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Human–wildlife interactions and zoonotic transmission of *Echinococcus multilocularis*

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The life cycle of the zoonotic cestode *Echinococcus multilocularis* depends on canids (mainly red foxes) as definitive hosts and on their specific predation on rodent species (intermediate hosts). Host densities and predation rates are key drivers for infection with parasite eggs. We demonstrate that they strongly depend on multifaceted human–wildlife interactions: vaccination against rabies, elimination of top predators, and changing attitude towards wildlife (feeding) contribute to high fox densities. The absence of large canids, low hunting pressure, and positive attitudes towards foxes modify their anti-predator response ('landscape of fear'), promoting their tameness, which in turn facilitates the colonization of residential areas and modifies parasite transmission. Such human factors should be considered in the assessment of any intervention and prevention strategy.

Main drivers of zoonotic transmission of *E. multilocularis*

The emergence of infective diseases is thought to be largely driven by socioeconomic, environmental, and ecological factors [1], and these factors largely shape human wildlife interactions which potentially are relevant for wildlife-borne diseases. The cestode *E. multilocularis* causes human alveolar echinococcosis (AE) and is among the zoonotic parasites with the highest burden of disease [2]. This tapeworm depends on a life cycle which involves predators as definitive hosts (mainly canids) and their prey as intermediate hosts (mainly cricetids). During the past decades, substantial changes in abundance and distribution patterns of *E. multilocularis* have been recorded in many countries, and AE is therefore considered as an emerging zoonosis [3].

E. multilocularis is a well-studied example of the diverse group of zoonotic agents with complex wildlife–parasite cycles depending on prey–predator interplay. In this Opinion article we have chosen *E. multilocularis* to highlight the hitherto underestimated significance of the human–wildlife interface for parasite transmission.

Main determinants affecting the zoonotic risk by E. multilocularis

The risk of developing AE depends on a variety of individual factors (e.g., susceptibility and behavior [4,5]) and external factors, of which the most important are the abundance and accessibility of infective parasite stages, particularly the environmentally resistant parasite eggs [2]. The density of infective parasite eggs in the environment depends mainly on the local density and behavior of the definitive host, and especially on the rate of predation on infected intermediate hosts [6]. As we show, these parameters are in many ways strongly affected by human–wildlife interactions.

Red fox: the main European definitive host of E. multilocularis

Canid species represent the major definitive hosts of *E. multilocularis*. Intestinal infections with usually very low numbers of gravid worms have occasionally been detected in feline species including domestic cats [7], and comparative experimental infections have confirmed the very low biotic potential (production of few infective parasite eggs) in domestic cats [8]. Therefore, cats are not considered as definitive hosts to maintain the parasite cycle, and thus are of no zoonotic relevance under normal circumstances. However, to our knowledge it has never been investigated to which extent domestic cats affect the transmission of *E. multilocularis* by competing with foxes in the predation of infected intermediate hosts near human settlements and in urbanized areas.

In contrast to cats, experimental studies revealed that red foxes (*Vulpes vulpes*), domestic dogs, and raccoon dogs (*Nyctereutes procyonoides*) excrete comparable high numbers of *E. multilocularis* eggs [8]. The potential high relevance of the domestic dogs in the zoonotic transmission of *E. multilocularis* has recently been reviewed for Europe [9,10] and described for Asian endemic areas [11,12]. The relevance of the raccoon dog as a wild definitive host and its contribution to parasite transmission in the parasite cycle remains controversial [13–16]. Comparative studies in endemic areas revealed that the prevalences in raccoon dogs

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were much lower than in foxes (examples in Bruzinskaite-Schmidhalter *et al.* [13]). Several behavioral traits indicate that raccoon dogs supposedly do not play a key role in maintaining the parasite cycle: they tend to defecate at few definite sites in latrines [17] (low potential to disperse parasite eggs in vole habitats), they are less active on meadows and pastures (where vole species are abundant) [17,18], and they reduce their activities or hibernate in cold winters [19].

