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Invited Review

The role of wildlife in the transmission of parasitic zoonoses in peri-urban and urban areas

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ABSTRACT

During the last 100 years in many countries of the world, there have been dramatic changes in natural/rural landscapes due to urbanization. Since many wildlife species are unable to adapt to these alterations in their environment, urbanization is commonly responsible for a decline of biodiversity in areas of urban development. In contrast, some wild animal species are attracted to peri-urban and urban habitats due to the availability of an abundant food supply and the presence of structures in which to shelter. Urban foxes and/or raccoons are common sights in many peri-urban and urban areas of Europe where they can reach far higher population densities than in their natural habitats. The same is true for foxes and dingoes in some urban areas of Australia. Unfortunately, some of these highly adaptable species are also hosts for a number of parasites of public health and veterinary importance. Due to the complexity of many parasitic life cycles involving several host species, the interactions between wild animals, domestic animals and humans are not fully understood. The role of potential hosts for transmission of a zoonotic disease in urban or peri-urban areas cannot be extrapolated from data obtained in rural areas. Since more than 75% of human diseases are of zoonotic origin, it is important to understand the dynamics between wildlife, domestic animal species and humans in urbanized areas, and to conduct more focused research on transmission of zoonotic parasites including arthropod vectors under such conditions.

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1. Introduction

Human induced landscape changes are believed to be an important factor causing modifications in the transmission of some zoonotic parasites, leading to outbreaks of human diseases, both endemic and emerging (Patz et al., 2004). Urbanization is one of those landscape alterations with the deepest impact on human health and is characterized by permanent and drastic land conversions (Patz et al., 2000, 2004). Urban areas currently contain more than 50% of the human population worldwide and this trend is increasing (United Nations Department of Economics and Social Affairs, 2003). However, it is not easy to define urban areas because they may comprise large and rapidly expanding cities, smaller towns and villages as well as smaller more diffuse human settlements. Areas defined as urban vary in size, density of human habitation, amount of vehicular traffic, infrastructure, population densities and ecological parameters. Bradley and Altizer (2007) addressed the need to find quantifiable parameters to distinguish between the different areas following the gradient from natural rural environment to core urban areas. Quantitative parameters such as population density or building density in urban, suburban and rural areas have been used (Shochat et al., 2006). Urbanization is generally accompanied by deforestation and habitat fragmentation linked with a progressive loss of biodiversity from rural areas to the central urban core, accompanied by a corresponding increase in human population density.

1.1. Wild animals in urban/peri-urban areas

According to McKinney (2006), urbanization is one of the leading causes of species extinction. The decline in species richness is explained by the inability of many native species to cope with the environmental alterations associated with urbanization, eventually leading to extinction in the urban core. However, the impact of urbanization on biodiversity depends on the ecological structure of the urban and peri-urban areas: replacement of natural ecosystems by densely populated uniform settlements in resource-poor countries has a clearly different effect than the spread of suburban landscapes into agricultural land in the industrialized world. Urban and peri-urban environments can be very attractive for adaptable wild animals. The biodiversity of plants and animals in these areas frequently exceeds the biodiversity in more natural environments due to the close proximity and variation of different habitat types (e.g. gardens and forest remnants). Additionally, the supply of food resources (waste food, pet food or garden produce) of urban and periurban areas in industrialized countries is far higher than in natural or rural environments. Urban and periurban areas are therefore very attractive for adaptable species, which may reach far higher population densities than in more natural or rural landscapes (Despommier et al., 2006; Bradley and Altizer, 2007). These species are typically food generalists. Shochat et al. (2006) discriminate between 1. synanthropic generalist species, able to tolerate a wide range of urban conditions; 2. urban adapters, able to adapt to urban habitats but also utilizing natural resources; and 3. urban exploiters which are dependent on urban resources. Species range and density of wild animals in urban areas are determined by the type of urban habitats. According to McKinney (2002, 2006), anthropogenic disturbances of various nature (noise, traffic, presence of humans and pet animals) vary in intensity between different urban, peri-urban or rural environments, which will select for the adaptability of individual species to these conditions. Observations in rapidly expanding urban areas have revealed that some wild animals not only cope well with urbanization but are actually attracted to urban environments. Therefore, urbanization is a very dynamic process and changes in the composition of wildlife communities in urban and peri-urban areas are also very important for zoonotic

vector-borne infections, because many of these highly adaptable species are important reservoir hosts for vector-transmitted pathogens. Therefore, changes in the abundance of certain wild animals will affect vector populations as well. Recently, abundant tick populations have been detected in peri-urban and urban areas worldwide, increasing the risk of zoonotic infections of humans and domestic animals. An increasing number of studies have been initiated to understand the complex processes involved in these developments (Daszak et al., 2000; Randolph, 2001; McKinney, 2002; Miller and Hobbs, 2002; Bradley, 2004; Patz et al., 2004; Polley, 2005; Despommier et al., 2006; Shochat et al., 2006; Bradley and Altizer, 2007; LoGiudice et al., 2008; Lambin et al., 2010; Reisen, 2010; Kellner et al., 2012; Pfäffle et al., 2013; Thompson, 2013; Rizzoli et al., 2014).

