Cryptosporidium infections in terrestrial ungulates with focus on livestock: a systematic review and meta-analysis

Kareem Hatam-Nahavandi¹, Ehsan Ahmadpour²*, David Carmena³, Adel Spotin⁴,⁵, Berit Bangoura⁶ and Lihua Xiao⁷*

Abstract
Background: Cryptosporidium spp. are causative agents of gastrointestinal diseases in a wide variety of vertebrate hosts. Mortality resulting from the disease is low in livestock, although severe cryptosporidiosis has been associated with fatality in young animals.

Methods: The goal of this systematic review and meta-analysis was to review the prevalence and molecular data on Cryptosporidium infections in selected terrestrial domestic and wild ungulates of the families Bovidae (bison, buffalo, cattle, goat, impala, mouflon sheep, sheep, yak), Cervidae (red deer, roe deer, white-tailed deer), Camelidae (alpaca, camel), Suinae (boar, pig), Giraffidae (giraffes) and Equidae (horses). Data collection was carried out using PubMed, Scopus, Science Direct and Cochran databases, with 429 papers being included in this systematic analysis.

Results: The results show that overall 18.9% of ungulates from the investigated species were infected with Cryptosporidium spp. Considering livestock species (cattle, sheep, goats, pigs, horses and buffaloes), analysis revealed higher Cryptosporidium infection prevalence in ungulates of the Cetartiodactyla than in those of the Perissodactyla, with cattle (29%) being the most commonly infected farm animal.

Conclusions: Overall, the investigated domestic ungulates are considered potential sources of Cryptosporidium contamination in the environment. Control measures should be developed to reduce the occurrence of Cryptosporidium infection in these animals. Furthermore, literature on wild populations of the named ungulate species revealed a widespread presence and potential reservoir function of wildlife.

Keywords: Cryptosporidiosis, Livestock, Cattle, Sheep, Goat, Pig, Horse, Wildlife

Background
Cryptosporidium, the causative agent of cryptosporidiosis, is an ubiquitous protozoan parasite. It causes gastrointestinal disease in a wide variety of vertebrate hosts, including ungulates of the orders Artiodactyla and Perissodactyla, as well as humans. Several Cryptosporidium species are known to be zoonotic with animals as major reservoirs [1]. In resource-limited settings, cryptosporidiosis is a leading cause of diarrhoeal death in children younger than five years across the globe, only second to rotaviral enteritis [2]. Cryptosporidiosis is also a significant contributor to health care cost in developed countries. It is estimated that in the USA 748,000 cases of human cryptosporidiosis occur annually [3]. Residents of and travelers to developing countries may be at greater risk of infection due to poor water treatment and food sanitation [4, 5]. Cryptosporidiosis typically induces self-limiting diarrhea in immunocompetent individuals, but the infection can be severe and life-threatening in immunocompromised subjects [6]. It is one of the most important diseases in young ruminants, especially neonatal calves [7, 8]. The clinical presentation of

*Correspondence: ehsanahmadpour@gmail.com; lxiao1961@gmail.com
² Infectious and Tropical Diseases Research Center, Tabriz University of Medical Sciences, Tabriz, Iran
³ College of Veterinary Medicine, South China Agricultural University, Guangzhou, China
Full list of author information is available at the end of the article

© The Author(s) 2019. This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The Creative Commons Public Domain Dedication waiver (http://creativecommons.org/publicdomain/zero/1.0/) applies to the data made available in this article, unless otherwise stated.
cryptosporidiosis varies from asymptomatic to deadly, leading to important economic losses due to growth retardation, reduced productivity and mortality [9, 10]. Considering that an infected bovine calf can shed up to $1.1 \times 10^8$ oocysts per gram of feces at the peak of the infection, cattle (and very likely wild ruminants) are significant contributors of environmental Cryptosporidium oocysts [11, 12], causing water-borne [13–15] and food-borne [16, 17] diarrhea outbreaks in humans worldwide. The worldwide annual excretion of Cryptosporidium spp. oocysts by livestock has been calculated to be $3.2 \times 10^{23}$ [18], with cattle being the host species causing most environmental contamination. Cattle are able to carry different species including C. hominis which implies an associated significant public health risk [19]. In addition, Cryptosporidium oocysts are infective at the time they are passed in feces and are highly resilient to a wide range of environmental factors including disinfection and water treatment processes. Moreover, low infection doses are sufficient to cause disease in suitable hosts, e.g. 10–100 oocysts are described to provoke diarrhea in humans [20, 21].

Over the past few decades, a major subject of debate and controversy in the epidemiology of Cryptosporidium is whether, and to what extent, domestic and wildlife species may act as natural reservoirs of human cryptosporidiosis [22, 23]. This is principally due to the fact that the genus Cryptosporidium encompasses nearly 40 valid species with marked differences in host range, among which over 10 (mainly C. hominis and C. meleagris) have been reported in humans [24] with a variety of genotypes being zoonotic [1, 22, 25]. The public health significance of animal cryptosporidiosis varies greatly depending on factors such as geographical variation in prevalence and genotype distribution, seasonality, load of environmental contamination with oocysts and access to surface waters intended for human consumption or recreation [9, 26]. In particular, genotyping data from epidemiological surveys conducted globally indicate that infected calves are the major reservoir for zoonotic C. parvum in many areas [26, 27], with lambs, kids and foals being potential additional sources of C. parvum infection for humans in some areas of the world [28–31]. Pigs are only sporadically infected with zoonotic Cryptosporidium species and are therefore considered minor contributors to the zoonotic transmission of cryptosporidiosis in humans [32]. Adult livestock typically harbor low level and asymptomatic infections but are epidemiologically important as cryptic carriers of the parasite, enabling re-infections at the herd level. Little is known of the molecular epidemiology and transmission cycles of cryptosporidiosis in wild ungulates. However, recent surveys have revealed the presence of C. parvum in wild hoofed species including the American mustang (Equus ferus caballus) [33], Scottish roe deer (Capreolus capreolus) and red deer (Cervus elaphus) [34], and Spanish wild boars (Sus scrofa scrofa) [35], which may represent a threat to water quality and public health [34].

In the present study, we conducted a systematic review of publications on the prevalence of Cryptosporidium infections and Cryptosporidium species distribution in domestic and wild ungulates in order to ascertain the extent to which hoofed animals should be considered as relevant reservoirs of human infection.

**Methods**

**Search strategy**

to evaluate the prevalence of Cryptosporidium infection in hoofed animals, we performed a comprehensive review of literatures (full text or abstracts) published online. English databases including PubMed, Scopus, Science Direct and Cochran were searched for publications related to Cryptosporidium infection of animals worldwide, from 1984 to 2016. We used the following MeSH terms alone or in combination: “Cryptosporidium” or “cryptosporidiosis” and “prevalence” and “livestock” or “cattle” or “buffaloes” or “sheep” or “pigs” or “camels” or “alpacas” or “horses” or “ruminants” or “wildlife”. To identify additional published articles, we used the PubMed option of “related articles” and checked the reference lists of the original and review articles. The more agricultural and veterinary focused database CAB abstracts was searched using the following search terms: “Cryptosporidium” or “cryptosporidiosis” and “prevalence” and “cattle” or “cows” or “calves” or “buffaloes” or “sheep” or “lambs” or “goats” or “kids” or “camels” or “alpacas” or “crias” or “llamas” or “pigs” or “piglets” or “horses” or “foals” or “deer” or “fawns” or “farm animals” or “ruminants” or “livestock” or “wildlife”. A protocol for the literature review was devised (Fig. 1) in accordance with the PRISMA guidelines [36] (Additional file 1: Table S1).

**Inclusion and exclusion criteria**

As part of the eligibility for inclusion, titles that suggested the topic Cryptosporidium in domestic and wild hoofed animals were selected. The abstracts from the selected reference titles were reviewed by two independent reviewers to determine if the studies met the inclusion criteria and, if so, the entire articles were reviewed in full. If more than one report was published from the same study, only one was included. Exclusion criteria included studies only on human cryptosporidiosis or case reports. Studies on epidemiology of Cryptosporidium spp. in groups unrelated to hoofed animals, or studies presenting overall prevalence estimates, where samples were collected from the ground, and data from each animal
were not independently retrievable, were also excluded. The language of data collection was limited to English. In order to provide contemporaneous and representative estimates, studies were excluded if they presented data collected prior to 1984. On several occasions, we contacted the authors for the collection of raw data.

Data extraction and tabulation
A data extraction form was used to collect the following data from each study: first author, year of publication, location of study, period of study, host species, age range, clinical signs (diarrhoeic versus non-diarrhoeic), population nature (e.g. domestic, captive or wild), total number of fecal samples, utilized detection method (conventional microscopy, CM; immunofluorescence antibody test, IFA; enzyme-linked immunosorbent assay, ELISA; immunochromatographic test, ICT; quantitative latex agglutination, QLAT; and polymerase chain reaction, PCR), number of Cryptosporidium-positive samples and identity of Cryptosporidium species and genotypes.

Retrieving sequences and phylogenetic analyses
To examine the genetic relationships among Cryptosporidium spp. (C. hominis, C. felis, C. parvum, C. erinacei, C. xiaoii, C. ryanae, C. scrofarum, C. muris, C. andersoni, C. ubiquitum, C. bovis and C. suis) in ungulates, a phylogenetic tree was constructed using the program Splits Tree v.4.0 based on the Neighbor-Net method and Median-Joining analysis of sequences.
of the 18S rRNA gene [37]. For this purpose, the sequences of the 18S rRNA gene of these Cryptosporidium spp. were retrieved from the GenBank database in the FASTA format. These sequences were initially obtained from various herbivores, including cattle, buffaloes, yaks, camels, goats, sheep and deer, as well as pigs.

