Journal of Helminthology

cambridge.org/jhl

Zoonotic helminths – why the challenge remains

R.C.A. Thompson

School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia, 6150, Australia

Centenary Review

Cite this article: Thompson RCA (2023). Zoonotic helminths – why the challenge remains. *Journal of Helminthology* **97**, e21, 1–15. https://doi.org/10.1017/S0022149X23000020

Received: 14 December 2022
Revised: 5 January 2023
Accepted: 5 January 2023

Keywords:
Zoonotic helminths; anthropogenic factors; urbanization; climate change; wildlife; *Echinococcus*; *Trichinella*; *Taenia*; *Ancylostoma*; *Schistosoma*

Author for correspondence:
R.C.A. Thompson,
E-mail: a.thompson@murdoch.edu.au

Abstract

Helminth zoonoses remain a global problem to public health and the economy of many countries. Polymerase chain reaction-based techniques and sequencing have resolved many taxonomic issues and are now essential to understanding the epidemiology of helminth zoonotic infections and the ecology of the causative agents. This is clearly demonstrated from research on *Echinococcus* (echinococcosis) and *Trichinella* (trichinosis). Unfortunately, a variety of anthropogenic factors are worsening the problems caused by helminth zoonoses. These include cultural factors, urbanization and climate change. Wildlife plays an increasingly important role in the maintenance of many helminth zoonoses making surveillance and control increasingly difficult. The emergence or re-emergence of helminth zoonoses such as *Ancylostoma ceylanicum*, *Toxocara*, *Dracunculus* and *Thelazia* exacerbate an already discouraging scenario compounding the control of a group of long neglected diseases.

Introduction

Given this is the centenary of the *Journal of Helminthology*, one might have expected great inroads to have been made into the control, and in some cases elimination, of helminth zoonoses. Unfortunately, this is not the case. Tremendous advances have been made over the last 100 years in the tools at our disposal and our understanding of the diversity, taxonomy, host range, distribution, ecology and public health significance of helminth zoonotic agents. However, this is not reflected in a reduction in their global impact and attempts at controlling the causative agents have largely been impeded by anthropogenic factors (Lindahl & Grace, 2015). For example, one of the best-known helminth zoonotic agents is *Toxocara canis*. The 'tools' available to control this parasite in dogs, in terms of prophylactic and therapeutic drugs have been available for several decades. However, whereas control has been readily accomplished in some countries, such as Australia, the parasite is an emerging issue elsewhere (see below). It is principally human behaviour in one way or another that allows the causative agents of helminth zoonoses to thrive. Helminths such as *T. canis* and *Echinococcus granulosus* can be effectively controlled in domestic dogs, but this requires education and a willingness by dog owners to administer prophylactic drugs to puppies or ensure dogs do not have access to raw uninspected meat, respectively.

Helminth parasites feature prominently in the World Health Organization's list of neglected diseases (8/17). Most are zoonotic with animal reservoirs playing a significant role in the epidemiology of human infections and thus they are a focus of control efforts. Most of the helminth species were described many years ago, but their zoonotic potential became clear much later. We have known about the zoonotic potential of helminths such as *Echinococcus* and *Trichinella* (echinococcosis and trichinosis) for over 150 years because of the pioneering experiments of researchers such as von Siebold, Zenker and Kuchenmeister, whereas the aetiology of visceral larva migrans was demonstrated much more recently by Beaver (see Grove, 1990). The history of helminth zoonoses is fascinating and detailed descriptions given by authors such as Calvin Schwabe (1969) and David Grove (1990) provide a valuable education on the types of investigations that would not be practical or possible today. The first papers on zoonotic helminths were published in the *Journal of Helminthology* in the 1920s on *Hymenolepis*, *Opisthorchis*, *Echinococcus*, *Trichinella* and *Toxocara*.

Education and public health measures, supported by drugs with some species, remain the main strategies in the control of helminth zoonoses. Considerable research has been undertaken on the development of helminth vaccines, including those with zoonotic potential, but vaccines have had no impact on the global burden. The technological advances that have been made in developing molecular-based vaccines have yet to be put into practice. No vaccines are approved for human or animal use (Bain, 2019; Perera & Ndao, 2021). The only successful vaccine against a helminth infection remains the oral vaccine containing live irradiated lungworm larvae (L3) developed by Jarrett and colleagues at the University of Glasgow to protect calves against infection with the bovine lung worm *Dictyocauls viviparus*

© The Author(s), 2023. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

(Jarrett *et al.*, 1960; Poynter, 1963). It is a live attenuated vaccine that allows larval development to the fourth stage in an immunogenic site, the mesenteric lymph nodes, following which there is no development to the adult stage. It is extremely effective in preventing infection and disease (parasitic bronchitis or 'husk') in cattle, but the other factor that made this vaccine a success was the clear market need given that there were no effective drugs to treat a potentially fatal infection (Poynter, 1963). In contrast, an effective vaccine developed against canine hookworm using a similar approach was not a commercial success given the availability of cheaper, effective therapeutic approaches (Miller, 1978). The attenuated vaccine approach taken in the development of the canine hookworm unfortunately would not be transferable to the development of a similar vaccine for human hookworm for reasons of registration. In the 60 years since the bovine lungworm vaccine was developed, molecular approaches have only resulted in potentially effective vaccines against *E. granulosus* in sheep and some species of *Taenia*. These vaccines are not yet used in control programmes, for a variety of reasons, principally economic, but trials have been undertaken and continue (e.g. Larrieu *et al.*, 2019; Nsadha *et al.*, 2021).

Nearly 30 years ago, Calvin Schwabe referred to the dynamic state of flux and new discovery that has always characterized studies on zoonoses (Schwabe, 1984). Helminth zoonoses are always changing in terms of host range, geographical distribution and the emergence of new or unexpected challenges. This is what makes them so interesting but at the same time so demanding.

In this review, the advances that have been made using molecular techniques in the characterization of the causative agents of helminth zoonotic infections are examined. The knowledge gained has provided comprehensive data on the epidemiology of zoonotic helminthiases yet progress in their control has been thwarted by increasingly problematic anthropogenic factors which are discussed.

Impact of molecular tools

The advent of polymerase chain reaction (PCR)-based techniques and sequencing has had a tremendous impact on our understanding of helminth zoonoses and developing strategies for their control.

Taxonomy

A sound taxonomy of helminths with accurate descriptions of individual species and accepted names is the first step in their control. The formal naming of a species is a prerequisite for effective communication which is particularly important when the species in question are of public health importance and require coordinated control efforts. The molecular characterization of numerous helminths has helped in resolving taxonomic issues, identifying new zoonoses and interpreting epidemiological observations.

Molecular approaches have proved useful where the taxonomic significance of morphological characters was questionable, for example in *Echinococcus*, or difficult to resolve, as with *Ancylostoma ceylanicum* (see below). The lack of morphological differences between many inter-specific and intra-specific variants has, in the past, compounded an often-confusing taxonomic picture, which in many cases has taken decades to resolve. For example, with *Trichinella*, there were no morphological characters that could complement increasing epidemiological evidence that *Trichinella spiralis* is not a uniform species (Zarlenga *et al.*, 2020).

Echinococcus has a long history of taxonomic and nomenclatural confusion, particularly regarding the species level taxonomy (Thompson, 2017). This has resulted not only from a lack of useful morphological characters, but also when taxonomic uncertainty overshadowed the importance of host occurrence (Thompson, 2017). The application of molecular tools has resolved much of the uncertainty of the past and there is now widespread agreement based on not only molecular but also morphological and ecological criteria that *Echinococcus* should be split into ten species (Thompson, 2020; table 1). Molecular approaches have been pivotal in resolving taxonomic issues and interestingly have largely confirmed original taxonomic considerations, and importantly, from a practical point of view, the reliability of differential morphological characters. As a consequence of establishing a sound taxonomy, the ecology of transmission of *Echinococcus* in areas where multiple host species are infected has only recently been interpreted with confidence. The life cycles and host range of all ten species are now well documented (Romig *et al.*, 2017; table 1) and represent an essential foundation for control efforts.

Of all the helminth zoonoses, *Trichinella* provides the best example of the value of molecular characterization in determining the genetic distinctness of inter-specific/intra-specific variants in the genus when differential morphological characters to support epidemiological observations are lacking. All developmental stages of currently recognized species and intra-specific variants/strains/genotypes of the genus (table 2) are morphologically indistinguishable. Until the 1950s, *T. spiralis* was considered a uniform species. The seminal studies by George Nelson and colleagues on *Trichinella* in the 1960s proved pivotal in establishing our current understanding of the intra-specific diversity of the genus and the epidemiology of trichinosis (trichinellosis) globally. Their studies in Africa were stimulated by observations that demonstrated differences in infectivity between local Kenyan isolates and 'typical' isolates of *T. spiralis*, particularly low infectivity to domestic pigs (Nelson & Mukundi, 1963). Locally acquired infections were also less clinically severe in humans than with 'typical' *T. spiralis*, and subsequent studies demonstrated that the local strain is principally maintained in a wild animal cycle (Nelson *et al.*, 1963; Capo & Despommier, 1996). Nelson's studies 'shattered many of the preconceived ideas about the parasite' (Nelson *et al.*, 1966) and importantly, complemented earlier observations of Rausch and colleagues in the Arctic who found that the local form of *Trichinella* was adapted to a wildlife cycle and not introduced but endemic to Arctic regions (Rausch *et al.*, 1956). The application of molecular tools has been instrumental in defining the taxonomy of both encapsulated and non-encapsulated forms of *Trichinella* thus providing a firm foundation on which to interpret the wealth of epidemiological data obtained over a period of more than 50 years since the discovery of what we now know as *Trichinella nelsoni*. A total of ten species (table 2) and three so far unresolved genotypes T6, T8 and T9, have been recognized in the genus *Trichinella* (Zarlenga *et al.*, 2020).

Characterization

The ability to diagnose and characterize a helminth infection based on faecal stages is an important factor both clinically and epidemiologically. However, morphology is often of limited

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

Table 1. Species and genotypes of *Echinococcus.*

Species strain/genotype	Distribution	Known intermediate hosts	Known definitive hosts	Infectivity to humans	Disease
Echinococcus granulosus (sheep/G1–G3)	worldwide	sheep, cattle, goats, macropods, etc.	dog, fox, dingo, jackal, hyena	yes	CE
Echinococcus equinus (horse/G4)	Europe, United States, Africa, Middle East	horses and other equines	dog	probably not	CE?
Echinococcus ortleppi (cattle/G5)	Europe, Asia, Africa, Central and South America	cattle, buffalo (sheep, goat)	dog	yes	CE
Echinococcus canadensis (cervid/G8, G10)	North America, Canada, Eurasia	cervids	wolf, dog	yes	CE
Echinococcus intermedius camel/G6 (Pig/G7)	Middle East, Africa, Asia, South America (pig) Worldwide	camels, sheep, pig	dog	yes	CE
Echinococcus felidis	Africa	warthog, other wildlife?	lion, hyena	not known	–
Echinococcus multilocularis	Northern Hemisphere: Alaska, United States, Canada, Asia, Europe	rodents, domestic and wild pig, dog, monkey, horse	fox, dog, cat, wolf, racoon-dog, coyote	yes	AE
Echinococcus shiquicus	Tibet	pika	Tibetan fox	not known	–
Echinococcus vogeli	Central and South America	rodents	bush dog	yes	PE
Echinococcus oligarthra	Central and South America	rodents	wild felids	yes	PE

Data updated from Thompson (2017) and Romig *et al.* (2017).
CE, cystic echinococcosis; AE, alveolar echinococcosis; and PE, polycystic echinococcosis.

value for the detection and characterization of helminth parasites as well as for the diagnosis of infections. This may be because of insufficient, or poor-quality material; no differential morphological characters between species of the same genus; and the need for staff well trained in microscopy (Singh, 1997; Betson *et al.*, 2020), a skill that is sadly very much in decline. Molecular tools have thus provided an important alternative or adjunct to the use of microscopy, providing better sensitivity as well as a means of characterizing helminth parasites genetically.

The eggs of *Taenia* species are morphologically identical which in the past has been a problem for studies on the epidemiology of taeniid infections where several species may coexist in an endemic area. Such situations require the use of molecular tools to determine the source of infection in humans and any cohabiting non-human definitive hosts. For example, in Laos *Taenia solium* is an important public health issue (Conlan *et al.*, 2012a; Ash *et al.*, 2017). However, in rural areas people may be infected with both, or either, *Taenia solium* and *Taenia saginata* and appropriate PCR-based assays are the only way to determine the prevalence of the two species from faecal samples (Conlan *et al.*, 2012b). Interestingly, in rural villages in Laos, dogs were found to be infected with *Taenia hydatigena* using PCR, raising questions about the possible competitive interactions of *T. solium* and *T. hyadatigena* in pigs acquiring infections with both species (Conlan *et al.*, 2009, 2012b).