1.2. Zoonotic parasites and urban/peri-urban areas

As a result of established wildlife populations in and around human settlements, zoonotic diseases (including such that are caused by parasites) can be transmitted in the immediate environment of humans. The range of pathogens transmitted not only depends on the species and abundance of individual host species, but, especially with parasites, on the host communities as a whole. Considering the complexity of parasitic life cycles (especially zoonotic vector-transmitted infections) which often include several different hosts, it is obvious that urbanization may be beneficial for the transmission of some parasites, but not for others to the point that the parasite's life cycle is inhibited completely. Therefore, the importance, transmission and prevalence of a parasite in a given host cannot be simply extrapolated from the natural (or rural) to the urban situation. Factors influencing the transmission of zoonotic parasites in urban areas are not well understood. As an example, rich food resources may increase the birth and litter survival rates of urban-adapted species, thus intensifying the parasite transmission due to the abundance of highly susceptible juvenile hosts. On the other hand, decreased hunting pressure may change the age pyramid in favour of older animals, which causes the opposite effect (Prange et al., 2003). Pet animals may be involved in the transmission cycles of these parasites in urban areas, and the presence and frequency of pets may have a significant effect on disease pressure to humans. In urban and peri-urban areas, the frequency of contact between wildlife and humans changes from sporadic encounters to permanently sharing the environment, thus greatly increasing the chance of parasite transmission to humans (Daszak et al., 2000; Polley, 2005). More than 75% of human diseases are of zoonotic origin and are related to wildlife and domestic animals (Taylor et al., 2001). Therefore, more information is required to better understand the dynamics between wildlife species, humans and domestic animals in urbanized areas (Blair, 1996; DeStefano and DeGraaf, 2003; Chace and Walsh, 2004; Faeth et al., 2005; Wilcox and Ellis, 2006).

In the following chapters, we address the state (most often, the lack) of knowledge on various helminths and ticks whose zoonotic potential in urban and peri-urban environments has been recognized. We review examples from contrasting types of urbanized areas in central Europe and Australia, respectively.

2. *Echinococcus multilocularis*

2.1. Background on transmission factors

Alveolar echinococcosis (AE), caused by the larval stage of the cestode *Echinococcus multilocularis*, is a zoonotic disease of increasing importance in the northern hemisphere (Davidson et al., 2012). Incidence and prevalence of human AE vary widely across the expansive range of *E. multilocularis* for reasons, which are only

partly understood. The wide geographical spread results from the ability of the parasite to use a large variety of local predator–prey systems for its transmission (Eckert et al., 2001). Thus, the parasite is endemic in natural ecosystems like arctic tundra or Tibetan high-altitude grassland, as well as in highly anthropogenic central European farming landscapes or Japanese city parks. In the far north, *E. multilocularis* cycles between arctic foxes (*Vulpes lagopus*) and northern voles (*Microtus oeconomus*). In the temperate parts of Eurasia, red foxes (*V. vulpes*) are the principal definitive hosts, although other canids may regionally also contribute to the life cycle, e.g. Tibetan foxes (*V. ferrilata*), raccoon dogs (*Nyctereutes procyonoides*), golden jackals (*Canis aureus*), coyotes (*C. latrans*), wolves (*C. lupus*) or domestic dogs (Eckert et al., 2001). Concerning intermediate hosts, the situation is even more complex. In most of Europe, *Microtus arvalis* seems to be the most important species, while e.g. in central Asia, other grassland-adapted rodents are principal intermediate hosts. In contrast, *Myodes* spp., living in dense forest undergrowth, maintain the life cycle in northern Japan (Eckert et al., 2001).

Therefore, factors that drive the transmission of this parasite – and risk factors for human disease – are necessarily different across geographical regions, and possibly even between different ecosystems of the same area:

- 1 **Definitive hosts:** wild and domestic canids as competent hosts are widespread and occur in all endemic regions. However, canid species differ in their capacities to support worm populations (Kapel et al., 2006), and their infection risk differs due to habitat and prey preference. Moreover, their population densities vary due to species-specific parameters and available food resources. As the age structure of the canid population is known to be important (juvenile red foxes have far higher worm burdens than adults – Hofer et al., 2000), hunting pressure or disease mortality has an impact on transmission. Repeated infections with *E. multilocularis* elicit intestinal immune responses, which act as a downregulating factor on parasite egg production in highly endemic areas (Torgerson, 2006).
- 2 **Intermediate hosts:** different rodent species differ drastically in their susceptibility to, and tolerance of, the parasite, as well as in their habitat preference on a small spatial scale. Some species maintain rather stable populations (at different densities), while others tend towards cyclic population outbreaks and crashes (Giraudoux et al., 2002). The amplitude of the population cycles, again, is determined by the landscape pattern (Raoul et al., 2001). Varying population densities of the same species not only change the predation rates of the canids, but may also change their predation behaviour with respect to other food sources. Availability (microhabitats, diurnal activity patterns) and attractiveness as prey is different among rodent species.
- 3 **Environmental conditions:** climate and anthropogenic influences determine the vegetation type and, thereby, the species composition and density of host species (Romig et al., 2006). Climatic factors (e.g. precipitation) and soil parameters act on the survival time of *E. multilocularis* eggs in the environment (Veit et al., 1995). Weather conditions (e.g. snow cover in winter) influence the survival of rodents and their availability as prey.
- 4 **Human behaviour:** Attitude to wildlife, hunting pressure and rodent pest control act on host populations. Intentional or accidental introduction of new host species can change life cycle patterns, and the parasite can be introduced into non-endemic areas via travelling dogs or translocated wild animals (Davidson et al., 2012). Dogs kept for various purposes may complement the life cycle (Deplazes et al., 2011), or may act as a specific risk factor for human AE (Kern et al., 2004). The presence or absence of good personal hygiene behaviour are likely to be key factors for the frequency of human disease.

