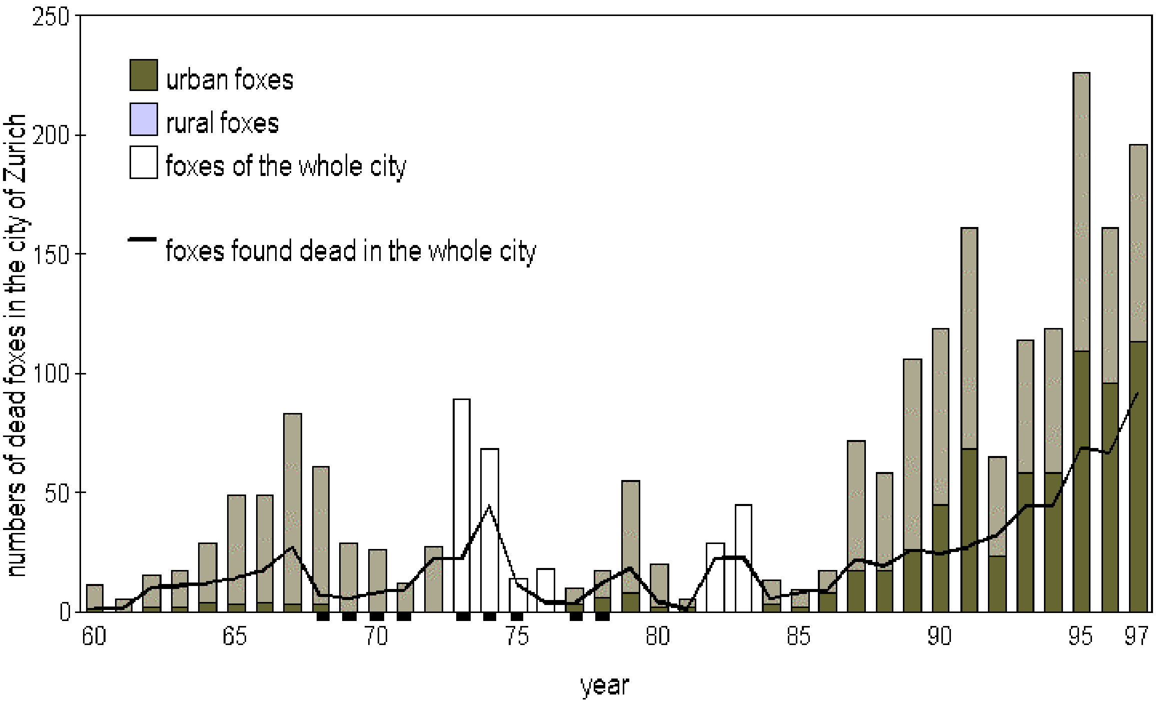

Fig. 1: Fox mortality (foxes shot or found dead) in urban and adjacent recrational areas in the city of Zürich (Switzerland) from 1960 to 1997. From the years 1973 – 1976 and 1982 - 1983 only total numbers of dead city foxes are available (white bars). The years with rabies cases within 5 km of the city centre are marked with small black bars (modified after [20]).

In order to study the spatial and habitat use of the urban fox population of Zürich, 20 adult foxes (12 females and 8 males) were observed by radiotracking [S. Gloor, unpublished data]. The study was carried out in a residential area of the city of about 11 km^2 between December 1996 and June 1999. The homeranges of the radiotracked foxes were analysed in three periods of the year (March to June; July to October; November to February). The homeranges of the vixens and of the resident male foxes were relatively small (Fig. 2) and comparable with those observed in British cities with high fox densities (e.g [29, 30]). According to preliminary homerange analyses, the homeranges of vixens were 30.6 ha ± 15.9, and the homeranges of resident male foxes were 42.0 ha ± 23.9 (100% MCP). However, three male foxes had significantly larger homeranges of 144.1 ha ± 39.2 and did not seem to be resident in an own area. Overlapping homeranges of foxes of the same sex and observations of more than two adult foxes at breeding dens indicate the establishment of familiy groups. This is in agreement with preliminary results of reproductive data from dead foxes collected in the city of Zürich which revealed that not all of the adult vixens do reproduce.

In the area of the radiotracked resident foxes (6.7 km^2) 23 dens with cubs were known in 1999. Assuming two adult foxes per breeding den, the fox densitiy in the area would be 6.9 adult foxes/km^2 or 10.3 adult foxes/km^2 with three adult foxes per den.