Similarly, the eggs of the zoonotic trematodes *Clonorchis* and *Opisthorchis* are identical which has made it difficult to determine their geographical distribution in endemic areas where both species occur. This is the case in south-east Asia where molecular epidemiological studies have provided a more accurate picture of the distribution of both species (Traub *et al.*, 2009; Saijuntha *et al.*, 2019). Similarly, with the faecal stages of zoonotic nematodes, PCR-based tools have proved valuable in differentiating between species, particularly of *Ancylostoma* (see below).

Smyth (1995) identified two nematodes as emerging zoonoses, *Angiostrongylus costaricensis* and *Oesophagostomum bifurcum*. Since then, the zoonotic significance of both parasites has increased and molecular tools have proved invaluable in terms of diagnosis, in the case of *A. costaricensis* (Rojas *et al.*, 2021) and determining prevalence and genetic diversity of *Oesophagostomum* (Sirima *et al.*, 2021).

Surveillance and biosecurity

Otranto & Deplazes (2019) predicted that the use of DNA-based analyses of clinical material would allow the specific diagnosis of exotic (i.e. unexpected) infections. This was demonstrated in a case of the diphyllobothriid cestode, *Adenocephalus pacificus* in a child in southern Australia (Moore *et al.*, 2016). Infection was traced to a locally caught marine finfish which was unexpected since recent food risk assessments in Australia did not recognize *A. pacificus* tapeworms as a potential zoonotic threat from locally caught finfish (Moore *et al.*, 2016). Morphologically, limited information could be obtained from strobilar material and eggs in the faeces of the infected child, and could only suggest diphyllobothriosis, not the genus or species. However, DNA sequencing confirmed this diagnosis and identified the causative agent as *A. pacificus*. This is the first human case of diphyllobothriosis reported in Australian waters which is discussed further below.

Opportunities for the introduction of exotic helminth parasites have increased with globalization and the expansion of tourism and illegal wildlife trade (Thompson *et al.*, 2003; Thompson, 2018; Betson *et al.*, 2020; Bezerra-Santos *et al.*, 2021), emphasizing the need for improved border security and surveillance. From an economic perspective *T. spiralis* has always been considered a major parasite threat to the biosecurity of many countries in terms of trade (Thompson *et al.*, 2003; Thompson, 2018). The importance of demonstrating *Trichinella*-free status is a

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

Table 2. Species and genotypes of *Trichinella.*

Species/genotype	Hosts*	Distribution
1. *Trichinella spiralis* (T1)	domestic and wildlife cycles, pig, wild boar, rat, fox, bear, horse, seals, many other mammals	Europe, the United States, South America, Africa, Asia, Middle East
2. *Trichinella nelsoni* (T7)	wildlife cycles, warthog, hyena, jackal, lion, bush pig, serval, leopard, genet, big-eared fox	Sub-Saharan Africa
3.*Trichinella britovi* (T3)	wildlife cycles, red fox, raccoon dog, wolf, jackal, wild cat, lynx, brown bear, badger, marten, otter, domestic pig, wild boar, horse	Eurasia, north-western Africa, south-western Asia
4. *Trichinella nativa* (T2)	wildlife cycles polar bear, walrus, seals, brown and black bear, wolf, polar fox, red fox, raccoon dog, lynx, wild cat, tiger, wild boar, mustelids, pig, dog, cat	Arctic and sub-Arctic regions of North America and Eurasia
5. *Trichinella murrelli* (T5)	wildlife cycles, red fox, raccoon, coyote, bobcat, black bear, cougar, mustelids, horse, dog, cat	Southern Canada, the United States
6. *Trichinella chanchalensis*	wildlife cycle, wolverine	North-west Canada
7. *Trichinella patagoniensis*	wildlife cycle, cougar	Argentina
8. *Trichinella pseudospiralis* (T4)	wildlife cycle, red fox, raccoon dog, lynx, badger, raccoon, wild boar, domestic pig, cat, rat, various bird species	cosmopolitan
9. *Trichinella papuae* (T10)	wildlife cycle, wild and domestic pig, saltwater crocodile	Papua New Guinea, Thailand
10. *Trichinella zimbabwensis* (T11)	wildlife cycle, Nile crocodile (and farmed crocodiles), Nile monitor, lion	Africa

Data from Deplazes *et al.* (2016) and Zarlenga *et al.* (2020).
*All zoonotic but no human cases reported for *T. patagoniensi*, *T. chanchalensis* and *T. zimbabwensis*.
1–7, encapsulated clade; and 8–10, non-encapsulated clade.

significant trade issue for many countries which is exacerbated by the limitations of meat inspection procedures, particularly in free-ranging situations, as well as a lack of appropriate surveillance in wildlife populations (Thompson, 2013). Pig producers need to show negligible risk of their animals becoming infected from wildlife. New molecular and biochemical-based methodologies have improved detection, differentiation and characterization of *Trichinella* species and genotypes (Zarlenga *et al.*, 2020). Confinement production systems, improvements in biosecurity, surveillance programmes and laws regulating commercial pork production are considered to have 'essentially eradicated' *Trichinella* in the United States and Europe (Diaz *et al.*, 2020; Shurson *et al.*, 2022). However, this view is not correct because of the numerous wildlife reservoir species in the United States and elsewhere in the world which may impact domestic environments (Pozio, 2013 and e.g. see Reichard *et al.*, 2021; and see below).

Australia has long been considered to be free of *T. spiralis* (Thompson, 2018). Australia's domestic pig population is free from *Trichinella pseudospiralis* and other *Trichinella* species (Wildlife Health Australia, 2022). Its discovery would be a significant impediment to trade. With the advent of molecular tools for surveillance the question of Australia's presumed *Trichinella*-free status has been questioned because in the past surveillance, particularly of potential wildlife reservoirs, has relied on traditional detection techniques (Thompson, 2013). *Trichinella spiralis* has never been reported in Australia. However, until relatively recently, surveys had not been undertaken on the mainland of Australia (Cuttell *et al.*, 2012a). Recent surveys detected *Trichinella papuae* in a wild pig from an Australian island in the Torres Strait *which has also* been described in pigs in New Guinea (Cuttell *et al.*, 2012a). *Trichinella papuae* is not only infective to other mammals, including humans, but also to crocodiles (Pozio *et al.*, 2009). *Trichinella pseudospiralis* infection has been detected in marsupials and birds in Tasmania (Obendorf *et al.*, 1990) and in a human from Tasmania (Andrews *et al.*, 1994). Real-time PCR has been developed as a surveillance tool for the detection of *Trichinella* in muscle samples from wildlife (Cuttell *et al.*, 2012b).

Unlike Australia, *Trichinella* is present in several South American countries apart from Peru, Colombia and Uruguay which have no documented evidence of *Trichinella* spp. in animals and humans (Ribicich *et al.*, 2020). However, these authors point to the lack of surveillance in other countries. In particular, the growth of the guinea pig meat market in the Andean region, and the high prevalence of *Trichinella* reported in free range pigs and wild boars, as well as other game animal species, are considered important risks. It is therefore considered important to focus on the role of biosecurity and risk management, while improving meat market regulations, and detection of infection prior to consumption. This will reduce the risk of transmission of *Trichinella* to humans (Ribicich *et al.*, 2020).

Trichinosis in humans is typically related to cultural food practices, including the consumption of raw, undercooked, fermented or cured meat and there has been an increasing reliance on testing to demonstrate food safety (Dorny *et al.*, 2009). As outlined above, in terms of control, much of the emphasis had focused on domestic environments and the role of pigs and synanthropic hosts such as the rat in transmission. However, globally, wildlife is now seen as playing the major role in maintaining cycles of

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

transmission (Rostami *et al.*, 2017; and e.g. see Sharma *et al.*, 2021; Gherman *et al.*, 2022). The consumption of undercooked commercial pork products is no longer considered the main source of human trichinosis, but in most regions, infection occurs following the consumption of raw or undercooked wild game meats, especially bear, moose, deer, walrus and wild/feral boar/hog (Diaz *et al.*, 2020). Thus, although biosecurity and ongoing surveillance is successful in domestic livestock settings, wildlife present an ongoing threat and if a true 'One Health' approach is taken it must take into account wildlife reservoirs.

Anthropogenic activities may exacerbate opportunities for spillover from wildlife to domestic foci which may threaten biosecurity for pig producers (Thompson, 2013). There are therefore growing demands for producers, not only to demonstrate that their pigs are *Trichinella*-free but that there is no risk of *Trichinella* infection spilling over to their pigs from wildlife. The situation has been exacerbated by the insensitivity of diagnostic assays used in meat inspection, and the growing demand for free-range pork (Thompson, 2014). Although routine screening for *Trichinella* in meat from endemic regions is mainly done using enzyme-linked immunosorbent assay-based techniques, molecular tools are playing a vital role in the screening of wildlife (Barlow *et al.*, 2021). It appears that political manoeuvring associated with market access is serving to artificially inflate this as an issue (Thompson, 2014). This may be the case in the United Kingdom where there is a perceived need for data gathering and assessment of *Trichinella* in United Kingdom wildlife even though it has rarely been detected in the past (Zimmer *et al.*, 2009; Food and Environmental Research Agency, 2013).

Epidemiology – understanding transmission

As discussed above, molecular tools have been invaluable in definitively characterizing many helminths genetically and thus settling taxonomic issues. It follows from the resolution of taxonomic issues that a better understanding of the epidemiology of zoonotic helminth infections, for example those caused by *Echinococcus* and *Trichinella*, is possible. However, with some species of helminth that have long been recognized as being distinct species, their zoonotic potential and geographical distribution have been uncertain. This has certainly been the case with the hookworm *A. ceylanicum*. The *A. ceylanicum* 'story' highlights better than no other how molecular tools led to the taxonomic and epidemiological recognition of a zoonotic hookworm, and in recent times has also demonstrated how widespread the parasite is globally (Traub, 2013; Thompson, 2015; Colella *et al.*, 2021; Traub *et al.*, 2021).

Dogs and cats are the definitive hosts of *A. ceylanicum* but it has long been known to have the ability to establish patent infections in humans. It is the only hookworm with this zoonotic potential and for many years, infections were considered to be uncommon in humans. This was undoubtedly because of difficulties in specific diagnosis since the eggs of hookworm species are morphologically identical (see above). However, with the development of PCR-based techniques that can differentiate between all species of hookworm in humans, dogs and cats, *A. ceylanicum* has been shown to have a much broader geographical distribution than previously thought (Palmer *et al.*, 2007; Conlan *et al.*, 2012a; Ngui *et al.*, 2012; Traub, 2013) and until recently was considered the most neglected of all human hookworm (Traub, 2013). As a consequence, the development and application of molecular epidemiological tools is now being undertaken in numerous hookworm endemic regions. Surveys in Asia have shown that *A. ceylanicum* is the second most common species of hookworm infecting humans and in developing areas of south-east Asia and India, there is now a growing awareness of the role of dogs in the zoonotic transmission of *A. ceylanicum* (Conlan *et al.*, 2012a; Inpankaew *et al.*, 2014; George *et al.*, 2015). In Australia, a recent study of wild dogs (dingoes and dingo hybrids) in peri-urban areas of northern Australia found that up to 100% were infected with *A. ceylanicum* thus constituting a zoonotic risk to communities in this tropical area of northern Australia (Smout *et al.*, 2013). Most recently, molecular tools have confirmed the presence of *A. ceylanicum* in the West Indies and South America (Sears *et al.*, 2022; Zendejas-Heredia *et al.*, 2022). In many areas where hookworm is endemic, dogs are common in villages and communities where a number of hookworm species may coexist in humans and dogs. *Ancylostoma ceylanicum* is not usually the dominant hookworm in such settings with *Ancylostoma duodenale* or *Necator americanus* more prevalent in humans (Conlan *et al.*, 2012a). Mixed infections may occur in both humans (e.g. *A. duodenale* ± *N. americanus* + *A. ceylanicum*) and dogs (*Ancylostoma caninum* + *A. ceylanicum*). Dogs therefore represent a reservoir of human infections which must be considered when using mass chemotherapy as a means of controlling hookworm infection in the human population. Studies in Laos suggest that the limited success of mass chemotherapy programmes targeted at humans in rural communities may have resulted from a proportion of human infections being due to *A. ceylanicum* from dogs (Conlan *et al.*, 2012a). The clinical management of hookworm disease in humans in endemic regions where more than one species of hookworm circulate will be optimized by specific diagnosis of the causative species given their different pathogenesis (Conlan *et al.*, 2012a).

The zoonotic trematodes *Clonorchis* and *Opisthorchis* are common throughout south-east Asia and their distributions may overlap (Traub *et al.*, 2009). It is important to differentiate between the two species because of differences in clinical presentation and the prognosis of infection in humans. There is therefore a need for the surveillance of human populations in endemic and potential new endemic regions. However, *Clonorchis* and *Opisthorchis* produce morphologically identical eggs, as do the more common, often co-occurring heterophyid flukes. Fortunately, direct characterization of the causative species of fluke from faecal samples is now possible using PCR-based tools. Recent surveys in Vietnam revealed that infection with several minute intestinal flukes, such as *Haplorchis pumilio* and *Haplorchis taichui*, are much more common than infection with *Clonorchis sinensis* or *Opisthorchis viverrini*, and they often co-infect humans (Doanh & Nawa, 2016). Further, previously reported prevalences of heterophyid infection in Vietnam were likely over-estimated due to misidentification of parasites in faecal examinations (Doanh & Nawa, 2016). For many years, *Opisthorchis* was thought to be the only species occurring in Thailand, but PCR-based tools identified the presence of *C. sinensis* for the first time in 2009 (Traub *et al.*, 2009).