Different large canids seem to be highly susceptible to patent *E. multilocularis* infections. In Canada, coyotes (*Canis latrans*) can therefore play a key role in the cycle of *E. multilocularis* and be the relevant definitive host in urban and peri-urban areas [20–23]. Wolves (*Canis lupus*) [24,25] and jackals (*Canis aureus*) [26,27] were also identified as definitive hosts, and these species could be crucial for the maintenance of the parasite life cycle in regions where they are the predominant canid species. However, they generally are rare in Europe, and thus have limited significance with regard to zoonotic transmissions in most European countries. Nevertheless, the spatial behavior of these large canids with generally large home-ranges and the potential of long-distance dispersals [28] supports the spread of the parasite.

The red fox (*Vulpes vulpes*) is highly susceptible to patent *E. multilocularis* infection and is a very effective predator of a wide range of cricetid species, which are known as predominant intermediate hosts. Contrary to racoon dogs, there is evidence that the marking behavior of foxes could play an important role in the transmission ecology. For example, in the city of Zurich, a surprisingly high number of fox feces (47 of 604) have been found directly on vole ground systems where signs of predation were observed [29]. Furthermore, the red fox is the canid species with the widest geographical range [30]. Therefore, the parasite life cycle is perpetuated to a large extent by red foxes in most ecological settings [2], and we therefore focus on this species to highlight the relevance of human–wildlife interactions to the transmission dynamics of *E. multilocularis*.

Densities of final hosts determine the environmental contamination with parasite eggs

The prevalence of *E. multilocularis* in red foxes is often used as a proxy to describe the infection risk for AE in endemic areas [2,31]. However, this disregards the finding that environmental contamination with *E. multilocularis* eggs depends strongly on the worm burdens and the population densities of the definitive hosts [32,33]. For example, domestic dogs are important for human infections because of their close contact as companion animals. In addition, because of their high population density in urbanized areas [9], they can substantially contribute to the overall production of *E. multilocularis* eggs even in regions where prevalence rates in dogs are much lower than in foxes. In addition, the density of foxes varies within a wide range and is strongly affected by several human–wildlife interactions.

Diseases and disease control programs are important determinants of fox densities

It is well known that fox population densities are driven by diseases such as mange or rabies. In Sweden and Great Britain, population declines of up to 95% have been recorded after outbreaks of mange, with long-lasting effects (>15–20 years) on the affected populations [34,35]. Although it is difficult to assess the density of fox populations, and there is a lack of absolute density estimates over larger regions and longer time-periods [36], hunting statistics give evidence that in many European countries fox populations started to strongly increase after successful implementation of baiting campaigns for oral rabies vaccination [37–40]. In Switzerland, for example, most rabies cases were recorded between 1972 and 1983 (>500 rabid foxes per year), before widespread oral vaccination campaigns became effective. At the end of the 1970s and the beginning of the 1980s, yearly hunting bags of roughly 10 000–12 000 foxes were recorded per year. These numbers increased to more than 40 000 in the mid 1990s, although the financial incentives and motivation of hunters to hunt foxes were decreasing during this period [38]. Similar patterns were also found in other European countries [39]. These observations provide clear evidence that fox population densities were negatively affected by the spread of rabies but positively by vaccine interventions.

Wildlife management

Hunting

It is apparent that human hunting activities can strongly affect wildlife populations. However, there is a broad debate to which extent hunting and culling measures are regulating and shaping red fox populations. Under strict conditions, intensive culling can reduce fox population densities even in extended areas [41]. However, it is well accepted that in most settings the regulation of fox populations on a larger scale is difficult to achieve [42]. Even in Australia, where introduced foxes are treated as pest species and poisoning programs are an accepted management method, control objectives are only partly achieved [43]. Legal hunting methods for native wildlife are much more restricted in Europe, and their application is controversially discussed [44–46]. Interestingly, intense hunting has profound effects on the population dynamics in the affected species, and this must be considered in regard to the dynamics of disease transmission [47]. For instance, culling can increase the proportion of sub-adult foxes, and this could increase the spatial dynamic of parasite transmission because sub-adults disperse over large distances [48,49] and/or boost the parasite biomass because sub-adult foxes can harbor higher worm burdens [33,50]. This is in accordance with a recent French study where, in culled foxes from a peri-urban area of Nancy, the proportion of immature foxes and also the prevalence of *E. multilocularis* (after an initial slight decrease) increased to a significantly higher level than in control areas [51].

