Plasticity of predation behaviour as a putative driving force for parasite life-cycle dynamics: the case of urban foxes and *Echinococcus multilocularis* tapeworm

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Summary

1. Parasite transmission frequently depends on an intermediate host species being subject to predation by a definitive host. We hypothesized that the population dynamics of this type of parasite would be affected by plasticity of the predation behaviour of the final host.

2. The zoonotic tapeworm *Echinococcus multilocularis* Leuckart is transmitted to foxes (*Vulpes vulpes* L.) by predation on infected rodents. One possible mechanism underlying the significant decrease in the prevalence of *E. multilocularis* in red foxes observed towards the centre of Zurich (Switzerland) is that the relative abundance of intermediate hosts varies between different urbanized habitats.

3. The water vole, *Arvicola terrestris scherman* L., which is the major intermediate host, was less abundant in urban compared with peri-urban areas, due to both a reduced availability of suitable habitats and lower numbers within those habitats. Stomach content analyses indicated that foxes in urban areas consumed more anthropogenic food but preyed less frequently on rodents – and those rodents taken belonged to species less susceptible to *E. multilocularis* infection.

4. We conclude that the functional response of final hosts to changes in supply of intermediate hosts and alternative food sources can significantly affect the transmission dynamic of dixenous parasites, such as this zoonotic tapeworm.

Introduction

Many macroparasites change their host species during their life cycle. Frequently, one or more asexual larval stages live in prey species and develop to an adult sexual stage in a predator species. It is assumed that a parasite enhances its transmission rate by having a larval stage in an abundant intermediate host that is a frequent prey species for a final host (Choisy *et al*. 2003), and that this strategy also increases the chances of finding a sexual mate (Brown *et al*. 2001). In addition, the different temporal and spatial dynamics of intermediate and definitive host species could enhance dispersal and increase the persistence of a parasite population

(Mackiewicz 1988). However, this alternation between species makes a parasite dependent on the prey–predator interaction, and changes in food acquisition by the definitive host (which can be caused by factors such as environmental change) could adversely affect the parasite's life cycle (Mackiewicz 1988).

The prey–predator interplay is therefore a key factor in understanding the transmission dynamics of obligatory heteroxenous parasites such as cestodes. For example, the small fox tapeworm *Echinococcus multilocularis* Leuckart is a zoonotic parasite with a dixenous life cycle (Eckert & Deplazes 2004). The adult, intestinal stage lives in various carnivores and eggs are excreted in faeces. Intermediate hosts are infected by ingestion of these eggs and harbour the parasite's larval stage (metacestode) in their liver. To complete the life cycle of the parasite, a definitive host

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must ingest fully developed metacestodes by preying on infected intermediate hosts.

In east and central Europe, the main definitive host is the red fox (*Vulpes vulpes* L.), with arvicolid species, predominantly the common vole (*Microtus arvalis* Pallas) and the fossorial form of the water vole (*Arvicola terrestris scherman* L.), acting as intermediate hosts (Eckert 1998). Although *E. multilocularis* is remarkably prevalent in foxes in endemic areas (20–70% individuals are infected), prevalence rates in intermediate species are generally low (<1–6%) (Eckert 1998), and rarely exceed 20% (Gottstein *et al.* 1996; Henttonen *et al.* 2001) with infection recorded only occasionally in murid rodents (Eckert *et al.* 2001).

Red foxes are the most widespread carnivore species in the Northern Hemisphere. Their behavioural plasticity enables them to live in a wide range of habitats. Their opportunistic feeding behaviour is an important factor in the recent colonization of urban areas (Harris 1981; Doncaster, Dickman & Macdonald 1990; Contesse *et al.* 2004). The high availability of food in urban environments allows urban foxes to live within small home ranges (Doncaster & Macdonald 1991; White, Saunders & Harris 1996; Gloor 2002) and foxes can reach very high densities that are not observed in other habitats (Voigt & Macdonald 1984; Harris & Smith 1987; Baker *et al.* 2000; Gloor 2002).

In the city of Zurich, the prevalence of *E. multilocularis* in foxes varies both temporally and spatially, with the highest prevalence rate (47%) occurring in winter (Hofer *et al.* 2000). Prevalence rates in potential intermediate host species are also variable, being remarkably high in water voles (22%), substantially lower in both common voles (4·9%) and bank voles (*Clethrionomys glareolus* Schreber) (2·4%), and zero in wood mice (*Apodemus sylvaticus* L.) and yellow-necked mice (*Apodemus flavicollis* Melchior) (Stieger *et al.* 2002; unpublished data). These different rodent species exhibit distinct differences in ecology and habitat preferences: arvicolid species (*A. terrestris* and *M. arvalis*) live mainly in meadows and pastures, whereas murid species (e.g. *A. sylvaticus*) prefer bushy habitats with more shelter, such as forests and hedges (Hausser 1995), but can also reach high density in urban habitats such as public parks and residential areas (Dickman & Doncaster 1987). Consequently, we would expect (1) the distribution of rodent species to vary with the size and fragmentation of these key habitat types in the urban environment; (2) that this variation would be reflected in the diet of the red fox; and (3) that this would, in turn, affect the transmission dynamics of *E. multilocularis*.