Of the zoonotic schistosome species, *S. japonicum* has the largest number of animal reservoirs. Over 40 species of domestic and wild mammals have been described as definitive hosts of *S. japonicum* (Carabin *et al.*, 2015; Budiono *et al.*, 2019; Gordon *et al.*, 2019). In south-east Asia, animal reservoirs are believed to play a significant role in the maintenance of the parasite and its transmission to humans, making control very difficult (Betson *et al.*, 2020). Surprisingly, few molecular epidemiological studies have been undertaken to confirm the actual role of different species of wild and domestic definitive hosts. These need to be undertaken at a local level in different countries and regions in south-east Asia.

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

The identity of which non-human definitive hosts contribute to zoonotic transmission of *S. japonicum* is important so that they can be targeted for control (Betson *et al.*, 2020).

In a number of endemic areas, molecular epidemiological studies have been instrumental in identifying and describing sympatric cycles of transmission involving more than one species of *Echinococcus* (Thompson, 2020). Although morphology can be used to differentiate between adult worms belonging to different species, this is not practical given the difficulties in recovering adult specimens from definitive hosts and the associated public health risks involved. However, molecular tools allow species identification from eggs in faeces. For example, a study of wild canids on both sides of the Canada–United States border in eastern North America, found wolves and coyotes infected with *Echinococcus canadensis* (Schurer *et al.*, 2018). This species comprises two genotypes, G8 and G10, and it was possible using appropriate PCR-based techniques to discriminate between the two genotypes, finding single and mixed infections in both canid species (Schurer *et al.*, 2018). In the Southern Italian Alps, a molecular-based faecal survey of. *Echinococcus granulosus* in wolves and dogs in the Southern Italian Alps, unexpectedly detected *Echinococcus multilocularis* eggs in four faecal samples from at least two shepherd dogs, and in five wolf faecal samples (Massolo *et al.*, 2018). Co-infection of *Echinococcus ortleppi* and *E. multilocularis* was also identified in two wolves. Similarly, co-infections of *E. multilocularis* and *E. canadensis* were detected by PCR in coyotes and red foxes in Alberta, Canada (Schurer *et al.*, 2018).

In some areas where multiple species of *Echinococcus* are endemic, it is important to determine the species responsible in clinical infections of humans as this will inform public health measures. Using molecular diagnostic techniques, a recent study in China characterized the species of *Echinococcus* in patients, with 22 isolates of *E. granulosus*, and *E. multilocularis* recovered from one patient and *Echinococcus intermedius* in another (Cao *et al.*, 2018). Another study of 42 patients in south-east Iran, found that 18 were infected with *E. granulosus* and 24 with the G6 genotype (=*Echinococcus intermedius*) (Lashkarizadeh *et al.*, 2019). In one patient, a mixed infection of *E. granulosus* in the liver and right lung, and *E. intermedius* in the left lung, was detected (Lashkarizadeh *et al.*, 2019). This study showed a significantly high proportion of patients infected with *E. intermedius*, particularly in the southern parts of the country (Lashkarizadeh *et al.*, 2019). In another recent molecular epidemiological study that examined 140 human cases in China, 108 were caused by *E. granulosus*, one by *E. intermedius*, and 31 by *E. multilocularis* (Shang *et al.*, 2019). Misdiagnosis between *E. granulosus* and *E. multilocularis* was common in these cases (Shang *et al.*, 2019) demonstrating the value of using molecular diagnostic procedures to ensure appropriate therapeutic interventions.

Anthropogenic factors

As Schwabe predicted in 1984, there are many situations yet to be discovered about how humans' changing activities may influence the transmission of zoonoses (Schwabe, 1984). How such activities will influence wildlife ecosystems as well as public health remain to be uncovered. Nearly 40 years later, anthropogenic factors are increasingly exacerbating the impact of zoonotic helminths on humans and animals. As discussed above, molecular tools have increased our knowledge about the diversity of helminth zoonotic agents which, in turn, has enabled a much better understanding of how anthropogenic factors, directly or indirectly, for example through climate change, are influencing the occurrence and emergence of helminth zoonoses.

Culture, poverty, poor hygiene and diet

The frequency of transmission of many helminth zoonoses is highest in poor and rural, often disadvantaged communities where cultural and educational issues, contact with contaminated water, poor hygiene and poverty, are major impediments to control. Under such conditions children are especially vulnerable to infection. Control is very difficult when it requires changes to long held cultural and community practices. For example, with schistosomiasis in areas where local populations spend much time close to contaminated water sources for washing, collecting water, agriculture and recreation.

Diet is a major factor with many zoonotic helminths and their transmission to humans, particularly in developing regions. The transmission of fish-borne flukes to humans and to intermediate hosts is influenced by human behaviour (Jones, 2015). The distribution of human infections in south-east Asia corresponds well with the availability of snail and fish intermediate hosts and the food consumption habits of local populations. Principally, eating raw or poorly cooked fish and inadequate sanitation leading to contaminated groundwater (Jones, 2015; Betson *et al.*, 2020). In the Arctic, indigenous communities are exposed to infection with *Trichinella* as a consequence of subsistence hunting and traditional methods of food preparation, particularly raw or poorly cooked food (Jenkins *et al.*, 2013). In poor rural communities, for whom livestock are a crucial source of income and economic security, zoonoses affecting livestock represent a double burden, in terms of their economy and health. There are many pig associated zoonoses in Asia and a lack of epidemiological studies may exacerbate their spread (Okello *et al.*, 2015). For example, in Laos, where *Taenia solium* is endemic in farmed pigs which are a source of income as well as serving as a food source for rural communities (Conlan *et al.*, 2008; Okello *et al.*, 2015), the dual routes of infection require a focus on basic hygiene and diet. In such situations, the vaccination of pigs, once available, is likely to have a beneficial impact on local levels of infection in pigs (Okello *et al.*, 2016).

Conversely, each year thousands of cases of anisakiasis are reported globally, particularly in developed countries with a significant fishing industry and high fish consumption, particularly of dishes comprising raw fish or squid (Adroher-Auroux & Benítez-Rodríguez, 2020; Sugiyama *et al.*, 2022). Using data from 2018 to 2019 health insurance claims, the average annual incidence of anisakiasis in Japan was estimated to be 19,737 cases (Sugiyama *et al.*, 2022).

The combination of traditional societal behaviours and subsistence hunting enhance the potential for zoonotic transmission. This is particularly the case in Arctic regions where trichinosis remains a public health challenge (Jenkins *et al.*, 2013). Unfortunately, 'spill-over' of such behaviour to tourists taking part in recreational hunting 'holidays' has resulted in local outbreaks of trichinosis when travellers, often illegally, take the meat from hunted animals back to their home countries (Dupouy-Camet *et al.*, 2016; Rostami *et al.*, 2017).

Urbanization

The importance of increasing urbanization has been neglected until relatively recently. The central driver that attracts wildlife

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

away from their natural habitats into urban areas is food. From an ecological standpoint, this is eloquently discussed by Altizer *et al.* (2018) and Becker *et al.* (2018) in terms of 'resource provisioning', which may be accidental, as when wildlife capitalize on refuse or agricultural by-products, or intentional, through supplemental feeding for management or recreation (in Becker *et al.*, 2018). Environmental encroachment, deforestation and agricultural intensification, also contribute to the movement of wildlife into urban areas (Otranto & Deplazes, 2019; Anon, 2020; Pozio, 2020). All these factors are likely to increase in the future due to human population expansion and increasing demand for resources (White & Razgour, 2020).

The most frequent wildlife to have exploited food resources available in urban areas are carnivores, and include the fox, coyote, bears, hyaenas, wolves, raccoons, raccoon dogs, mountain lions, as well as wild boars and stone martins. As a consequence of adapting to urban environments, their ecology has been altered. Such urban invasions are seen throughout Europe, Canada, the United States, Australia and Japan (Otranto & Deplazes, 2019; Pozio, 2020; Waindok *et al.*, 2021). The urbanization of some of these animals, for example raccoons and raccoon dogs, has been exacerbated by translocations (Otranto & Deplazes, 2019). From a zoonotic and public health perspective, the most important parasites infecting such urban wild carnivores are helminths.

Echinococcus multilocularis 'evolved' with a successful wild, sylvatic life cycle involving foxes as definitive hosts and microtine, principally arvicolid, rodents as intermediate host. Initially, in natural ecosystems such as the Arctic tundra or Tibetan high-altitude grasslands, and subsequently in highly anthropogenic central European farming landscapes or Japanese city parks (Rausch, 1986; Mackenstedt *et al.*, 2015). It is a cycle now perfectly suited to transmission in an urban environment once its principal hosts successfully adapted to urban environments with the result that spillover to domestic hosts has occurred along with additional wild invaders playing increasingly important roles in transmission, such as the raccoon dog (*Nyctereutes procyonoides*).

The urbanization of *E. multilocularis* has now emerged as a significant public health issue, particularly in Europe. Fox densities can build up to be larger in urban than rural areas representing an enhanced contact zone between humans and infected foxes (Mackenstedt *et al.*, 2015). *Echinococcus multilocularis* is the cause of alveolar echinococcosis in humans, which is considered one of the most potentially fatal zoonotic diseases in the Northern Hemisphere (Avcioglu *et al.*, 2021), because of the metastasizing nature of infection with the larval (metacestode) parasite (Thompson, 2017).

In the past, zoonotic transmission of *E. multilocularis* was principally associated with occupations such as fox trapping (Schantz *et al.*, 1995) and other rural activities. However, over the last 40 years it has emerged as a major urban zoonosis as a consequence of various human interventions, most notably vaccinating foxes against rabies which has led to an increase in the numbers of foxes in many European countries, exacerbated by provisioned urban red foxes in Europe (Schweiger *et al.*, 2007; Scott *et al.*, 2014; Romig *et al.*, 2017; Altizer *et al.*, 2018). The arvicolid rodent intermediate hosts have also, like the fox, proved to be very successful urban adaptors (Romig *et al.*, 2017). Since the 1980s the autochthonous presence of *E. multilocularis* has been reported in over 20 European countries that were previously considered non-endemic (Davidson *et al.*, 2012; Deplazes *et al.*, 2017; Avcioglu *et al.*, 2021). In addition, another urban adaptor, the raccoon dog, has successfully invaded Western Europe from the east, and is an excellent definitive host for *E. multilocularis*, comparable to the fox (Kapel *et al.*, 2006; Thompson *et al.*, 2006), although its future role in transmission is uncertain given differences in the ecology of foxes and raccoon dogs (Bružinskaitė-Schmidhalter *et al.*, 2012; Romig *et al.*, 2017).

The urbanization of the life cycle of *E. multilocularis* has become a major public health issue not only in Europe but also Japan (Uraguchi *et al.*, 2022), and more recently in Canada where both foxes and coyotes are involved in transmission of the parasite (Romig *et al.*, 2017). Anthropogenic landscape changes such as deforestation and overgrazing (White & Razgour, 2020) have resulted in an expansion of known intermediate hosts in North America and Tibet (Schantz *et al.*, 1995; Giradoux *et al.*, 2003; Deplazes *et al.*, 2004; Romig *et al.*, 2006, 2017; Wang *et al.*, 2007; Davidson *et al.*, 2012) and new intermediate hosts, such as the southern red-backed vole (*Myodes gapperi*) have been identified in urban areas in Canada (Liccioli *et al.*, 2012). It has been known for some time that domestic dogs are also capable of acting as suitable definitive hosts of *E. multilocularis* (Thompson *et al.*, 2006). Recently domestic dogs have been found to be an increasing risk as definitive hosts in urban areas in Germany (Schmidberger *et al.*, 2022), especially considering the rapidly increasing number of dog owners. Schmidberger *et al.* (2022) reported that dog ownership in Germany is associated with increased odds of human alveolar echinococcosis. A recent literature review and meta-analysis drew attention to the need to re-assess the role of dogs in the epidemiology of *E. multilocularis* infections (Toews *et al.*, 2021).

In other areas of the world such as Canada, the public health significance of *E. multilocularis* is also an emerging issue in urban areas, and communities with interaction between coyotes, red foxes and most recently wolves, as well as free roaming domestic dogs, with access to abundant populations of intermediate hosts (Davidson *et al.*, 2012; Romig *et al.*, 2017). Further, the interaction between wild and domestic cycles raises the possibility of 'mixing' of the recently introduced 'European' strain of *E. multilocularis* (Jenkins *et al.*, 2012), which may differ in pathogenicity, zoonotic potential and host specificity (Jenkins *et al.*, 2013; Deplazes *et al.*, 2017; Romig *et al.*, 2017; Santa *et al.*, 2021).