**Meta-analysis**

A meta-analysis was performed for studies describing Cryptosporidium infection prevalence in domestic animals that are common in many parts of the world, i.e. cattle, sheep, goats, buffaloes, horses and pigs. This analysis was performed to enhance knowledge on the potential role of livestock in zoonotic Cryptosporidium

Table 1  Summarized Cryptosporidium prevalence data for major domestic farmed animals. Data for wild populations of the given species not included (see for full datasets and other host species in Additional file 2: Table S2)

| Host species  | Region     | No. of studies | Utilized diagnostic methods      | Retrieved minimum prevalence (%) | Retrieved maximum prevalence (%) |
|--------------|------------|----------------|----------------------------------|---------------------------------|---------------------------------|
| Buffalo (Bubalus bubalis) | Africa     | 6              | CM, PCR                          | 1.3 (CM)                        | 52.0 (CM)                       |
|              | Asia       | 16             | CM, ICT, PCR                     | 3.6 (CM)                        | 50.0 (CM)                       |
|              | Australia  | 2              | PCR                              | 13.1 (PCR)                      | 30.0 (PCR)                      |
|              | Europe     | 1              | ELISA                            | 14.7 (ELISA)                    |                                 |
|              | South America | 2        | CM, PCR                          | 9.4 (CM)                        | 48.2 (PCR)                      |
| Cattle (Bos taurus) | Africa     | 29             | CM, ELISA, PCR                   | 0.5 (CM)                        | 86.7 (CM)                       |
|              | Asia       | 74             | CM, ICT, IFA, PCR                | 1.5 (CM)                        | 93.0 (CM)                       |
|              | Australia  | 7              | CM, IFA, PCR                     | 3.6 (IFA)                       | 73.5 (PCR)                      |
|              | Europe     | 60             | CM, ELISA, ICT, IFA, PCR, QLAT   | 0.0 (CM)                        | 71.7 (CM)                       |
|              | New Zealand| 5              | CM, IFA                         | 2.6 (IFA)                       | 21.2 (CM)                       |
|              | North America | 29       | CM, IFA, PCR                     | 1.1 (IFA)                       | 78.0 (CM)                       |
|              | South America | 11        | CM, ICT, PCR                     | 3.0 (CM)                        | 56.1 (CM)                       |
| Goat (Capra hircus) | Africa | 10 | CM, ELISA | 0.0 (CM) | 76.5 (ELISA) |
|              | Asia       | 15             | CM, ICT, IFA                     | 0.0 (IFA)                       | 42.9 (CM)                       |
|              | Australia  | 1              | PCR                              | 4.4 (PCR)                       |                                 |
|              | Europe     | 22             | CM, ELISA, IFA                   | 0.0 (CM)                        | 93.0 (IFA)                      |
|              | North America | 3        | CM                              | 20.0 (CM)                       | 72.5 (CM)                       |
|              | South America | 3        | CM                              | 4.8 (CM)                        | 100 (CM)                        |
| Sheep (Ovis aries) | Africa | 10 | CM, ELISA, PCR | 1.3 (CM) | 41.8 (ELISA) |
|              | Asia       | 17             | CM, ELISA, ICT, PCR             | 1.8 (CM)                        | 66.6 (CM)                       |
|              | Australia  | 7              | PCR                              | 2.2 (PCR)                       | 81.3 (PCR)                      |
|              | Europe     | 22             | CM, IFA, ELISA                   | 1.4 (CM)                        | 100.0 (CM)                      |
|              | North America | 9        | CM, IFA, PCR                     | 20.0 (CM)                       | 77.4 (PCR)                      |
|              | South America | 5        | CM, PCR                         | 0.0 (CM)                        | 25.0 (PCR)                      |
| Pig (Sus scrofa) | Africa | 5 | CM, ELISA, IFA, PCR | 13.6 (CM) | 44.9 (ELISA) |
|              | Asia       | 13             | CM, IFA, PCR                     | 0.4 (IFA)                       | 55.8 (PCR)                      |
|              | Australia  | 3              | CM, PCR                          | 0.3 (CM)                        | 22.1 (PCR)                      |
|              | Europe     | 13             | CM, IFA, PCR                     | 0.1 (CM)                        | 40.9 (IFA)                      |
|              | North America | 6        | CM, IFA                         | 2.8 (ns)                        | 19.6 (CM)                       |
|              | South America | 3        | CM, PCR                         | 0.0 (CM)                        | 2.2 (PCR)                       |
| Horse (Equus caballus) | Africa | 3 | CM, PCR | 0.0 (CM) | 2.9 (PCR) |
|              | Asia       | 7              | CM, PCR                          | 2.7 (PCR)                       | 37.0 (CM)                       |
|              | Europe     | 10             | CM, ELISA, IFA, PCR              | 3.4 (PCR)                       | 25.0 (IFA)                      |
|              | New Zealand| 2              | CM                              | 18.0 (CM)                       | 83.3 (CM)                       |
|              | North America | 6        | CM, IFA, PCR                     | 0.0 (IFA/PCR)                   | 17.0 (IFA)                      |
|              | South America | 7        | CM                              | 0.0 (CM)                        | 100.0 (CM)                      |

* Multiple studies revealed the same prevalence data

Abbreviation: ns, not stated
## Table 2  Statistical analysis of *Cryptosporidium* infection prevalence in domestic ungulates using CM and PCR methods

| Method/host | CM | PCR |
|-------------|----|-----|
|             | Pooled (%) | OR (95% CI) | Heterogeneity | Publication bias | Pooled (%) | OR (95% CI) | Heterogeneity | Publication bias |
|             | Q statistic | df | I² (%) | Egger bias (P-value) | Q statistic | df | I² (%) | Egger bias (P-value) |
| Cattle      | 22.5 | 19.6–25.6 | 11,038.9 | 127 | 98.8 | 10.51 (P<0.0001) | 29.1 | 23.1–35.6 | 1591.1 | 34 | 97.9 | 11.52 (P<0.0001) |
| Sheep       | 20.7 | 15.2–26.8 | 1391.9 | 30 | 97.8 | 6.77 (P=0.0086) | 24.4 | 16.4–33.4 | 916.7 | 14 | 98.5 | 818 (P=0.014) |
| Goat        | 18.7 | 12.36–26.2 | 1852.1 | 28 | 98.5 | 9.01 (P=0.0004) | 8.2 | 3.7–14.3 | 11.2 | 2 | 82.2 | – |
| Pig         | 15.5 | 10.5–21.3 | 1545.4 | 21 | 98.6 | 12.42 (P=0.0485) | 22.6 | 13.7–33.0 | 99.8 | 5 | 95.0 | 2.36 (P=0.6452) |
| Horse       | 13.8 | 6.6–22.9 | 621.6 | 16 | 97.4 | 6.71 (P=0.0002) | 4.7 | 2.0–8.4 | 22.5 | 4 | 82.3 | 3.67 (P=0.0452) |
| Buffalo     | 18.6 | 11.1–27.4 | 991.4 | 17 | 98.3 | 8.76 (P=0.0004) | 26.0 | 12.2–42.8 | 152.4 | 4 | 97.4 | 9.28 (P=0.1434) |
Fig. 2 Forest plot of prevalence of Cryptosporidium spp. infection in cattle using molecular methods (first author, year and country)
transmission since these animals feature a close contact to humans. The pooled prevalence of *Cryptosporidium* infection as well as its 95% confidence interval (CI) was calculated for each study. A forest plot was generated to display the summarized results and heterogeneity among the included studies. To ensure comparable sensitivity of tests used in analyzed studies, only results from studies based on PCR as a diagnostic method were included. Studies using PCR methods only for molecular *Cryptosporidium* species/genotype identification but utilizing alternative diagnostic methods to determine prevalence were not included. The heterogeneity was expected in advance and statistical analyses including $I^2$ and Cochrane’s Q test (with a significance level of $P<0.1$) were used to quantify these variations. The meta-analysis considering the random effects model [38] was performed using the Stats Direct statistical software (http://www.statsdirect.com).

**Results**

The initial database search retrieved 14,970 publications. The screening of these records enabled us to exclude 14,456 studies due to not meeting the inclusion criteria. Altogether, 514 studies were retained for further investigation. During the secondary assessment of these papers, another 85 were excluded because of one of the following reasons: other host species including wild hoofed animals; report of the same results as another paper published by the same author; and language of publication (e.g. Chinese, Spanish, etc.). Papers evaluating cryptosporidiosis in camels, yaks, donkeys, alpacas and llamas were excluded in the secondary analysis of data, as the meta-analysis focused on *Cryptosporidium* infection in cattle, sheep, goats, pigs, buffaloes and horses. Eventually, 429 studies which evaluated *Cryptosporidium* infection during three decades met our eligibility criteria and were retained for analysis (Fig. 1).

Different diagnostic procedures were used for the detection of *Cryptosporidium* oocysts to a varying extent in the different studies. The included publications featured CM examination ($n=371$), IFA ($n=107$), ELISA ($n=25$), ICT ($n=9$), quantitative latex agglutination (QLAT) ($n=1$) and polymerase chain reaction (PCR) ($n=99$) (Additional file 2: Table S2).

In total, 196,638 stool samples from Artiodactyla and Perissodactyla ungulates were evaluated, of which 37,206 (18.9%) subjects were positive for *Cryptosporidium* infection. Among the 196,638 stool samples, 90,744 were associated with the domestic hoofed animals (including camels, yaks, donkeys, alpacas and llamas), displaying a *Cryptosporidium* infection prevalence of 13.6% ($n=12,377$) (Table 1 and Additional file 2: Table S2).

All subsequent analyses included only the studies that focused on *Cryptosporidium* infection in cattle, sheep,
goats, pigs, buffaloes and horses (n = 429). Among them, 201 provided data on cattle, 66 on sheep, 55 on goats, 39 on pigs, 37 on horses and 28 on buffaloes (Additional file 2: Table S2).

A total of 105,894 samples from 245 studies on common livestock, defined as cattle, sheep, goats, pigs, horses and buffaloes, were examined for Cryptosporidium infection, with 24,829 (23.4%) being positive for Cryptosporidium spp. using CM and PCR methods. Most of the studies were conducted on cattle (n = 163) and sheep (n = 46).

The pooled prevalence rates using the CM method were 22.5% (95% CI: 19.6–25.6%), 20.7% (95% CI: 15.2–26.8%), 18.7% (95% CI: 12.36–26.2%), 15.5% (95% CI: 10.5–21.3%), 13.8% (95% CI: 6.6–22.9%) and 18.6% (95% CI: 11.1–27.4%) for cattle, sheep, goats, pigs, horses and buffaloes, respectively (Table 2). The pooled prevalence rates using the PCR method were 29.1% (95% CI: 23.1–35.6%), 24.4% (95% CI: 16.4–33.4%), 8.2% (95% CI: 3.7–14.3%), 22.6% (95% CI: 13.7–33%), 4.7% (95% CI: 2–8.4%) and 26.0% (95% CI: 12.2–42.8%) for cattle, sheep, goats, pigs, horses and buffaloes, respectively (Table 2). Analysis of available data by regions (continents and New Zealand) showed a moderate geographical variation of observed prevalence (Table 1). Although diagnostic tests varied among regions, the observed prevalence mostly fell within the 5–30% range (Table 2). Regarding cattle, a considerably lower maximum prevalence was seen in New Zealand compared to other regions. Cryptosporidium prevalence in goat tended to be lower in Asia; however, only one study was available for Australia. For sheep it was the highest in the regions with most intensive sheep production, i.e. Australia, Europe and North America (Table 1). Cryptosporidium prevalence in pigs was the highest in Asia, Africa and Europe. In horses,

![Forest plot of prevalence of Cryptosporidium spp. infection in sheep using molecular methods (first author, year and country)](image-url)

Fig. 4 Forest plot of prevalence of Cryptosporidium spp. infection in sheep using molecular methods (first author, year and country)
studies in South America reported the highest *Cryptosporidium* prevalence.