Central Zurich is a densely built urban area which is ringed by residential areas with more green space; beyond the city border are rural areas dominated by forests and agriculture. Within the urban area a high supply of anthropogenic food is available for urban foxes (Contesse *et al.* 2004). Thus we made the following predictions: (1) the supply of suitable habitat for

voles – and thus their availability – decreases from peri-urban areas towards urban areas; (2) as a functional response, foxes in urban areas would consume fewer voles and more anthropogenic food sources than in the adjacent peri-urban area; and (3) the prevalence of *E. multilocularis* in foxes would correspond to the predation rate of suitable intermediate hosts.

Methods

STUDY AREA

The political community of Zurich covers 92 km^2, with 360 000 human inhabitants, and consists of 53% built-up area, 24% forest, 17% agricultural land and 6% water (Anonymous 2000). The built-up area and the lake are situated in the centre, while the agricultural areas and the forests are located in the urban periphery. The study area was therefore divided into three zones, with the central urban and outer peri-urban zones (39 and 20% of the area) separated by a border zone (41%; Fig. 1). The urban zone contained little green space, and we defined its limit by a line following properties where buildings were in daily use and which were no more than 100 m from the next such building. The border zone was a 500-m-wide belt, extending 250 m either side of this boundary, which consisted mostly of residential areas, allotment gardens, cemeteries, sports fields and public parks. The peri-urban zone consisted of forests, fields, pastures and meadows, which are intensively used for recreational activities.

An extensive telemetry study in the city of Zurich has demonstrated that resident foxes rarely range between the urban and the peri-urban zones (Minimal Convex Polygon (MCP) home range sizes of 28·8 ± 22·7 ha for females and 30·8 ± 11·0 ha for males; Gloor 2002). Correspondingly, significant differences in the prevalence rates of *E. multilocularis* in foxes have been detected over distances of just 500 m (Hegglin, Ward & Deplazes 2003).

INTERMEDIATE HOSTS: HABITAT AVAILABILITY AND DENSITY ESTIMATES

Habitat suitability for the arvicolid species *A. terrestris* and *M. arvalis* was assessed by calculating the area of meadows and pastures on-screen with the help of the GIS software package ARCVIEW 3·3 (Environmental Systems Research Institute, Redlands, CA, USA). The relative population density of *A. terrestris* and *M. arvalis* was calculated according to Giraudoux *et al.* (1995) and Quéré *et al.* (2000), respectively. The methods are based on counting superficial signs of the activity of the two rodent species on predefined transects. The fossorial form of *A. terrestris* builds extended subterraneous burrow systems, which are accompanied by superficial earth tumuli. The common vole establishes clearly visible runways above the ground, where they also deposit their faeces. A total of 35 1-m-wide transects were paced out
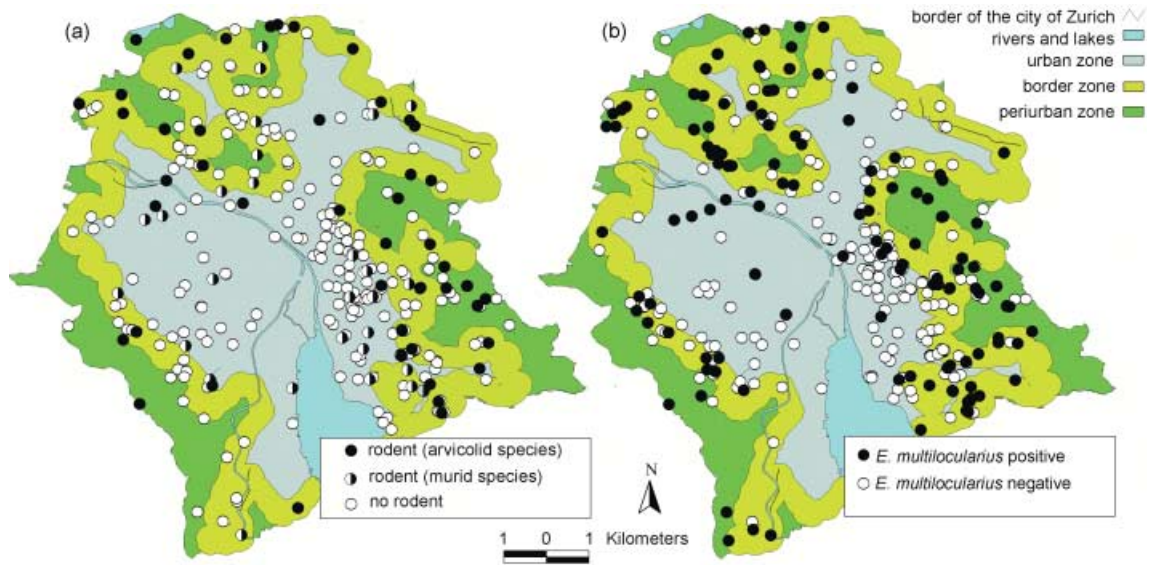
Fig. 1. Distribution of foxes (places shot or found dead) in the urban, border and peri-urban zones of the city of Zurich. Dots represent (a) foxes that had remains of arvicolid rodents, murid rodents or no rodents in their stomach ($N = 450$); (b) foxes with and without *Echinococcus multilocularis* infection ($N = 582$).

by the same observer (each 200 steps long, about 150 m) and at randomly selected locations in meadows and pastures (10 transects in the urban, 13 in the border and 12 in the peri-urban zone), and the proportion of 10-step intervals with tumuli of *A. terrestris* or faeces of *M. arvalis* was used as relative index of abundance for the two species (ranging from 0 to 100%). All transects were walked in the period 2–19 December 2003, when vegetation was low and the bare ground was visible.