Accidental and deliberate wildlife translocations have also allowed the range expansion of *E. multilocularis* in different parts of the world. The unfortunate accidental introduction of microtine rodents to Svalbard in the Norwegian Arctic, where foxes were also present, led to the establishment of a successful *E. multilocularis* cycle (Romig *et al.*, 2017). In contrast, foxes were deliberately translocated within the south-eastern United States to enhance recreational hunting, whereas the movement of foxes from endemic Kuriles to Rebun Island off the north-western coast of Hokkaido, Japan was for rodent control (Davidson *et al.*, 1992, 2012; Schantz *et al.*, 1995; Romig *et al.*, 2006, 2017).

Unlike the urbanization of *E. multilocularis* from wildlife foci, in Australia, early settlers introduced *E. granulosus* with their sheep which subsequently resulted in the establishment of *E. granulosus* in a wildlife cycle involving dingoes and macropod marsupials (Thompson & Jenkins, 2014). Recently, dingoes (increasingly referred to as wild dogs) infected with *E. granulosus* have been reported in peri-urban areas of Queensland and New South Wales (Harriott *et al.*, 2019). Dingoes/wild dogs in urban Australia are associated with the transmission of a number of helminth zoonoses, apart from *E. granulosus* including *A. ceylanicum* and *Toxocara canis*, as they can reach higher population densities

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

in urban areas than in their natural habitats (Smout *et al.*, 2013, 2017; Mackenstedt *et al.*, 2015; White & Razgour, 2020).

Raccoons are native to North America and are the principal definitive host of *Baylisascaris procyonis* which was highlighted by Smyth (1995) as a potential emerging zoonosis. There is no doubt now that *Baylisascaris* has emerged and is a significant public health issue. As a result of introductions of raccoons from North America, principally for hunting, raccoons are now widely distributed across Europe, Russia and Japan. Like the fox, due to its adaptability, the raccoon has been able to colonize urban areas as a habitat where it readily co-exists with humans often making an engaging pet which can readily transmit *Baylisascaris* to humans via its faeces. The parasite seems to thrive better in terms of prevalence in association with human-dominated landscapes which put paratenic hosts (rodents and other mammals, birds) under pressure and where domestic dogs can become infected and extend the range of environmental contamination (Page, 2013).

Apart from the public health significance of *Baylisascaris* in urban areas, the impact of the parasite on conservation is an emerging issue that should not be overshadowed by the public health issue (Otranto & Deplazes, 2019). The low host specificity for paratenic hosts and the pathogenic potential of the migratory larval parasite is considered to be a potential contributor to the extinction of vulnerable species of wildlife (Page, 2013). For example, *B. procyonis* is believed to have contributed to local declines and extinctions of the Allegheny woodrat (*Neotoma magister*) in the United States (LoGiudice, 2003), but other wildlife species are also thought to be at risk and not just in the United States, but also in Europe and Japan (Bauer, 2013; Page, 2013). The fact that raccoons have caused the introduction and spread of 'exotic' parasites, such as *B. procyonis* in Central European countries, with a potential risk of spill-over to other autochthonous species should be considered as a threat to the conservation of biodiversity (Otranto & Deplazes, 2019).

Climate change

It is difficult to predict how a changing climate will affect the structure and functioning of terrestrial, freshwater and marine parasite ecosystems (Jenkins *et al.*, 2013), as well as the biology of definitive and intermediate hosts, given the diversity of parasite life cycles (Froeschke *et al.*, 2010). In this context, of most significance perhaps are saprozoonoses such as the taeniids, ascarids and hookworm, which all produce resistant stages which will be directly affected by climate change, increasing or decreasing their survival in the environment. Some require sojourn in the environment to embryonate and they are all capable of prolonged survival under suitable conditions of temperature and humidity. For example, climate change is predicted to favour the survival of *Toxocara* eggs in the soil (Blum & Hotez, 2018). *Trichinella* is unusual among the helminth zoonoses in having one species, *T. britovi*, that is specifically adapted to cooler climatic zones. *Trichinella britovi* larvae survive longer in carcasses beneath than in those above the snow (Pozio, 2022). During the past 60 years, there has been a significant reduction in *T. britovi* prevalence in red foxes from Alpine regions (Pozio, 2022) of between 20 and 30% (Marazza, 1960; Rossi *et al.*, 2019) which correlates with a significant decrease in snow depth and snow cover in the Alps (Scherrer *et al.*, 2004; Marty, 2013).

Globally, a warming climate and the associated ecological disturbances are modifying the structure of helminth ecosystems (Jenkins *et al.*, 2013). For example, with the diphyllobothriid cestodes (Kuchta *et al.*, 2015), these changes will influence patterns of distribution, seasonal timing of migration and reproduction of their definitive hosts, as well as the development and survival of fish hosts (second intermediate, and paratenic, hosts), as well as invertebrate intermediate hosts and free-living parasite stages (eggs and coracidia). Recently, the first human case of a patent diphyllobothriid infection with *A. pacificus* was reported in humans in South Australia (see above). Infection was acquired by the ingestion of raw locally caught marine fish (Moore *et al.*, 2016). It will be interesting to see if plerocercoids are recovered from more marine fish off the coast of South Australia in the future and determine the possible influence of climate change on this apparent change in distribution.

These effects will be especially felt in the Arctic where a recent study concluded that it has warmed nearly four times faster than the rest of the world since 1979 (Rantanen *et al.*, 2022). Since the current distribution of *E. multilocularis* is restricted to the Northern Hemisphere, it is likely to be highly susceptible to the effects of climate change (Jenkins *et al.*, 2013). Already, this parasite is emerging (increasing in distribution and prevalence) in wildlife and human hosts in the Arctic and is colonizing new regions through anthropogenic and natural movements of wild and domestic hosts (in Jenkins *et al.*, 2013).

As discussed above, the raccoon dog is rapidly expanding in Europe and is likely to exacerbate the already worsening problem caused by the spread of the fox as a definitive host of *E. multilocularis*. Although the raccoon dog occupies a similar ecological niche to that of foxes, particularly in terms of diet and urbanization, competition has not been observed (Kauhala & Kowalczyk, 2011). However, the raccoon dog has a greater reproductive potential than the fox and this may increase with the effects of global warming (Mustonen & Nieminen, 2018). This is because climate is likely to have a marked effect on the productivity of the raccoon dog, especially on the proportion of reproducing females and annual birth rate (Kauhala & Helle, 1995).

Anisakiasis is an emerging zoonosis where the causative agents have complex multi-host aquatic life cycles. Like the diphyllobothriids, all stages of the life cycles will be very sensitive to environmental factors including temperature. Climate change will adversely affect the complex trophic webs that form part of the complex life cycles of anisakid nematodes involving different species of marine mammals, fish and invertebrates which act as definitive and intermediate hosts (Mattiucci & Nascetti, 2007). For example, in south-east Asia anisakiasis is an emerging zoonosis and new fish hosts have been identified (Betson *et al.*, 2020). The prevalence of anisakid infection in two species of Croaker fish (*Johnius carouna* and *Dendrophysa ruselli*) were found to be 31.7% and 87.5%, respectively (Nuchjangreed *et al.*, 2006), highlighting the potential reservoirs present that could favour zoonotic emergence. Mature adult anisakids have been found in marine animals in Indonesia, the Philippines and Thailand (Wiwanitkit & Wiwanitkit, 2016). Although cases in humans are not well reported in the literature, examples of anisakiasis have been recorded in Thailand and Malaysia (Hemsrichart, 1993; Amir *et al.*, 2016).

Wildlife

Some wildlife cycles are a major impediment to the eventual control of certain helminth zoonoses, and in the case of *T. spiralis*, they can be of economic significance with respect to trade (see

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

above). With *T. spiralis*, much of the emphasis has been on the control of the parasite in domestic environments, principally involving pigs and synanthropic hosts such as the rat. However, the maintenance of *Trichinella* spp. in a variety of wildlife transmission cycles and the involvement of humans in these cycles is central to the zoonotic transmission of the parasite (Pozio *et al.*, 2009).

Globally, most *Trichinella* infections occur in wildlife (Pozio, 2013). Infections in wildlife have been documented in 66 (33%) countries worldwide compared with 43 (21.9%) countries for domestic animals (Pozio, 2007). Therefore, the spillover from wildlife to domestic foci represents a constant challenge for control in both endemic regions and from a biosecurity viewpoint for those countries which are considered to be *Trichinella*-free (discussed in detail above).

Wildlife is essential for maintaining the life cycle of some species of *Echinococcus* in nature. For *E. multilocularis*, foxes and microtine rodents serve this role whereas for *E. canadensis* it is wolves and cervids, *Echinococcus oligarthra* wild felids and large rodents, and for *Echinococcus felidis* lions and warthogs (Thompson, 2008; Romig *et al.*, 2017). Throughout most of its geographical range, *E. granulosus* exists almost invariably under conditions modified by humans (Rausch, 1986) perpetuated by domestic animals with infection of humans principally a result of domestic dogs having access to infected livestock. Unfortunately, anthropogenic activities allowing spillover from the domestic sheep/dog cycle, led to the establishment on the Australian mainland of a cycle involving native wildlife, macropod marsupials and dingoes, that not only impacts on public health and livestock industries but also on wildlife health (Jenkins *et al.*, 2005; Thompson *et al.*, 2009). This artificial, man-made cycle also represents a barrier to the control or eradication of *E. granulosus* in sheep on the Australian mainland due to infected dingoes contaminating sheep pasture (Jenkins *et al.*, 2005). There is no evidence of an indigenous species of *Echinococcus* in Australia or that *E. granulosus* was present before the arrival of European settlers, with whom *E. granulosus* was introduced in sheep (Thompson *et al.*, 2010).

From a conservation perspective, indigenous macropodid marsupials in Australia, particularly small species of wallabies, are highly susceptible to infection with the cystic stage of *E. granulosus* which may seriously impair respiratory function enhancing their predation (Barnes *et al.*, 2007). As discussed above, the urban encroachment of infected dingoes is also an emerging public health issue.

Echinococcus felidis is confined to Africa and may represent an indigenous form perpetuated in wildlife cycles involving the lion as the principal definitive host and the warthog as an intermediate host. With the introduction and domestication of livestock in Africa, *E. granulosus* has become widespread in domestic livestock including sheep, cattle and goats, with *E. intermedius* also occurring in camels (Hüttner *et al.*, 2009; Addy *et al.*, 2012). Over 18 species of wild herbivores from different parts of southern, central and eastern Africa have been found to be infected with hydatid cysts (Macpherson, 1983; Romig *et al.*, 2017). These include the most common prey species of the lion although the role of other intermediate hosts is as yet unknown (Schantz *et al.*, 1995; Huttner & Romig, 2009; Hüttner *et al.*, 2009; Romig *et al.*, 2017). The existence of an independent cycle in wild mammals in Africa has been proposed (Macpherson *et al.*, 1983; Rausch, 1986), and there was speculation that *E. felidis* was responsible for infections in domestic livestock and other wildlife intermediate hosts of *Echinococcus* in Africa. However, without molecular characterization of isolates from intermediate hosts it was not possible until recently, to determine the extent of transmission cycles of *E. felidis* in African wildlife. Molecular epidemiological studies support an indigenous wildlife cycle in Africa involving the lion and spotted hyaena as definitive hosts, with the warthog and possibly other wild Suidae as intermediate hosts (Romig *et al.*, 2017).

Echinococcus canadensis (formerly genotypes G8 and G10) is also maintained in a wild animal cycle involving wolves and large cervids (moose and caribou), originally referred to as the 'northern form' of *E. granulosus* (Rausch, 2003), and principally occurring in northern Canada, Alaska, parts of Scandinavia, Eastern Europe and the United States (Himsworth *et al.*, 2010; Thompson, 2015; Romig *et al.*, 2017; Dell *et al.*, 2020). Domestic or free-roaming dogs have long been recognized as important 'bridging hosts' between the wild, sylvatic cycle of *E. canadensis* and people (Rausch, 2003; Himsworth *et al.*, 2010). In northern Canada, interaction between the wildlife cycle and indigenous communities occurs due to subsistence hunting within indigenous communities where domestic dogs have access to offal and carcasses leading to infection with *E. canadensis* (Lichtenwalner *et al.*, 2014; Oksanen & Lavikainen, 2015; Schurer *et al.*, 2018). A domestic cycle of transmission involving domestic dogs and farmed elk was also identified in western Canada (Thompson, 2013). Recent reports of *E. canadensis* in coyotes in Canada suggest the emergence of this species in new endemic regions (Santa *et al.*, 2018; Priest *et al.*, 2021) and given that, the urbanization of the coyote in Canada is of potential public health significance.

Wildlife also plays an increasingly important role in the epidemiology of schistosome infections. For example, with *S. japonicum*, wild animals play a very significant role as reservoirs of transmission to humans, making *S. japonicum* difficult to control. Over 40 species of domestic and wild mammals have been described as definitive hosts (Gordon *et al.*, 2019). Riley *et al.* (2008) explored the rate of transmission of *S. japonicum* from different mammals using mathematical modelling. The model inferred that rats are key hosts in the infection cycle, while water buffaloes are found to be a less important reservoir host in the Philippines situation than the bovines in China (Riley *et al.*, 2008). However, most emphasis over the last ten years has focused on the role of bovines in zoonotic transmission. A recent study found that rodents are likely to become the main reservoir of ongoing transmission of *S. japonicum* and a severe risk to not attaining elimination goals in China (Zou *et al.*, 2020). In West Africa, Catalano *et al.* (2018) reported that rodents may be an important local reservoir for zoonotic schistosomiasis, amplifying transmission to humans and acting as natural definitive hosts of schistosome hybrids.