The forest plot diagrams of prevalence of *Cryptosporidium* infection in domestic hoofed animals derived from studies using a PCR method are shown in Figs. 2, 3, 4, 5, 6, 7. As forest plots show, there is a considerable variation of study numbers and observed prevalence in a given host species within each defined geographical region, even if only studies based on PCR methodology are included. Considering a wider range of studies, i.e. studies that use either CM or PCR (Table 2), cattle are most commonly infected globally while horses feature the lowest *Cryptosporidium* prevalence.

The highest and lowest prevalence rate of *Cryptosporidium* infection in domestic hoofed animals was observed in America (26%) and Africa (14%) continents, respectively (Table 3, Fig. 8). Among 53 countries with data, Canada (60%) showed the highest infection rate whereas China, Thailand and Germany (8%) had the lowest infection rate (Table 3, Fig. 8).

The distribution of *Cryptosporidium* species/genotypes by host and geographical region is summarized in Table 4. *Cryptosporidium parvum* (monoinfections 4172/10,583; 39.4%) and *C. andersoni* (monoinfections 1992/10,583; 18.8%) were the most commonly detected *Cryptosporidium* species (Table 4). A phylogenetic network was constructed based on sequences of *Cryptosporidium* spp. (Fig. 9) using the Neighbor-Net method. On the basis of this phylogenetic analysis, 10 clades (I, II, III, IV, V, VI, VII, VIII, IX and X) containing 12 *Cryptosporidium* spp. were identified (Fig. 9). Interestingly, *C. andersoni* and *C. muris* were placed together in Clade I, and *C. xiaoii* and *C. bovis* were both placed in Clade III. It further demonstrated a pairwise sister relationship between clades III and IV (clustering *C. xiaoii*, *C. bovis*, and *C. ryanae*), VI and VII (containing *C. ubiquitum* and *C. suis*) and VIII and IX (containing *C. hominis* and *C. erinacei*), respectively. Interestingly, the result of the phylogenetic analysis indicated that clades II (*C. scrofarum*), III (*C. bovis* and *C. xiaoii*) and IV (*C. ryanae*) could have originated from a common ancestor. The distribution of *Cryptosporidium* spp. in a wide range of domestic and wild ungulates is presented in Table 4. The *C. parvum* is the most common genotype in cattle (54.1%), goats (42.1%) and horses (40.2%), followed by *C. ryanae* in buffaloes (66.6%), *C. suis* in pigs (54.1%), and *C. xiaoii* in sheep (48.9%). In terms of transmission dynamics and clinical importance of zoonotic *Cryptosporidium* spp., *C. hominis*, *C. parvum*, *C. andersoni*, *C. bovis* and *C. ubiquitum* were identified in sheep/goats, cattle/goats/horses/pigs/sheep, cattle/camels/sheep/yaks, bufaloes/cattle/sheep/pigs/red deer and alpacas/bufaloes/cattle/goats/impalas/sheep/red deers, respectively (Table 4).
Fig. 6 Forest plot of prevalence of *Cryptosporidium* spp. infection in horses using molecular methods (first author, year and country)

Fig. 7 Forest plot of prevalence of *Cryptosporidium* spp. infection in buffaloes using molecular methods (first author, year and country)
| Continent                        | Country   | Prevalence, pooled proportion (95% CI) (%) |
|---------------------------------|-----------|------------------------------------------|
| Africa (43 studies; 17,424 samples) | Egypt  | 10 (4.44–19.32)                          |
|                                 | Ethiopia | 17 (7.15–30.13)                         |
|                                 | Ghana    | 29                                       |
|                                 | Kenya    | 15 (10.72–21.30)                        |
|                                 | Malawi   | 18 (10.48–28.78)                        |
|                                 | Nigeria  | 17 (13.07–22.33)                        |
|                                 | South Africa | 0.5                                     |
|                                 | Tanzania | 11 (1.59–29.29)                         |
|                                 | Tunisia  | 14 (2.09–44.93)                         |
| **Total prevalence in Africa:** |           | **14 (11.12–18.31)**                    |
| America (37 studies; 15,860 samples) | Argentina | 25 (18.83–33.58)                        |
|                                 | Brazil   | 16 (5.82–30.23)                         |
|                                 | Canada   | 60 (23.32–91.14)                        |
|                                 | Chile    | 56                                       |
|                                 | Costa Rica | 11 (1.59–29.29)                   |
|                                 | Mexico   | 41 (31.81–52.23)                        |
|                                 | Trinidad | 32 (6.47–67.24)                         |
|                                 | USA      | 11 (2.84–24.39)                         |
| **Total prevalence in America:** |           | **26 (18.41–34.67)**                   |
| Asia (90 studies; 37,458 samples) | Bangladesh | 9 (2.93–20.36)                          |
|                                 | China    | 8 (5.62–12.95)                          |
|                                 | India    | 21 (16.02–28.47)                        |
|                                 | Iraq     | 17 (11.36–25.23)                        |
|                                 | Japan    | 24 (6.02–72.52)                         |
|                                 | Malaysia | 24 (8.43–46.55)                         |
|                                 | Myanmar  | 56                                       |
|                                 | Nepal    | 35 (28.81–43.45)                        |
|                                 | Pakistan | 16 (9.05–25.96)                         |
|                                 | South Korea | 17 (11.53–23.57)        |
|                                 | Sri Lanka | 28                                       |
|                                 | Taiwan   | 35 (32.44–38.15)                        |
|                                 | Thailand | 8 (3.08–17.41)                          |
|                                 | Vietnam  | 18                                       |
| **Total prevalence in Asia:**   |           | **17 (14.94–20.30)**                   |
| Australia (4 studies; 923 samples) | Australia | 23 (0.00–71.85)                          |
|                                 | New Zealand | 20 (15.42–25.92)        |
| **Total prevalence in Australia:** |           | **21 (7.28–40.02)**                   |
| Europe (71 studies, 34,229 samples) | Austria | 11 (9.87–27.11)                          |
|                                 | Czech Republic | 17 (9.87–27.11)          |
|                                 | Denmark  | 33 (14.90–55.60)                        |
|                                 | France   | 17 (2.56–41.08)                        |
|                                 | Germany  | 8 (3.62–48.31)                         |
|                                 | Greece   | 17 (9.87–27.11)                        |
|                                 | Ireland  | 23 (3.84–52.25)                        |
|                                 | Netherlands | 60 (15.42–25.92)       |
|                                 | Poland   | 11 (3.62–21.85)                        |
|                                 | Portugal | 17                                       |

Table 3 The prevalence of Cryptosporidium infection in terrestrial ungulates (cattle, sheep, goat, pig, horse and buffalo) using conventional microscopic methods. Data are presented separately by continent and country.
Discussion

In this systematic review and meta-analysis, we found that 18.9% of the overall populations of the investigated ungulate species were infected with *Cryptosporidium* spp. Our study showed that although the prevalence of *Cryptosporidium* infection was higher in ungulates of the Cetartiodactyla than in Perissodactyla, the prevalence in the latter was not negligible and needs to be considered in terms of pathogen transmission and cycling. From the data collected and summarized on wild animals (as included in Table 4, and Additional file 2: Table S2), it is obvious that sylvatic cycles play a major role in *Cryptosporidium* transmission. Wild terrestrial ungulates are likely serving as important reservoir for the parasite, and certainly the infection of livestock and humans may occur by contact to wildlife feces. For meta-analysis, worldwide *Cryptosporidium* prevalence and species/genotype identity common livestock species have been scrutinized. Overall, *Cryptosporidium* prevalence in farmed animals is the highest in the Americas and Europe (Table 3) which could be attributed to the intensive farm animal production in these regions. More specifically, considering domestic farm animals, the pooled prevalence of equine *Cryptosporidium* infection was 4.7%, compared to the pooled prevalence of 29.1%, 26.0%, 24.4%, 22.6% and 8.2% in cattle, buffaloes, sheep, pigs and goats, respectively. Regarding the number of studies published for the different geographical regions, our analysis does not support under investigation of certain regions (e.g. Asia) as cause of a detection bias. This reinforces the suggestion that animal production intensity affects the prevalence of *Cryptosporidium* spp. Concentrated animal feeding operations (CAFOs) are most common in cattle and pigs. For example, in the USA, in 2002 more than 71% of all produced beef were derived from operations holding more than 5000 heads of cattle each. It is known that CAFOs pose a major problem due to the high amounts of manure that are released to the environment, facilitating potential pathogen transmission to humans, wildlife and other agricultural operations [39]. Furthermore, pathogen transmission within a CAFO seems much more likely than in more extensive farming systems. Accordingly, a high prevalence of *Cryptosporidium* was observed in animals from countries with many CAFO operations, especially in studies in Asia and Europe, with both regions harboring the majority of the commercial pig raising industry [40]. High prevalences in pigs in Africa may be attributed to the opposite effect of extensive farming with high exposure to environmental contamination. Other host animals displaying a high prevalence, such as buffaloes and sheep, are also generally kept in larger groups on commercial operations. The comparatively low prevalence rates in equines and goats may potentially result from smaller animal groups and free-range nature of the animal management.

Between wild and domestic animals, it appears that *Cryptosporidium* prevalence is lower in wild populations than in farmed populations in the same host species. For example, Zahedi et al. [41] reported *Cryptosporidium* infection rates of 30% in farmed buffalo but 12% in wild buffalo. This suggests that animal density and confinement to the same (contaminated) environment facilitate *Cryptosporidium* transmission in domestic animals, and there is no clear host species disposition in terms of general susceptibility to infection with the genus *Cryptosporidium* despite the observed variation in *Cryptosporidium* infection rates among host species (Table 4).