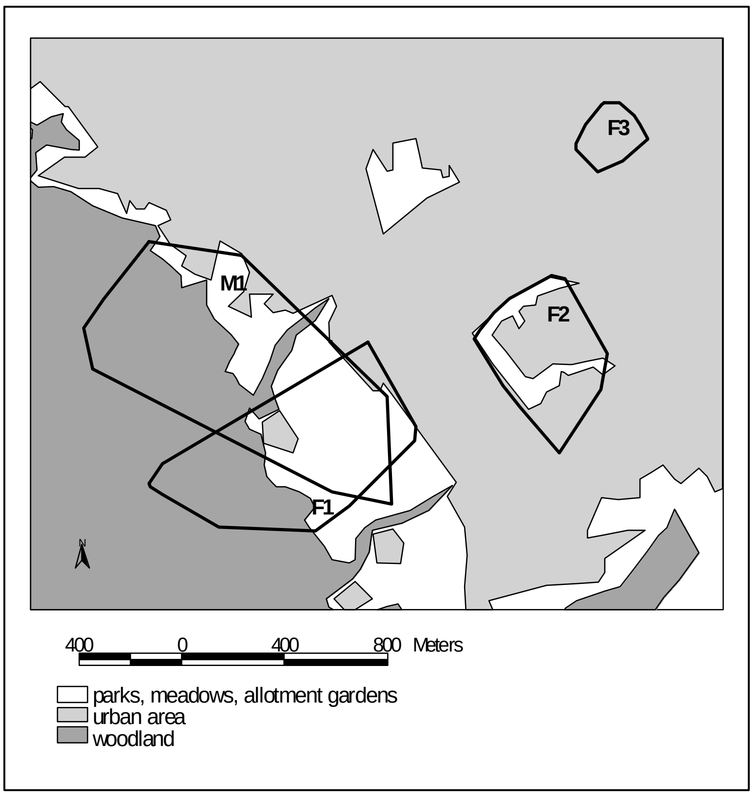

Fig. 2: Homeranges of three female foxes (F1, F2, F3) and one male fox (M1) from July to October 1998, in urban and adjacent recreational areas in the city of Zürich (Switzerland).

3. Epidemiology of *E. multilocularis* in urban settings

3.1. Infection pressure in urban areas

In recent years, the occurrence of *E. multilocularis* in urban foxes has been reported from several European cities, e.g. Copenhagen, Geneva, Munich, Stuttgart, Zürich [7, 9, 31] and from Sapporo (Japan) [24]. However, there is no detailed data available about the transmission ecology of *E. multilocularis* in the urban environment. A preliminary study on the epidemiological role of red foxes in the urban area of Sapporo was based on the detection of parasite coproantigen in faecal samples collected around active fox dens most of them being located in the urban fringe [24]. Thirty-three of the 155 samples (21%) which tested positive originated from the surroundings of 11 dens including one from the urban area. In this study, *E. multilocularis* was not detected in a small number of 23 rodents at necropsy. The authors pointed out that the life-cycle of *E. multilocularis* may not easily be maintained in the central urban area, whereas the outskirts of Sapporo offer a good habitat for the most suitable intermediate host *Clethrionomys spp*. [24].

3.2. Urban cycle of *E. multilocularis* in the city of Zürich (Switzerland)

Over a period of 26 months (1996-1998), 388 foxes from the city of Zürich were examined for intestinal infections with *E. multilocularis* and other helminths [9]. Seasonal differences in the prevalence of *E. multilocularis* were only found in urban subadult male foxes which were significantly less frequently infected in summer than in winter. The prevalence of *E. multilocularis* in 252 foxes sampled during winter increased significantly from 47% in the urban to 67% in the adjacent recreational area whereas a decrease of the *Mesocestoides* prevalence was observed (Table 1). The prevalence rates of other helminths were similar in both areas.
The distribution of the *Echinococcus* biomass, as expressed by worm numbers per fox, was overdispersed in 133 infected foxes randomly sampled in winter (Fig. 3) [9]. Therefore, a few highly infected foxes (carrying thousands of fertile worms) can be responsible for most of the environmental egg contamination. For example, 7.5% of the fox population (10/133) harboured more than 72% of the total worm number with a maximum individual worm burden of about 57,000. Prevalences did not differ significantly in these foxes in regard to age and sex, but worm burdens were significantly higher in subadult foxes as compared with adult foxes (Fig. 3). A total of 82.7% of the worm burden was detected in 68 subadult foxes, and 65 adult foxes harboured the remainig 17.3%. In the same study [9], metacestodes of *E. multilocularis* were found in 14% (19/135) of water voles (*Arvicola terrestris*) in a city park. This investigation provided evidence for the existence of an urban wild-

life cycle of *E. multilocularis* in the city of Zürich. Therefore, a new project was initiated in 1998 focusing on the assessment of the infection pressure with *E. multilocularis* eggs in urban environments by investigating faecal samples of foxes collected in the field and by further studies of rodents.