2.2. *E. multilocularis* in urban and peri-urban areas of Europe

Until the 1990s, AE in central Europe was considered to be a disease associated with rural areas and farming activities (Auer and Aspöck, 1991). Since then, the annual incidence of human AE has increased at least in parts of the region (Schweiger et al., 2007), a development which seems to be correlated with the general increase of European fox populations beginning in the early 1990s (Chautan et al., 2000). In addition, human cases are being reported increasingly from urban areas (cit. in Deplazes et al., 2011), which appear to be a consequence of the urbanization of the *E. multilocularis* life cycle.

For most of the 20th century, foxes outside Britain were not known to occur in larger towns and cities, and the principal intermediate hosts, *M. arvalis* and *Arvicola scherman*, are typical rodents of meadows, pastures and orchards in rural landscapes. From that time onwards, however, habitat preferences of some red fox populations have changed. Regular sightings of foxes inside larger human settlements were first reported from the middle of the 1990s, and by the early 2000s several larger cities of central Europe were known to support resident fox populations (Deplazes et al., 2004). The most obvious characteristic of these ‘urban foxes’ is tolerance of disturbing factors like traffic and the immediate vicinity of humans and pet animals. Initially, this phenomenon was thought to be the result of population pressure from rural areas to less suitable urban habitats in the wake of general fox population increases in the 1990s (probably aided by reduced mortality after successful rabies vaccinations – Chautan et al., 2000). Genetic studies, however, showed that populations of ‘urban foxes’ are self-sustaining and show reduced gene flow to and from surrounding rural populations (Wandeler et al., 2003). Typically, these synanthropic foxes live in higher population densities than their rural counterparts, aided by sufficient and seasonally stable food from anthropogenic sources (Contesse et al., 2004). For urban and suburban areas in Switzerland and southern Germany, radio-tracking data suggest densities of >10 resident adult foxes per km² (Deplazes et al., 2004), compared with <3 per km² in rural areas (Heydon et al., 2000; Thoma, 2008; Janko et al., 2012).

Relatively few studies have been conducted on the infection of such foxes with *E. multilocularis*. Reported prevalences in different cities and towns vary drastically, being e.g. 4% in Nancy (France) and 44% in Zurich (Switzerland) (Deplazes et al., 2004; Robardet et al., 2008). ‘Urban’ *E. multilocularis* life cycles are assumed to result from the establishment of these synanthropic fox populations. However, earlier presence of the parasite in urban areas cannot be excluded, since relevant studies were only initiated after the urban fox phenomenon was recognized. At least in the periphery of cities and towns, rural (‘shy’) foxes are known to utilize anthropogenic food sources and might be able to maintain a certain level of transmission inside the settlement area. The same applies for domestic dogs, whose generally low *E. multilocularis* prevalence is compensated by their extremely large numbers in urban and peri-urban areas (Deplazes et al., 2011; Hegglin and Deplazes, 2013). In any case, the prevalence of *E. multilocularis* in synanthropic foxes is the only practically available indicator for presence and frequency of the parasite. Data suggest that, even as fox population densities increase from rural through peri-urban to urban areas, *E. multilocularis* frequency shows the opposite trend, e.g. in the cities of Zurich, Geneva, Stuttgart and Nancy (Deplazes et al., 2004; Robardet et al., 2008; Reperant et al., 2009). This is usually explained by decreased availability of suitable intermediate hosts in highly urbanized areas, which either depend on extensively managed grassland which becomes increasingly rare towards city centers (*M. arvalis*), or which are not as easily accessible as prey for foxes due to low density, burrowing habits or size (*A. scherman*, *M. glareolus*, *Ondatra zibethicus*) (Robardet et al., 2011). Based on population densities of both foxes

