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Echinococcus multilocularis – a zoonosis of anthropogenic environments?

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Abstract

Transmission of the fox tapeworm *Echinococcus multilocularis*, the causative agent of human alveolar echinococcosis, is known to depend on various environmental factors which are subject to human influence. Epidemiological data suggest that in most endemic regions anthropogenic landscape changes (e.g. deforestation and agricultural practices) have led to more favourable conditions for the parasite's animal hosts, especially arvicolid rodents, thereby increasing the risk for parasite transmission and human disease. Examples are the conversion of forests or crop fields into meadows and pastures in Europe, China and North America, and overgrazing of natural grassland in central Asia. Other anthropogenic factors include interference with host population densities by wildlife disease control, changing hunting pressure and provision of new habitats, e.g. in urban areas. Domestic dogs may, under certain conditions, get involved in the otherwise largely wildlife-based transmission, and thereby greatly increase the infection pressure to humans. The introduction of neozootic host species may increase transmission, or even initiate the parasite's life-cycle in previously non-endemic regions. Lastly, the parasite itself may be accidentally introduced into non-endemic areas, if suitable host populations are present (e.g. in northern Japan).

Introduction

The fox tapeworm *Echinococcus multilocularis* (Cestoda: Taeniidae) is one of eight currently recognized species of the genus *Echinococcus* (Jenkins *et al.*, 2005), all of them exploiting predator–prey systems between carnivores (mainly canids) and their principal prey species for their transmission. Intermediate hosts for most *Echinococcus* species are large herbivores (*E. granulosus* s.s., *E. ortleppi*, *E. equinus*), large-bodied rodents (*E. vogeli, E. oligarthrus*), or lagomorphs (*E. shiquicus*). In contrast, the metacestodes of *E. multilocularis* are adapted to small rodents (usually species of Arvicolidae). The characteristic vesicular growth form of the metacestode seems to be a morphological response to the limited space available in such small mammals. Thereby, most of the mature metacestode is eventually filled with protoscolices, in contrast to other *Echinococcus* species whose metacestodes contain large amounts of cyst fluid. The principal definitive hosts for *E. multilocularis* are canids specialized on rodents as prey, e.g. foxes (*Vulpes* spp., *Alopex lagopus*) and coyotes (*Canis latrans*) (Eckert *et al.*, 2001).

Echinococcus multilocularis occurs througout the northern hemisphere, although its small scale distribution and frequency is unknown in most parts of the range. Due to the zoonotic potential of this parasite – alveolar echinococcosis is considered one of the most severe human parasitoses in non-tropical regions – it has received considerable attention in recent years, particularly in Europe, Japan and most recently China. Although risk factors are still incompletely understood, it is apparent that environmental parameters, including climatic conditions, play a key role for the transmission intensity of the parasite and for the infection risk to humans (fig. 1). These factors are thought to act on two targets: firstly, sufficient ground moisture will increase the survival period of eggs in the environment, and secondly, certain vegetation types will provide the habitat

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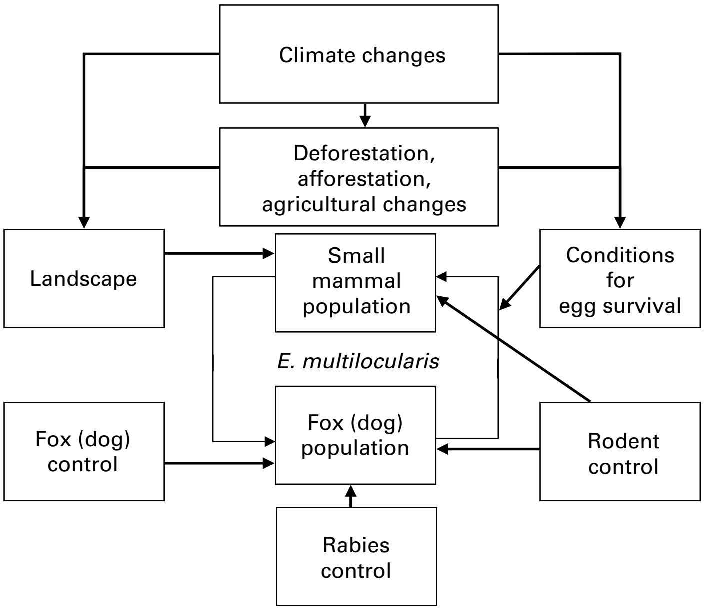