From the 'landscape of fear' to the 'urban tameness'

Hunting activity on wildlife by humans can be considered as a type of predation on a prey species. Predation has not only the direct effect of mortality but results in various indirect effects on prey species. The mortality risk and additional disturbances increase vigilance, which competes with other fundamental activities such as browsing, foraging, or mating, and they restrict the spatial behavior and therewith limit access to essential resources which determine individual fitness and finally population dynamics [52,53]. In addition, hunting by humans induces behavioral changes in the affected prey species which indirectly affect their population dynamics. While traditional hunting aims to kill animals (which is hunting for mortality), Cromsigt *et al.* [54] introduced the concept 'hunting for fear' when hunting focuses on the indirect effects of predation. However, to what extent hunting affects the anti-predator behavior of foxes has surprisingly, to our knowledge, never been investigated. Cromsigt and co-authors point out that such behavioral changes can only be achieved if the hunted species has the opportunity to learn that the proximity to humans can be dangerous [54]. Such learning effects can probably be achieved for foxes that have a complex social behavior and live in social groups at high density. Furthermore, we assume that the effectiveness of this hunting concept strongly depends on the hunting techniques.

The concept of 'hunting for fear' is based on the broader concept of the 'landscape of fear' [55], meaning that the perceived predation risk is a fundamental factor determining the anti-predator behavior and thus spatial and temporal distribution, habitat use, and finally also the population dynamics of wildlife. In fact, the 'landscape of fear' concept originates from Darwin – who observed that animals on remote islands were less afraid of people, permitting close approaches, a concept later referred to as 'island tameness' [56]. It postulates that wildlife reduces the costly escape behavior in the absence of strong natural selection of mortality by predators. A high predation risk can minimize the access to essential resources such as feeding places or resting sites, and thus not only limits the distribution of wildlife but also reduces the carrying capacity of its environment [57]. 'Island tameness' could have the opposite effect.

Although these concepts have been developed mainly in studies on lizards and ungulates, the underlying mechanism can be also observed in many other species [58]. A very evident phenomenon which can be explained by these concepts is the daily activity pattern of foxes. Generally, foxes are known as nocturnal, but in protected areas where foxes are not hunted, they quickly shift their activity pattern and become active during the daytime [59]. If hunting pressure increases vigilance and wariness, and thereby governs their activity cycle, the absence of hunting increases tameness of foxes which in turn allows them to colonize new habitats. Such new habitats are residential areas, which provide access to key resources – for example, abundant anthropogenic food and protected denning sites [35,40,60]. This access to abundant resources can significantly boost the population density, and it is therefore not surprising that the highest fox densities with >10 adult foxes km^2 are observed in urban areas [35,61,62]. This could at least partly be explained by the 'island tameness' phenomenon. In this context, we suggest the term 'urban tameness', a phenomenon which could be crucial for wildlife to exploit more efficiently the profitable resources in this strongly human-shaped environment, leading to extraordinarily high population densities as observed for urban foxes.

The comeback of large carnivores: competition and intraguild predation

Interactions between predators that exploit similar resources frequently shape the distribution, behavior, and density of intraguild predators [63,64]. It is known that larger canid species do not tolerate smaller canid species in their habitat. As a consequence, wolves reduce densities of coyotes and coyotes negatively affect grey, swift, and red fox populations, by agonistic behavior, competition, or by direct predation [65,66]. In many areas of Europe, wolves and also lynx are returning as a result of better protection and active conservation programs. This might negatively affect fox populations [67–69] and thus alter zoonotic transmission of *E. multilocularis* in those regions.

Human attitude

Changing attitude towards foxes

It is a well-known phenomenon that attitudes towards wildlife may sharply change over time. For example, the perception of wolves in Croatia changed within only a few years [70]. Foxes certainly have been regarded as pest species in earlier times [71]. Predation of foxes on livestock such as poultry was certainly a more severe economic threat to farmers in times when subsistence farming was common practice. During decades with rabies epizootic, all encounters with foxes were linked to fears of direct transmission of this life-threatening disease. In recent times a better economic situation, the fact that rabies disappeared from many European countries, and a general interest and desire in 'wilderness' has favored the positive image of the fox in Europe [72]. A public survey in the Czech Republic, France, Germany, and Switzerland revealed that 25% (Czech Republic) to 42% (Switzerland) of people gave a favorable opinion on foxes living in urban areas [73].