and rodents, peri-urban areas appear to be focal points for transmission of *E. multilocularis*. Such areas are characterized by (1) higher population densities of foxes compared to strictly rural landscapes (as foxes are able to supplement their 'natural' food sources with anthropogenic sources like waste or pet food), (2) presence of intermediate host species at sufficient frequency to serve as regular fox prey (even though at reduced densities or with patchy distribution compared to strictly rural landscapes), and (3) high density of humans and their pet animals. *E. multilocularis* prevalence of foxes in such areas is usually lower than in adjacent rural habitats (reflecting the reduced availability of intermediate hosts), but this is counteracted by the larger fox densities. Such peri-urban areas are a contact zone between humans and infected foxes and therefore – hypothetically – more important than rural (few humans) or highly urbanized areas (few infected animals). In addition, dogs and cats can complement the life cycle of *E. multilocularis* when preying on rodents, e.g. in the city periphery or in parks and gardens (Deplazes et al., 2004). Although cats are known to be inferior hosts for this parasite, and dogs are generally rarely infected, dogs in particular are thought to be an important conduit for human infection due to their frequent and close contact (compared to foxes) with people (Kapel et al., 2006). In addition, even at very low prevalences, dogs may also contribute substantially to transmission due to their large number: it has been estimated that, under urban conditions, dogs may contribute 6.8–18.9% of the total egg output of all definitive hosts combined (Hegglin and Deplazes, 2013).

A definition of 'urban' or 'peri-urban' life cycles for *E. multilocularis* is difficult to formulate for a number of reasons. Even within a region like central Europe, the character of urbanization varies considerably. Size, distribution and management of 'green' areas inside human settlements differ, which has an impact on the suitability of these areas as habitats for host species. At the periphery of cities, there is necessarily a contact zone between typical synanthropic fox populations and those from surrounding rural areas that also exploit anthropogenic food sources using different strategies. The dependency of urban *E. multilocularis* life cycles on these 'periphery' foxes (whose home ranges can include both agricultural grassland and urban parts) is not known. Likewise, it is unclear which species of intermediate hosts can maintain the life cycle in urban/peri-urban areas. For open landscapes of central Europe, stable populations of common voles (*M. arvalis*) seem to be more important for the parasite than any other rodent species (Guerra et al., 2014), and some data from France suggest that this may also be the case for cities and towns (Robardet et al., 2011). Water voles (*A. sherman*) can be frequently infected in city parks and gardens (e.g. 9.1% in Zurich – Stieger et al., 2002), although their role in transmission is less clear. Likewise, 15.2% of 46 muskrats (*O. zibethicus*) were found to be infected at a recreational lake within the city of Stuttgart, Germany (Romig, unpublished), but their impact on transmission may be marginal due to localized occurrence and low predation by foxes. There are considerable gaps of knowledge concerning such basic epidemiological parameters. Better understanding of urban/periurban life cycles and their link with the surrounding 'rural' landscape, however, is crucial for the development of countermeasures against the parasite which have been specifically recommended for peri-urban areas with increased fox–human contact (Hegglin and Deplazes, 2013). Various deworming schemes using anthelmintic fox baits have been described from Europe and Japan (Ito et al., 2003; Hegglin and Deplazes, 2013). In urban areas, they were conducted with different degrees of success, and comparative data from two French studies indicate that failure in one area is linked to parasite infection pressure from surrounding landscapes (Comte et al., 2013). In conclusion, it is apparent that even within Europe, there is no uniform pattern of urban/peri-urban transmission of *E. multilocularis*, and even less so when comparing areas (e.g. in Japan or North America) where other host species with different ecological requirements occur.

3. *Baylisascaris procyonis* in Europe

Raccoons are opportunistic carnivores native to North and Central America. They are highly adaptable to various environments and settle in rural, as well as peri-urban and urban areas. Raccoons have been introduced to Europe in the early 20th century and are now known to occur in at least 20 European countries (Bartoszewicz, 2011; Beltrán-Beck et al., 2012). Stable populations are presently developing in Spain and France and a few raccoons appear occasionally in Denmark and other Scandinavian countries. Raccoons have been released deliberately for hunting purposes (in Russia and Poland), escaped from fur farms or set free by pet owners. High population densities are recorded in Germany and it is estimated that at least 500,000 raccoons are living there. In 2012, the hunting index increased up to 67,000 individuals (Michler and Michler, 2012). In some urban areas in Germany, raccoons may reach a population density of up to 100 individuals/km² due to their adaptable behaviour, their omnivorous feeding habits, their high reproductive potential and the lack of natural predators (Beltrán-Beck et al., 2012). The high population density of raccoons in some European urban settlements greatly exceeds the known density of other wild carnivores in these environments (Michler and Hohmann, 2005).