Fig. 1. Principal external factors influencing the transmission of *Echinococcus multilocularis* (modified from Giraudoux *et al.*, 2003).

for large densities of suitable intermediate host species. Although in most parts of its range *E. multilocularis* is transmitted in wildlife cycles, it is increasingly clear that anthropogenic alterations of landscape and accidental introductions of the parasite or new hosts play a key role for the human infection risk (Giraudoux *et al.*, 2002).

Transmission in natural environments

Most recent epidemiological studies on environmental transmission factors were undertaken in densely settled regions of Europe and Asia, while comparatively lttle is known about the parasite in unaltered natural landscapes. One example of such an environment is the circumpolar tundra region, where the life-cycle includes the Arctic fox *Alopex lagopus* as the sole final host, and several species of arvicolid rodents, e.g. the northern vole *Microtus oeconomus* and the brown lemming *Lemmus sibiricus*. The most detailed epidemiological data are available from St Lawrence Island in the Bering Sea (Rausch & Fay, 2002), where the life-cycle is characterized by limited fluctuations of the host populations. This results in a stable *E. multilocularis* transmission and prevalence rates of >70% in foxes and up to 80% in rodents. In other Arctic regions of North America and Eurasia, host populations may undergo strong fluctuations, which are thought to result in low *E. multilocularis* prevalence rates. Although no detailed studies are available from most tundra regions, available data suggest that transmission there is unstable, leading to a patchy distribution and high prevalence foci within large areas of low or sporadic endemicity (Bessonov, 1998; Rausch & Fay, 2002).

An additional example for (semi-) natural transmission of *E. multilocularis* is the grassland (steppe) region of central Asia, including, e.g. parts of Kazakhstan, the Tibetan plateau, northwestern China and Mongolia. While in most of this vast region the natural ecosystems, characterized by herds of large grassland herbivores, have been replaced by pastoral land with livestock, the vegetation and small mammal fauna is thought still to be close to the natural state in many areas. The range of host species for *E. multilocularis* is far more diverse than in the Arctic, including different species of foxes (*V. vulpes, V. corsac, V. ferrilata*), and a large number of *Microtus* species, e.g. *M. brandti* in Mongolia, *M. limnophilus* on the Tibetan plateau, and other rodents (Eckert *et al.*, 2001). A detailed survey on host species and landscape characteristics is available from Kazakhstan (Shaikenov & Torgerson, 2002), which shows that the transmission intensity is ruled by a moisture gradient. The most favourable habitat appears to be the moist forested steppe, and transmission gradually decreases in dry steppe, semi-desert and desert areas. However, even in arid regions the parasite can be present in foci of higher moisture and on the banks of lakes and rivers, where muskrats *Ondatra zibethicus* are important intermediate hosts.

Impact of anthropogenic landscape alterations

In its natural state, the largest part of the temperate region would be covered by taiga or deciduous forests. Both vegetation types seem to be less suitable for intense transmission of *E. multilocularis*. This hypothesis is supported by distribution data from Europe and North America (Schantz *et al.*, 1995; Eckert *et al.*, 2001), and is thought to be due to the low density of arvicolid rodent species, which are suitable as intermediate hosts and, at the same time, form a major proportion of fox prey.

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An exception may be forest areas of temperate eastern Asia, where dense undergrowth of bamboo provides suitable conditions for dense and stable vole populations (*Clethrionomys* spp.).