Human behavior towards foxes affects their boldness

A positive attitude towards wildlife is linked not only to an interest in observing but also in many cases to attempts to interact with wild animals [74]. Wildlife authorities are increasingly confronted with problematic situations linked to reduced wariness of wild animals because they are actively fed by people [75]. It is not surprising that stories regularly arise in the mass media about tame foxes in residential areas approaching and interacting with people, or even entering apartments to explore the site or to search for food – often, subadult foxes are involved in these encounters. It seems that young foxes that grow up in urban environments learn that humans are beneficial and harmless.

From the animal welfare point of view, and because the efficacy of hunting is controversially discussed, non-lethal methods should be considered to deter foxes and to induce in foxes a behavior to avoid the close proximity to humans. Therefore, management practices that aim to reduce the contact between foxes and wildlife should include recommendations to keep foxes shy and to abstain from feeding [76]. New approaches to deter foxes are needed and the effectiveness of these methods should be evaluated.

Economic development and land use

The effect of anthropogenic food resources

Considering the processes outlined above, it is not surprising that long-term increases in fox population densities have also been recorded in regions where rabies has never been detected (e.g., Doñana National Park and the UK [39]). In many regions the hunting bag today is much higher than in the period before the rabies epizootic, despite the fact that the motivation to hunt foxes is markedly reduced (low prizes for fox fur, higher regulation of hunting methods, lower acceptance of fox hunting). A likely very important driver for the long-term increase of many fox population is that foxes are opportunistic feeders, profiting from anthropogenic food resources which have increased during the past decades due to increased agricultural productivity and a throwaway mentality in prosperous economies. Especially in densely populated areas, the available food resources are enormous. For example, it has been shown in the city of Zurich that, on average, four households provide sufficient foodstuffs (rubbish, compost, etc.) to feed one adult fox [60]. By contrast, experimental food shortage by reducing anthropogenic food resources has been shown to be effective in reducing fox densities near villages [77]. Therefore, to understand the dynamics of fox populations it is crucial to determine to what extent they can access anthropogenic food resources and how access to food resources can be limited by counter-measures, for example, by using closed rubbish bins or by measures to reduce littering.

Less obvious, but important for zoonotic transmissions, is that urban foxes also shift their diet. They raise the amount of anthropogenic food in their diet in parallel with reduced predation on rodents. This explains why foxes in central urban areas frequently have a lower *E. multilocularis* prevalence than foxes in urban peripheries [62,78,79].

Human land use as a determinant of intermediate host communities

The *E. multilocularis* cycle can only be completed locally if foxes have access to infected intermediate hosts. Vole availability and *E. multilocularis* prevalence in voles can vary strongly over time and within short distances because many species occur only in specific habitats and can undergo strong population cycles over time [80–82]. Especially in urbanized environments, where suitable intermediate-host habitats are patchily distributed within the small fox home-ranges, *E. multilocularis* prevalence in foxes can vary substantially at a local scale (<500 m [79]).

The dynamic changes in land use in urban environments, but also agricultural practices and landscape management, strongly affect the composition of the rodent community. Such changes in the habitat of the intermediate hosts can increase the occurrence and frequency of *E. multilocularis*, and thus accelerate transmission dynamics to humans, resulting in increased incidence of human AE [83,84]. However, the density of suitable intermediate hosts does not necessarily directly affect the prevalence of *E. multilocularis* in definitive hosts [85]. Because foxes have a selective predation behavior (e.g., a preference for *Microtus* species [86]), some intermediate hosts are predated frequently even if they occur at low densities, thus buffering the effect of reduced supply of *E. multilocularis*-infected voles. Changes in land management practices have been shown to considerably enhance the incidence of human AE based on fundamental changes of rodent communities that favor suitable intermediate hosts for *E. multilocularis* [83,87,88]. Therefore, it is worth considering how land use, agricultural practice, and landscape management, especially in proximity to densely populated areas, could prevent the development of high densities of relevant intermediate hosts. It is likely that appropriate management of rodent habitats [89–91], combined with other control measures such as traditional trapping and/or the promotion of vole-consuming raptors or owl species [92], contributes within an integrated approach to reducing the risk of *E. multilocularis* infection and AE.