Table 1: Small intestinal helminths discovered in 252 foxes collected from January 1996 to February 1998 during winter (November to February) in the city of Zürich (Switzerland) [9]. Numbers, prevalences and confidence intervals are shown separately for foxes originating from the urban area (urban foxes) and from the adjacent recreational area (rural foxes).

	129 urban foxes			123 rural foxes			
	N	P (%)	CI(%)	N	P (%)	CI(%)	χ^2 test*
Echinococcus multilocularis	61	47.3	38.5 - 56.1	82	66.7	58.1 - 75.2	0.002
Taenia spp.	25	19.4	12.4 - 26.4	28	22.8	15.2 - 30.4	n.s.
Mesocestoides sp.	13	10.1	4.8 - 15.4	3	2.4	0.0 - 5.2	0.018
Dipylidium sp.	1	0.8	0.0 - 2.3	0	0.0	0.0 - 0.0	n.s.
Uncinaria stenocephala	92	71.3	63.3 - 79.4	89	72.4	64.3 - 80.5	n.s.
Toxocara canis	56	43.4	34.7 - 52.2	59	48.0	38.9 - 57.0	n.s.
Alaria sp.	2	1.6	0.0 - 3.7	6	4.9	1.0 - 8.8	n.s.

* Significance (two-tailed) of differences in prevalence of urban foxes and foxes from the adjacent recreational area (rural foxes).

Faecal samples were identified as of fox or dog origin by using the criteria, sample size, shape and smell. Since domestic dogs are numerous in urban areas, our sampling strategy was evaluated by comparing the parasite spectrum and the composition of the sample content of three types of samples, namely field samples identified as fox or dog faeces and samples taken from deposit boxes into which dog owners are advised to dispose their animals' faeces collected in plastic bags. Samples identified as fox field faeces contained significant more helminth eggs (68%) than dog field faeces (3%). Results from dog samples from the deposit boxes were comparable to those of the field samples judged as dog faeces. In fox samples fruit remnants and feathers were found frequently but not in samples of putative dog origin [C. Stieger and P. Deplazes, unpublished data].

The diagnostic strategy for the detection of *E. multilocularis* in the collected samples was performed as described by Mathis and Deplazes [32]. A coproantigen

ELISA (EM-ELISA) [33] was used as a screening test and the results were confirmed by PCR [34] using 22 coproantigen positive and 18 negative samples [C. Stieger and P. Deplazes, unpublished data]. The sensitivity of the ELISA for patent infections, as determined by egg isolation and PCR, was 89% and comparable with the sensitivity (84%) of the same test determined with samples obtained from killed animals [33]. These data confirm other results of *E. multilocularis* coproantigen studies applied in the field [35, 36].

