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Trophic ecology, behaviour and host population dynamics in *Echinococcus multilocularis* transmission

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ABSTRACT

The life cycle of the cestode *Echinococcus multilocularis* primarily involves canids and small mammals (rodents, lagomorphs) as definitive and intermediate hosts, respectively. Several surveys have identified marked temporal and geographical variations at different scales in the parasite's prevalence in both types of hosts, suggesting variations in the biological and ecological factors that control transmission processes. The parasite transmission from intermediate to definitive hosts is determined by the predator–prey relationship, which theoretically depends on prey population dynamics and the complex dietary response of predators to varying densities of prey species and other food items. Parasite eggs are transmitted to intermediate hosts *via* carnivore faeces, whose distribution in the environment is driven by the defecating behaviour of final hosts. We reviewed field-based studies that address issues related to the trophic ecology and behaviour of definitive hosts, interactions between definitive and intermediate hosts, and *E. multilocularis* transmission both in wild and domestic animals in rural and urban environments. Two density-dependent mechanisms control the transmission dynamics in definitive hosts: one is based on the variations in the availability of intermediate hosts, and the other is based on the variations in the density of the definitive host and its faeces. Non-linearity and the direct and delayed responses of definitive host contamination in relation to intermediate host population variations were recorded. The dietary response of the red fox was shown to be complex when abundant alternative resources were available (anthropogenic food, multiple intermediate host prey species). Micro-local hotspots of parasite transmission to intermediate hosts in a landscape, as well as areas of higher risk for human contamination in village and urban settings, may be explained by the definitive hosts' activity patterns and defecation behaviour.

1. Introduction

The life cycle of the cestode *Echinococcus multilocularis* primarily involves canids and a large number of small mammal species (rodents, lagomorphs) as definitive and intermediate hosts, respectively (Rausch, 1995). The predator-prey relationship determines the transmission of the parasite from intermediate to definitive hosts, whereas the release of canid faeces in the environment allows the parasite's eggs to be transmitted to intermediate hosts. Many publications have been issued over decades that report the local prevalence of the parasite in definitive (several species of foxes such as *Vulpes vulpes*, *Vulpes ferrilata* or *Vulpes lagopus*, raccoon dogs, coyotes, golden jackal, wolves and dogs) and intermediate host populations. Some authors have associated the variation in prevalence to the variations in host life-history traits (mostly age structure of populations) and/or in environmental parameters, such as climate, landscape characteristics or geographical location (for recent reviews see Atkinson et al., 2013; Otero-Abad and Torgerson, 2013). For example, a number of surveys on regional or national scales have identified a high spatial heterogeneity in the prevalence of the parasite in red fox (*V. vulpes*) populations (Miterpakova et al., 2006; Combes et al., 2012; Guerra et al., 2014). In a recent screening in the north-eastern half of France covering an area of 240,000 km^2, Combes et al. (2012) showed prevalence variation from more than 60% to less than 10% within only some tens of kilometres. At this spatial scale, differences in climatic conditions are

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not likely to explain such gradients. Instead, it has been proposed that small scale variations in the distribution, abundance and population dynamics of intermediate hosts (*e.g.* Guerra et al., 2014) and interactions between host populations *via* predator-prey relationship could play a critical role in the transmission intensity of the parasite (Giraudoux et al., 2003). On a more local scale, the transmission of the parasite's eggs to intermediate hosts is governed by the distribution of the definitive host's faeces in the environment and the micro-climatic conditions controlling egg survival (Giraudoux et al., 2002). The definitive hosts' defecating behaviour, and thus the patterns of environmental contamination, is determined by several factors, including habitat use, social interactions among congenerics, local habitat features and the distribution of resources in the environment. Here, we aim to review field-based studies that (1) correlate *E. multilocularis* prevalence in definitive hosts (foxes and dogs) in urban and rural environments to at least one of the following factors: small mammal intermediate host population density, definitive host population density or diet; (2) report definitive host faeces distribution or activity patterns in relation to environmental characteristics or to intermediate host spatial distribution (see Table 1 for a list of publications). We then highlight gaps in knowledge and propose research perspectives.