Concluding remarks

We feel that the consequences of human–wildlife interactions are still underestimated with regard to the transmission of parasitic zoonoses. As we have shown in the case of the well-documented parasite cycle of *E. multilocularis*, many factors act (Figure 1) and interact with the distribution and abundance of this zoonotic agent, and thereby govern the risk of infection. While it is evident that the environmental parasite density (responsible for the infection risk) mainly depends on definitive host populations and on the predation rate of infected intermediate hosts, these parameters are strongly affected by multi-faceted human–wildlife interactions. These include spatial and temporal factors that influence host density, wildlife disease, and actions for their control, as well as the positive attitudes of people towards wildlife, which alter 'landscape of fear' of the definitive host and allow them to establish new habitats and to exploit new food resources ('urban tameness'). It includes intraguild interactions such as predation and competition. In addition, intermediate host communities are strongly affected by human–wildlife interactions because land use practices modify their habitats and landscape features shape the predation pattern of their predators.

An understanding of these human–wildlife interactions is of major importance in developing intervention strategies to minimize the risk of *E. multilocularis* infection and human AE. One approach is to target the parasite by the delivery of deworming baits for definitive hosts. However, it is difficult and expensive to control *E. multilocularis* on a larger scale and over a longer period by this measure [9]. Measures to control wild host species are discussed as alternative or supplementary intervention methods. However, the evaluation of such interventions should consider all possible side effects. For example, the effect of increased hunting pressure should carefully be evaluated not only with regard to its capacity to reduce the number of foxes but also regarding its effects on the spatial and demographic dynamics (e.g., higher dispersal rates [93], higher proportion of juvenile foxes). In addition, it is important to critically scrutinize the effectiveness of reducing host densities because, for example, a reduction of intermediate host populations could possibly boost parasite transmission if foxes aggregate in small patches to prey on the rodent intermediate hosts.