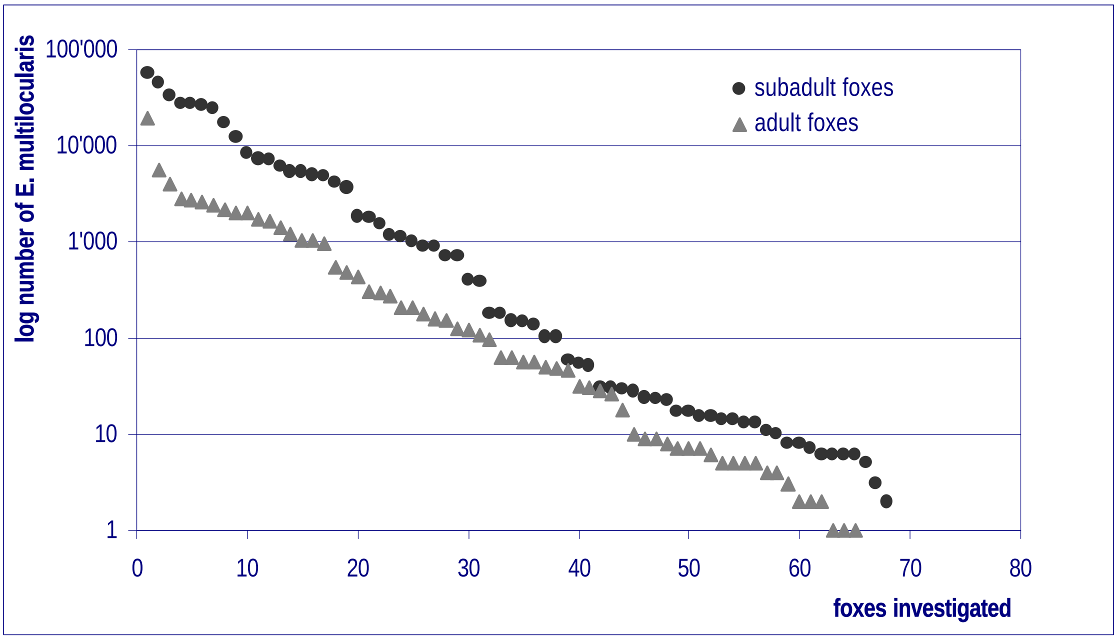

Fig. 3: Distribution of the *E. multilocularis* biomass in 65 adult foxes and 68 subadult foxes sampled in the city of Zürich (Switzerland) in winter (November- February).

The analyses of 647 fox faecal specimens collected within the city revealed coproantigen-positive samples in 10% up to 60% in different areas. The spatial distribution of coproantigen positive samples (Fig. 4, A and B) was in accordance with the different prevalences found in necropsied foxes [9] and gave evidence for a high contamination with *E. multilocularis* in the recreational area. Furthermore, it is worth to note that 47 faecal samples were found directly on vole ground systems of *A. terrestris* where signs of predation activities of carnivores were observed. Metacestodes of *E. multilocularis* were identified morphologically, by PCR [32] and by an ELISA specific for *E. multilocularis* antigen [37]. In 72 (9.2%) of 781 *A. terrestris* trapped in the recreational area mainly at the city border *E. multilocularis* were detected (Fig. 4, C and D). Protoscolices (14-240,000) were seen in 24 animals. However, other important intermediate hosts, such as *Microtus* and *Clethrionomys* species need to be investigated to assess their role in this urban cycle.