In central Europe, the transmission of *E. multilocularis* was shown to be most intense in areas dominated by grassland or agriculturally altered landscape, while forested and urban areas were associated with decreased prevalences in foxes (A.-K. Weible & T. Romig, unpublished data). This suggests that in this region, high endemicity of *E. multilocularis* depends on the presence of anthropogenic landscapes. The principal factor seems to be the necessity of short-grass habitats (regularly mowed meadows or pastures) for the development of high population densities of common voles *Microtus arvalis* and the terrestrial form of water voles *Arvicola terrestris* (Delattre *et al.*, 1996). Both species are highly suitable hosts for the parasite, and form the preferred prey for red foxes. In eastern France (Doubs departement), where crop fields were converted into grassland (pastures) from the 1950 s onwards, a correlation was found between the number of human echinococcosis patients, population fluctuations of rodents and the proportion of permanent grassland (Viel *et al.*, 1999; Giraudoux *et al.*, 2003). In a separate study in southern Gansu, China, a similar pattern emerged. The area suffered increasing deforestation within the past 30 years, and the vegetation succession provided increasingly suitable habitats for intermediate hosts of *E. multilocularis*, particularly *Microtus limnophilus*. The prevalence of echinococcosis in humans (although 100 times higher than in France) appears to follow a gradient of deforestation (Giraudoux *et al.*, 2003). The correlation between the number of human cases and the proportion of grass- or shrubland (as opposed to forest) both in Europe and China is caused by the fact that in both regions, the most suitable hosts for *E. multilocularis* are adapted to this habitat type. This is not necessarily the case elsewhere, e.g. in Japan (see below). Although the proportion of grassland in a given area emerges as a risk factor in the studies mentioned above, other parameters are likely to influence transmission intensity on different spatial scales. In a large-scale approach covering all of China, the distribution of grassland coincided with the occurrence of human echinococcosis in some regions, but not in others (Danson *et al.*, 2003). Additional factors have not been identified, but are likely to include climatic factors acting on the survival of eggs in the environment, host species abundance controlled by factors other than landscape (e.g. rodent or fox control measures), or human behaviour. In a small scale approach in southwestern Germany, the prevalence of *E. multilocularis* in foxes was not convincingly correlated to the proportion of grassland within the area of individual communes. Areas with large, coherent pastures and meadows showed lower prevalence levels than areas with more fragmented landscapes dominated by crop production (A.-K. Weible & T. Romig, unpublished data). As a conclusion of the data available so far, the influence of landscape is evident. However, the impact of individual landscape parameters on transmission appears to vary among regions. As a hypothesis, landscape parameters do not define precise prevalence levels, but provide a broader frame within which other parameters are likely to influence transmission.

Even in areas where grassland is the naturally predominating vegetation type, the transmission of *E. multilocularis* may be influenced by human activities. In the Tibetan plateau of western China, overgrazing of pastures by livestock (yak) was found to favour populations of one of the major intermediate host species, the lagomorph *Ochotona curzoniae*, by providing patches of bare soil and facilitating the digging of dens. This may explain the correlation between the density of yak populations and the risk for human echinococcosis found in that area (Wang *et al.*, 2004).

In addition to the Arctic tundra, there is a second endemic region for *E. multilocularis* in North America in the temperate zone of southern Canada to the central USA. No records exist from the interspersed Canadian taiga zone which is either a non-endemic area, or prevalence levels are too low to allow detection (Schantz *et al.*, 1995). In central North America, red foxes *Vulpes vulpes* and coyotes *Canis latrans* are the most important final hosts, main intermediate hosts being the meadow vole *Microtus pennsylvanicus* and the deer mouse *Peromyscus maniculatus* (Eckert *et al.*, 2001). This endemic region may be of rather recent origin, after becoming suitable for *E. multilocularis* transmission due to anthropogenic deforestation. Both the range of the area and the transmission seem to be increasing rapidly. While a survey of red foxes in South Dakota during the late 1960s resulted in one infected fox out of 222, prevalence in the period 1987–1991 had increased to 74.5% of 137 red foxes; in addition, 4 of 9 coyotes were also found infected (Schantz *et al.*, 1995; Hildreth *et al.*, 2000; Storandt *et al.*, 2002). It is believed that the parasite will spread further, since suitable hosts for *E. multilocularis* are more widespread than the currently known range of their parasite (Storandt *et al.*, 2002).