Cryptosporidiosis in ungulates, especially ruminants, has several economic and health implications. Cryptosporidiosis in neonatal calves can lead to profuse watery diarrhea, loss of appetite, lethargy, dehydration and even death, thus may require costly treatments [42]. Moreover, as shown in sheep and goats, cryptosporidiosis can exhibit long-term effects on the growth of animals [43, 44]. Additionally, infected calves can shed over $1 \times 10^{10}$ oocysts each day, which can survive in the environments for months. The ingestion of very few oocysts can cause infection in susceptible hosts, including humans [23, 45].

### Table 3 (continued)

| Continent | Country | Prevalence, pooled proportion (95% CI) (%) |
|-----------|---------|------------------------------------------|
| Romania   | 21      | (15.02–27.97)                           |
| Serbia    | 40      | (31.95–49.48)                           |
| Spain     | 29      | (19.80–39.75)                           |
| Sweden    | 8a      |                                          |
| Switzerland | 55a    |                                          |
| Turkey    | 34      | (19.82–50.61)                           |
| UK        | 34      | (0.59–85.50)                            |

* One study was performed in these countries

Between wild and domestic animals, it appears that *Cryptosporidium* prevalence is lower in wild populations than in farmed populations in the same host species. For example, Zahedi et al. [41] reported *Cryptosporidium* infection rates of 30% in farmed buffalo but 12% in wild buffalo. This suggests that animal density and confinement to the same (contaminated) environment facilitate *Cryptosporidium* transmission in domestic animals, and there is no clear host species disposition in terms of general susceptibility to infection with the genus *Cryptosporidium* despite the observed variation in *Cryptosporidium* infection rates among host species (Table 4).

Cryptosporidiosis in ungulates, especially ruminants, has several economic and health implications. Cryptosporidiosis in neonatal calves can lead to profuse watery diarrhea, loss of appetite, lethargy, dehydration and even death, thus may require costly treatments [42]. Moreover, as shown in sheep and goats, cryptosporidiosis can exhibit long-term effects on the growth of animals [43, 44]. Additionally, infected calves can shed over $1 \times 10^{10}$ oocysts each day, which can survive in the environments for months. The ingestion of very few oocysts can cause infection in susceptible hosts, including humans [23, 45].
It has been shown that the median infection dose of C. parvum for humans range from below 10 to over 1000 oocysts [22]. Zoonotic transmission of Cryptosporidium spp. can easily occur seasonally from young animals such as bovine calves to humans, frequently as an occupational hazard [45, 46].

Nearly 40 Cryptosporidium species have been recognized based on molecular, morphological and biological characteristics of the parasites. Previous studies have shown that four major species are responsible for bovine cryptosporidiosis, namely C. parvum, C. andersoni, C. bovis and C. ryanae [1]. We showed that the most prevalent Cryptosporidium species in ungulates are C. parvum and C. andersoni, comprising 39.4% and 18.8% of detected parasites, respectively.

The data also suggest that some Cryptosporidium species are shared among ungulate hosts (Table 4). This indicates the occurrence of some inter-species transmission of Cryptosporidium spp. among ungulate species, making wildlife an important reservoir for infections in domestic animals. Currently, most data on the distribution of Cryptosporidium species and genotypes are available on domestic animal populations. Amazingly, there are clear differences in the distribution of Cryptosporidium species within the same host species among geographical regions. For example, studies from Ethiopia and Nigeria indicate that C. andersoni and C. bovis are the most prevalent species in cattle. In contrast, in countries with concentrated animal feeding operations (CAFO) such as Australia, Iran, Japan and New Zealand, as well as many European and North American countries, C. parvum is prevalent in cattle (Table 4). Similarly, alpacas in their region of origin are mostly infected with C. parvum and C. ubiquitum, while alpacas in the UK only tested positive for C. parvum (Table 4). Calves, lambs and goat kids in areas with more human activities can even have C. hominis infections [19, 41, 47, 48]. Thus, it might be speculated that husbandry systems and contact to other livestock and humans strongly influence the distribution of Cryptosporidium species in an ungulate population.

Our meta-analysis had several limitations. We observed a substantial heterogeneity among the included studies. Heterogeneity in the meta-analyses of prevalence is not uncommon, and the random-effect

![Fig. 8 Overall prevalence of Cryptosporidium in different geographical regions in the world. The prevalence in each country was determined from conventional microscopy data in farmed animals (cattle, sheep, goats, pigs, horses and buffaloes)](image)
### Table 4: Worldwide occurrence of Cryptosporidium species or genotypes in selected domestic and wild populations of ungulate species; where applicable, available data are summarized from different sources per country