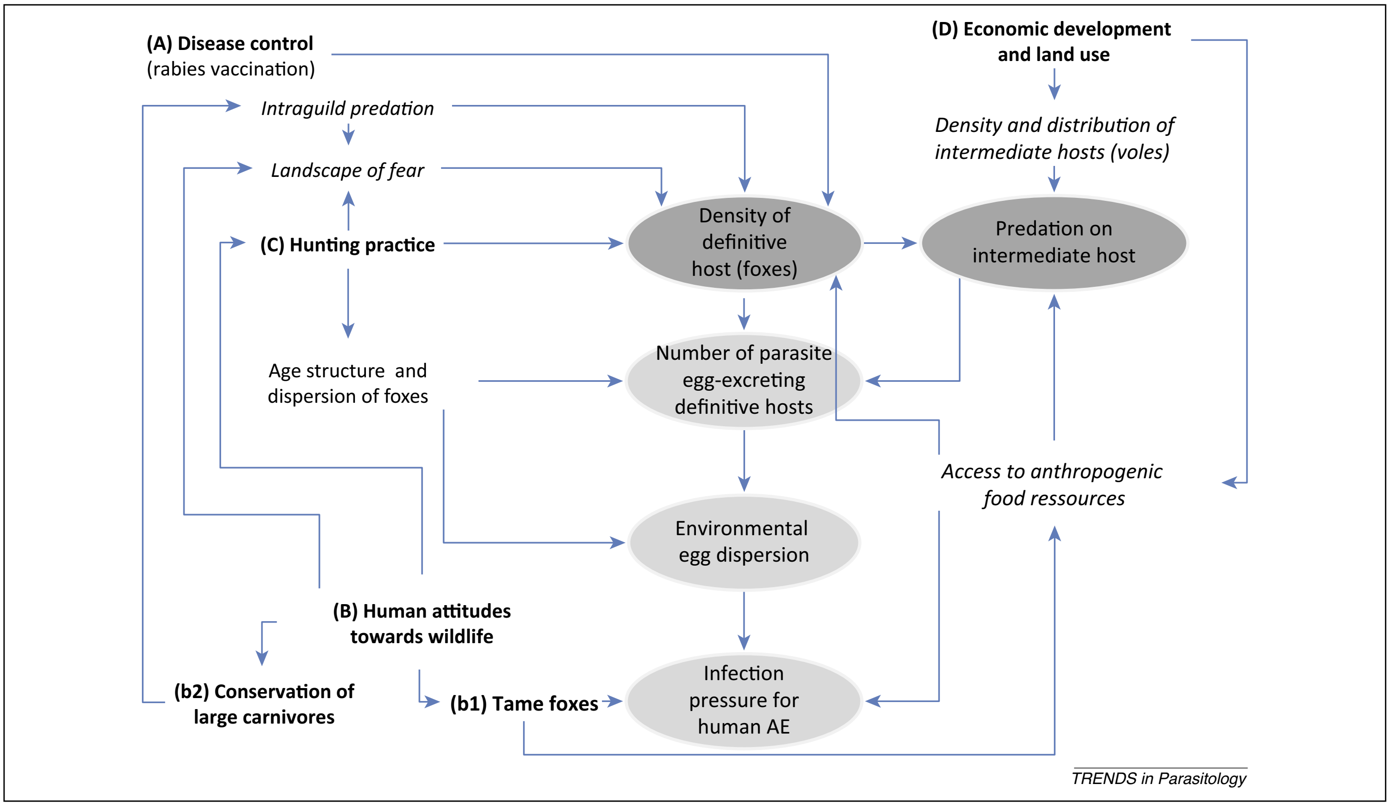

Figure 1. Human–wildlife interactions affecting environmental *Echinococcus multilocularis* egg contamination of red foxes. The figure shows interactions between humans and wildlife (bold) that directly or indirectly (italic) affect fox densities and their predation on intermediate hosts (dark-grey ellipses), and thus the infection pressure of humans with infective *E. multilocularis* eggs in the environment (grey ellipses) and the risk of developing alveolar echinococcosis (AE). **(A)** Disease control: rabies vaccinations eliminate an important, density-dependent mortality factor and contribute to increased fox densities. **(B)** Human attitudes towards wildlife have different effects which directly or indirectly affect transmission pathways of *E. multilocularis* by shaping the population dynamics and behavior of foxes; for example, positive attitudes suggest that people tame foxes (b1) and foxes gain easy access to anthropogenic food resources in urbanized areas. It also affects the conservation (b2) and thereby the abundance of top predators such as wolves and lynx, which negatively affect fox densities (via the mechanisms of intraguild predation and landscape of fear, see text for further explanations). Human attitudes towards wildlife also determine the intensity and type of fox hunting. **(C)** Hunting practices can influence fox population dynamics in many ways. Direct control of fox numbers on a larger scale is difficult to achieve. Higher mortality via strong hunting pressure could decrease the numbers of foxes that excrete eggs on a regional scale, but could also increase the proportion of juvenile foxes which frequently have higher worm burdens, thereby increasing the spatial dynamics of a fox population and thus parasite transmission. If foxes learn that humans can be dangerous, hunting could keep foxes at a greater distance from humans and away from the rich food resources in human settlements. **(D)** Economic development and land use: increased productivity of agriculture and a throwaway mentality in prosperous economies lead to increased anthropogenic food supply for foxes, which contributes to increasing fox densities. Foxes contaminate the environment only with *E. multilocularis* eggs if they have access to susceptible intermediate hosts. The occurrence and abundance of many rodent species depend strongly on land use (agricultural practices, green space management).

The concept of the 'landscape of fear' helps in understanding which resources can be exploited by foxes and in considering the interface between the definitive host and humans. Correspondingly, we hypothesize that it is likely that wariness towards humans ('urban tameness') is relevant for the transmission of *E. multilocularis* to humans. As a consequence, promoting the wariness of foxes by public campaigns that ask people not to feed or tame foxes, and to keep at a distance, is a recommended part of every prevention strategy.

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