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Infection, colonization and shedding of *Campylobacter* and *Salmonella* in animals and their contribution to human disease: A review

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Abstract

Livestock meat and offal contributes significantly to human nutrition as sources of high-quality protein and micronutrients. Livestock products are increasingly in demand, particularly in low- and middle-income settings where economies are growing and meat is increasingly seen as an affordable and desirable food item. Demand is also driving intensification of livestock keeping and processing. An unintended consequence of intensification is increased exposure to zoonotic agents and a contemporary emerging problem is infection with *Campylobacter* and *Salmonella* spp. from livestock (avian and mammalian), which can lead to disease, malabsorption and undernutrition through acute and chronic diarrhoea. This can occur at the farm, in households or through the food chain. Direct infection occurs when handling livestock and through bacteria shed into the environment, on food preparation surfaces or around the house and surroundings. This manuscript critically reviews *Campylobacter* and *Salmonella* infections in animals, examines the factors affecting colonization and faecal shedding of bacteria of these two genera as well as risk factors for human acquisition of the infection from infected animals or environment and analyses priority areas for preventive actions with a focus on resources-poor settings.

Keywords: *Campylobacter* spp.; diarrhoea; foodborne pathogens; *Salmonella* spp.; zoonosis

Impact

1. Hosts, environments, bacteria and management-related factors determine *Campylobacter* and *Salmonella* species colonization in domestic and non-domestic animals with subsequent shedding of bacteria into the environments.
2. In resource-poor settings, infections with *Campylobacter* and *Salmonella* spp. are more likely transmitted through extended human-animal interactions, poor sanitation and hygiene services, unlike in areas with improved services where the infections are mostly acquired from contaminated animal-source foods.
3. Sustained exposure of susceptible humans to colonized animals predisposes humans to *Campylobacter* and *Salmonella* spp. infections; however, this interaction does not always result in clinical disease and/or infection in humans.

1. Introduction

Human campylobacteriosis caused by infection with different species of *Campylobacter* and non-typhoid salmonellosis due to infection with *Salmonella enterica* subsp. *enterica*, are amongst the top causes of foodborne gastroenteritis worldwide (Kirk et al., 2015). *Campylobacter* and non-typhoid Salmonellae are recurrently isolated from different types of animal-source foods, with most of them implicated in foodborne disease outbreaks (Friesema et al., 2014; Gharieb et al., 2015; Marotta et al., 2015; Olobatoke & Mulugeta, 2015; Taylor et al., 2013).

Campylobacter and *Salmonella* spp. infections in high-income countries are mostly acquired through consumption of the contaminated food of animal origin (Dallman et al., 2016; Taylor et al., 2013;), and the most common source of infection is poultry (EFSA, 2015). In contrast, in low- and middle-income countries (LMICs), the main sources of infection appear to be contaminated environment, food, water and close contact with infected live animals (Coker et al., 2002; El-Tras et al., 2015; Lyimo et al., 2016). Clinically and silently infected animals harbour and shed bacteria in the environment and act as a source of infection to uninfected animals and susceptible humans through direct contact or indirectly through faecal-contaminated environments (Gopinath et al., 2012). Several factors including physiological stress and concurrent infection can aggravate prolonged infection and faecal shedding in infected animals, with subsequent environmental contamination (Cummings et al., 2009). Gastrointestinal microbiota plays a large role in the control of pathogenic microbes and a minor disturbance in normal microflora may result in even a pathogen of low virulence colonizing the gastrointestinal tract with subsequent faecal shedding (Gopinath et al., 2012).

This paper discusses the clinical signs of *Campylobacter* and *Salmonella* spp. infections in domestic animals. It examines the role of normal gastrointestinal flora and possible consequences associated with its imbalance. The factors predisposing animals to *Campylobacter* and *Salmonella* spp. colonization and subsequent faecal shedding are also reviewed. In addition, this paper explores the contribution of infected animals leading to human infections and the critical components which facilitate the movement of these bacteria from infected animals to humans.

2. Methods

A search was conducted to find the studies which cover the subject areas tackled by this review: "*Salmonella* infections", "*Salmonella* colonization", "*Salmonella* shedding", "*Campylobacter* infections", "*Campylobacter* colonization", "*Campylobacter* shedding", and "Non-typhoid *Salmonella*". Searches based on these subject areas in BioOne, CAB ebook, CAB abstract and Web of science databases, yielded 2766 results from 7th to 9th January 2019. The article titles were assessed for relevance in relation to infection, colonization and shedding in domestic and non-domestic animals and the terms "non-typhoid *Salmonella*" which eliminated 1924 titles. The remaining 842 publications were examined through thorough assessment of the abstracts whereby 673 articles were eliminated and the remaining 169 articles were included in the review. The first exclusion criteria was the host whereby studies conducted in insects, non human primates, acquatic animals and *in vitro* (cell culture) were not included in this review. All studies related to clinical signs of diseases in animals other than domestic animals, treatment of diseases, vaccine testing and studies conducted in more specialised production systems were also not included in the review. Google search, shelf literature and the reference lists of selected publications were used to source additional information relavant to the sub-topics under review.