| Host | Country | No. of isolates | No. of Cryptosporidium species/genotypes | Reference |
|------|---------|----------------|-----------------------------------------|-----------|
|      |         |                | Mono-infection (n)                       | Mixed infection (n) | |
|      | Alpaca  | Peru           | 3 | C. parvum (2); C. ubiquitum (1)         | – | Gómez-Couso et al. [51] |
|      | Alpaca  | UK             | 9 | C. parvum (9)                           | – | Twomey et al. [52]; Wessels et al. [53] |
|      | Bison   | Portugal       | 1 | C. tyzzeri (1)                          | – | Alves et al. [54] |
|      | Boar    | Czech Republic | 32| C. suis (13); C. scrofa (7)             | C. suis + C. scrofa (12) | Nêméc et al. [55] |
|      | Buffalo | Egypt          | 70| C. parvum (41); C. ryanae (17); C. bovis (2) | C. parvum + C. ryanae (7); C. parvum + C. bovis (3) | Amer et al. [56]; Helmy et al. [57]; Mahfouz et al. [58]; Ibrahim et al. [59] |
|      | Buffalo | South Africa   | 2 | C. ubiquitum (1); C. bovis (1)          | – | Abu Samra et al. [60] |
|      | Buffalo | Australia      | 72| C. parvum (9); C. ryanae (58); C. scrofa (1); C. bovis (4) | – | Abeywardena et al. [61]; Zahedi et al. [62] |
|      | Buffalo | Italy          | 6 | C. parvum (6)                           | – | Caccio et al. [63] |
|      | Buffalo | Brazil         | 63| C. parvum (1); C. ryanae (60); unknown genotype (2) | – | Aquino et al. [64] |
|      | Camel   | China          | 3 | C. andersoni (3)                        | – | Wang et al. [65]; Liu et al. [66] |
| Cattle | Egypt   |                | 238| C. parvum (146); C. andersoni (7); C. ryanae (35); C. bovis (13) | C. parvum + C. ryanae (15); C. parvum + C. bovis (10); C. parvum + C. andersoni (3); C. ryanae + C. bovis (7) | Amer et al. [56]; Helmy et al. [57]; Mahfouz et al. [58]; Ibrahim et al. [59] |
| Cattle | Ethiopia |                | 71 | C. andersoni (54); C. ryanae (3); C. bovis (14) | – | Wegayehu et al. [67] |
| Cattle | Kenya   |                | 27 | C. parvum (17); C. andersoni (3); C. ryanae (6); C. ubiquitum (1) | – | Szonyi et al. [68]; Kang et al. [69] |
| Cattle | Madagascar |            | 17 | C. suis (17)                           | – | Bodager et al. [70] |
| Cattle | Nigeria |                | 65 | C. andersoni (5); C. ryanae (13); C. bovis (32) | C. ryanae + C. bovis (111); C. bovis + C. andersoni (4) | Ayinmode et al. [71]; Maikai et al. [72] |
| Cattle | South Africa |          | 6 | C. parvum (1); C. andersoni (2); C. ubiquitum (3) | – | Abu Samra et al. [80]; Abu Samra [73] |
| Cattle | Tunisia |                | 7 | C. parvum (7)                           | – | Soitane et al. [74] |
| Cattle | Zambia  |                | 45 | C. parvum (29); C. ubiquitum (1); C. bovis (15) | – | Geurden et al. [75] |
| Cattle | China   |                | 299| C. parvum (69); C. andersoni (100); C. ryanae (19); C. bovis (89) | C. parvum + C. bovis (6); C. parvum + C. andersoni (3); C. ryanae (4); C. parvum + C. andersoni (3); C. bovis + C. ryanae (9) | Wang et al. [76, 77]; Huang et al. [78] |
| Cattle | India   |                | 21 | C. parvum (6); C. andersoni (3); C. ryanae (3); C. bovis (8); C. occultus (1) | – | Khan et al. [79] |
| Cattle | Iran    |                | 54 | C. parvum (50); C. andersoni (4)        | – | Meamar et al. [80]; Fotouhi et al. [81]; Pirestani et al. [82] |
| Cattle | Israel  |                | 61 | C. parvum (61)                          | – | Tannirvedi et al. [83] |
| Cattle | Japan   |                | 33 | C. parvum (32); C. bovis (1)            | – | Karanis et al. [84] |
| Cattle | Malaysia |               | 14 | C. parvum (11); C. ryanae (3)           | – | Halim et al. [85] |
| Host | Country       | No. of isolates | No. of *Cryptosporidium* species/genotypes | Reference                                                                 |
|------|---------------|-----------------|-------------------------------------------|---------------------------------------------------------------------------|
| Cattle | Australia    | 439             | *C. parvum* (297); *C. andersoni* (20); *C. ryanae* (30); *C. bovis* (72); *C. hominis* (3) | Waldron et al. [86]; Nolan et al. [87]; Ferguson et al. [88]; Ng et al. [89]; McCarthy et al. [90]; O’Brien et al. [91]; Ralston et al. [92] |
| Cattle | New Zealand  | 127             | *C. parvum* (85); *C. bovis* (42) | Learmonth et al. [93]; Grinberg et al. [94]; Al-Mawly et al. [95] |
| Cattle | Belgium      | 114             | *C. parvum* (105); *C. suis* (1); *C. bovis* (8) | Geurden et al. [96] |
| Cattle | Czech Republic | 2019           | *C. parvum* (699); *C. andersoni* (1315); *C. bovis* (5) | Kvac et al. [97]; Kvac et al. [98]; Ondrackova et al. [99] |
| Cattle | Denmark      | 244             | *C. parvum* (100); *C. andersoni* (59); *C. bovis* (11); *C. occultus* (3); unknown genotype (4) | Langkjaer et al. [100]; Enemark et al. [101] |
| Cattle | France       | 91              | *C. parvum* (32); *C. ryanae* (14); *C. ubiquitum* (1); *C. bovis* (11) | Follet et al. [102] |
| Cattle | Hungary      | 22              | *C. parvum* (21); *C. ryanae* (1) | Plutzer et al. [103] |
| Cattle | UK (Northern Ireland) | 224            | *C. parvum* (213); *C. ryanae* (3); *C. bovis* (8) | Thompson et al. [104] |
| Cattle | Italy        | 101             | *C. parvum* (101) | Durant et al. [105] |
| Cattle | Poland       | 113             | *C. parvum* (36); *C. andersoni* (17); *C. ryanae* (8); *C. bovis* (52) | Rzezutka & Kaupke [106] |
| Cattle | Portugal     | 82              | *C. parvum* (82) | Mendonca et al. [107] |
| Cattle | Romania      | 65              | *C. parvum* (65) | Imre et al. [108] |
| Cattle | Scotland     | 411             | *C. parvum* (409); *C. hominis* (2) | Smith et al. [109] |
| Cattle | Serbia       | 62              | *C. parvum* (63) | Masic & Abe [110] |
| Cattle | Spain        | 267             | *C. parvum* (255); *C. andersoni* (11); *C. bovis* (4); *C. felis* (4); unknown genotype (8) | Mendonca et al. [107]; Quileiz et al. [111]; Cardona et al. [112] |
| Cattle | Sweden       | 359             | *C. parvum* (33); *C. andersoni* (4); *C. ryanae* (40); *C. bovis* (262); *C. ubiquitum* (1) | Silverlas et al. [113]; Silverlas et al. [114]; Silverlas et al. [115]; Bjorkman et al. [116] |
| Cattle | Switzerland  | 81              | *C. parvum* (81) | Uhde et al. [117] |
| Cattle | Turkey       | 15              | *C. parvum* (15) | Tannirvedi et al. [83] |
| Cattle | UK           | 306             | *C. parvum* (240); *C. andersoni* (20); *C. ryanae* (1); *C. bovis* (81) | Thompson et al. [104]; Brook et al. [118]; Featherstone et al. [119]; Moriarty et al. [120]; Smith et al. [121] |
| Cattle | Canada       | 134             | *C. parvum* (51); *C. andersoni* (38); *C. ryanae* (11); *C. bovis* (94) | Coklin et al. [122]; Coklin et al. [123]; Budu-Amoako et al. [124]; Budu-Amoako et al. [125] |
| Host     | Country   | No. of isolates | No. of Cryptosporidium species/genotypes                                                                 | Reference                                      |
|----------|-----------|-----------------|----------------------------------------------------------------------------------------------------------|-----------------------------------------------|
|          |           |                 |                                                                                                          |                                               |
| Cattle   | USA       | 698             | C. parvum (240); C. andersoni (203); C. ryanae (83); C. bovis (171); C. suis (1)                           | Santín et al. [126]; Fayer et al. [127–129]; Szonyi et al. [130] |
| Cattle   | Brazil    | 57              | C. parvum (15), C. andersoni (33); C. ryanae (4); C. bovis (5)                                          | Meireles et al. [131]; Sevá et al. [132]; Silva et al. [133] |
| Giraffe  | Czech Republic | 1           | C. muris (1)                                                                                              | Kodádková et al. [134]                        |
| Goat     | Tanzania  | 5               | C. xiao (5)                                                                                                | Parsons et al. [135]                          |
| Goat     | Zambia    | 1               | C. parvum (1)                                                                                                | Goma et al. [136]                             |
| Goat     | China     | 44              | C. andersoni (16); C. ubiquitum (24); C. xiao (4)                                                          | Wang et al. [137]                             |
| Goat     | Papua New Guinea | 10          | C. parvum (2); C. hominis (6); C. xiao (1); rat genotype II (1)                                           | Koinari et al. [138]                         |
| Goat     | Belgium   | 11              | C. parvum (11)                                                                                             | Geurden et al. [139]                          |
| Goat     | France    | 31              | C. parvum (1); C. ubiquitum (12); C. xiao (18)                                                             | Rieux et al. [140]; Paraud et al. [141]        |
| Goat     | Greece    | 14              | C. parvum (2); C. ubiquitum (5); C. xiao (7)                                                               | Tzanidakis [142]                              |
| Goat     | Spain     | 68              | C. parvum (61); C. xiao (7)                                                                                    | Díaz et al. [143]; Díaz et al. [144]          |
| Goat     | UK        | 1               | C. hominis (1)                                                                                              | Giles et al. [46]                             |
| Horse    | Algeria   | 4               | C. erniace (4)                                                                                              | Laatamna et al. [145]                         |
| Horse    | China     | 2               | C. andersoni (2)                                                                                            | Liu et al. [146]                              |
| Horse    | New Zealand | 9            | C. parvum (9)                                                                                               | Grinberg et al. [31]                          |
| Horse    | Czech Republic | 12         | C. parvum (1); C. muris (9); C. ryanae (1); horse genotype (1)                                              | Wagnerová et al. [33]                         |
| Horse    | Italy     | 35              | C. parvum (5); horse genotype (21)                                                                        | Galuppi et al. [147]                          |
| Horse    | UK        | 3               | C. parvum (3)                                                                                                | Smith et al. [121]; Chalmers et al. [148]      |
| Horse    | USA       | 29              | C. parvum (20); horse genotype (9)                                                                          | Wagnerová et al. [133]; Burton et al. [149]   |
| Impala   | South Africa | 2            | C. ubiquitum (2)                                                                                           | Abu Samra et al. [60]                         |
| Mouflon sheep | Czech Republic | 1        | C. muris (1)                                                                                                | Kotková et al. [150]                          |
| Pig      | Madagascar | 4               | C. parvum (1); C. suis (3)                                                                                   | Bodager et al. [70]                           |
| Pig      | Australia | 87              | C. scrofarum (48); C. suis (35); C. bovis (4)                                                               | McCarthy et al. [90]; Morgan et al. [151]; Johnson et al. [152]; Ryan et al. [153] |
| Pig      | Czech Republic | 1031      | C. parvum (2); C. muris (5); C. scrofarum (374); C. suis (621)                                              | Vítovec et al. [154]; Kváč et al. [155, 156]; Němejc et al. [157] |
| Pig      | Denmark   | 239             | C. scrofarum (171); C. suis (68)                                                                             | Langkjæer et al. [100]; Petersen et al. [158]  |
| Pig      | Ireland   | 28              | C. parvum (2); C. muris (1); C. scrofarum (11); C. suis (14)                                               | Zint et al. [32]                              |
| Pig      | UK        | 42              | C. parvum (11); C. scrofarum (25); C. suis (6)                                                               | Smith et al. [121]; Featherstone et al. [159]  |
| Host     | Country          | No. of isolates | No. of Cryptosporidium species/genotypes                                                                 | Mixed infection (n) | Reference                                      |
|----------|------------------|-----------------|----------------------------------------------------------------------------------------------------------|---------------------|-----------------------------------------------|
| Pig      | Brazil           | 2               | *C. scrofarum* (2)                                                                                      | –                   | Fiuza et al. [160].                           |
| Red deer | Czech Republic   | 6               | *C. muris* (1); *C. ubiquitum* (5)                                                                       | –                   | Kotková et al. [150].                         |
| Roe deer | Spain            | 6               | *C. ryanae* (3); *C. bovis* (3)                                                                          | –                   | García-Presedo et al. [161].                 |
| Sheep    | Egypt            | 3               | *C. xiaoi* (3)                                                                                           | –                   | Mahfouz et al. [58].                          |
| Sheep    | Tanzania         | 2               | *C. xiaoi* (2)                                                                                           | –                   | Parsons et al. [135].                         |
| Sheep    | Tunisia          | 3               | *C. bovis* (3)                                                                                            | –                   | Soltane et al. [74].                          |
| Sheep    | Zambia           | 6               | *C. parvum* (5); *C. ubiquitum* (1)                                                                      | –                   | Wang et al. [162]; Li et al. [163].           |
| Sheep    | China            | 125             | *C. andersoni* (4); *C. ubiquitum* (78); *C. xiaoi* (43)                                                 | –                   | Sweeny et al. [43]; Yang et al. [164]; Ryan et al. [165]; Yang et al. [166, 167]. |
| Sheep    | Australia        | 1005            | *C. parvum* (78), *C. andersoni* (6); Sheep genotype I (7); *C. scrofarum* (8); *C. suis* (2); *C. ubiquitum* (148); *C. hominis* (1); *C. xiaoi* (41); *C. bovis* (66); *C. macropodum* (4); unknown genotype (1) | –                   | Sweeny et al. [43]; Yang et al. [164]; Ryan et al. [165]; Yang et al. [166, 167]. |
| Sheep    | Papua New Guinea | 6               | *C. parvum* (4); *C. andersoni* (1); *C. scrofarum* (1)                                                 | –                   | Koinari et al. [138].                        |
| Sheep    | Belgium          | 9               | *C. parvum* (9)                                                                                          | –                   | Geurden et al. [139].                         |
| Sheep    | Greece           | 10              | *C. parvum* (7); *C. ubiquitum* (3)                                                                      | –                   | Tzanidakis [142].                             |
| Sheep    | Romania          | 24              | *C. parvum* (20); *C. ubiquitum* (2); *C. xiaoi* (2)                                                     | –                   | Imre et al. [168].                            |
| Sheep    | Scotland         | 16              | *C. parvum* (16)                                                                                         | –                   | Galuppi et al. [147].                         |
| Sheep    | Spain            | 57              | *C. parvum* (46); *C. ubiquitum* (11)                                                                   | –                   | Díaz et al. [144, 169].                      |
| Sheep    | UK               | 133             | *C. parvum* (121); *C. hominis* (2); *C. bovis* (10)                                                     | –                   | Mueller-Dobies et al. [28]; Giles et al. [46]; Smith et al. [121]; Pritchard et al. [170]; Galuppi et al. [147]. |
| Sheep    | Brazil           | 42              | *C. parvum* (3); *C. ubiquitum* (24); *C. xiaoi* (15)                                                    | –                   | Fiuza et al. [171]; Paz e Silva et al. [172]; Zucatto et al. [173]. |
| White-tailed deer | Czech Republic | 3   | *C. muris* (1); *C. ryanae* (2)                                                                            | –                   | Kotková et al. [150].                         |
| Yak      | China            | 158             | *C. andersoni* (72); *C. ryanae* (37); *C. bovis* (47); *C. occultus* (Q)                                | –                   | Yang et al. [164].                            |

**Notes:** *C. suis* (previously known as pig genotype I); *C. scrofarum* (previously known as pig genotype II); *C. ryanae* (previously deer-like genotype); *C. erinacei* (previously described as hedgehog genotype); *C. bovis* (previously bovine genotype B); *C. macropodum* (previously marsupial genotype II); *C. xiaoi* (previously bovis-like genotype); *C. hominis* (synonym: *C. parvum* genotype 1); *C. parvum* (synonym: *C. parvum* genotype 2); *C. ubiquitum* (previously identified as *Cryptosporidium* cervine genotype)

**Abbreviations:** *n*, numbers in parentheses are number of positive samples genotypes for each species or genotype
model implicitly incorporates some of the heterogeneity [49]. Nevertheless, we investigated several factors that can contribute to the observed heterogeneity. The diagnostic method used for the detection of Cryptosporidium infection was one of the main confounding variables. For example, the pooled prevalence of bovine Cryptosporidium infection was estimated 29.1% using PCR compared to 22.5% using conventional microscopy. This seems to indicate that molecular methods such as PCR are highly sensitive and specific for the detection of Cryptosporidium infection, but compared with conventional microscopic methods, they are more expensive and require a higher degree of expertise [50].