Disease control and other anthropogenic factors

Prevalence rates of *E. multilocularis* in foxes have increased drastically in many countries of Europe during the 1990s. In central Europe, this occurred in clear temporal correlation with the onset of large-scale rabies eradication programmes by vaccinating foxes with baits (Chautan *et al.*, 2000), and a subsequently observed drastic increase of fox population density (Romig *et al.*, 1999). The regional eradication of rabies is likely to be only one of several factors leading to the population increase of foxes, since a similar development was observed in Britain where fox rabies had never occurred. Other contributing factors may include changing hunting practices (decreased hunting pressure due to commercial devaluation of fox fur), changing attitudes of the public towards wildlife (better acceptance of foxes in the vicinity of humans), and improved availability of anthropogenic food. As a result of increased host density and parasite prevalence, the density of *E. multilocularis*, i.e. parasites per unit area, is estimated to have increased by a factor of 10 during the 1990s in Germany (Romig, 2002).

Synanthropic lifecycles

Synanthropic transmission of *E. multilocularis* may become established under a variety of circumstances. In this context, synanthropic is defined as taking place in or near human habitations, while transmission may or may not involve domestic animals. This is opposed to a true domestic life-cycle maintained by dogs or cats as definitive hosts. Such cycles have been variously proposed to exist (Eckert *et al.*, 2001), but there is no convincing evidence that these are self-maintaining and run independently from the common sylvatic transmission based on wildlife species.

Human alveolar echinococcosis can be extremely frequent where domestic dogs are substantially involved in the life-cycle. This is the case in some villages on St Lawrence Island (Alaska) from where an annual incidence of 98/100.000 has been reported. Although Arctic foxes are known to be frequently infected in that region, the infection pressure to humans is clearly caused by dogs, which acquire the parasites by preying on northern voles *Microtus oeconomus* near human habitation (Eckert *et al.*, 2001; Rausch & Fay, 2002). Similar situations exist in western China, from where far more human cases are reported than from any other country, e.g. in hyperendemic foci of southern Gansu, the prevalence in humans can reach 4% (Craig *et al.*, 2000). Also in China, such situations are known or suspected to be associated with life-cycles involving free-roaming dogs as definitive hosts. These dogs become infected by preying on rodents or lagomorphs in the vicinity of the villages, thereby interacting with the sylvatic lifecycle maintained by foxes.

Synanthropic transmission of *E. multilocularis* may also occur where wildlife species become adapted to urban areas. An example is the adaptation of foxes to live in cities and towns. This is known from Britain since the 1940s, but occurred rather recently in continental Europe, possibly in the wake of generally increasing fox populations following rabies control (Chautan *et al.*, 2000). Today, urban foxes are known from many towns and cities of south-central Europe, e.g. southern Germany and Switzerland (Gloor *et al.*, 2001). In these locations, fox population densities can be much higher than in rural environments due to the abundant and seasonally stable availability of anthropogenic food (Contesse *et al.*, 2004). Infection rates with *E. multilocularis* can be high (e.g. 44% in Zurich, 43% in Geneva, 17% in Stuttgart) (Deplazes *et al.*, 2004), but are generally lower than in surrounding rural areas, due to the limited presence of suitable vole habitats. However, due to the high population density the absolute number of infected foxes may still be higher than in agricultural landscapes, and the close proximity between foxes and humans poses a considerable infection risk. Transmission to humans may not only occur directly from infected foxes, but also via pet dogs and cats which become infected by preying upon rodents in city parks and gardens. Up to 9% of water voles were found infected in the urban to peri-urban areas of Zurich (Stieger *et al.*, 2002).

Neozoa

Neozoa are animals which were introduced, by purpose or accident, into areas outside their native range. In the case of *E. multilocularis*, this applies both to final and intermediate host species, and to the parasite itself.

The raccoon dog *Nyctereutes procyonoides*, originating from eastern Asia, is a neozootic species in Europe, which presently experiences a drastic increase in population densitiy in Poland and eastern Germany. This species is highly susceptible to infection (Deplazes *et al.*, 2004), and naturally infected animals were found in northwestern Germany and northern Poland (Thiess *et al.*, 2001; Machnicka-Rowinska *et al.*, 2002). Since raccoon dogs do not seem to compete directly with foxes (thereby decreasing their populations), an additional pool of definitive hosts may be developing in central Europe. However, more information is needed on the ecology of this species in Europe, before any conclusion on increasing parasite densities can be drawn for a given area.