Emerging issues

Aquaculture

Whenever animals are farmed, increased density will enhance the transmission of parasites. As with livestock industries, this applies to aquaculture for which the impact of parasite infections has long been recognized. In particular, fish-borne zoonotic trematodes are an emerging and rapidly growing concern in developing countries due to associated economic losses and public health concerns (Labony *et al.*, 2020). The diseases of most concern include

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

those caused by opisthorchid, heterophyid and echinostomid flukes (Betson *et al.*, 2020; Caffara *et al.*, 2020). The situation is not improving as the global demand for farmed fish continues to rise and developing countries seize opportunities to develop their aquaculture capabilities to serve export markets. For example, Vietnam is a densely populated developing country and aquaculture forms part of their economic development strategy, with fisheries accounting for 3.7% of its gross domestic product (Nguyen *et al.*, 2021). It has become one of the largest aquaculture producers worldwide, accounting for 4.5% of the global production, and the third largest world fish exporter after China and Norway (United Nations Food and Agriculture Organization, 2018; Nguyen *et al.*, 2021). As such, the ability to rapidly detect zoonotic trematodes in farmed fish is very important but has been difficult as the infective metacercariae are hard to detect visually in fish (Caffara *et al.*, 2020). An important advance has been the development of a rapid and cost-effective multiplex PCR for the simultaneous detection of opisthorchid and heterophyid metacercariae in fish or fish products (Caffara *et al.*, 2020).

Dracunculus *(Guinea worm)*

Dracunculus has been known since early recorded history, undoubtedly because of the female's spectacular behaviour when releasing L1 larvae from infected humans into fresh water which are infective to *Cyclops* crustaceans. Intensive global eradication efforts spanning several decades which focused on education and clean drinking water raised optimism that this zoonotic helminth would be the first to be eradicated (Callaway, 2016). However, in Africa, dogs are playing an increasingly important role as reservoirs of infection contaminating water sources and thus enhancing transmission to humans. In addition to increasing reports of the role of dogs in the epidemiology of dracunculiasis in humans, has been the recognition of novel paratenic hosts such as fish and amphibians. This has raised awareness of the potential for *Dracunculus medinensis* to emerge in new geographical areas (Molyneux & Sankara, 2017; Hopkins *et al.*, 2020).

Most of the focus on controlling Guinea worm has, understandably, been on *D. medinensis*. However, the application of molecular tools has also revealed more definitive data on the diversity of species in the genus *Dracunculus* and the limitations of past knowledge based on morphology. These emerging concerns recently culminated in the report of a human patient in Vietnam infected with *Dracunculus* (Thach *et al.*, 2021). Molecular characterization demonstrated that infection was not with *D. medinensis*, but with a previously undescribed species, in a different clade phylogenetically to *D. medinensis*. It clustered with the animal infective *Dracunculus insignis* and *Dracunculus lutrae*, (Thach *et al.*, 2021) and thus is potentially of zoonotic significance.

Toxocara canis

There is increasing concern that *T. canis* and its impact on human health have been neglected. For many years, anthelmintics have been available to prevent *T. canis* infection in domestic dogs and the veterinary profession has done much to educate dog owners about the public health significance of *T. canis* and how it can be readily controlled. This has had dramatic effects in countries such as Australia where the prevalence in domestic dogs has fallen to less than 1% (Palmer *et al.*, 2008; Massetti *et al.*, 2022). Surprisingly, this has not been the case in other Western countries (Deplazes *et al.*, 2011; Mathison & Pritt, 2018) where the parasite is still persisting in large endemic areas despite the availability, as in Australia, of effective anthelmintics (Deplazes *et al.*, 2011), perhaps due to human complacency or variable levels of dog owner education.

Hotez (2020) considers that insufficient attention is given to the potential emergence of toxocariasis in developing countries where increasing urbanization in tropical and sub-tropical areas coupled with large numbers of stray dogs and cats will lead to increasing levels of environmental contamination with *Toxocara* eggs (Hotez, 2017). In addition, increasing urbanization of the red fox in many parts of the developed world with a reproductive cycle giving rise to large numbers of cubs with high *T. canis* worm burdens, will contribute significantly to environmental contamination with eggs (Otranto & Deplazes, 2019). In addition, climate change in some areas such as the Arctic may extend the range of *Toxocara* through increasing numbers of wildlife hosts such as the red fox, leading to a spillover into local wildlife such as wolves and Arctic foxes (Jenkins *et al.*, 2013).

Thelazia callipaeda

Thelazia callipaeda is a zoonotic filarial nematode transmitted by lachryphagous drosophilids that was first described in a dog from India in 1910 (Railliet & Henry, 1910). Seven years later the first case of infection in the eye of a human in China was reported (Stuckey, 1917). Subsequently, occasional human cases have been reported throughout south-east Asia and India (Sillman, 1953; Otranto & Deplazes, 2019). However, since the late 1980s when it was first reported in dogs in Italy, *T. callipaeda* has rapidly expanded its distribution throughout Europe with infections in domestic and wild animal species as well as increasing numbers of cases reported in humans (Otranto & Deplazes, 2019). Not surprisingly, canine thelaziosis is considered an emerging vector borne helminth with significant zoonotic potential. The reason why it has emerged, and continues to do so, in Europe is not clear but may be associated with the increasing importance of wildlife, such as the fox, but also animals such as bears and wolves (Papadopoulos *et al.*, 2021) and mustelids (Ionică *et al.*, 2019) in maintaining infection in their natural habitats which increasingly encroach into domestic environments. Another zoonotic filarial nematode, *Brugia malayi*, has re-emerged in Sri Lanka after a quiescent period of four decades with dogs and cats the potential reservoirs for human infections (Mallawarachchi *et al.*, 2018). Overall microfilaraemia rates of over 80% in dogs and 75% in cats were found with higher levels in rural than urban areas.

Haycocknema perplexum

The nematode, *H. perplexum*, cannot be considered an emerging zoonotic helminth but remains a curiosity in terms of its zoonotic potential. *Haycocknema perplexum* is a minute muspiceoid nematode with related species in native wildlife including koalas, bats and kangaroos (Spratt, 2005; Ward *et al.*, 2022). However, the natural host of *H. perplexum* remains unknown. It has been identified in 12 human patients, who have contracted infection in Australia (Northern Australia and Tasmania) since 1998 (Dennett *et al.*, 1998; Spratt, 2005; Basuroy *et al.*, 2008; McKelvie *et al.*, 2013; Vos *et al.*, 2016; Koehler *et al.*, 2018; Pritt *et al.*, 2022; Ward *et al.*, 2022). Clinical features common to infection are limb wasting and weakness associated with myositis, dysphagia and persistent eosinophilia, suggesting a long

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

period of subclinical infection (Basuroy *et al.*, 2008; Ward *et al.*, 2022). Diagnosis based on symptoms alone is difficult given that they are similar to those of muscular dystrophy and inflammatory myopathy (Pritt *et al.*, 2022). The source of infection with *H. perplexum* is not known and its zoonotic potential remains to be proven, although some of the cases were associated with the consumption of bush meat (Spratt, 2005; Ward *et al.*, 2022).

Identifying zoonotic potential

Recently, Majewska *et al.* (2021) developed a predictive model from a global dataset to identify factors contributing to spillover of helminths from wildlife to domestic animals and humans. By doing this with well recognized zoonotic helminths, their model identified several non-zoonotic helminths with zoonotic potential. Among these were *Paramphistomun cervi*, followed by *Schistocephalus solidus* and *Strongyloides papillosus*. Predisposing factors for zoonotic potential included the nature of the intermediate hosts, involvement of wildlife and livestock in the life cycles, free-living environmental stage in the case of *Strongyloides* and likely scenarios of transmission to humans. These authors concluded that their results highlight the importance of the often-changing interface between wildlife, companion animals and humans in determining the risk of zoonotic helminth infections (Majewska *et al.*, 2021).

One Health

Finally, I would like to mention 'One Health'. It seems mandatory nowadays to advocate taking a One Health approach in the context of controlling zoonotic infections, including helminths. Unfortunately, the term is increasingly mentioned in papers, often in just the title or abstract, without qualification or explanation for its relevance to the published study. It is therefore losing its significance in ecological and epidemiological studies of infectious diseases. This is a shame as there are important elements, particularly with respect to parasite zoonoses (Thompson, 2013), that form part of 'One Health' as originally proposed (Gibbs, 2014). In terms of zoonotic helminths, effective control must take a One Health approach, and this has been clearly demonstrated in the successful control programmes of *Echinococcus* infections in different parts of the world. Although implemented before the term One Health was adopted, their control by necessity included collaborative strategies encompassing environmental, human and animal health as envisioned by the 'father' of One Health Calvin Schwabe (Schwabe, 1969; Zinsstag *et al.*, 2011).

Concluding comments

We have the 'tools' that have enabled the characterization of the causative agents of helminth zoonotic infections and significant inroads have been made into understanding their ecology and epidemiology. Molecular tools and improved surveillance continue to provide information on emerging zoonoses and to identify 'new' zoonoses. Importantly, we now better understand transmission patterns more than ever before and know from past experience that breaking the cycles of transmission is the key to control. So, theoretically, we are in the best position possible to control helminth zoonoses. However, this is not the case. For example, *T. canis* remains a problem in developed countries and is an emerging issue in developing countries, even though effective cheap, prophylactic drugs have been available for decades. Unfortunately, we cannot rely on vaccines to control helminth zoonoses but even if they were available, would they really have an impact? They would still have to be administered, which, in regions where they would be most effective would require financial support. This would need to come from governments and aid agencies, given the likely lack of commercial interest. We need to act now, not procrastinate, with well utilized, successful approaches that require education and government support. If not, the situation will only worsen due to anthropogenic factors such as urbanization and climate change which are exacerbating the problem of helminth zoonoses.

References

Addy F, Alakonya A, Wamae N, *et al.* (2012) Prevalence and diversity of cystic echinococcosis in livestock in Masailand, Kenya. *Parasitology Research* **111**(6), 2289–2294.

Adroher-Auroux FJ and Benítez-Rodríguez R (2020) Anisakiasis and anisakis: an underdiagnosed emerging disease and its main etiological agents. *Research in Veterinary Science* **132**, 535–545.

Altizer S, Becker DJ, Epstein JH, *et al.* (2018) Food for contagion: synthesis and future directions for studying host–parasite responses to resource shifts in anthropogenic environments. *Philosophical Transactions of the Royal Society B* **373**(1745), 20170102.

Amir A, Ngui R, Ismail WHW, Wong KT, Ong JS, Lim YA, Lau Y-L and Mahmud R (2016) Anisakiasis causing acute dysentery in Malaysia. *American Journal of Tropical Medicine and Hygiene* **95**(2), 410–412.

Andrews JR, Ainsworth R and Abernethy D (1994) *Trichinella pseudospiralis* in humans: description of a case and its treatment. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **88**(2), 200–203.

Anon (2020) Zoonoses: beyond the human–animal–environment interface. *The Lancet* **396**(10243), 1.

Ash A, Okello A, Khamlome B, Inthavong P, Allen J and Thompson RCA (2017) Controlling *Taenia solium* and soil transmitted helminths in a northern Lao PDR village: impact of a triple dose albendazole regime. *Acta Tropica* **174**(1), 171–178.

Avcioglu H, Guven E, Balkaya I, Kirman R, Akyuz M, Bia MM, Gulbeyen H and Yaya S (2021) *Echinococcus multilocularis* in Red Foxes in Turkey: increasing risk in urban [sic]. *Acta Tropica* **216**(1), 105826.

Bain PK (2019) Irradiated vaccines for helminth control in livestock. *International Journal for Parasitology* **29**(1), 185–191.

Barlow A, Roy K, Hawkins K, Ankarah A and Rosenthal B (2021) A review of testing and assurance methods for *Trichinella* surveillance programs. *Food and Waterborne Parasitology* **24**(11), e00129.

Barnes TS, Morton JM and Coleman GT (2007) Clustering of hydatid infection in macropodids. *International Journal for Parasitology* **37**(8–9), 943–952.

Basuroy R, Pennisi R, Robertson T, Norton R, Stokes J, Reimers J and Archer J (2008) Parasitic myositis in tropical Australia. *Medical Journal of Australia* **188**(4), 254–256.

Bauer C (2013) Baylisascariosis—infections of animals and humans with 'unusual' roundworms. *Veterinary Parasitology* **193**(4), 404–412.

Becker DJ, Hall RJ, Forbes KM, Plowright RK and Altizer S (2018) Anthropogenic resource subsidies and host–parasite dynamics in wildlife. *Philosophical Transactions of the Royal Society B* **373**(1745), 2017086.

Betson M, Alonte AJI, Ancog RC, *et al.* (2020) Zoonotic transmission of intestinal helminths in southeast Asia: implications for control and elimination. *Advances in Parasitoloy* **108**(1), 47–131.