There are geographical differences in the estimated pooled prevalence of Cryptosporidium infection. The prevalence was highest in the continent of America, followed by Europe, Australia, Asia and Africa. Canada had the highest prevalence among countries. Study design, time of sampling, age of animals, and conditions of keeping animals are other factors that can contribute to the observed heterogeneity in cryptosporidiosis prevalence, in addition to the nature of animal management.

The outcome of our study is probably affected by the publication bias. Publication bias occurs when the results of studies affect the likelihood of their inclusion in the systematic review and meta-analysis [49]. Our systematic review was limited to studies published after 1984 in English. Moreover, many studies did not provide enough information to be included in the meta-analysis.

**Conclusions**

Results of the meta-analysis suggest that Cryptosporidium infection is highly prevalent in ungulates, especially ruminants. Geographical differences in Cryptosporidium prevalence and distribution of Cryptosporidium species are seen for most domestic ungulate hosts. These within-host-species differences could be partially attributed to differences in animal management among geographical regions. The highest prevalence in farmed ungulates occurs in America and Europe where CAFO is widely practiced. The major farm animal hosts of Cryptosporidium spp. appear to be cattle, buffalo, sheep and pigs. These farm animals are potent reservoirs for a variety of Cryptosporidium species. Cryptosporidium prevalence is also clearly higher in farmed animals than in wild ungulate populations. Inter-species transmission of Cryptosporidium spp. appears to be affected by contact with other host species (humans or other animals) and infection pressure (intensive farming), rendering the investigated ungulate hosts capable of propagating both zoonotic and non-zoonotic Cryptosporidium species.

---

*Fig. 9* The phylogeny of Cryptosporidium spp
Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s13071-019-3704-4.

Additional file 1: Table S1. PRISMA checklist.
Additional file 2: Table S2. Worldwide prevalence of Cryptosporidium spp. in herbivorous animals.

Abbreviations
CM: conventional microscopy; ELISA: enzyme-linked immunosorbent assay; ICT: immunochromatographic test; PCR: polymerase chain reaction; PRISMA: Preferred Reporting Items for Systematic Reviews and Meta-Analyses; QLAT: quantitative latex agglutination test.

Acknowledgements
We would like to thank Mr. F. Shahrivar and Dr. A.S. Pagheh for their assistance and kind help.

Authors’ contributions
KHN, EH, DC and LX contributed to the design of the study. KHN, EA and AS conducted the systematic review of the literature and extracted data. EA, AS, DC and LX analyzed data and drafted the first version of the manuscript. EA, DC, BB and LX contributed to the interpretation of data and writing of the first draft. All authors read and approved the final manuscript.

Funding
The authors received no financial support for the research.

Availability of data and materials
Data supporting the conclusions of this article are included within the article and its additional files.

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
1 Iranshahr University of Medical Sciences, Iranshahr, Iran. 2 Infectious and Tropical Diseases Research Center, Tabriz University of Medical Sciences, Tabriz, Iran. 3 Parasitology Reference and Research Laboratory, National Centre for Microbiology, Carlos III Health Institute, Ctra Majadahonda-Pozuelo Km 2, 28220 Majadahonda, Madrid, Spain. 4 Immunology Research Center, Tabriz University of Medical Sciences, Tabriz, Iran. 5 Drug Applied Research Center, Tabriz University of Medical Sciences, Tabriz, Iran. 6 Department of Veterinary Sciences, College of Agriculture and Natural Resources, University of Wyoming, Laramie, WY, USA. 7 College of Veterinary Medicine, South China Agricultural University, Guangzhou, China.

Received: 9 May 2019 Accepted: 5 September 2019
Published online: 14 September 2019

References
1. Feng Y, Ryan UM, Xiao L. Genetic diversity and population structure of Cryptosporidium. Trends Parasitol. 2018;34:997–1011.

2. Khalil IA, Troeger C, Rao PC, Blacker BF, Brown A, Brewer TG, et al. Morbidity, mortality, and long-term consequences associated with diarrhoea from Cryptosporidium infection in children younger than 5 years: a meta-analysis study. Lancet Glob Health. 2018;6:e758–68.

3. Scallan E, Hoekstra RM, Angulo FJ, Tauxe RV, Widdowson MA, Roy SL, et al. Foodborne illness acquired in the United States—major pathogens. Emerg Infect Dis. 2011;17:7–15.

4. DuPont HL. Persistent diarrhea: a clinical review. JAMA. 2016;315:2712–23.

5. Hatam-Nahavandi K, Mohabadi M, Mahvi AH, Keshavarz H, Khamaliha K, Tangi F, et al. Evaluation of Cryptosporidium oocyst and Giardia cyst removal efficiency from urban and slaughterhouse wastewater treatment plants and assessment of cyst viability in wastewater effluent samples from Tehran, Iran. J Water Reuse Desal. 2015;5:372–90.

6. Marcos LA, Gotuzzo E. Intestinal protozoal infections in the immunocompromised host. Curr Opin Infect Dis. 2013;26:295–301.

7. Cho YI, Han JI, Wang C, Cooper V, Schwartz K, Engelken T, et al. Case–control study of microbiological etiology associated with calf diarrhea. Vet Microbiol. 2013;166:375–85.

8. Meganck V, Hoflack G, Opsomer G. Advances in prevention and therapy of neonatal dairy calf diarrhea: a systematic review with emphasis on colostrum management and fluid therapy. Acta Vet Scand. 2014;56:75.

9. Thompson RA, Palmer CS, O’Yandley R. The public health and clinical significance of Giardia and Cryptosporidium in domestic animals. Vet J. 2008;177:18–25.

10. Santin M. Clinical and subclinical infections with Cryptosporidium in animals. N Z Vet J. 2013;61:1–10.

11. Oates SC, Miller MA, Hardin D, Conrad PA, Melli A, Jessup DA, et al. Prevalence, environmental loading, and molecular characterization of Cryptosporidium and Giardia isolates from domestic and wild animals along the Central California Coast. Appl Environ Microbiol. 2012;78:8762–72.

12. Silverlås C, Bosaeus-Reineck H, Näslund K, Björkman C. Is there a need for improved Cryptosporidium diagnostics in Swedish calves? Int J Parasitol. 2013;43:155–61.

13. Karanis P, Plutzer J, Hakim NA, Igori K, Nagazewa H, Ongerth J, et al. Molecular characterization of Cryptosporidium from animal sources in Qinghai province of China. Parasitol Res. 2007;101:1575–80.

14. Efstratiou A, Ongerth JE, Karanis P. Waterborne transmission of protozoan parasites: review of worldwide outbreaks—an update 2011–2016. Water Res. 2017;11:14:14–22.

15. Hatam-Nahavandi K, Mohebali M, Mahvi AH, Keshavarz H, Najafian HR, Mirjalali H, et al. Microscopic and molecular detection of Cryptosporidium andersoni and Cryptosporidium xiaoai in wastewater samples of Tehran Province, Iran. Iran J Parasitol. 2016;11:499–506.

16. Budu-Amoako E, Greenwood SJ, Dixon BR, Barkema HW, McClure J. Foodborne illness associated with Cryptosporidium and Giardia from livestock. J Food Prot. 2011;74:1944–55.

17. Ryan U, Hijawi N, Xiao L. Foodborne cryptosporidiosis. Int J Parasitol. 2018;48:1–12.

18. Vermeulen LC, Benders J, Medema G, Hofstra N. Global Cryptosporidium loads from livestock manure. Environ Sci Technol. 2017;51:8663–71.

19. Razakandrainibe R, Costa D, Le Goff L, Lemeteil D, Ballet JJ, Gargala G, et al. Common occurrence of Cryptosporidium hominis in asymptomatic and symptomatic calves in France. PLoS Negl Trop Dis. 2018;12:e006355.

20. Roberts CL, Morin C, Addiss DG, Wahlquist SP, Mshar PA, Hadler JL. Factors influencing Cryptosporidium testing in Connecticut. J Clin Microbiol. 1996;34:2292–3.

21. Chappell CL, Okhuysen PC, Sterling CR, DuPont HL. Cryptosporidium parvum: intensity of infection and oocyst excretion patterns in healthy volunteers. J Infect Dis. 1996;173:232–6.

22. Ryan U, Fayer R, Xiao L. Cryptosporidium species in humans and animals: current understanding and systematic reviews. Parasitol. 2014;141:1667–85.

23. Thompson R, Ash A. Molecular epidemiology of Giardia and Cryptosporidium infections. Infect Genet Evol. 2016;40:315–23.

24. Nichols GL, Chalmers RM, Hadfield SJ. Molecular epidemiology of human cryptosporidiosis. Cryptosporidium: parasite and disease. Vienna: Springer; 2014. p. 81–147.

25. Xiao L. Molecular epidemiology of cryptosporidiosis: an update. Exp Parasitol. 2010;124:80–9.

26. Gong C, Cao XF, Deng J, Li W, Huang XM, Lan JC, et al. Epidemiology of Cryptosporidium infection in cattle in China: a review. Parasite. 2017;24:1.

27. Xiao L, Feng Y. Zoonotic cryptosporidiosis. FEMS Immunol Med Microbiol. 2008;52:309–23.
28. Mueller-Doblies D, Giles M, Elwin K, Smith RP, Clifton-Hadley FA, Chalmers RM. Distribution of Cryptosporidium species in sheep in the UK. Vet Parasitol. 2008;154:214–9.

29. Quílez J, Torres E, Chalmers RM, Hadfield SJ, del Cacho E, Sánchez-Acedo C. Cryptosporidium genotypes and subtypes in lambs and goat kids in Spain. Appl Environ Microbiol. 2008;74:6026–31.