Raccoons are competent hosts for various pathogens (Beltrán-Beck et al., 2012), but only *Baylisascaris procyonis*, the common raccoon roundworm, poses a serious threat to humans in Europe. Apart from raccoons, this nematode can also develop into the mature stage in dogs (but not cats) (Beltrán-Beck et al., 2012). Larvae, however, may start their body migration in a wide range of hosts (birds, reptiles and mammals including humans). The eggs of *B. procyonis* remain infectious for months in humid soil or water. Raccoons apparently acquire the infection by the uptake of embryonated eggs from contaminated environments, but especially adult raccoons may also become infected by the consumption of third-stage larvae in intermediate hosts (Bauer, 2013). Raccoons defecate at latrines close to their resting and sleeping places, and in case of raccoons adapted to peri-urban and urban areas these can be located in barns, lofts, attics, chimneys and garages (Bauer, 2013). The surroundings of such latrines may become heavily contaminated with *B. procyonis* eggs, increasing the risk of human infections. In humans, the larval stages may cause ocular and visceral larva migrans, which may become fatal when larvae invade the central nervous system (Wise et al., 2005). The prevalences of *B. procyonis* in European raccoon populations vary considerably, as high as 70% in parts of Germany (Hesse) (Michler and Hohmann, 2005) and as low as 3% in adjacent countries. Although the prevalence of *B. procyonis* may be very high in 'urban' raccoons, human cases of baylisascariasis are rare both in Europe and elsewhere. Infection is usually restricted to patients who had close contact with raccoons, i.e. pet owners (Küchle et al., 1993). The results of serological studies indicated, however, that many more individuals showed increased antibody levels against *B. procyonis*, although clinical symptoms were lacking (Conraths et al., 1996).

4. Parasitic zoonoses of peri-urban wildlife carnivores in Australia

The wildlife hosts of parasitic zoonoses occurring in peri-urban areas of Australia comprise wild dogs (dingoes – *Canis lupus dingo* – and dingo/domestic dog hybrids), foxes (*Vulpes vulpes*) and feral cats (*Felis catus*).

4.1. Origin of wild dogs, foxes and feral cats in Australia

Dingoes, foxes and cats were all introduced into Australia at various times. Dingoes by south-east Asian seafarers somewhere between 4000 and 5000 years ago (Breckwoldt, 1988; Corbett, 1995).

Over time, they out-competed the indigenous Australian marsupial predators, Thylacines (*Thylacinus cynocephalus*) and Tasmanian Devils (*Sarcophilus harrisii*), and established themselves as a new Australian top-order predator. From 1788, European settlers with dogs began arriving in Australia and it soon became evident that dingoes and domestic dogs could hybridize and produce fertile young (Claridge et al., 2014). The result has been that currently in much of the suitable dingo habitat in Australia, the top-order predators consist no longer of pure-bred dingoes but dingo/domestic dog hybrids together with a few pure-bred dingoes (Claridge et al., 2014). These populations of wild canids are commonly referred to as wild dogs, but importantly dingoes and their hybrids are readily susceptible to infection with all parasitic zoonoses associated with domestic dogs.

Foxes arrived in Australia much more recently than dingoes, having been introduced by the early settlers for sport and to control rabbits (*Oryctolagus cuniculus*) (also introduced). However, within a few decades foxes themselves had become a major agricultural pest. It is generally accepted that the first successful introduction of foxes occurred in 1871 in southern Victoria; they spread rapidly, reaching Western Australia in the 1920s (Saunders et al., 1995). Foxes are now found in all parts of Australia except the tropical north. They were also recently illegally introduced into Tasmania and there followed an intense eradication campaign, but the current status of foxes in Tasmania is unclear (Sarre et al., 2012). Foxes, like dingoes and their hybrids, can act as definitive host for the same suite of potential helminth zoonoses found infecting dogs, including *E. granulosus*.

Cats were introduced into Australia in the early 1800s by settlers intending to have them as companion animals, but some soon became feral. Feral cats are now widespread, in almost all environments of Australia, and a major environmental pest. Cats share a number of the zoonotic helminths found in wild dogs and foxes, but importantly they do not act as a definitive host for *E. granulosus* (Jenkins and Macpherson, 2003).

The most important zoonotic helminth parasite recorded infecting wild dogs and foxes living in peri-urban and urban environments is *Echinococcus granulosus* (Jenkins and Craig, 1992; Jenkins et al., 2008). However, a number of other zoonotic helminths including *Dipylidium caninum* (Brown and Copeman, 2003; Jenkins et al., 2008; Smout et al., 2013), *Spirometra erinacei* (Jenkins et al., 2008; Smout et al., 2013), *Toxocara canis* and *Toxascaris leonina* (Jenkins et al., 2008; Smout et al., 2013), *Ancylostoma caninum* (Brown and Copeman, 2003; Jenkins et al., 2008; Smout et al., 2013), *A. ceylanicum* (Smout et al., 2013) and *A. braziliense* (Smout et al., 2013) also occur. Zoonotic helminths of feral cats include *Toxocara cati*, *T. canis* and *T. leonina* and *Ancylostoma tubaeforme*, but they can also become infected with *S. erinacei* and *D. caninum*. Although *S. erinacei* and *D. caninum* are zoonotic parasites, their transmission to humans is indirect, requiring ingestion of parasite stages residing in intermediate hosts, not a parasite stage emanating from the definitive host. Therefore, *S. erinacei* and *D. caninum* will not be included in this review of parasitic zoonoses of peri-urban wildlife carnivores in Australia.

4.2. *Echinococcus granulosus* in peri-urban wild dogs (dingoes) and foxes in Australia

Humans are accidental intermediate hosts for *E. granulosus* becoming infected through ingestion of eggs passed into the environment in the faeces of infected carnivores. Infection (cystic echinococcosis, or hydatid disease) manifests as large fluid-filled cysts developing mainly in the liver and/or lungs, causing morbidity and occasionally death.