Bezerra-Santos MA, Mendoza-Roldan JA, Thompson RCA, Dantas-Torres F and Otranto D (2021) Illegal wildlife trade: a gateway to zoonotic infectious diseases. *Trends in Parasitolgy* **37**(3), 181–184.

Blum AJ and Hotez PJ (2018) Global 'worming': climate change and its projected general impact on human helminth infections. *PLoS Neglected Tropical Diseases* **12**(7), e0006370.

Bružinskaitė-Schmidhalter R, Šarkūnas M, Malakauskas A, Mathis A, Torgerson PR and Deplazes P (2012) Helminths of red foxes (*Vulpes*

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

vulpes) and raccoon dogs (*Nyctereutes procyonoides*) in Lithuania. *Parasitology* **139**(1), 120–127.

Budiono NG, Satrija F, Ridwan Y, Handharyani E and Murtini S (2019) The contribution of domestic animals to the transmission of *Schistosomiasis japonica* in the Lindu Subdistrict of the Central Sulawesi Province, Indonesia. *Veterinary World* **12**(10), 1591–1598.

Caffara M, Gustinelli A, Mazzone A and Fioravanti ML (2020) Multiplex PCR for simultaneous identification of the most common European opisthorchiid and heterophyid in fish or fish products. *Food and Waterborne Parasitology* **19**(1), e00081.

Callaway E (2016) Dogs thwart end to Guinea worm. *Nature* **529**(7584), 10–11.

Cao M, Chen K, Li W, Ma J, Xiao Z, Wang H and Gao J (2018) Genetic characterization of human-derived hydatid fluid based on mitochondrial gene sequencing in individuals from northern and western China. *Journal of Helminthology* **94**(1), e2.

Capo V and Despommier DD (1996) Clinical aspects of infection with *Trichinella* spp. *Clinical Microbioloigy Reviews* **9**(1), 47–54.

Carabin H, McGarvey ST, Sahlu I, Tarafder MR, Joseph L, De Andrade BB, Balolong E and Olveda R (2015) *Schistosoma japonicum* in Samar, the Philippines: infection in dogs and rats as a possible risk factor for human infection. *Epidemiology and Infection* **143**(8), 1767–1776.

Catalano S, Sène M, Diouf ND, Fall CB, Borlase A, Léger E, Bâ K and Webster JP (2018) Rodents as natural hosts of zoonotic *Schistosoma* species and hybrids: an epidemiological and evolutionary perspective from West Africa. *Journal of Infectious Diseases* **218**(3), 429–433.

Colella V, Bradbury R and Traub R (2021) *Ancylostoma ceylanicum*. *Trends in Parasitology* **37**(9), 844–845.

Conlan J, Khounsy S, Inthavong P, Fenwick S, Blacksell S and Thompson RCA (2008) A review of taeniasis and cysticercosis in the Lao People's Democratic Republic. *Parasitology International* **57**(3), 252–255.

Conlan JV, Vongxay K, Fenwick S, Blacksell S and Thompson RCA (2009) Does interspecific competition have a moderating effect on *Taenia solium* transmission dynamics in Southeast Asia? *Trends in Parasitology* **25**(9), 398–403.

Conlan JV, Khamlome B, Vongxay K, Elliot A, Pallant L, Sripa B, Blacksell SD, Fenwick S and Thompson RCA (2012a) Soil-transmitted helminthiasis in Lao People's Democratic Republic: a community-wide cross-sectional study of humans and dogs in a mass drug administration environment. *American Journal of Tropical Medicine and Hygiene* **86**(4), 624–634.

Conlan JV, Vongxay K, Khamlome B, Dorny P, Sripa B, Elliot A, Blacksell SD, Fenwick S and Thompson RCA (2012b) A cross-sectional study of *Taenia solium* in a multiple taeniid-endemic region reveals competition may be protective. *American Journal of Tropical Medicine and Hygiene* **87**(2), 281–291.

Cuttell L, Cookson B, Jackson L, Gray C and Traub R (2012a) First report of a *Trichinella papuae* infection in a wild pig (*Sus scrofa*) from an Australian island in the Torres Strait region. *Veterinary Parasitology* **185**(2–4), 343–345.

Cuttell L, Corley SW, Gray CP, Vanderlinde PB, Jackson LA and Traub RJ (2012b) Real-time PCR as a surveillance tool for the detection of *Trichinella* infection in muscle samples from wildlife. *Veterinary Parasitology* **188**(3–4), 285–293.

Davidson WR, Appel MJ, Doster GL, Baker OE and Brown JF (1992) Diseases and parasites of red foxes, gray foxes, and coyotes from commercial sources selling to fox-chasing enclosures. *Journal of Wildlife Diseases* **28**(4), 581–589.

Davidson RK, Romig T, Jenkins E, Tryland M and Robertson LJ (2012) The impact of globalisation on the distribution of *Echinococcus multilocularis*. *Trends in Parasitology* **28**(6), 239–247.

Dell B, Newman SJ, Purple K, Miller B, Ramsay E, Donnell R and Gerhold RW (2020) Retrospective investigation of *Echinococcus canadensis* emergence in translocated elk (*Cervus canadensis*) in Tennessee, USA, and examination of canid definitive hosts. *Parasites & Vectors* **13**(1), 330.

Dennett X, Siejka SJ, Andrews JR, Beveridge I and Spratt DM (1998) Polymyositis caused by a new genus of nematode. *Medical Journal of Australia* **168**(5), 226–227.

Deplazes P, Gloor S, Hegglin D and Romig (2004) Wilderness in the city – the urbanization of *Echinococcus multilocularis*. *Trends in Parasitology* **20** (2), 77–84.

Deplazes P, van Knapen F, Schweiger A and Overgaauw PAM (2011) Role of pet dogs and cats in the transmission of helminthic zoonoses in Europe, with a focus on echinococcosis and toxocarosis. *Veterinary Parasitology* **182**(1), 41–53.

Deplazes P, Eckert J, Mathis A, von Samson-Himmelstjerna G and Zahner H (2016) *Parasitology*. 652pp. In *Veterinary medicine*. Wageningen, Wageningen Academic Publishers.

Deplazes P, Rinaldi L, Alvarez Rojas CA, *et al.* (2017) Global distribution of cystic and alveolar echinococcosis. *Advances in Parasitology* **95**(1), 315–493.

Diaz JH, Warren RJ and Oster MJ (2020) The disease ecology, epidemiology, clinical manifestations, and management of trichinellosis linked to consumption of wild animal meat. *Wilderness and Environmental Medicine* **31**(2), 235–244.

Doanh PN and Nawa Y (2016) *Clonorchis sinensis* and *Opisthorchis* spp. in Vietnam: current status and prospects. *Transactions of the Royal Society for Tropical Medicine and Hygiene* **110**(1), 13–20.

Dorny P, Praet N, Deckers N and Gabriel S (2009) Emerging food-borne parasites. *Veterinary Parasitology* **163**(3), 196–206.

Dupouy-Camet J, Yera H, Dahane N, Bouthry E and Kapel CM (2016) A cluster of three cases of trichinellosis linked to bear meat consumption in the Arctic. *Journal of Travel Medicine* **23**(5).

Food and Environment Research Agency (2013) *Trichinella* in UK wildlife. 96pp. Final Report, Food Standards Agency, York, UK. Available at https://www.food.gov.uk/sites/default/files/media/document/843-1-1543_Final_Trichinella_Report_March_2012_FS231058_v4_plus_extensionplusNIdata.pdf (accessed October, 2022).

Froeschke G, Harf R, Sommer S and Matthee S (2010) Effects of precipitation on parasite burden along a natural climatic gradient in southern Africa – implications for possible shifts in infestation patterns due to global changes. *Oikos* **119**(6), 1029–1039.

George S, Kaliappan SP, Kattula D, Roy S, Geldhof P, Kang G, Vercruysse J and Levecke B (2015) Identification of *Ancylostoma ceylanicum* in children from a tribal community in Tamil Nadu, India using a semi-nested PCR-RFLP tool. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **109**(4), 283–285.

Gherman CM, Boros Z, Baies M-H, Cozman-Petrut A and Cozma V (2022) A review of *Trichinella* species infection in wild animals in Romania. *Food and Waterborne Parasitology* **28**(1), e00178.

Gibbs EPJ (2014) The evolution of One Health: a decade of progress and challenges for the future. Veterinary Record **174**, 85–91.

Giradoux P, Craig PS, Delattre P, *et al.* (2003) Interactions between landscape changes and host communities can regulate *Echinococcus multilocularis* transmission. *Parasitology* **127**(Supplement), S121–S131.

Gordon CA, Kurscheid J, Williams GM, Clements ACA, Li Y, Zhou XN, Utzinger J, Mcmanus DP and Gray DJ (2019) Asian schistosomiasis: current status and prospects for control leading to elimination. *Tropical Medicine and Infectious Diseases* **4**(1), 40.

Grove DI (1990) *A history of human helminthology*. 848pp. Wallingford, CAB International.

Harriott L, Gentle M, Traub R, Cobbold R and Magalhaes RS (2019) Geographical distribution and risk factors for *Echinococcus granulosus* infection in peri-urban wild dog populations. *International Journal for Parasitology: Parasites and Wildlife* **10**(1), 149–155.

Hemsrichart V (1993) Intestinal anisakiasis: first reported case in Thailand. *Journal of the Medical Association of Thailand* **76**(2), 117–121.

Himsworth CG, Jenkins E, Hill J, *et al.* (2010) The emergence of sylvatic *Echinococcus granulosus* as a parasitic zoonosis of public health concern in an indigenous Canadian community. *American Journal of Tropical Medicine and Hygiene* **82**(4), 643–645.

Hopkins DR, Weiss AJ, Roy SL, Yerian S and Sapp SGH (2020) Progress toward global eradication of dracunculiasis, January 2019–June 2020. *Morbidity and Mortality Weekly Report* **69**(43), 1563–1568.

Hotez PJ (2017) Global urbanization and the neglected tropical diseases. *PLoS Neglected Tropical Diseases* **11**(2), 2.

Hotez PJ (2020) Toxocariasis: a neglected infection for the Anthropocene epoch. *Advances in Parasitology* **109**(1), 879–883.

Hüttner M and Romig T (2009) *Echinococcus* species in African wildlife. *Parasitology* **136**(10), 1089–1095.

Hüttner M, Siefert L, Mackenstedt U and Romig T (2009) A survey of *Echinococcus* species in wild carnivores and livestock in East African. *International Journal for Parasitology* **39**(11), 1269–1276.

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

Inpankaew T, Schar F, Dalsgaard A, *et al.* (2014) High prevalence of *Ancylostoma ceylanicum* hookworm infections in humans, Cambodia, 2012. *Emerging Infectious Diseases* **20**(6), 976–982.

Ionică AM, Deak G, D'Amico G, *et al.* (2019) *Thelazia callipaeda* in mustelids from Romania with the European badger, *Meles meles*, as a new host for this parasite. *Parasites & Vectors* **12**(1), 370.

Jarrett WF, Jennings FW, McIntyre WI, Mulligan W and Urquhart GM (1960) Immunological studies on *Dictyocaulus viviparus* infection; immunity produced by the administration of irradiated larvae. *Immunology* **3**(2), 145–151.

Jenkins DJ, Romig T and Thompson RCA (2005) Emergence/re-emergence of *Echinococcus* spp. – a global update. *International Journal for Parasitology* **35**(11–12), 1205–1219.

Jenkins EJ, Peregrine AS, Hill JE, Somers CM, Gesy KM, Barnes B, Gottstein B and Polley L (2012) Detection of a European strain of *Echinococcus multilocularis* in North America. *Emerging Infectious Diseases* **18**(6), 1010–1012.

Jenkins EJ, Castrodale LJ, de Rosemond SJC, *et al.* (2013) Tradition and transition: parasitic zoonoses of people and animals in Alaska, northern Canada, and Greenland. *Advances in Parasitology* **82**(1), 33–204.

Jones SRM (2015) Transmission dynamics of foodborne parasites in fish and shellfish. pp. 149–164. In Gajadhar AA (*Ed.*) *Foodborne parasites in the food supply web*. Cambridge, Woodhead Publishing.

Kapel CM, Torgerson PR, Thompson RCA and Deplazes P (2006) Reproductive potential of *Echinococcus multilocularis* in experimentally infected foxes, dogs, raccoon dogs and cats. *International Journal for Parasitology* **36**(1), 79–86.

Kauhala K and Helle E (1995) Population ecology of the raccoon dog in Finland – a synthesis. *Wildlife Biology* **1**(1), 3–9.

Kauhala K and Kowalczyk R (2011) Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: history of colonization, features behind its success, and threats to native fauna. *Current Zoology* **57**(5), 584–598.

Koehler AV, Leung P, McEwan B and Gasser RB (2018) Using PCR-based sequencing to diagnose *Haycocknema perplexum* infection in a human myositis case, Australia. *Emerging Infectious Diseases* **24**(12), 2368–2370.