DEFINITIVE HOST: PREDATION ON INTERMEDIATE HOSTS AND CONSUMPTION OF ANTHROPOGENIC FOOD

The game wardens of the city of Zurich collected and recorded all foxes shot or found dead between January 1996 and June 2001 ($n = 789$). The foxes were categorized as urban (31%), border (49%) or peri-urban (19%) according to the site of their collection, as well as by season of collection [spring (March–June, 16% of the sample), summer/autumn (July–October, 35%) and winter (November–February, 49%)], sex (equal numbers of males and females) and age (younger than 1 year *vs* 1 year or older, determined according to Kappeler 1991: 55% juveniles, 45% adults.

After dissection of the stomach of each fox, the contents were washed in a sieve and possible remains of rodents were separated (for details see Contesse *et al.* 2004). Stomachs that contained <2 ml were classified as empty. Rodents were identified to species level according to Niethammer & Krapp (1982), if recognizable feet, tails or teeth were present. The keys of Day (1966) and Teerink (1991) were used to identify species by their hairs. A subset of 402 of these fox stomachs were analysed for remains of food of anthropogenic

origin (Contesse *et al.* 2004). For this study, a fox was classified as having consumed anthropogenic food when its stomach contained at least one of the following: scavenged meat (processed meat and bones), other scavenge (mainly vegetable kitchen waste, processed food), pets and domestic stock, pet food or bird seed (bird-feeding mixtures).

PARASITE: PREVALENCE IN DEFINITIVE HOST

Of the 789 foxes, 582 were used for parasitological analyses. Foxes collected after April 2000 were excluded because anthelmintic baits had been distributed in parts of the study area as part of a study on the control of *E. multilocularis*.

Echinococcus multilocularis infection in foxes was detected by the sedimentation and counting technique (for details see Hofer *et al.* 2000). Briefly, the small intestine was cut longitudinally and shaken in 0·9% NaCl solution. The sediment was washed by a standardized procedure of repeated dilution, shaking and decanting in a glass bottle, then small portions (about 5–10 ml) were examined in square Petri dishes for the presence of *E. multilocularis*.

STATISTICAL ANALYSIS

Density indices for *A. terrestris* and *M. arvalis* could not be normalized and were compared between the three zones using the non-parametric Kruskal–Wallis test. Dunn's *post hoc* tests were performed to identify significant differences between zones.

Feeding behaviour of foxes and prevalence rates of *E. multilocularis* in foxes can be affected not only by

spatial factors, but also by temporal (season, year; Weber & Aubry 1993; Stieger *et al.* 2002) and individual factors (age, sex; Tackmann *et al.* 1998). Logistic regressions were used for modelling predation rates on rodents in general (and voles in particular), the consumption rate of anthropogenic food and the prevalence rates. The factors zone, season and age were selected as the most promising independent variables for the modelling procedure. Furthermore, the age × season interaction was considered because the age structure of a fox population varies during seasons, with most young foxes in spring and fewest in winter. The age × zone interaction was included because hunting pressure was lower in the built-up areas than in the urban periphery (unpublished data), and this may have caused differences in the age structure of the fox population between the zones.

We fitted logistic regression models using all possible combinations of the selected predictor variables (zone, season, age, age × season, age × zone), but only models that significantly explained variation in the data set (log-likelihood ratio test) were included in the model-selection process. Best models were then selected using Akaike's information criterion (AIC; Akaike 1973; Burnham & Anderson 1998) corrected for small sample sizes (AICc, Burnham & Anderson 1998). The model with the lowest AICc can be viewed as the most parsimonious. Models with ΔAICc < 2 compared with the model with the lowest AICc were selected. We then calculated Akaike model weights (Burnham & Anderson 1998) to determine the degree to which a model is supported by the data. Weights of selected models sum to 1 by definition, and higher weights indicate better explanatory power.

To evaluate the relative importance of each explanatory variable, the AICc weights were summed up over all models where that variable was present. A variable that is included in all selected models sums up to 1, whereas a variable present in just one model gets the value of the corresponding model. Subsequently, the variables were ranked according to the resulting AICc weight sums. Odds ratios and their 95% confidence interval are given for the best of the selected models. An odds ratio of 1 indicates that an event is equally likely in both groups. Therefore the only factors that were interpreted were those that comprised at least one odds ratio with a 95% CI that did not include 1.

Statistical analyses were conducted using SPSS 10·0 (Norusis 1986). The fit of the logistic regression models were tested by likelihood ratio and Hosmer–Lemeshow goodness-of-fit tests. The minimal *P* value (P_{min}) of the Hosmer–Lemeshow goodness-of-fit tests and the maximal *P* value (P_{max}) for the likelihood ratio tests are given for the selected models. To express the sensitivity and specificity of the best models, receiver operating characteristic analyses were performed and threshold probabilities were determined by minimizing the absolute value of the difference between sensitivity and specificity (Cantor *et al.* 1999).