Infection with *E. granulosus* is common and it is often present in large numbers in the small intestine, not only in the wild dogs

living in the bush (Jenkins and Morris 2003), but also in those encroaching into peri-urban and urban areas (Brown and Copeman, 2003; Jenkins et al., 2008).

Reports of wild dogs encroaching into peri-urban and urban areas are increasing. In a recent study by Allen et al. (2013), satellite tracking collars were attached to a number of urban wild dogs that were released back into their territories and followed for varying periods of time. It was clear from the data of Allen et al. (2013) that these animals were including urban, peri-urban and adjacent bushland in their home range, moving freely between all three habitats.

The few published reports containing data on *E. granulosus* in wild dogs encroaching into peri-urban and urban areas have all originated from studies in Queensland. However, the migration of wild dogs into urban and peri-urban areas is not restricted to Queensland; it is also happening in and around urban centres in New South Wales (Jenkins, unpublished data). The prevalence of *E. granulosus* in a study of wild dogs moving between adjacent bushland and peri-urban and urban habitat in Townsville (North Queensland) was 22.2% (Brown and Copeman, 2003). The prevalence of *E. granulosus* in 108 wild dogs caught around Maroochydore (south-eastern Queensland) was 46.3%, with individual worm burdens in excess of 100,000 worms in some animals (Jenkins et al., 2008). Of particular importance is that at least some of these animals are moving close to, and in some cases, entering the gardens of residents and defecating (Jenkins et al., 2008). It is of interest to note that in their study of the intestines and scats from wild dogs collected in bushland adjacent to northern and southern Cairns in northern tropical Queensland, Smout et al. (2013) found no evidence of *E. granulosus* either in scats or in wild dogs examined *post mortem*.

The prevalence of *E. granulosus* in foxes in rural areas in Australia can be as high as 45.8%, but the worm burdens of infected foxes are always low, usually less than 50 tapeworms (Jenkins and Morris, 2003). However, more commonly the prevalence of *E. granulosus* in foxes in rural areas and in peri-urban areas is lower, with worm burdens also less than 50 worms (Jenkins and Craig, 1992). The contribution of Australian foxes in contaminating the environment with eggs of *E. granulosus*, particularly in the bush, is small by virtue of their small worm burdens and the generally low prevalence of infected animals. However, their importance may increase in peri-urban and urban areas, particularly around areas such as popular barbecue or picnic sites. These locations attract foxes to come and scavenge rubbish bins looking for food scraps left by visitors. If several foxes visit one of these barbecue or picnic sites, the area can become heavily contaminated with fox faeces, and if one or more of these animals is infected with *E. granulosus*, this may present an important potential public health risk (Jenkins and Craig, 1992).

An important consideration in respect of the epidemiology of *E. granulosus* in peri-urban and urban environments infiltrated by *E. granulosus*-infected wild dogs and/or foxes is the role of coprophagous flies in egg dispersal. A study by Lawson and Gemmell (1985) demonstrated the capacity of several species of coprophagous flies for the dispersal of eggs of taeniid cestodes. They showed that individual flies can ingest more than 800 eggs, over 80 percent of the eggs were excreted within 24 hours and that eggs ingested by flies remained infective to sheep. These data suggest that the potential role of coprophagous flies in the transmission of *E. granulosus* in peri-urban and urban environments also inhabited by wild dogs and foxes infected with *E. granulosus* could be more important than is currently realized.

4.3. *Ancylostoma species* and *Uncinaria stenocephala*

Human infection with hookworm species commonly causes cutaneous larval migrans, with painful, itchy eruptions along the path of migrating larvae. Lesions occur most commonly in the skin on

Table 1
Zoonotic hookworm species recovered from Australian peri-urban wild dogs and foxes.

Location	Definitive host (n)	Parasite species	Prevalence % (n)	Reference
Townsville	Wild dogs (27)	<i>A. caninum</i>	74 (20)	Brown and Copeman, 2003
Maroochy Shire	Wild dogs (108)	<i>A. caninum</i>	37 (40)	Jenkins et al., 2008
Fraser Island	Wild dogs (18)	<i>A. caninum</i>	83.3 (15)	Jenkins et al., 2008
Cairns	Wild dog (38)	<i>A. caninum</i>	78.9 (30)	Smout et al., 2013
	scats	<i>A. ceylanicum</i>	55.3 (21)	
		<i>A. braziliense</i>	2.6 (1)	
Canberra	Foxes (45)	<i>U. stenocephala</i>	80 (36)	Jenkins and Craig, unpublished data
Maroochy Shire	Foxes (7)	<i>A. caninum</i>	42.8 (3)	Jenkins et al., 2008

the feet, legs, buttocks and hands, but lesions can occur anywhere on the body. Lesions from *A. braziliense* and *U. stenocephala* may persist for many weeks to a year before the larvae die, while lesions caused by *A. caninum* are small and transient (Stevenson and Hughes, 1988). Complications may be secondary bacterial infection following scratching lesions with dirty hands. *A. caninum* has also been implicated in causing eosinophilic enteritis in humans. Until the cause of this eosinophilic enteritis was revealed, patients had large sections of intestine resected (Prociw and Croese, 1996).