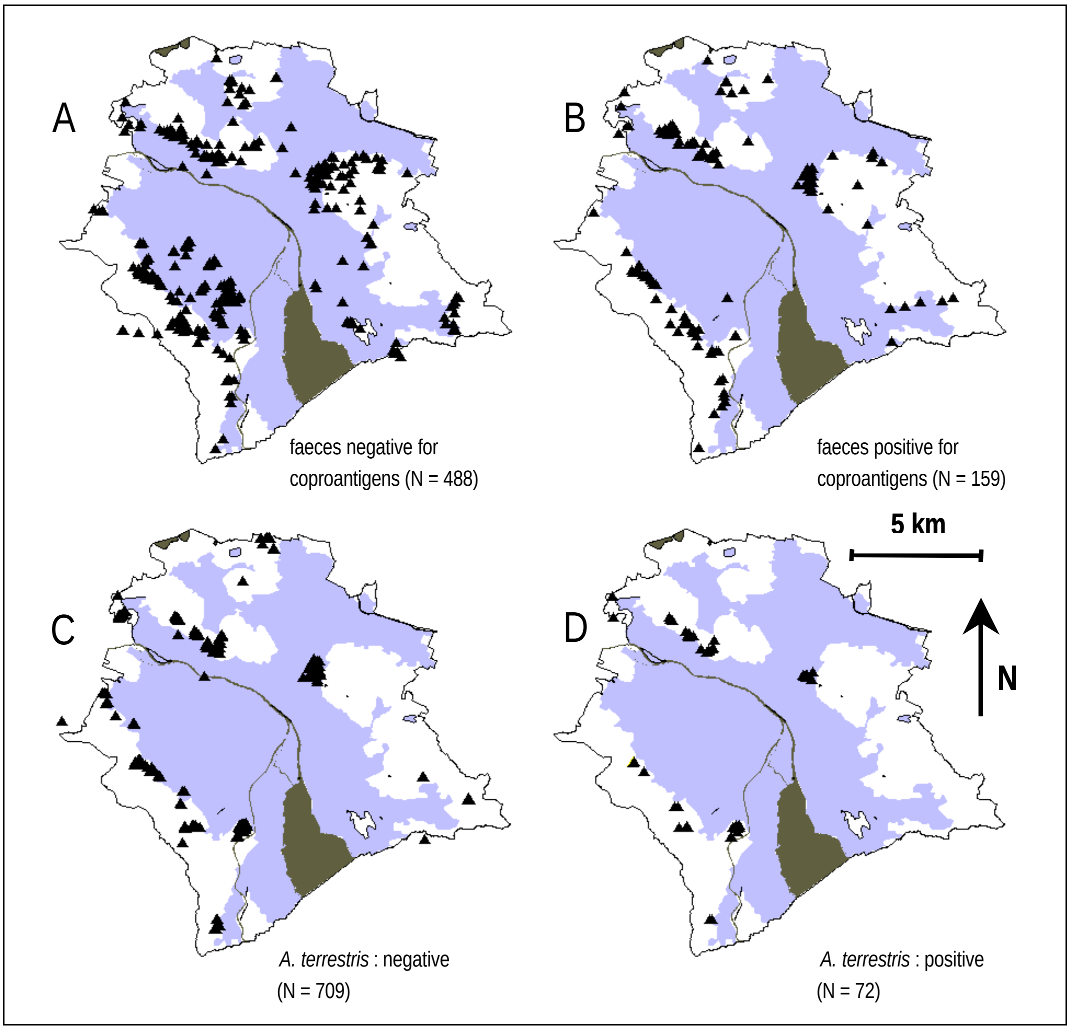

Fig. 4 (A-D): Distribution of coproantigen negative and positve faeces (A and B), and of Arvicola terrestris negative and positive for Echinococcus multilocularis (C and D) in the city of Zürich (Switzerland). Dark grey: rivers and lakes; bright grey: densly populated area; white: recreational area; black line: border of the city.

4. *E. multilocularis* infection in urban domestic carnivores

Our data show that an urban wild-life cycle of *E. multilocularis* in Zürich does exist and hence, a potential infection risk not only for urban residents, but also for domestic dogs and cats which may acquire the infection by preying on metacestode-infected rodents. In certain epidemiological situations in Alaska and China high prevalences of *E. multilocularis* have been found in domestic dogs (1-12%) which apparently were mainly responsible for the transmission of the infection to humans [3, 4]. In other endemic areas, e.g. Europe, USA, Japan, the epidemiological significance of domestic carnivores is uncertain. In France and Germany, studies performed on dogs and cats at necropsy revealed local *E. multilocularis* prevalences of 0.5% to 5.6% [38, 39]. Such necropsy studies have the disadvantage that the animals mostly represent a selected population and only low numbers of animals can be examined. Nowadays, modern techniques allow surveys of larger populations of living animals. Low *E. multilocularis* prevalences of 0.3% and 0.4%, respectively, were found in Switzerland in 660 randomly selected living domestic dogs and in 263 cats by detection of specific coproantigen and confirmation of positive results by PCR [33]. Higher infection rates of 7% in 86 dogs and of 3% in 33 cats were discovered in a rural area of western Switzerland with a high prevalence of *E. multilocularis* in fox and rodent populations [40].

The high prevalence of *Taenia taeniaeformis* (11.4%) in the *Arvicola terrestris* population in the city of Zürich, and the fact that *T. taeniaeformis* was not found in foxes in this area [9] indicate that domestic cats also could acquire *E. multilocularis* infections. However, the zoonotic significance of *E. multilocularis* infections in cats is probably low due to a retarded development and strongly reduced egg production of the worms [41].

Irrespective of the relative significance of dogs and cats for contaminating the environment with *E. multilocularis* eggs it should be stressed that all dogs and cats in endemic areas with access to rodents should be regarded as potential sources of human infection [42].

5. Future control of AE in urban areas

In view of the stable epidemiological situation of human AE in Switzerland [see introduction] there doesn’t seem to be an urgent requirement for control measures against *E. multilocularis*. Nevertheless, the high prevalence of *E. multilocularis* in a growing urban fox population and the emerging public awareness concernig urban zoonosis might force officals to implement control strategies in the future. Therefore, active and throroughly planned information campaigns about the presence of this zoonosis and its associated potential risks should be carried out [43] paralleled by further research on possible control strategies.