Results

INTERMEDIATE HOSTS: HABITAT AVAILABILITY AND DENSITY ESTIMATES

Meadows and pastures comprised a substantially greater proportion of the border (18·4%) and peri-urban (12·0%) zones than the urban zone (1·5%; Fig. 2a). The relative abundance of *A. terrestris* differed significantly between the three zones (Kruskal–Wallis test: $\chi^2 = 10·5$, df = 2, *P* < 0·01), being significantly higher in the border area (41·5%) than in the urban area (8·5%; Fig. 2b, Dunn's *post hoc* test, *P* < 0·05). The index of relative abundance of *M. arvalis* was much lower than that observed for *A. terrestris* and did not differ significantly between the three zones (Kruskal–Wallis test: $\chi^2 = 0·1$, df = 2, *P* > 0·1).

DEFINITIVE HOST: PREDATION ON INTERMEDIATE HOSTS AND CONSUMPTION OF ANTHROPOGENIC FOOD

Of the 789 stomachs analysed, 339 were empty. Only fox stomachs with content were considered for our analyses (*N* = 450). Remains of rodents were detected in 95 stomachs (21%). Of the 97 remains recorded (some stomachs contained more than one species), 56 originated from arvicolids (21, 22 and 13 remains of the genera *Arvicola*, *Microtus* and *Clethrionomys*, respectively); 32 from murids (26, four and two remains of the genera *Apodemus*, *Mus* and *Rattus*, respectively); three from the red squirrel (*Sciurus vulgaris*) and six from unidentified rodents.

The model-selection process to explain predation by foxes on rodents yielded eight logistic-regression models, all showing significant zonal variations (Table 1). The adequacy of all these multivariate models was supported with non-significant results from the Hosmer–Lemeshow goodness-of-fit test ($P_{min} = 0·60$) and significant results from the log-likelihood ratio test ($P_{max} = 0·004$). Ranking of the independent variables revealed zone as the most relevant factor (AICc weight sum = 1), followed by season (0·70), age (0·65), and the interaction terms for zone × age (0·33) and season × age (0·17). The best model comprised the two factors zone and season, while zone was the only factor with 95% confidence intervals of the odds ratios that did not include 1 (urban and border zone *vs* peri-urban zone; Table 2). In the urban and peri-urban zones, 16·5 and 18·8%, respectively, of stomachs contained rodents compared with 39·7% in the peri-urban zone (Fig. 2c).

A second model-selection process, based only on stomachs with rodent remains, was used to explain the fox predation rate on voles (*N* = 95), and yielded two models (Hosmer–Lemeshow goodness-of-fit test: $P_{min} = 0·93$; log-likelihood ratio test, $P_{max} = 0·003$). Again, zone turned out to be the most relevant factor (AICc weight sum = 1), followed by season (0·27). No other factor entered the selected models (Table 1). The
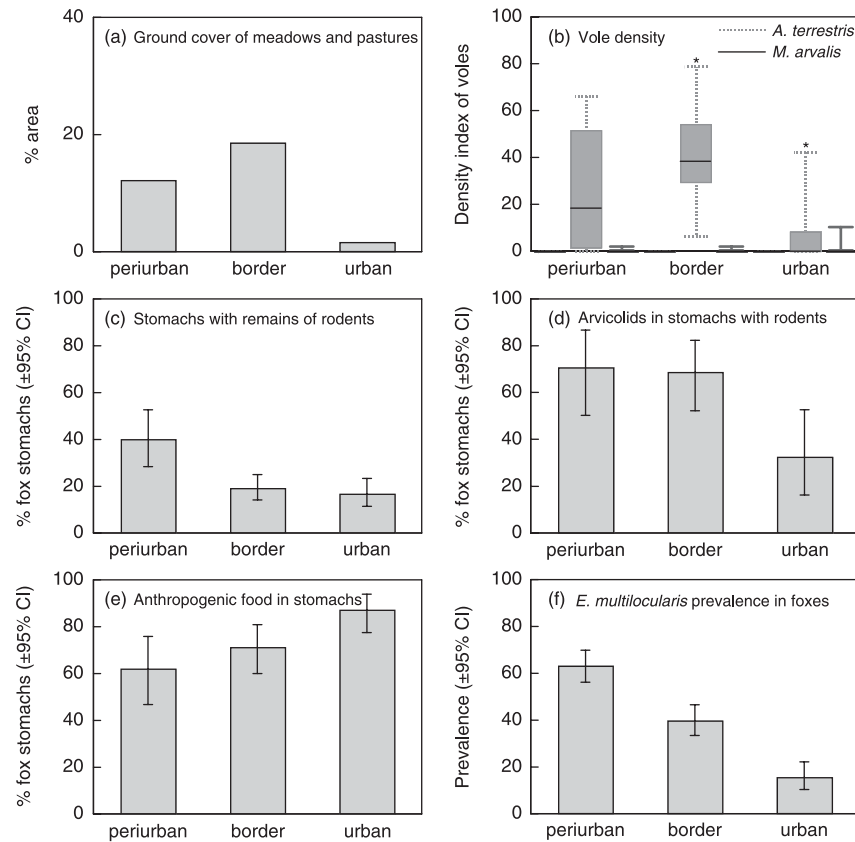
Fig. 2. Zonal variation of parameters relevant for the life cycle of *Echinococcus multilocularis* (see Methods for definition of the peri-urban, border and urban zones). (a) Proportion of area covered by meadows and pastures; (b) density index for *Arvicola terrestris* and *Microtus arvalis* [box plots with median, interquartile range and 10–90% whiskers: portion of intervals with signs of *A. terrestris* (grey) and of *M. arvalis* (black), respectively; $N = 35$ transects]; (c) portion of fox stomachs with remains of rodents ($N = 450$ non-empty fox stomachs); (d) proportion of arvicolid species in fox stomachs containing rodents ($N = 95$ fox stomachs with rodents); (e) proportion of anthropogenic food in fox stomachs ($N = 202$ fox stomachs with content); (f) prevalence of *E. multilocularis* in foxes ($N = 582$ foxes). Bars in (a) represent absolute areas, therefore no statistical analysis was performed. Data from (b) were analysed using a Kruskal–Wallis test and Dunn's *post hoc* test (*, $P < 0.05$); (c–f) were analysed by binary logistic regressions (Table 2).