Kuchta R, Serrano-Martínez ME and Scholz T (2015) Pacific broad tapeworm *Adenocephalus pacificus* as a causative agent of globally reemerging diphyllobothriosis. *Emerging Infectious Diseases* **21**(10), 1697–1703.

Labony SS, Abdul Alim M, Muhammad Mehedi Hasan MD, Hossain S, Islam A, Alam ZM, Tsuji N and Anisuzzaman (2020) Fish-borne trematode infections in wild fishes in Bangladesh. *Pathogens and Global Health* **114**(2), 91–98.

Larrieu E, Gavida CM and Lightowlers MW (2019) Control of cystic echinococcosis: background and prospects. *Zoonoses and Public Health* **66**(8), 889–899.

Lashkarizadeh MR, Hooshmand N, Nasibi S, Mohammadi MA, Shamsaddini S, Kamyabi H, Rostami S and Harandi MF (2019) Genetic profile of hydatid cysts in patients with multi-organ involvement: mixed infections by different strains. *Vector Borne Zoonotic Diseases* **19**(10), 724–730.

Liccioli S, Duignan PJ, Lejeune M, Deunk J, Majid S and Massolo A (2012) A new intermediate host for *Echinococcus multilocularis*: the southern red-backed vole (*Myodes gapperi*) in urban landscape in Calgary, Canada. *Parasitology International* **62**(4), 355–357.

Lichtenwalner A, Adhikari N, Kantar L, Jenkins E and Schurer JM (2014) *Echinococcus granulosus* genotype G8 in Maine moose (*Alces alces*). *Alces* **50**(1), 27–33.

Lindahl JF and Grace D (2015) The consequences of human actions on risks for infectious diseases: a review. *Infection Ecology and Epidemiology* **5**(1), 30048.

LoGiudice K (2003) Trophically transmitted parasites and the conservation of small populations: raccoon roundworm and the imperilled Allegheny woodrat. *Conservation Biology* **17**(1), 258–266.

Mackenstedt U, Jenkins D and Romig T (2015) The role of wildlife in the transmission of parasitic zoonoses in peri-urban and urban areas. *International Journal for Parasitology: Parasites and Wildlife* **4**(1), 71–79.

Macpherson CNL (1983) An active intermediate host role for man in the life cycle of *Echinococcus granulosus* in Turkana, Kenya. *American Journal of Tropical Medicine and Hygiene* **32**(2), 397–404.

Macpherson CNL, Karstad L, Stevenson P and Arundel JH (1983) Hydatid disease in the Turkana district of Kenya. III. The significance of wild animals in the transmission of *Echinococcus granulosus*, with particular reference to Turkana and Masailand in Kenya. *Annals of Tropical Medicine and Parasitology* **77**(1), 61–73.

Majewska AA, Huang T, Han B and Drake J (2021) Predictors of zoonotic potential in helminths. *Philosophical Transactions B* **376**(1837), 2020356.

Mallawarachchi CH, Chandrasena NT, Wickramasinghe S, Premaratna R, Gunawardane NY, Mallawarachchi NS and de Silva NR (2018) A preliminary survey of filarial parasites in dogs and cats in Sri Lanka. *PLoS One* **13**(11), e0206633.

Marazza V (1960) La trichinosi della volpe in Italia [Fox trichinosis in Italy]. *Archivio Veterinario Italiano* **11**(3), 507–566. [In Italian.]

Marty C (2013) Climate change and snow cover in the European Alps. pp. 30–44. In Rixen C, Rolando A (Eds) *The impacts of skiing on mountain environments*. Bussum, The Netherlands, Bentham Books.

Massetti L, Wiethoelter A, McDonagh P, Rae L, Marwedel L, Beugnet F, Colella V and Traub RJ (2022) Faecal prevalence, distribution and risk factors associated with canine soil-transmitted helminths contaminating urban parks across Australia. *International Journal for Parasitology* **52**(10), 637–646.

Massolo A, Valli D, Wassermann M, *et al.* (2018) Unexpected *Echinococcus multilocularis* infections in shepherd dogs and wolves in south-western Italian Alps: a new endemic area? *International Journal for Parasitology: Parasites and Wildlife* **7**(3), 309–316.

Mathison BA and Pritt BS (2018) A systematic overview of zoonotic helminth infections in North America. *Laboratory Medicine* **49**(4), e61–e93.

Mattiucci S and Nascetti G (2007) Genetic diversity and infection levels of anisakid nematodes parasitic in fish and marine mammals from Boreal and Austral hemispheres. *Veterinary Parasitology* **148**(1), 43–55.

McKelvie P, Reardon K, Bond K, Spratt DM, Gangell A, Zochling J and Daffy J (2013) A further patient with parasitic myositis due to *Haycocknema perplexum*, a rare entity. *Journal of Clinical Neuroscience* **20**(7), 1019–1022.

Miller TA (1978) Industrial development and field use of the canine hookworm vaccine. *Advances in Parasitology* **16**(1), 333–342.

Molyneux D and Sankara DP (2017) Guinea worm eradication: progress and challenges — should we beware of the dog? *PLoS Neglected Tropical Diseases* **11**(4), e0005495.

Moore CV, Thompson RCA, Jabbar A, Williams J, Rasiah K, Pallant L, Koehler AP, Graham C and Weldhagen GF (2016) Rare human infection with Pacific broad tapeworm *Adenocephalus pacificus*, in Australia. *Emerging Infectious Diseases* **22**(8), 1510–1512.

Mustonen A-M and Nieminen P (2018) A review of the physiology of a survival expert of big freeze, deep snow, and an empty stomach: the boreal raccoon dog (*Nyctereutes procyonoides*). *Journal of Comparative Physiolgy B* **188**(1), 15–25.

Nelson GS and Mukundi J (1963) A strain of *Trichinella spiralis* from Kenya of low infectivity to rats and domestic pigs. *Journal of Helminthology* **37**(4), 329–338.

Nelson GS, Guggisberg CW and Mukundi J (1963) Animal hosts of *Trichinella spiralis* in East Africa. *Annals of Tropical Medicine and Parasitology* **57**(3), 332–346.

Nelson GS, Mukundi J and Blackie EJ (1966) Comparative studies on geographical strains of *Trichinella spiralis*. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **60**(4), 471–480.

Ngui R, Lim YA, Traub R, Mahmoud R and Mistam MS (2012) Epidemiological and genetic data supporting the transmission of *Ancylostoma ceylanicum* among humans and domestic animals. *PLoS Neglected Tropical Diseases* **6**(2), e1522.

Nguyen TH, Dorny P, Nguyen TTG and Dermauw V (2021) Helminth infections in fish in Vietnam: a systematic review. *International Journal for Parasitology: Parasites and Wildlife* **14**(1), 13–32.

Nsadha Z, Rutebarika C, Ayebazibwe C, *et al.* (2021) Control trial of porcine cysticercosis in Uganda using a combination of the TSOL18 vaccination and oxfendazole. *Infectious Diseases of Poverty* **10**(1), 34.

Nuchjangreed C, Hamzah Z, Suntornthiticharoen P and Sorosjinda-Nunthawarasilp P (2006) Anisakids in marine fish from the coast of

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

Chon Buri Province, Thailand. *Southeast Asian Journal of Tropical Medicine and Public Health* **37**(Suppl 3), 35–39.

Obendorf D, Handlinger J, Mason R, Clarke K, Forman A, Hooper P, Smith S and Holdsworth M (1990) *Trichinella pseudospiralis* infection in Tasmanian wildlife. *Australian Veterinary Journal* **67**(3), 108–110.

Okello AL, Burniston S, Conlan JV, Inthavong P, Khamlome B, Welburn SC, Gilbert J, Allen J and Blacksell SD (2015) Prevalence of endemic pig-associated zoonoses in Southeast Asia: a review of findings from the Lao People's Democratic Republic. *American Journal of Tropical Medicine and Hygiene* **92**(5), 1059–1066.

Okello AL, Thomas L, Inthavong P, *et al.* (2016) Assessing the impact of a joint human-porcine intervention package for *Taenia solium* control: results of a pilot study from northern Lao PDR. *Acta Tropica* **159**(1), 185–191.

Oksanen A and Lavikainen A (2015) *Echinococcus canadensis* transmission in the North. *Veterinary Parasitology* **213**(3–4), 182–186.

Otranto D and Deplazes P (2019) Zoonotic nematodes of wild carnivores. *International Journal for Parasitology: Parasites and Wildlife* **9**(1), 370–383.

Page KL (2013) Parasites and the conservation of small populations: the case of *Baylisascaris procyonis*. *International Journal for Parasitology: Parasites and Wildlife* **2**(1), 203–210.

Palmer CS, Traub RJ, Robertson ID, Hobbs RP, Elliot A, While L, Rees R and Thompson RCA (2007) The veterinary and public health significance of hookworm in dogs and cats in Australia and the status of *A. ceylanicum*. *Veterinary Parasitology* **145**(3–4), 304–313.

Palmer CS, Thompson RCA, Traub RJ, Rees R and Robertson ID (2008) National study of the gastrointestinal parasites of dogs and cats in Australia. *Veterinary Parasitology* **151**(2–4), 181–190.

Papadopoulos E, Komnenou A, Karamanlidis AA, Bezerra-Santos MA and Otranto D (2021) Zoonotic *Thelazia callipaeda* eyeworm in brown bears (*Ursus arctos*): a new host record in Europe. *Transboundary and Emerging Diseases* **69**(2), 235–239.

Perera DJ and Ndao M (2021) Promising technologies in the field of helminth vaccines. *Frontiers in Immunology* **12**(1), 711650.

Poynter D (1963) Parasitic bronchitis. *Advances in Parasitology* **1**(1), 179–212.

Pozio E (2007) World distribution of *Trichinella* spp. infections in animals and humans. *Veterinary Parasitology* **149**(1–2), 3–21.

Pozio E (2013) The opportunistic nature of *Trichinella* – exploitation of new geographies and habitats. *Veterinary Parasitology* **194**(2–4), 128–132.

Pozio E (2020) How globalization and climate change could affect foodborne parasites. *Experimental Parasitology* **208**(1), 107807.

Pozio E (2022) The impact of globalization and climate change on *Trichinella* spp. epidemiology. *Food and Waterborne Parasitology* **27**(S2), e00154.

Pozio E, Hoberg E, La Rosa G and Zarlenga DS (2009) Molecular taxonomy, phylogeny and biogeography of nematodes to the *Trichinella* genus. *Infection Genetics and Evolution* **9**(4), 606–616.

Priest JM, McRuer DL, Stewart DL, Boudreau M, Power JWB, Conboy G, Jenkins EJ, Kolapo TU and Shutler D (2021) New geographic records for *Echinococcus canadensis* in coyotes and moose from Nova Scotia, Canada. *International Journal for Parasitology: Parasites and Wildlife* **16**(1), 285–288.

Pritt BS, Mathison BA, Bradbury RS, *et al.* (2022) Imported *Haycocknema perplexum* infection, United States. *Emerging Infectious Diseases* **28**(11), 2281–2284.

Railliet A and Henry AC (1910) Nouvelles observations sur les thelazies, nematodes parastes de l'oeil [New observations on thelazies, parasitic nematodes of the eye]. *Comptes Rendus Hebdomedaires des Seances et Memoires de la Societe de Biologie* **68**, 783–785.

Rantanen M, Karpechko AY, Lipponen A, Nordling K, Hyvarinen O, Rousteenoja K, Vihma T and Laaksonen A (2022) The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth and Environment* **3**(1), 168.

Rausch RL (1986) Life-cycle patterns and geographic distribution of echinococcus species. pp. 274–284. In Thompson RCA (Ed.) *The biology of echinococcus and hydatid disease*. London, UK, Allen and Unwin.

Rausch RL (2003) Cystic echinococcosis in the Arctic and sub-Arctic. *Parasitology* **127**(Supplement), S73–S85.

Rausch RL, Babero BB, Rausch RV and Schiller EL (1956) Studies on the helminth fauna of Alaska, XXVII. The occurrence of larvae of *Trichinella spiralis* in Alaskan mammals. *Journal of Parasitology* **42**(3), 259–271.

Reichard MV, Sanders TL, Prentiss NL, Cotey SR, Koch RW, Fairbanks WS, Interisano M, La Rosa G and Pozio E (2021) Detection of *Trichinella murrelli* and *Trichinella pseudospiralis* in bobcats (*Lynx rufus*) from Oklahoma. *Veterinary Parasitology: Regional Studies and Reports* **25**(1), 100609.

Ribicich MM, Fariña FA, Aronowicz T, Ercole ME, Bessi C, Winter M and Pasqualetti MI (2020) A review on *Trichinella* infection in South America. *Veterinary Parasitology* **285**(1), 109234.

Riley S, Carabin H, Belisle P, *et al.* (2008) Multi-host transmission dynamics of *Schistosoma japonicum* in Samar province, the Philippines. *PLoS Medicine* **5**(1), E18.

Rojas A, Maldonado-Junior A, Mora J, Morassutti A, Rodriguez R, Solano-Barquero A, Tijerino A, Vargas M and Graeff-Teixeira C (2021) Abdominal angiostrongyliasis in the Americas: fifty years since the discovery of a new metastrongylid species. *Angiostrongylus costaricensis*. *Parasites & Vectors* **14**(1), 374.