The prevalences of hookworm infections in wild dogs and foxes from peri-urban and urban environments are high (Table 1). *U. stenocephala* is a cold adapted species and is found almost exclusively in domestic and wild dogs and foxes inhabiting the cooler areas of southeastern Australia, especially areas associated with the Great Dividing Range where cold winters with severe frosts occur (Wilson, 1994; Palmer et al., 2007). Whereas *A. caninum* occurs along the warmer coastal fringe of eastern Australia, becoming more widespread in the damper, warmer areas of tropical Australia (Palmer et al., 2007). *A. ceylanicum* and *A. braziliense* also occur mainly in more tropical areas (Palmer et al., 2007). *A. ceylanicum* is able to cause patent enteric infection in humans and patent infections have been identified in dingoes in the Cairns district in Queensland (Smout et al., 2013).

4.4. *Toxocara species* and *Toxascaris leonina*

The most important of these parasites is *T. canis* because of its impact on human hosts. Accidental ingestion of embryonated *T. canis* eggs, usually by children, results in visceral larval migrans and in some cases larvae migrate to the eyes, leading to blindness, commonly unilateral (Stevenson and Hughes, 1988). *T. cati* and *T. leonina* have not been definitely implicated as causes of visceral larval migrans in humans, but *T. cati* has been shown to produce a similar impact in pigs (Stevenson and Hughes, 1988).

T. canis occurs in wild dogs and foxes encroaching into peri-urban and urban areas; however, the prevalence of infection is commonly low, but can be unexpectedly high. In wild dogs from the Maroochy Shire, 5/108 (4.6%) of the animals examined were infected (Jenkins et al., 2008), but none of 7 foxes examined was infected. However, in the same study, 5/18 (27.8%) wild dogs from Fraser Island were infected, a likely reflection of the close proximity of the Fraser Island wild dogs with human habitation. In the Townsville study, Brown and Copeman (2003) did not recover *T. canis* in any of the 27 wild dogs examined in contrast to Smout et al. (2013) who reported a prevalence of 46% in their study in Townsville. Data from a survey of 25 road-killed urban foxes and 43 shot peri-urban foxes in and around Canberra (Wilson, 1994), revealed prevalences of *T. canis* of 12% and 0%, respectively (Craig, 1990).

4.5. Feral cats

Domestic cats also accompanied some settlers to Australia and the progeny of these animals soon established feral populations in the bush. Cats in Australia do not act as definitive host for *E. granulosus* (Jenkins and Macpherson, 2003). There are a few data available regarding the zoonotic parasites of peri-urban feral cats. However, cats living in and around urban rubbish dumps and cats from council shelters (Palmer et al., 2007) have been found infected with *Ancylostoma tubaeforme*, *Toxocara cati*, *T. leonina*, *D. caninum*, *S. erinacei*, *Cryptosporidium*, *Giardia*, and *Toxoplasma*. However, the habit of cats to bury their faeces may reduce the transmission of potential zoonoses.

In a study of 54 cats trapped over three rubbish dumps around Canberra, the average prevalence of *A. tubaeforme* was 3.8% (range 0–7%), and in the study of Palmer et al. (2007) the mean prevalence of hookworm was reported as 2.9% (range 1.4–4.4%) but the species present were not reported.

5. *Ixodes species* and the transmission of parasites/pathogens in peri-urban/urban areas

Ticks, mosquitoes and fleas are important arthropod vectors in the transmission of parasites and other pathogens, some of which are zoonotic. In the northern hemisphere, the majority of vector-borne infections are transmitted by ticks (Randolph, 2001), especially *Ixodes* species that are highly competent vectors for a variety of different pathogens including parasites, bacteria and viruses (Sonenshine and Roe, 2014). In general, the eco-epidemiology of zoonotic vector-borne diseases is still little understood, as it depends on the interaction of a vector with (often several) reservoir hosts and a pathogen which is transferred from the reservoir to the human host (Pfäffle et al., 2013). *Ixodes* species have a three-host life cycle with larvae feeding predominantly on small mammals whereas adults prefer larger mammals. Nymphs tend to feed on small as well as large mammals. The most abundant tick in central Europe, *Ixodes ricinus*, has the capacity to feed on more than 300 different vertebrate host (Bowmann and Nuttall, 2008), including small rodents, lizards, hares, hedgehogs as well as larger animals like deer, red foxes or wild boar. *I. ricinus* populations are usually associated with deciduous and mixed forests, but recent studies show that this tick species can also be highly abundant in peri-urban and urban areas (Rizzoli et al., 2014). As already mentioned above, urbanization changes the local wildlife composition drastically. This has important consequences for tick densities, because the local composition of host species and their abundance affects the capacity of the environment to support tick populations. Roe deer (*Capreolus capreolus*), red foxes (*Vulpes vulpes*) and wild boar (*Sus scrofa*) are particularly important for the maintenance and the geographical distribution of *I. ricinus*, because they host all three different developmental stages of *I. ricinus*, can carry a large number of ticks and may migrate over long distances. Importantly, they are often attracted by peri-urban and urban areas (Gassner et al., 2011; Medlock et al., 2013; Overzier et al., 2013; Rizzoli et al., 2014). Roe deer and other cervids as well as foxes or wild boar are important reservoir hosts of numerous pathogens which may be transmitted by ticks to humans, so their high abundances in peri-urban and urban areas increase zoonotic infection risks (Medlock et al., 2013; Rizzoli et al., 2014; Sonenshine and Roe, 2014). Schorn et al. (2011) collected *I. ricinus* in several parks within different cities in southern Germany, which were found to contain *Babesia* and several bacterial pathogens. Interestingly, the composition of pathogens in “urban” ticks revealed differences when compared to woodlands. Overzier et al. (2013) collected more than 10000 *I. ricinus* ticks from four different urban parks, a pasture and a natural area in Bavaria, Germany. The prevalence of *Babesia* spp. was generally higher in the pasture and the