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best model comprised only the factor zone (Table 2). The proportion of rodents belonging to the Arvicolidae (*Arvicola*, *Microtus* and *Clethrionomys*) was less than half in the urban zone compared with the border and peri-urban zones (30·4 *vs* 68·3 and 70·4%; Figs 1a and 2d).

A total of 202 of the 402 fox stomachs investigated for anthropogenic food contained food remains. Remains of anthropogenic food were found in 151 of these stomachs (74·8%). Only one model (Hosmer–Lemeshow goodness-of-fit test, $P = 0.99$; log-likelihood ratio test, $P = 0.003$) with the independent factors age and zone remained after the model-selection process (Table 1). A higher proportion of fox stomachs contained food from anthropogenic food sources in the urban zone (86·8%; Fig. 2e) than in the peri-urban zone (61·7%; Table 2).

PARASITE PREVALENCE IN DEFINITIVE HOST

A total of 582 fox intestines were analysed for *E. multilocularis* infections. Three models explained best prevalence rates in foxes (Hosmer–Lemeshow goodness-of-fit test, $P_{min} = 0.41$; log-likelihood ratio test, $P_{max} < 0.001$). All included the factors zone and season (Table 1). Accordingly, the ranking of the independent variables revealed zone and season as the most relevant factors (AICc weight sum = 1 for both), followed by age and season × age (0·69 for both), and zone × age (0·45). The best model comprised all factors that were added to the model-selection procedure (Table 2). However, the odds ratio 95% CIs of season and age comprised 1, and were therefore not interpreted (Table 2). The prevalence rates in foxes decreased from the peri-urban (62·9%) to the border (39·5%) and the urban zones (16·5%' Fig. 2f). The interaction term zone × age revealed that this decrease was more pronounced for adult foxes (63·1% peri-urban, 41·2% border and 7·5% urban zone) than for juvenile foxes (62·6% peri-urban, 37·6% border and 19·2% urban zone). Furthermore, seasonal changes of prevalence rates proved to be more pronounced in juvenile (13·2% spring, 20·4% summer/autumn and 56·7% winter) than in adult foxes (28·9% spring, 31·0% summer/autumn and 50·0% winter).

Table 1. Results from logistic-regression model selection to explain (a) predation by foxes on rodents (*N* = 450 fox stomachs with content); (b) proportion of arvicolids in predated rodents (*N* = 95 fox stomachs with rodents); (c) consumption of anthropogenic food (*N* = 202 fox stomachs with content); (d) prevalence rates of *Echinococcus multilocularis* in foxes (*N* = 582 fox intestines)

Model	AICc	ΔAICc	Weight
(a) Predation on rodents (*N* = 450)			
Zone, season	2·18	0·00	0·22
Zone, season, age, zone × age	2·70	0·52	0·17
Zone, season, age	3·12	0·94	0·14
Zone	3·42	1·24	0·12
Zone, age	3·98	1·80	0·09
Zone, season, age, season × age	4·06	1·88	0·09
Zone, age, zone × age	4·13	1·94	0·08
Zone, season, age, zone × age, season × age	4·16	1·98	0·08
(b) Predated arvicolid rodents (*N* = 95)			
Zone	26·78	0·00	0·73
Zone, season	28·75	1·97	0·27
(c) Anthropogenic food (*N* = 202)			
Zone, age	22·08	0·00	1·00
(d) Prevalence rates (*N* = 582)			
Zone, season, age, zone × age, season × age	103·23	0·00	0·45
Zone, season	103·94	0·70	0·32
Zone, season, age season × age	104·51	1·27	0·24

AICc, the Akaike information criterion corrected for small sample sizes and ΔAICc, the difference in AICc to the best model, are given. Weight indicates relative support of a particular model compared with the other models, higher values indicating better support. Selected models with ΔAICc < 2 were used for model averaging (Table 2).

Discussion

Parasites depending on a prey–predator system are limited to locations where the distributions of definitive and intermediate hosts intersect. Their occurrence and persistence depend on the availability of host species and the specific environmental conditions that enable the survival of free-living stages.

Our data indicate that the supply of intermediate hosts for *E. multilocularis* is strongly reduced in urban areas. The intermediate hosts *A. terrestris* and *M. arvalis* are strongly associated with meadows and pastures (Hausser 1995), but these habitats were 12·3 times less abundant in the urban area than in the adjacent border area (Fig. 2a). Furthermore, meadows and pastures sustained substantially lower densities of *A. terrestris* in the urban zone (Fig. 2b), possibly because of the increased fragmentation of these habitats, which would affect the connectivity of subpopulations, and because of the lower dispersal potential of arvicolid species relative to murid species (Dickman & Doncaster 1989). Consequently, the rodent community in the urban zone is likely to consist of a substantially greater proportion of murid species.