30. Grinberg A, Learmonth J, Kwan E, Pomroy W, Lopez Villalobos N, Gibson I, Widow M. Genetic diversity and zoonotic potential of Cryptosporidium parvum causing foetal diarrhoea. J Clin Microbiol. 2008;46:2396–8.

31. Zintl A, Neville D, Maguire D, Fanning S, Mulcahy G, Smith H, et al. Prevalence of Cryptosporidium species in intensively farmed pigs in Ireland. Parasitology. 2007;134:1575–82.

32. Wells B, Shaw H, Hotchkiss E, Gilray J, Ayton R, Green J, et al. Prevalence, species identification and genotyping Cryptosporidium from livestock and deer in a catchment in the Cairngorms with a history of a contaminated public water supply. Parasit Vectors. 2015;8:66.

33. Garcia-Presedo I, Pedraza-Díaz S, González-Warleta M, Mezo M, Gómez-Bustamante M, Ortega-Mora LM, et al. Presence of Cryptosporidium scrofae, C. suis and C. parvum subtypes IlA16G2R1 and IlA3G1R1 in Eurasian wild boars (Sus scrofa). Vet Parasitol. 2013;196:497–502.

34. Moher D, Liberati A, Tetzlaff J, Altman DG. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. PLoS Med. 2009;6:e100097.

35. DerSimonian R, Laird N. Meta-analysis in clinical trials. Control Clin Trials. 1980;1:177–88.

36. Zahedi A, Phasey J, Boland T, Ryan U. First report of Cryptosporidium species in farmed and wild buffalo from the Northern Territory, Australia. Parasitol Res. 2016;115:1349–53.

37. Wessels J, Wessels M, Featherstone C, Pike R. Cryptosporidiosis in eight-month-old weaned alpacas. Vet Rec. 2013;173:426–7.

38. Alves M, Xiao L, Lemos V, Zhou L, Cama V, da Cunha MB, et al. Occurrence and molecular characterization of Cryptosporidium spp. in mammals and reptiles at the Lisbon Zoo. Parasitol Res. 2005;97:108–12.

39. Néméc K, Sak B, Kvetonová D, Hanzel V, Jenikova M. The first report on Cryptosporidium suis and Cryptosporidium pig genotype II in European wild boars (Sus scrofa) (Czech Republic). Vet Parasitol. 2012;184:122–5.

40. Amer S, Zidan S, Feng Y, Adamu H II, N X, Xiao L. Identity and public health potential of Cryptosporidium spp. in water buffalo calves in Egypt. Vet Parasitol. 2013;191:123–7.

41. Helmy AY, Krücken J, Nöckler K, Samson-Himmelstjerna G, Zes-Gómez-Bautista M, Ortega-Mora LM, et al. Presence of Cryptosporidium in dairy cows, cattle, and deer in a catchment in the Ismailia province of Egypt. Vet Parasitol. 2013;193:15–24.

42. Hribar A. Understanding concentrated animal feeding operations and environmental contamination. Epidemiol Infect. 2009;137:913–21.

43. Jacobson C, Al-Habsi K, Ryan U, Williams A, Anderson F, Yang R, et al. Zoonotic cryptosporidiosis in the UK–challenges for control. J Appl Microbiol. 2010;109:1487–97.

44. Thomson S, Hamilton CA, Hope JC, Katzer F, Mabbott NA, Morrison LJ, et al. Multilocus genotyping of Cryptosporidium parvum infecting domesticated, public water supply. Parasit Vectors. 2015;8:66.

45. Benschop J, Booker C, Shadbolt T, Weston J. A Retrospective cohort study of an outbreak of cryptosporidiosis among veterinary students. Vet Sci. 2017;4:22.

46. Giles M, Chalmers RM, Hadfield SJ, del Cacho E, Sánchez-Acedo C. Cryptosporidium genotypes and subtypes in lambs and goat kids in Spain. Appl Environ Microbiol. 2008;74:6026–31.

47. Grinberg A, Learmonth J, Kwan E, Pomroy W, Lopez Villalobos N, Gibson I, Widow M. Genetic diversity and zoonotic potential of Cryptosporidium parvum causing foetal diarrhoea. J Clin Microbiol. 2008;46:2396–8.

48. Giles M, Chalmers RM. Zoonotic cryptosporidiosis in the UK–challenges for control. J Appl Microbiol. 2010;109:1487–97.

49. Connelly L, Craig B, Jones B, Alexander C. Genetic diversity of Cryptosporidium parvum and Enterocytozoon bieneusi in American mustangs and Chincoteague ponies. Exp Parasitol. 2013;139:24–7.

50. Wessels J, Wessels M, Featherstone C, Pike R. Cryptosporidiosis in eight-month-old weaned alpacas. Vet Rec. 2013;173:426–7.

51. Alves M, Xiao L, Lemos V, Zhou L, Cama V, da Cunha MB, et al. Occurrence and molecular characterization of Cryptosporidium spp. in mammals and reptiles at the Lisbon Zoo. Parasitol Res. 2005;97:108–12.

52. Twooney DF, Barlow AM, Bell S, Chalmers RM, Elwin K, Giles M, et al. Cryptosporidiosis in two alpaca (Lama pacos) holdings in the South-West of England. Vet J. 2008;175:419–22.

53. Helmy AY, Krücken J, Nöckler K, Samson-Himmelstjerna G, Zes-Gómez-Bautista M, Ortega-Mora LM, et al. Presence of Cryptosporidium in dairy cows, cattle, and deer in a catchment in the Ismailia province of Egypt. Vet Parasitol. 2013;193:15–24.
or livestock interface of the Kruger National Park, South Africa. Onderstepoort J Vet Res. 2015;83:a1024.

74. Soltane R, Guyot K, Dei-Cas E, Ayadi A. Prevalence of Cryptosporidium spp. (Eucoccidiorida: Cryptosporiidae) in seven species of farm animals in Tunisia. Parasite. 2007;14:335–8.

75. Geurden T, Goma FY, Siwila J, Phiri IGK, Mwanza AM, Gabriel S, et al. Prevalence and genotyping of Cryptosporidium in three cattle husbandry systems in Zambia. Vet Parasitol. 2006;138:217–22.

76. Wang R, Wang H, Sun Y, Zhang L, Jian F, Qi M, Ning C, Xiao L. Characteristics of Cryptosporidium transmission in preweaned dairy cattle in Henan, China. J Clin Microbiol. 2011;49:1077–82.

77. Wang R, Ma G, Zhao J, Lu Q, Wang H, Zhang L, Jian F, Ning C, Xiao L. Cryptosporidium andersoni is the predominant species in post-weaned and adult dairy cattle in China. Parasitol Int. 2011;60:1–4.

78. Huang J, Yue D, Meng Q, Wang R, Zhao J, Li J, et al. Prevalence and molecular characterization of Cryptosporidium spp. and Giardia duodenalis in dairy cattle in Ningxia, northernwestern China. BMC Vet Res. 2014;10:292.

79. Khan SM, Debnath C, Pramanik AK, Xiao L, Nozaki T, Ganguly S. Molecular characterization and assessment of zoonotic transmission of Cryptosporidium from dairy cattle in West Bengal, India. Vet Parasitol. 2010;171:41–7.

80. Meamar AR, Guyot K, Certad G, Dei-Cas E, Mohraz M, Mohebali M, et al. Molecular characterization of Cryptosporidium isolates from humans and animals in Iran. Appl Environ Microbiol. 2007;73:1033–5.

81. Fotouhi Ardakani R, Fasihi Harandi M, Soleiman Banaei S, Kamyabi H, Pirestani M, Sadraei J, Dalimi A, Zawar M, Vaeznia H. Molecular characterization of Cryptosporidium isolates from humans and bovine using 18S rRNA gene in Shahriar county of Tehran, Iran. Parasitol Res. 2008;103:447–67.

82. Tanriverdi S, Markovic A, Arslan MO, Itik A, Shkap V, Widmer G. Emergence of distinct genotypes of Cryptosporidium parvum in structured by mutation scanning of the 60 kDa glycoprotein gene sequences. Parasitol Res. 2007;100:516–20.

83. Brien E, McInnes L, Ryan U. GP60 genotypes from ’C. andersoni’ and expected finding of feline-specific Cryptosporidium feline in asymptomatic adult cattle in Northern Spain. Parasitology. 2008;135:1613–20.

84. Ferguson C. Quantifying Infectious Pathogen Sources in WA Drinking Water Catchments. Report by ASL Water services group. 2010.

85. Halim NA, Plutzer J, Bakheit MA, Karanis P. First report of Cryptosporidium in dam and diagnosis and genotyping of Cryptosporidium spp. in diarrheic pre-weaned calves in Hokkaido. Vet Parasitol. 2010;169:387–90.

86. Meisner L, Bień A, Certad G, Dei-Cas E, Halama P. Occurrence and molecular identification of Cryptosporidium sp. in diarrheic pre‑weaned calves in Belgium. Parasitology. 2007;134:335–8.

87. Costas JM, Canada N. Molecular characterization of Cryptosporidium isolates from pre‑weaned calves in Spain: is there an actual risk of zoonotic infections? Vet Parasitol. 2011;181:321–4.

88. Al-Mawly JA, Grinberg A, Velanthanthiri N, French N. Cross-sectional study of prevalence, genetic diversity and zoonotic potential of Cryptosporidium parvum cycling in New Zealand dairy farms. Parasit Vectors. 2015;8:240.

89. Guyot K, Bértévens D, Martens C, Cazaert S, Verleysen J, Claerbeaut E. Molecular epidemiology with subtype analysis of Cryptosporidium in calves in Belgium. Parasitology. 2007;134:1981–7.

90. Kvac M, Kovač M, Vitézová J. Age-related and housing-dependence of Cryptosporidium infection of calves from dairy and beef herds in South Bohemia. Czech Republic. Vet Parasitol. 2006;137:202–9.

91. Langkjaer RB, Vigele P, Enemark HL, Maddox-Hyttel C. Molecular and phylogenetic characterization of Cryptosporidium and Giardia from pigs and cattle in Denmark. Parasitology. 2007;134:339–50.

92. Meisner L, Bień A, Certad G, Dei-Cas E, Halama P. Distribution of Cryptosporidium and Giardia isolates from cattle in Hungary. Vet Parasitol. 2007;146:357–62.