On the Norwegian Arctic island of Svalbard, Arctic foxes were always present as potential definitive hosts, but the transmission of *E. multilocularis* did not occur due to the absence of suitable intermediate hosts. This changed after the accidental introduction of the sibling vole *Microtus rossiaemeridionalis*, probably from Russia. By now, the parasite is established in a stable life-cycle between the voles and Arctic foxes (Henttonen *et al.*, 2001).

Muskrats *Ondatra zibethicus* are native to North America, and are ubiquitous neozoa in large parts of temperate Eurasia. They are highly suitable hosts for *E. multilocularis* and, in Europe, the prevalence of the parasite in muskrats usually exceeds that in other sympatric, intermediate host species (Romig *et al.*, 1999). However, the quantitative contribution for transmission in a given area is unclear. In Kazakhstan, muskrats are thought to be an important source of infection for foxes and wild cats near lakes and rivers (Shaikenov & Torgerson, 2002).

The coypu *Myocastor coypus*, a neozootic rodent originating from South America which has established feral populations in Europe, was shown to be less susceptible to *E. multilocularis* infection than arvicolid rodents, and seems to play only a marginal role in transmission. In a recent survey in western Germany only 1 of 119 feral coypu harboured fertile metacestodes, compared to 13 of 92 muskrats from the same habitat (Hartel *et al.*, 2004).

Non-human primates are susceptible to alveolar echinococcosis and a large number of case reports with fertile metacestodes are known from captive animals in endemic countries (Deplazes & Eckert, 2001; Plesker *et al.*, 2001; Rehmann *et al.*, 2003; Bacciarini *et al.*, 2004). However, there are no natural or feral populations of non-human primates anywhere within the endemicity range of *E. multilocularis* (with the possible exception of the southern and eastern slopes of the Tibetan plateau), so they do not contribute to the transmission of this parasite.

Where suitable populations of host animals exist in non-endemic areas, the parasite itself can be introduced as a neozoon. This was the case in Japan, where *E. multilocularis* is presently restricted to the northern island of Hokkaido. It was probably introduced together with infected foxes from the Kurile Islands early in the 20th century. Since the early 1980s the parasite has rapidly spread from the easternmost part of Hokkaido through the entire island, and has recently entered a phase of drastic prevalence increase in animal hosts (Ito *et al.*, 2003). In contrast to Europe and continental Asia, no rodent species is adapted to grassland in northern Japan. There, grey-sided voles *Clethrionomys rufocanus*, which form large populations in dense bamboo undergrowth (*Sasa* spp.) of forests and scrubland, are the most important intermediate hosts. Since forests with such undergrowth represent the natural vegetation type, *E. multilocularis* transmission in Japan is not adapted to anthropogenically changed landscape (meadows, pastures) as is the case in most other parts of the world. Despite this, a certain infection pressure to the human population is maintained, especially in rural areas. The number of human echinococcosis cases is moderate with 373 records between 1937 and 1997 and approximately ten new cases diagnosed annually (Eckert *et al.*, 2001).

Non-endemic regions at risk for accidental introduction of *E. multilocularis* as a neozoon include the British Isles, Fennoscandia, and the Japanese main island of Honshu. In these regions, the climate is favourable for the parasite, and a susceptible host animal fauna exists. Introductions could take place via infected companion animals (dogs or cats) travelling from endemic countries. Although the prevalence in dog and cat populations is estimated at $< 1\%$ even in high endemicity regions of Switzerland (Deplazes *et al.*, 1999), every animal should be regarded as a potential carrier of the parasite and treated accordingly. Other routes of introduction could be the transfer of wildlife without appropriate veterinary control. A potential candidate could be the European beaver *Castor fiber*, a highly susceptible species (Janovsky *et al.*, 2002) which, for conservation purposes, is being translocated, e.g. from *E. multilocularis*-endemic Bavaria (Germany) to other countries. Such activities are certainly problematic given the unreliable diagnostic methods for echinococcosis in intermediate host animals, and should only be performed with caution under strict veterinary control.

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