Predation by foxes on *A. terrestris* and *M. arvalis* correlates in general with the abundance of these two prey species (Weber & Aubry 1993; Kjellander & Nordström 2003), with foxes switching to alternative prey when voles become rare (Kjellander & Nordström

Table 2. Odds ratios (OR), 95% confidence intervals (CI), threshold probabilities, sensitivities and specificities of the best models (for *N* see Table 1)

Model factors	(a) Predation on rodents OR	95% CI	(b) Predated arvicolid rodents OR	95% CI	(c) Anthropogenic food OR	95% CI	(d) Prevalence rates OR	95% CI
Zone								
Urban *vs* peri-urban	0·30	0·15–0·61	0·17	0·05–0·54	4·81	1·92–12·0	0·05	0·02–0·17
Border *vs* peri-urban	0·35	0·19–0·64	0·89	0·31–2·56	1·74	0·79–3·84	0·46	0·25–0·85
Season								
Spring *vs* winter	0·46	0·20–1·09	–	–	–	–	0·70	0·30–1·67
Summer/autumn *vs* winter	1·15	0·68–1·94	–	–	–	–	0·78	0·38–1·61
Age (juvenile *vs* adult)	–	–	–	–	0·55	0·27–1·10	1·17	0·65–2·11
Zone × age								
Urban × juvenile *vs* peri-urban × adult	–	–	–	–	–	–	4·76	1·26–17·39
Border × juvenile *vs* peri-urban × adult	–	–	–	–	–	–	1·29	0·55–3·07
Season × age								
Spring × juvenile *vs* peri-urban × adult	–	–	–	–	–	–	0·23	0·06–0·89
Summer/autumn × juvenile *vs* winter × adult	–	–	–	–	–	–	0·36	0·14–0·91
Constant	0·67	–	2·36	–	2·04	–	1·75	–
Threshold probability		0·201		0·481		0·726		0·419
Sensitivity		0·516		0·854		0·645		0·715
Specificity		0·673		0·475		0·490		0·627

(a) Predation by foxes on rodents; (b) proportion of arvicolids in predated rodents; (c) consumption of anthropogenic food; (d) prevalence rates of *Echinococcus multilocularis* in foxes.

2003). Few signs of the arvicolid *M. arvalis* were detected in the meadows and pasture investigated here, although we recorded *M. arvalis* as frequently as *A. terrestris* in fox stomachs. Despite their dietary plasticity, different studies point out that foxes show preferences for certain prey species (Macdonald 1977; Green 2002). *Microtus* species appear to be more attractive than other arvicolid species, and arvicolid species in general are more attractive than murid species (Macdonald 1977). Correspondingly, we found that the decrease in predation on vole species (Fig. 2c,d) was much less pronounced than one would expect given the observed decrease in the supply of vole prey towards the city centre (Fig. 2a,b).

Nevertheless, in accordance with prediction 2, the analyses of stomach content indicate that foxes can shift their diet to murid species (which are less susceptible to *E. multilocularis* infection) if arvicolid species are rare (Fig. 2d). In addition, the total predation rate on rodents was significantly lower for foxes in urban areas than for foxes in the urban periphery, further reducing the total uptake of intermediate hosts (Fig. 2c). This functional response may be caused by the surplus of anthropogenic food accessible to foxes in urban areas, reflected in the increased contribution of such items to the fox diet (Fig. 2e).

A high amount of anthropogenic food available enables foxes to fulfil their requirements within small home ranges encompassing not more than 30 ha (Gloor 2002). We have shown in a preceding experimental study that this small-scale spatial organization of urban foxes is reflected in a low spatial dynamic of the life cycle of *E. multilocularis*. In six areas, each 1 km^2, foxes were dewormed regularly by the delivery of anthelmintic baits over 2 years. However, the effect of this treatment was detectable only within a range of 500 m around the baiting areas (Hegglin *et al*. 2003). This finding corresponds to the manifold decrease of *E. multilocularis* prevalence within a distance of not more than 500 m along the urban periphery (prediction 3; Fig. 2f). Hence we believe that the low supply of suitable intermediate hosts and the high levels of anthropogenic food sources available, combined with the resulting small-scale spatial organization of urban foxes, are responsible for the pronounced differences in the prevalence of *E. multilocularis* over small distances.

Conversely, however, anthropogenic food sources could enhance the transmission of *E. multilocularis* by increasing host densities. In urban areas, fox densities can exceed 10 adults per km^2, much higher than observed in rural areas (Baker *et al*. 2000; Gloor 2002). Thus the transmission of *E. multilocularis* could be especially intense in the transition zone between urban and peri-urban areas where high fox population densities are sustained by high anthropogenic food resources and suitable habitat for arvicolid species is abundant (Deplazes *et al*. 2004).

Our results suggest that the temporal and spatial dynamics of *E. multilocularis* is also affected by the age structure of fox populations. In juvenile foxes, the spatial variation of the prevalence rates was less pronounced than in adult foxes. This may reflect the spatial behaviour of juvenile foxes, which frequently show exploratory behaviour and/or disperse before they establish a territory. Furthermore, dispersion occurs mainly during late autumn and winter (Trewhella 1988), the period when the prevalence in juvenile foxes was highest in our study. Thus juvenile foxes may have best access to voles, and their roaming behaviour may play an important role in the spread of this parasite.