93. Ondrackova Z, Kvac M, Vogelova A, Kvetova D, Rost M, Jakubal M. Prevalence and molecular characterization of Cryptosporidium spp. in dairy cattle in South Bohemia, the Czech Republic. Vet Parasitol. 2009;163:141–4.

94. Misic Z, Abe N. Subtype analysis of Cryptosporidium parvum isolates from calves on farms around Belgrade, Serbia and Montenegro, using the 60 kDa glycoprotein gene sequences. Parasitol Res. 2007;103:351–8.

95. Quilez J, Torres E, Chalmers RM, Robinson G, Del Cacho E, Sanchez-Acedo C. Cryptosporidium species and subtype analysis from dairy calves in Spain. Parasitology. 2008;135:1613–20.

96. Cardona GA, de Lucio A, Bailo B, Cano L, de Fuentes I, Carmena D. Unexpected finding of feline-specific Giardia duodenalis assemblage F and Cryptosporidium felis in asymptomatic adult cattle in Northern Spain. Vet Parasitol. 2015;30:258–63.

97. Silverlas C, Blasco-Fenedo I. Cryptosporidium infection in cattle and cows from conventional and organic dairy herds. Epidemiol Infect. 2013;141:529–39.

98. Silverlas C, Náslund K, Björkman C, Mattsson JG. Molecular characterisation of Cryptosporidium isolates from Swedish dairy cattle in relation to age, diarrhoea and region. Vet Parasitol. 2010;169:289–95.

99. Silverlas C, de Verdiere K, Emanuelsen U, Mattsson JG, Björkman C. Cryptosporidium infection in herds with and without calf diarrheal problems. Parasitol Res. 2010;107:1435–44.
116. Bjorkman C, Lindstrom L, Owston C, Ahola H, Troel K, Axen C. Cryptosporidium infections in suckler herd beef calves. Parasitology. 2015;142:1108–14.

117. Uhde FL, Kaufmann T, Sager H, Albini S, Zanoni R, Schelling E, Meylan M. Prevalence of four enteropathogens in the faeces of young diarrhoeic dairy calves in Switzerland. Vet Rec. 2008;163:362–6.

118. Brook EJ, Hart CA, French NP, Christley RM. Molecular epidemiology of Cryptosporidium spp. in cattle in England. Vet J. 2009;179:378–82.

119. Featherstone CA, Giles M, Marshall JA, Mawhinney IC, Holliman A, Pritchard GC. Cryptosporidium species in calves submitted for post-mortem examination in England and Wales. Vet Rec. 2010;167:979–80.

120. Moriarty EM, McEvoy JMV, Lowery CJ, Thompson HP, Finn M, Sheridan JJ, et al. Prevalence and characterisation of Cryptosporidium species in cattle faeces and on beef carcasses at slaughter. Vet Rec. 2005;156:165–8.

121. Smith RP, Chalmers RM, Mueller-Doblies D, Clifton-Hadley FA, Elwin K, Coklin T, Farber J, Parrington L, Dixon B. Prevalence and molecular characterization of Cryptosporidium species in dairy calves in 11 farms in Prince Edward Island, Canada. Vet Parasitol. 2009;160:323–6.

122. Santín M, Trout JM, Xiao L, Zhou L, Greiner E, Fayer R. Prevalence of species and genotypes in calves submitted for post-mortem examination in England and Wales. Vet Rec. 2010;167:979–80.

123. Santín M, Trout JM, Greiner E, Fayer R, Santín M, Dargatz D. Species of Cryptosporidium in pre-weaned kids in a dairy goat farm in western France. Vet Parasitol. 2013;192:268–72.

124. Pritchard GC, et al. Prevalence and characterization of Cryptosporidium spp. in dairy cattle in the New York City Watershed. Parasitol Res. 2009;107:317–25.

125. Liu A, Zhang J, Zhao J, Zhao W, Wang R, Zhang L. The first report of Cryptosporidium in horses with diarrhea and multilocus subtype analysis. Parasit Vectors. 2015;8:483.

126. Galuppi R, Piva S, Castagnetti C, Iacono E, Tanel S, Pallaver F, et al. Epidemiological survey on Cryptosporidium in an Equine Perinatology Unit. Vet Parasitol. 2015;210:10–8.

127. Chalmers AM, Thomas AL, Butler BA, Davies Morel MCG. Identification of Cryptosporidium parvum genotype 2 in domestic horses. Vet Rec. 2002;150:49–50.

128. Burton AJ, Nydam DV, Dearen TK, Mitchell K, Bowman DD, Xiao L. The prevalence of Cryptosporidium, and identification of the Cryptosporidium horse genotype in foals in New York State. Vet Parasitol. 2010;174:139–44.

129. Vitovec J, Hamadejova K, Landova L, Kvac M, Kvetonova D, Sak B. Occurrence of Cryptosporidium in pre- and post-weaned pigs in Australia. Exp Parasitol. 2008;119:418–21.

130. Ryan UM, Samarasinghe B, Read C, Buddle JR, Robertson ID, Thompson RCA. Identification of a novel Cryptosporidium genotype in pigs. Appl Environ Microbiol. 2003;69:3970–4.

131. Vitovec J, Hamadejova K, Landova L, Kruc M, Kvetonova D, Sak B. Prevalence and pathogenicity of Cryptosporidium suis in pre- and post-weaned pigs. J Vet Med B. 2006;53:239–43.

132. Kvač M, Sak B, Hanzlíková D, Katoliová J, Kvetová D. Molecular characterization of Cryptosporidium isolates from pigs at slaughterhouses in South Bohemia, Czech Republic. Parasitol Res. 2009;104:425–8.

133. Kvač M, Hanzlíková D, Sak B, Kvetová D. Prevalence and age-related infection of Cryptosporidium suis, C. muris and Cryptosporidium pig genotype II in pigs on a farm complex in the Czech Republic. Vet Parasitol. 2009;160:319–22.

134. Německ J, Sak B, Kvetová D, der Kvetová N, Rost M, Cama VA, Kvač M. Occurrence of Cryptosporidium suis and Cryptosporidium scotti on commercial swine farms in the Czech Republic and its associations with age and husbandry practices. Parasitol Res. 2013;112:1143–54.

135. Petersen HH, Jannin W, Katakan KM, Meier H, Thamsborg SM, Anders Dalsgaard A, et al. Cryptosporidium and Giardia in Danish organic pig
farms: seasonal and age-related variation in prevalence, infection intensity and species/genotypes. Vet Parasitol. 2015;214:29–39.

159. Featherstone CA, Marshall JA, Giles M, Sayers AR, Pritchard GC. Cryptosporidium species infection in pigs in East Anglia. Vet Rec. 2010;166:51–2.

160. Fiuza VRS, Gallo SSM, Frazao-Teixeira E, Santin M, Fayer R, Oliveira FCR. Cryptosporidium pig genotype II diagnosed in Pigs from the State of Rio de Janeiro. Brazil J Parasitol. 2011;17:146–7.

161. García-Presedo I, Pedraza-Díaz S, González-Warleta M, Mezo M, Gómez-Bautista M, Ortega-Mora LM, et al. The first report of Cryptosporidium bovis, C. ryanae and Giardia duodenalis sub-assemblage A-II in roe deer (Capreolus capreolus) in Spain. Vet Parasitol. 2013;197:658–64.

162. Wang Y, Feng Y, Cui B, Jian F, Ning C, Wang R, Zhang L, Xiao L. Cervine genotype is the major Cryptosporidium genotype in sheep in China. Parasitol Res. 2010;106:341–7.

163. Li P, Cai J, Cai M, Wu W, Li C, Lei M, et al. Distribution of Cryptosporidium species in Tibetan sheep and yaks in Qinghai, China. Vet Parasitol. 2016;215:58–62.

164. Yang R, Jacobson C, Gardner G, Car michael I, Campbell AJD, Ng-Hublin J, et al. Longitudinal prevalence, oocyst shedding and molecular characterisation of Cryptosporidium species in sheep across four states in Australia. Vet Parasitol. 2014;200:50–8.

165. Ryan UM, Bath C, Robertson I, Read C, Elliot A, McInnes L, Traub R, Besier B. Sheep may not be an important zoonotic reservoir for Cryptosporidium and Giardia parasites. Appl Environ Microbiol. 2005;71:4992–7.

166. Yang R, Jacobson C, Gordon C, Ryan U. Prevalence and molecular characterisation of Cryptosporidium and Giardia species in pre-weaned sheep in Australia. Vet Parasitol. 2009;161:19–24.

167. Yang R, Gardner GE, Ryan U, Jacobson C. Prevalence and pathogen load of Cryptosporidium and Giardia in sheep faeces collected from saleyards and in abattoir effluent in Western Australia. Small Ruminant Res. 2015;130:216–22.

168. Imre K, Luca C, Costache M, Sala C, Morar A, Moraroiu S, et al. Zoonotic Cryptosporidium parvum in Romanian newborn lambs (Ovis aries). Vet Parasitol. 2013;191:119–22.

169. Díaz P, Quílez J, Chalmers RM, Panadero R, López C, Sánchez-Acedo C. Genotype and subtype analysis of Cryptosporidium isolates from calves and lambs in Galicia (NW Spain). Parasitology. 2010;137:1187–93.

170. Pritchard GC, Marshall JA, Giles M, Muller-Doblies D, Sayers AR, Marshall RN, et al. Cryptosporidium species in lambs submitted for diagnostic postmortem examination in England and Wales. Vet Rec. 2008;163:688–9.

171. Fiuza VR, Cosendey RI, Frazão-Teixeira E, Santin M, Fayer R, Oliveira FC. Molecular characterization of Cryptosporidium in Brazilian sheep. Vet Parasitol. 2011;175:360–2.

172. Paz e Silva FM, Lopes RS, Saraiva Bresciani KD, Talamini Amarante AF, Araujo JP Jr. High occurrence of Cryptosporidium ubiquitum and Giardia duodenalis genotype E in sheep from Brazil. Acta Parasitol. 2014;59:193–6.

173. Zucatto AS, Aquino MCC, Inácio SV, Figueiredo RN, Pierucci JC, Perri SHV, et al. Molecular characterisation of Cryptosporidium spp. in lambs in the South-Central region of the State of São Paulo. Arq Bras Med Vet Zootec. 2015;67:441–6.

Publisher’s Note
Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

• fast, convenient online submission
• thorough peer review by experienced researchers in your field
• rapid publication on acceptance
• support for research data, including large and complex data types
• gold Open Access which fosters wider collaboration and increased citations
• maximum visibility for your research: over 100M website views per year

Learn more biomedcentral.com/submissions