Romig T, Thoma D and Weible A-K (2006) *Echinococcus multilocularis* – a zoonosis of anthropogenic environments? *Journal of Helminthology* **80**(2), 207–212.

Romig T, Deplazes P, Jenkins D, Giraudoux P, Massolo A, Craig PS, Wassermann M, Takahashi K and de la Rue M (2017) Ecology and life cycle patterns of *Echinococcus* species. *Advances in Parasitology* **95**(1), 213–314.

Rossi L, Interisano M, Deksne G and Pozio E (2019) The subnivium, a haven for *Trichinella* larvae in host carcasses. *International Journal for Parasitology: Parasites and Wildlife* **8**(1), 229–233.

Rostami A, Gamble HR, Dupouy-Camet J, Khazan H and Bruschi F (2017) Meat sources of infection for outbreaks of human trichinellosis. *Food Microbiology* **64**(1), 65–71.

Saijuntha W, Sithithaworn P, Kiatsopit N, Andrews RH and Petney TN (2019) Liver flukes: *Clonorchis* and *Opisthorchis*. pp. 139–180. In Toledo R and Fried B (Eds) *Digenetic trematodes*. 2nd edition. *Advances in experimental medicine and biology*. Cham, Switzerland, Springer Nature.

Santa MA, Pastran SA, Klein C, Duignan P, Ruckstuhl K, Romig T and Massolo A (2018) Detecting co-infections of *Echinococcus multilocularis* and *Echinococcus canadensis* in coyotes and red foxes in Alberta, Canada using real-time PCR. *International Journal for Parasitology: Parasites and Wildlife* **7**(2), 111–115.

Santa MA, Rezansoff AM, Chen R, Gilleard JS, Musiani M, Ruckstuhl KE and Massolo A (2021) Deep amplicon sequencing highlights low intra-host genetic variability of *Echinococcus multilocularis* and high prevalence of the European-type haplotypes in coyotes and red foxes in Alberta, Canada. *PLoS Neglected Tropical Diseases* **15**(5), e0009428.

Schantz PM, Chai J, Craig PS, Eckert J, Jenkins DJ, Macpherson CNL and Thakur A (1995) Epidemiology and control of hydatid disease. pp 2334–2331. In Thompson RCA and Lymbery AJ (Eds) *Echinococcus and hydatid disease*. Wallingford, UK, CAB International.

Scherrer SC, Appenzeller C and Laternser M (2004) Trends in Swiss Alpine snow days: the role of local- and large-scale climate variability. *Geophysics Research Letters* **31**(1), L13215.

Schmidberger J, Uhlenbruck J, Schlingeloff P, Maksimov P, Conraths FJ, Mayer B and Kratzer W (2022) Dog ownership and risk for alveolar echinococcosis, Germany. *Emerging Infectious Diseases* **28**(8), 1597–1605.

Schurer JM, Bouchard E, Bryant A, Revell S, Chavis G, Lichtenwalner A and Jenkins EJ (2018) *Echinococcus* in wild canids in Québec (Canada) and Maine (USA). *PLoS Neglected Tropical Diseases* **12**(8), e0006712.

Schwabe CW (1969) *Veterinary medicine and human health*. 2nd edn. 713pp. Baltimore, Williams and Wilkins.

Schwabe CW (1984) *Veterinary medicine and human health*. 3rd edn. 680pp. Baltimore, Williams and Wilkins.

Schweiger A, Ammann RW, Candinas D, *et al.* (2007) Human alveolar echinococcosis after fox population increase, Switzerland. *Emerging Infectious Diseases* **13**(6), 878–882.

Scott DM, Berg MJ, Tolhurst BA, Chauvenet ALM, Smith GC, Neaves K, Lochhead J and Baker PJ (2014) Changes in the distribution of red foxes (*Vulpes vulpes*) in urban areas in Great Britain: findings and limitations of media-driven nationwide survey. *PLoS One* **9**(6), e99059.

Sears WJ, Cardenas J, Kubofcik J, Nutman TB and Cooper PJ (2022) Zoonotic *Ancylostoma ceylanicum* hookworm infections, Ecuador. *Emerging Infectious Diseases* **28**(9), 1867–1869.

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press

Shang J, Zhang G, Yu W, *et al.* (2019) Molecular characterization of human echinococcosis in Sichuan, Western China. *Acta Tropica* **190**(1), 45–51.

Sharma R, Harms NJ, Kukka PM, *et al.* (2021) High prevalence, intensity, and genetic diversity of *Trichinella* spp. in wolverine (*Gulo gulo*) from Yukon, Canada. *Parasites & Vectors* **14**(1), 146.

Shurson GC, Urriola PE and van de Ligt JLG (2022) Can we effectively manage parasites, prions, and pathogens in the global feed industry to achieve One Health? *Transboundary and Emerging Diseases* **69**(1), 4–30.

Sillman EI (1953) A Korean case of infestation with *Thelazia callipaeda* with notes on human thelaziasis. *Journal of Parasitology* **39**(6), 669–670.

Singh B (1997) Molecular methods for diagnosis and epidemiological studies for parasitic infections. *International Journal for Parasitology* **27** (10), 1135–1145.

Sirima C, Bizet C, Hamou H, *et al.* (2021) Soil-transmitted helminth infections in free-ranging non-human primates from Cameroon and Gabon. *Parasites & Vectors* **14**(1), 354.

Smout FA, Thompson RCA and Skerratt LF (2013) First report of *Ancylostoma ceylanicum* in wild canids. *International Journal for Parasitology: Parasites and Wildlife* **2**(1), 173–177.

Smout FA, Skerratt LF, Butler JRA, Johnson CN, Congdon BC and Thompson RCA (2017) The hookworm *Ancylostoma ceylanicum*: an emerging public health risk in Australian tropical rainforests and Indigenous communities. *One Health* **3**(1), 66–69.

Smyth JD (1995) Rare, new and emerging helminth zoonoses. *Advances in Parasitology* **36**(1), 1–45.

Spratt DM (2005) Australian ecosystems, capricious food chains and parasitic consequences for people. *International Journal for Parasitology* **35**(7), 717–724.

Stuckey EJ (1917) Circumocular filariasis. *China Medical Journal* **31**(1), 24–25.

Sugiyama H, Shiroyama M, Yamamoto I, Ishikawa T and Morishima Y (2022) Anisakiasis annual incidence and causative species, Japan, 2018–2019. *Emerging Infectious Diseases* **28**(10), 2105–2108.

Thach PN, van Doorn HR, Bishop HS, Fox MS, Sapp SGH, Cama VA and Van Duyet L (2021) Human infection with an unknown species of *Dracunculus* in Vietnam. *International Journal of Infectious Diseases* **105**(1), 739–742.

Thompson RCA (2008) The taxonomy, phylogeny and transmission of *Echinococcus*. *Experimental Parasitology* **119**(4), 439–446.

Thompson RCA (2013) Parasite zoonoses and wildlife: One Health, spillover and human activity. *International Journal for Parasitology* **43**(12–13), 1079–1088.

Thompson RCA (2014) Parasites and food: ripe for exploitation. *Trends in Parasitology* **30**(1), 1–3.

Thompson RCA (2015) Neglected zoonotic helminths: *Hymenoleps nana*, *Echinococcus canadensis* and *Ancylostoma ceylanicum*. *Clinical Microbiology and Infection* **21**(5), 426–432.

Thompson RCA (2017) Biology and systematics of *Echinococcus*. *Advances in Parasitology* **95**(1), 65–109.

Thompson RCA (2018) Exotic parasite threats to Australia's biosecurity—trade, health, and conservation. *Tropical Medicine and Infectious Disease* **3**(3), 76.

Thompson RCA (2020) The molecular epidemiology of *Echinococcus* infections. *Pathogens* **9**(6), 453.

Thompson RCA and Jenkins DJ (2014) *Echinococcus* as a model system: biology and epidemiology. *International Journal for Parasitology* **44**(12), 865–877.

Thompson RCA, Owen IL, Puana I, Banks D, Davis TME and Reid SA (2003) Parasites and biosecurity—the example of Australia. *Trends in Parasitology* **19**(9), 410–416.

Thompson RCA, Kapel CM, Hobbs RP and Deplazes P (2006) Comparative development of *Echinococcus multilocularis* in its definitive hosts. *Parasitology* **132**(5), 709–716.

Thompson RCA, Kutz SJ and Smith A (2009) Parasite zoonoses and wildlife: emerging issues. *International Journal of Environmental Research and Public Health* **6**(2), 678–693.

Thompson RCA, Lymbery AJ and Smith A (2010) Parasites, emerging disease and wildlife conservation. *International Journal for Parasitology* **40** (10), 1163–1170.

Toews E, Musiani M, Checkley S, Visscher D and Massolo A (2021) A global assessment of *Echinococcus multilocularis* infections in domestic dogs: proposing a framework to overcome past methodological heterogeneity. *International Journal for Parasitology* **51**(5), 379–392.

Traub RJ (2013) *Ancylostoma ceylanicum*, a re-emerging but neglected parasitic zoonosis. *International Journal for Parasitology* **43**(12–13), 1009–1015.

Traub RJ, Macaranas J, Mungthin M, Leelayoova S, Cribb T, Murrell KD and Thompson RCA (2009) A new PCR-based approach indicates the range of *Clonorchis sinensis* now extends to Central Thailand. *PLoS Neglected Tropical Diseases* **3**(1), e367.

Traub RJ, Zendejas-Heredia PA, Massetti L and Colella V (2021) Zoonotic hookworms of dogs and cats - lessons from the past to inform current knowledge and future directions of research. *International Journal for Parasitology* **51**(13–14), 1233–1241.

United Nations Food and Agriculture Organization (2018) *The state of world fisheries and aquaculture 2018 – meeting the sustainable development goals*. Rome, United Nations Food and Agriculture Organization.

Uraguchi K, Irie T, Kouguchi H, Inamori A, Sashika M, Shimozuru M, Tsubota T and Yagi K (2022) Anthelmintic baiting of foxes against *Echinococcus multilocularis* in small public area, Japan. *Emerging Infectious Diseases* **28**(8), 1677–1680.

Vos LJ, Robertson T and Binotto E (2016) *Haycocknema perplexum*: an emerging cause of parasitic myositis in Australia. *Communicable Disease Intelligence Quarterly Report* **40**(4), E496–E499.

Waindok P, Raue K, Grilo ML, Siebert U and Strube C (2021) Predators in northern Germany are reservoirs for parasites of One Health concern. *Parasitology Research* **120**(12), 4229–4239.

Wang Q, Xiao YF, Vuitton DA, Schantz PM, Raoul F, Budke C, Campos-Ponce M, Craig PS and Giraudoux P (2007) Impact of overgrazing on the transmission of *Echinococcus multilocularis* in Tibetan pastoral communities of Sichuan Province, China. *Chinese Medical Journal* **120** (3), 237–242.

Ward K, Krishnan A, Iyengar KR, Robertson T, White R and Urkude R (2022) *Haycocknema perplexum* myositis: the first description of subclinical disease and a proposed distinctive triad to evoke clinical suspicion. *BMJ Neurology Open* **4**(1), e000290.

White RJ and Razgour O (2020) Emerging zoonotic diseases originating in mammals: a systematic review of effects of anthropogenic land-use change. *Mammal Review* **50**(4), 336–352.

Wildlife Health Australia (2022) *Trichinellosis and Australian wildlife*. Available at https://wildlifehealthaustralia.com.au/Portals/0/Documents/FactSheets/Public health/Trichinella_and_Australian_Wildlife.pdf (accessed September 2022).

Wiwanitkit S and Wiwanitkit V (2016) Anisakiasis in Southeast Asia: a story of new tropical disease? *Asian Pacific Journal of Tropical Biomedicine* **6**(5), 382–383.

Zarlenga D, Thompson P and Pozio E (2020) *Trichinella* species and genotypes. *Research in Veterinary Science* **133**(1), 289–296.

Zendejas-Heredia PA, Colella V, Macphersopn MLA, Sylvester W, Gasser RB, Macpherson CNL and Traub RJ (2022) *Ancylostoma ceylanicum* hookworms in dogs, Grenada, West Indies. *Emerging Infectious Diseases* **28**(9), 1870–1872.

Zimmer IA, Fee SA, Spratt-Davison S, *et al.* (2009) Report of *Trichinella spiralis* in a red fox (*Vulpes vulpes*) in Northern Ireland. *Veterinary Parasitology* **159**(3–4), 300–303.

Zinsstag J, Schelling E, Waltner-Toews D and Tanner M (2011) From 'one medicine' to 'one health' and systemic approaches to health and well-being. *Preventive Veterinary Medicine* **101**(3–4), 148–156.

Zou H-Y, Yu Q-F, Qiu C, Webster JP and Lu D-B (2020) Meta-analyses of *Schistosoma japonicum* infections in wild rodents across China over time indicates a potential challenge to the 2030 elimination targets. *PLoS Neglected Tropical Diseases* **14**(9), e0008652.

https://doi.org/10.1017/S0022149X23000020 Published online by Cambridge University Press