2. Intermediate host populations, predation and *E. multilocularis* prevalence in definitive hosts

2.1 E. multilocularis *transmission in foxes*

An early major contribution to the transmission ecology of *E. multilocularis* between small mammals and foxes was given by Saitoh and Takahashi (1998). They investigated *E. multilocularis* winter prevalence dynamics in a sample of 9828 foxes (*V. vulpes*) and *Myodes rufocanus* population variations in three localities of Hokkaido, the northernmost island of Japan, over 8 years. In this area, *M. rufocanus* populations were monitored by private foresters as part of the forest pest management programmes. The parasite prevalence in foxes greatly varied among years (average ranging between 20.2% and 44.7%) and was correlated with the *M. rufocanus* density of the current year in the three sites. Moreover, a delayed effect of vole abundance was suspected in Kushiro and Nemuro, where the parasite prevalence was also correlated with the intermediate host population density of the previous year. The effect of the current year vole density on prevalence was attributed to the direct dietary response of the fox to its main prey density variation: if the fox consumption rate on the prey is dependent on its density, the parasite transmission intensity to foxes should be as well. The one year-delayed effect observed in the two sites was attributed to the effect of the lower snow cover in winter that allowed foxes to hunt more easily on rodents, compared to the third site where a thick snow cover prevented predation and drastically reduced transmission. Thus, differences in the winter food habits of foxes may explain differences in the overwintering patterns of the parasite. In this study, the hypothesis on transmission mechanisms was grounded on fox dietary studies undertaken in the 1970s and 80s, but no data on the fox diet collected in parallel to prevalence and intermediate host density were available to confirm or reject those hypotheses. In the northern ecosystem of Spitsbergen, Svalbard, Stien et al. (2010) reported an average 8.5% *E. multilocularis* prevalence in 353 Arctic foxes (*V. lagopus*, formerly known as *Alopex lagopus*). They showed that prevalence significantly decreased with increasing distance from the *Microtus levis* population (formerly known as *M. rossiaemeridionalis*), known to be the only intermediate host (with a 19% average parasite prevalence).

The landscape composition of the mid-altitude plateau of the Jura Mountains in eastern France is dominated by grassland and is favourable to regular and spatially asynchronous population outbreaks of two grassland rodent species, *Arvicola scherman* (formerly *A. terrestris*) and *Microtus arvalis* (Delattre et al., 1999; Giraudoux et al., 1997; Raoul, Defaut et al., 2001), which are considered the main *E. multilocularis* intermediate hosts in Europe and an important food resource for foxes. This place is located in the historical area of higher endemicity of Western Europe, and the average parasite prevalence in fox populations ranged from 20% to 65% (Raoul, Deplazes et al., 2001). Based on the copro-ELISA diagnostic on 1252 faeces collected in the field, Raoul et al. (2010) showed that *E. multilocularis* infection in foxes was asymptotically related to both *A. scherman* and *M. arvalis* relative density in the field, suggesting a non-linear parasitic response: infection rose quickly up to a plateau that may be partly attributed to immunity mechanisms regulating infection level. In the Slovak Republic, 3096 red foxes were collected in the entire country between 2000 and 2004 and analysed for *E. multilocularis* infection using the sedimentation and counting technique (Miterpakova et al., 2006). In a sub-sample of foxes from southern and northern regions the prevalence of *E. multilocularis* was correlated with the density of small mammals, although the species actually trapped were not identified by the authors.

The transmission of *E. multilocularis* within large and medium cities, firstly reported in early 2000, represents a new context that should result from the general increase in fox populations worldwide. The urban cycle of the parasite is now documented in Zurich and Geneva (Switzerland), Stuttgart (Germany), Copenhagen (Denmark), Sapporo (Japan), Nancy, Annemasse and Pontarlier (France), and Calgary (Canada) (Hofer et al., 2000; Tsukada et al., 2000; Deplazes et al., 2004; Fischer et al., 2005; Robardet et al., 2008; Catalano et al., 2012; Comte et al., 2013). A general pattern that seems to emerge is a decrease in *E. multilocularis* prevalence in foxes according to the following gradient: rural periphery/residential peri-urban area/urban centre. The distribution of intermediate host populations has been investigated in Zurich and Nancy (Hegglin et al., 2007; Robardet et al., 2008) with similar findings (see Table 2 for a comparison between Zurich and Nancy cities, where key ecological parameters of the cycles have been documented). Indeed, one of the main fox prey species displayed a higher density in the rural periphery (*M. arvalis* in Nancy) and/or in the residential peri-urban area (*A. scherman* in Zurich) compared to the urban centre where the relative densities of both prey species were lower due to reduced availability of suitable habitats (grasslands) and the lower numbers of animals within these habitats. The spatial and temporal patterns of the cycle involving coyote (*Canis latrans*) as definitive host have been investigated in urban parks of the city of Calgary (Liccioli et al., 2014). There, *E. multilocularis* faecal prevalence peaked in spring (43.47% of positive faeces) and strongly varied across parks, ranging between 5.34% and 61.48%. Higher faecal prevalence in two parks was associated with both the local small mammal assemblage being dominated by species known to be intermediate hosts (*vs.* non intermediate hosts) and higher prevalence of the parasite in these intermediate hosts.

At least two non-exclusive ecological mechanisms are likely to explain the dependence of *E. multilocularis* prevalence in foxes to the intermediate hosts' density variations: the functional and numerical response of the predator. The numerical response is the capacity of a predator to change its population density through demographic (alteration of reproduction success) and aggregation (modification of spatial behaviour and aggregation to prey patches) processes according to the changes in its prey density (Ricklefs and Miller, 2000). The functional response reflects the variation of the predator's diet following the variation of the density of its prey (Arditi and Ginzburg, 2012). In the context of *E. multilocularis* transmission, a numerical response would theoretically lead to higher fox populations when prey density increases, thereby increasing