The larval stage of *E. multilocularis* can cause human alveolar echinococcosis, a severe helminthic zoonosis which is fatal if left untreated (Ammann & Eckert 1995). However, low incidence rates of human alveolar echinococcosis have been recorded in Europe to date (Kern *et al*. 2003). Apart from individual risk factors (e.g. owning dogs, living in a farmhouse; Kern *et al*. 2004), ecogeographical factors such as a high vole densities appear to increase the risk for human alveolar echinococcosis (Viel *et al*. 1999). The growing fox population in Western Europe (Chautan, Pontier & Artois 2000), and the newly observed colonization of urban habitats in many central European cities (Gloor *et al*. 2001), raise concern about the risk of a possible increased infection pressure for this disease in densely populated areas (Eckert & Deplazes 2004). Therefore knowledge about the factors affecting the population dynamic of this zoonotic parasite is relevant to public health.

This study confirmed our predictions that the relative supply of arvicolids does correlate with the predation of foxes on these rodent species and, as a consequence, corresponds with the spatial differences in the prevalence of *E. multilocularis* in foxes. Our results support the hypothesis that the supply of prey species, acting as intermediate hosts, and the abundance of alternative food sources, can significantly affect the population dynamics of dixenous parasites and confirm the crucial role of plasticity in predation behaviour of definitive hosts for this type of parasite. Hence the functional response of final hosts to a varying supply of intermediate hosts and alternative food sources can be considered as a key factor for the transmission dynamics of parasites that depend on a predator–prey interplay.

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References

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *Second International Symposium on Information Theory, Tsahkadsor, Armenian SSR* (eds B.N. Petrov and F. Csaki), pp. 267–281. Akademiai Kiado, Budapest.

Ammann, R. & Eckert, J. (1995) Clinical diagnosis and treatment of *Echinococcosis* in humans. *Echinococcus and Hydatid Disease* (eds R.C.A. Thompson and A.J. Lymbery). CAB International, Wallingford, UK.

Anonymous (2000) *Statistisches Jahrbuch der Stadt Zürich 2000* (in German). Statistical Department of the City of Zurich, Zurich.

Baker, P.J., Funk, S.M., Harris, S. & White, P.C.L. (2000) Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Animal Behaviour* **59**, 127–146.

Brown, S.P., Renaud, F., Guegan, J.F. & Thomas, F. (2001) Evolution of trophic transmission in parasites: the need to reach a mating place? *Journal of Evolutionary Biology* **14**, 815–820.

Burnham, K. & Anderson, D. (1998) *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.

Cantor, S.B., Sun, C.C., Tortolero-Luna, G., Richards-Kortum, R. & Follen, M. (1999) A comparison of *C*/*B* ratios from studies using receiver operating characteristic curve analysis. *Journal of Clinical Epidemiology* **52**, 885–892.

Chautan, M., Pontier, D. & Artois, M. (2000) Role of rabies in recent demographic changes in red fox (*Vulpes vulpes*) populations in Europe. *Mammalia* **64**, 391–410.

Choisy, M., Brown, S.P., Lafferty, K.D. & Thomas, F. (2003) Evolution of trophic transmission in parasites: why add intermediate hosts? *American Naturalist* **162**, 172–181.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. & Deplazes, P. (2004) The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian Biology* **69**, 81–95.

Day, M.G. (1966) Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Journal of Zoology (London)* **148**, 201–217.

Deplazes, P., Hegglin, D., Gloor, S. & Romig, T. (2004) Wilderness in the city: the urbanization of *Echinococcus multilocularis*. *Trends in Parasitology* **20**, 77–84.

Dickman, C.R. & Doncaster, C.P. (1987) The ecology of small mammals in urban habitats. I. Populations in a patchy environment. *Journal of Animal Ecology* **56**, 629–640.

Dickman, C.R. & Doncaster, C.P. (1989) The ecology of small mammals in urban habitats. II. Demography and dispersal. *Journal of Animal Ecology* **58**, 119–127.

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

Doncaster, C.P. & Macdonald, D.W. (1991) Drifting territoriality in the red fox *Vulpes vulpes*. *Journal of Animal Ecology* **60**, 423–440.

Eckert, J. (1998) Alveolar echinococcosis (*Echinococcus multilocularis*) and other forms of echinococcosis (*Echinococcus vogeli* and *Echinococcus oligarthrus*). *Zoonoses* (eds S.R. Palmer, L. Soulsby and D.I.H. Simpson), pp. 689–716. Oxford Medical Publications, Oxford, UK.

Eckert, J. & Deplazes, P. (2004) Biological, epidemiological and clinical aspects of echinococcosis: a zoonosis of increasing concern. *Clinical Microbiology Reviews* **17**, 107–135.

Eckert, J., Schantz, P.M., Gasser, R.B. *et al.* (2001) *Geographic Distribution and Prevalence. WHO/OIE Manual on Echinococcosis in Humans and Animals* (eds J. Eckert, M.A. Gemmel, F.-X. Meslin and Z.S. Pawlowski), pp. 100–142. World Health Organization/World Organisation for Animal Health, Paris.

Giraudoux, P., Pradier, B., Delattre, P., Deblay, S., Salvi, D. & Defaut, R. (1995) Estimation of water vole abundance by using surface indices. *Acta Theriologica* **40**, 77–96.

Gloor, S. (2002) *The rise of urban foxes* (Vulpes vulpes) *in Switzerland and ecological and parasitological aspects of a population in the recently colonised city of Zurich*. PhD thesis, University of Zurich, Zurich.

Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P. & Breitenmoser, U. (2001) The rise of urban fox populations in Switzerland. *Mammalian Biology* **66**, 155–164.

Gottstein, B., Saucy, F., Wyss, C. *et al.* (1996) Investigations on a Swiss area highly endemic for *Echinococcus multilocularis*. *Applied Parasitology* **37**, 129–136.

Green, K. (2002) Selective predation on the broad-toothed rat, *Mastacomys fuscus* (Rodentia: Muridae), by the introduced red fox, *Vulpes vulpes* (Carnivora: Canidae), in the Snowy Mountains, Australia. *Austral Ecology* **27**, 353–359.

Harris, S. (1981) The food of suburban foxes (*Vulpes vulpes*), with special reference to London. *Mammal Review* **11**, 151–168.

Harris, S. & Smith, G.C. (1987) Demography of two urban fox (*Vulpes vulpes*) populations. *Journal of Animal Ecology* **24**, 75–86.

Hausser, J. (1995) *Säugetiere der Schweiz*. Birkhäuser-Verlag, Basel, Switzerland.

Hegglin, D., Ward, P. & Deplazes, P. (2003) Anthelmintic baiting of foxes against urban contamination with *Echinococcus multilocularis*. *Emerging Infectious Diseases* **9**, 1266–1272.

Henttonen, H., Fuglei, E., Gower, C.N. *et al.* (2001) *Echinococcus multilocularis* on Svalbard: introduction of an intermediate host has enabled the local life-cycle. *Parasitology* **123**, 547–552.

Hofer, S., Gloor, S., Muller, U., Mathis, A., Hegglin, D. & Deplazes, P. (2000) High prevalence of *Echinococcus multilocularis* in urban red foxes (*Vulpes vulpes*) and voles (*Arvicola terrestris*) in the city of Zurich, Switzerland. *Parasitology* **120**, 135–142.

Kappeler, A. (1991) *Die orale immunisierung von Füchsen gegen Tollwut in der Schweiz*. PhD thesis, University of Bern, Bern, Switzerland.

Kern, P., Bardonnet, K., Renner, E. *et al.* (2003) European echinococcosis registry: human alveolar echinococcosis, Europe, 1982–2000. *Emerging Infectious Diseases* **9**, 343–349. http://www.cdc.gov/ncidod/EID/vol9no3/02-0341.htm

Kern, P., Ammon, A., Kron, M. *et al.* (2004) Risk factors for alveolar echinococcosis in humans. *Emerging Infectious Diseases* **10**, 2088–2093.

Kjellander, P. & Nordström, J. (2003) Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. *Oikos* **101**, 338–344.

Macdonald, D.W. (1977) On food preference in the red fox. *Mammal Review* **7**, 7–23.

Mackiewicz, J.S. (1988) Cestode transmission patterns. *Journal of Parasitology* **74**, 60–71.

Niethammer, J. & Krapp, F. (1982) *Nagetiere I and 2/I, Nagetiere II*. Akademische Verlagsgesellschaft, Wiesbaden, Germany.

Norusis, M.J. (1986) *spss/pc + Advanced Statistics* SPSS, Chicago, IL, USA.

Quéré, J.-P., Raoul, F., Giraudoux, P. & Delattre, P. (2000) An index method of estimating relative population densities of the common vole (*Microtus arvalis*) at landscape scale. *Revue d'Ecologie: La Terre et la Vie* **55**, 25–32.

Stieger, C., Hegglin, D., Schwarzenbach, G., Mathis, A. & Deplazes, P. (2002) Spatial and temporal aspects of urban

transmission of *Echinococcus multilocularis*. *Parasitology* **124**, 631–640.

Tackmann, K., Löschner, U., Mix, H., Staubach, C., Thulke, H.-H. & Conraths, F.J. (1998) Spatial distribution patterns of *Echinococcus multilocularis* (Leuckart 1863) (Cestode: Cyclophylldea: Taeniidae) among red foxes in an endemic focus in Brandenburg, Germany. *Epidemiology and Infection* **120**, 101–109.

Teerink, B.J. (1991) *West European Mammals Atlas and Identification Key*. Cambridge University Press, Cambridge, UK.

Trewhella, W.J., Harris, S. & Mcallister, F.E. (1988) Dispersal distance, home-range size and population density in the red fox (*Vulpes vulpes*): a quantitative analysis. *Journal of Applied Ecology* **25**, 423–434.

Viel, J.F., Giraudoux, P., Abrial, V. & Bresson-Hadni, S. (1999) Water vole (*Arvicola terrestris* Scherman) density as risk factor for human alveolar echinococcosis. *American Journal of Tropical Medicine and Hygiene* **61**, 559–565.

Voigt, D.R. & Macdonald, D.W. (1984) Variation in the spatial and social behaviour of the red fox, *Vulpes vulpes*. *Acta Zoologica Fennica* **171**, 261–265.

Weber, J.M. & Aubry, S. (1993) Predation by foxes *Vulpes vulpes* on the fossorial form of the water vole, *Arvicola terrestris Scherman*, in western Switzerland. *Journal of Zoology (London)* **229**, 553–559.

White, P.C.L., Saunders, G. & Harris, S. (1996) Spatio-temporal patterns of home range use by foxes (*Vulpes vulpes*) in urban environments. *Journal of Animal Ecology* **65**, 121–125.