natural area compared to the urban parks. Three species, *Babesia microti*, *B. venatorum* and *B. capreoli*, were detected in ticks collected in the natural area, whereas in the pasture and the urban habitats only one species, *B. venatorum*, was frequent. It is important to note that *B. venatorum* may infect humans and that roe deer are reservoir hosts of this parasite (Pfäffle et al., 2013; Rizzoli et al., 2014). Pichon et al. (1999) pointed out that tick abundance is positively correlated with deer abundance, and those habitats with high densities of deer or cervids in general are therefore areas with a higher risk of infection. Habitat fragmentation and landscape conversion may also favour high population densities of small mammals, mainly rodents, which are crucial as hosts for tick larvae and nymphs as well as important reservoirs for many tick transmitted pathogens (Boyard et al., 2008; Paziewska et al., 2010; Medlock et al., 2013; Pfäffle et al., 2013; Rizzoli et al., 2014). The most prevalent tick-borne infection in the northern hemisphere is Lyme borreliosis. In northeastern North America, extensive studies were conducted on the interactions between *Borrelia burgdorferi* and the different hosts which are involved in the transmission of this pathogen from wild animals to humans (Allan et al., 2003; LoGiudice et al., 2003). Adult *Ixodes scapularis*, as the most important vector, feeds on white-tailed deer (*Odocoileus virginianus*), which is important for the maintenance of the tick population and reaches high population densities in peri-urban areas. *I. scapularis* becomes infected with *B. burgdorferi* when feeding on *Peromyscus leucopus*, the white-footed mouse which is the most competent reservoir host for the pathogen and reaches high population densities due to habitat fragmentation in the vicinity of humans settlements. An infected *I. scapularis* transmits the pathogen to humans. The importance of rodents and other small mammals as “bridge” hosts is more and more recognized, because some species are well adapted to urban environments, are competent reservoir host of many pathogens and may introduce the parasites or pathogens to new habitats (Rizzoli et al., 2014). In addition, small mammals are maintenance hosts for different tick species, which means that pathogens can be exchanged between the different ticks. This host switch may be important because the behaviour and the habitat requirements of tick species differ concerning biotic and abiotic parameters (Pfäffle et al., 2013; Sonenshine and Roe, 2014). European hedgehogs (*Erinaceus europaeus*) can serve as an example for such a host switch. They are common animals, well adapted to urban areas and are frequently infested with two different tick species (*I. ricinus* and *I. hexagonus*), both competent vectors for many pathogens. *I. ricinus* is a generalist, whereas *I. hexagonus* feeds almost exclusively on hedgehogs. *I. hexagonus* was shown to maintain a high infection rate of pathogens within hedgehog populations, whereas *I. ricinus*, becoming infected when feeding on hedgehogs, can transmit these pathogens to various other hosts due to their low host specificity (Estrada-Penã and Jongejan, 1999; Skuballa et al., 2010). These so-called subcycles are important for maintaining stable pathogen populations in urban areas (Pfäffle et al., 2013).

In summary, peri-urban and urban areas are complex and diverse ecosystems which can favour tick transmitted pathogens, although there are still many unsolved questions about the interactions of vectors, reservoir hosts and the transmission of pathogens to humans and/or domestic animals which need to be answered.

6. Conclusion

Urbanization is an ongoing worldwide phenomenon that has important impacts not only on landscapes and ecosystems, but also on the host–parasite interaction within those landscapes. Even as an impressive amount of data on wild animals in urban environments and new parasite transmission routes are now available, we are still far from understanding many of the complex transmission systems within or near urban areas. An important part of this

problem is the ecological diversity of peri-urban and urban environments, which differ even between adjacent areas of Europe, and even more so between different continents due to varying climatic conditions, presence of different animal species and differing cultural backgrounds and attitudes of the human population. Therefore, it is difficult to extrapolate knowledge on transmission routes and risk factors from one area to another, and the application of such data in prevention and control programmes has to be done with care. We are still in the process of understanding some of the basic rules in the complex interactions between zoonotic parasites and their hosts in the light of rapidly changing environmental conditions.

Conflict of interest

The authors declared that there is no conflict of interest.

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