A reduction of the abundance of intermediate hosts is very difficult and ecologically questionable. The impact of fox culling is controversialy discussed and is dependent on different parameters (e.g. [44]). A study on an urban fox population in London showed that hunting mainly affects the population structure and that a reduction in fox numbers can hardly be achieved with conventional control methods [13]. Culling could even have a counterproductive effect on zoonosis prevention [45], because recolonization of areas and spatial perturbation caused by culling could facilitate disease transmission.

A control strategy by repeated treatment of rural foxes with baits containing 50 mg praziquantel (20 baits per km2 distributed by aircraft) over large areas in Germany has shown that the prevalence of the parasite can be significantly reduced in the fox population. [7, 8]. However, the long-term effects and the cost-effectiveness remain to be determined. Fox baiting in urban areas has so far not been critically studied, not even for rabies control.

In a preliminary investigation we documented the uptake of baits in urban areas by means of camera traps. These results revealed that domestic cats and foxes were most frequently photographed at baiting places but neither cats nor the few observed stone martens and badgers did eat the baits [D. Hegglin, unpublished data]. Most of the 144 baits delivered in summer 1999 were taken up within three days by foxes (39 baits), followed by hedgehogs (14 baits) and domestic dogs (2 baits).
The cycle of E. multilocularis in urban settings seems to be determined by the small homeranges of foxes and the distribution of suitable intermediate hosts. Therefore, local interaction in the cycle reducing the infection pressure in defined areas (e.g. public parks, swimming pool areas, private gardens) should be feasible. Field studies in Zürich on the control of the E. multilocularis infection in urban areas by distributing praziquantel-containing baits manually are currently being carried out. Similarly, a baiting campaign is planned in Sapporo (Japan) [Y. Oku, personal communication].

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Im Verlaufe meines Studiums besuchte ich Vorlesungen folgender DozentInnen:

Bachofen, R; Barbour, A.D., Biegert, J.; Burla, H.; Chanson, R.; Chen, P.S.; Christen, Ph.; Cook, C.D.K.; Dübendorfer, A.; Endress, P.K.; Eugster, C.H.; Gigon, A.; Gomez, P.; Graf, K.; Haffner, M.; Hegelbach, J.; Honegger, R.; Honegger, Th.; Kägi, J.; Klötzli, F.; Kramer, C.U.; Kummer, H.; Landolt, E.; Matile, P.; Meyer, V.; Nievergelt, B.; Oswald, H.R.; Raboud, C.; Rast, D.; Ribi, G.; Rieber, H.; Schaffner, W.; Schanz, F.; Schelbert-Syfrig, H.; Schmid, P.; Stolba, A.; Storrer, H.H.; Stutz, H.-P. B.; Tardent, P.; Turner, D.C.; Wehner, R.; Wildermuth, H.; Ziswiler, V..

List of publications

Hegglin, D.; Bontadina, F.; **Gloor, S.** (1998): From the alpine to the urban fox - adaptive behaviour of the red fox (*Vulpes vulpes*). Advances in Ethology 33: 119, Supplements to Ethology. Abstract.

Hofer, S.; **Gloor, S.**; Müller, U.; Mathis, A.; Hegglin, D.; Deplazes, P. (2000): Urban cycle of *Echinococcus multilocularis* in the city of Zurich, Switzerland. Parasitology 120, 135-142.

Breitenmoser-Würsten, C., Robin, R., Landry, J.-M., **Gloor, S**., Olsson, P., Breitenmoser, U. (2001): Die Geschichte von Fuchs, Luchs, Bartgeier, Wolf und Braunbär in der Schweiz – ein kurzer Überblick. For. Snow Landsc. Res. 76: 9-22.

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Gloor, S.: Spatial organisation of foxes in the recently colonised city of Zurich, Switzerland. (Submitted)

Gloor, S.: Adaptations to urban environment in habitat association of foxes. (Submitted)

Wandeler, P; Funk, St. M.; Largiadèr, C. R., **Gloor, S.**, Breitenmoser, U.: The city-fox phenomenon: genetic consequences of a recent colonisation of urban habitat. (Submitted)

Contesse, P.; Hegglin, D.; **Gloor, S.;** Bontadina, F.; Breitenmoser, U.; Deplazes, P.: Anthropogenic food resources allow increase in a Swiss urban fox (*Vulpes vulpes*) population. (Submitted)

Hegglin, D.; Bontadina, F.; **Gloor, S**.; Romer, J.; Müller, U.; Breitenmoser, U.; Deplazes, P.: Baiting red foxes in urban area: a camera trap study. (Submitted)