3. *Campylobacter* infection in domestic animals

Campylobacter spp. are often isolated from clinically healthy domestic animals (Corry, 2014; Döhne et al., 2012; Khan et al., 2013; Marotta et al., 2015; Rahimi et al., 2017). In most studies carried out, *C. jejuni* is commonly isolated followed by *C. coli* (Anderson et al., 2012; Mdegela et al., 2011; Nonga & Muhairwa, 2010). The chicken gastrointestinal tract, especially the caecum, is highly colonized by *Campylobacter*, particularly *C. jejuni* and *C. coli* (Rosenquist et al., 2006). The ability of these bacteria to grow at 42 ^{0}C reflects their adaptation to the gastrointestinal tract of birds (Crushell et al., 2004; Stanley & Jones, 2003). Although *Campylobacter* is considered commensal in both domestic and non-domestic birds, *C. jejuni* infection in intensively raised, modern, fast-growing breeds of chickens may elicit a strong inflammatory response leading to diarrhoea (Humphrey et al., 2014).

Campylobacter fetus subspecie *fetus* causes clinical campylobacteriosis in cattle and sheep and C. *fetus* subspecie *veneralis* causes clinical disease in cattle only. Clinical disease in cattle and sheep is characterized by infertility, abortion and foetal death, (Debruyned et al., 2008; Schulze et al., 2006; Truyers et al., 2014). However, *C. jejuni* has been also implicated in sheep abortion (Mannering et al., 2006). Cattle infected with species other than *C. fetus* remain asymptomatic and continue to shed bacteria through faeces (Abley et al., 2011). *C. jejuni, C. coli* and *C. upsaliensis* are commonly found in clinically asymptomatic as well as diarrhoeic and vomiting dogs and cats. Experimentally inoculated dogs do not show clinical signs of disease, suggesting a primary or opportunistic nature of *Campylobacter* infection in dogs and cats predisposed to several factors such as concurrent virus infections and stress (Macartney et al., 1988; Olson & Sandstedt, 1987; Sokolow et al., 2005).

4. *Salmonella* infection in domestic animals

More than 1,454 serotypes of *Salmonella enterica* subsp. *enterica* depend on warm-blooded animals and humans for habitat (Brenner et al., 2000; Grimont & Weill, 2007). Although almost all species of domesticated animals harbour *Salmonella*, poultry under intensive production systems, are represented more frequently (Akbarmehr, 2011; Paião et al., 2013, Vinueza-Burgos et al., 2016). Infections in birds by avian-adapted serovars, *S.* Pullorum and non-avian adapted *S.* Enteritidis result in clinical disease primarily in chicks, and in all ages in case of avian-adapted *S.* Gallinurum infections (Gast, 2013; Shivarprasad & Barrow, 2013). The faeco-oral is the main route of transmission with the exception of *S.* Enteritidis which can also be transmitted transovarially (Gast, 2013; Lutful Kabir, 2010; Ricke & Gast, 2014; Saha et al., 2012). The vertically or horizontally infected survivor chicks can remain carriers until the adult stage, infecting subsequent eggs and continuing to shed bacteria in the environment (Ishola, 2009; Takata et al., 2003; Van Immerseel et al., 2004).

Salmonella are often isolated from healthy domestic pigs (Parada et al., 2017; Stevens & Gray, 2013). Occasionally, *Salmonella*-infected pigs may develop signs from transient fever to severe disease depending on strain virulence, immune resistance, route of infection and dose (Alsop, 2005; Schwartz, 1999). A wide range of serovars have been isolated in domestic ovines but only serovars Brandenburg, Arizonae and Typhimurium cause gastroenteritis, pneumonia and death, and sheep-specific serovar Abortusovis have been reported to cause epidemic abortion in healthy looking ewes during the third trimester, stillbirths, premature and nonviable lambs (Uzzau, 2013).

Cattle of all ages can suffer from clinical salmonellosis characterized by diarrhoea, but most serious disease occurs in newborns, young calves 2-6 weeks of age, and cows approaching calving. Bovine salmonellosis is mostly caused by serovars Newport, Typhimurium, Infantis, 4,5,12:i:-, Agona, Montevideo, Anatum, Mbadaka, Enteritidis and cattle-adapted serovar Dublin (Cummings et al., 2012; Ragione et al., 2013). Occasionally, adult cattle become carriers following recovery from the disease and continuously or intermittently shed pathogens through faeces for years or lifelong (Ragione et al., 2013).

5. Animal gastrointestinal microbiome

Gastrointestinal microbes contribute to the breakdown of food components and host nutrient acquisition through a symbiotic association with host and immune system education which enables the host to differentiate between normal flora and harmful bacteria (Callaway et al., 2014; Hanning & Diaz-Sanchez, 2015). Well-developed normal flora protects the host through creating gastrointestinal resistance environments which prevent external pathogenic bacteria from colonizing the gut (Han et al., 2017; Monack, 2012). The microbial community in the gastrointestinal tract stimulates production, maintenance of normal structure and functioning of the mucosal lining, hence render the animal protection from pathogenic bacteria (Hanning & Diaz-Sanchez, 2015). Also, some gut commensals produce metabolites which inhibit growth of pathogenic organisms through disrupting intercellular metabolisms (Jacobson et al., 2018).

Stress factors, including starvation, changes in ration, overcrowding, age, pregnancy, parturition, intercurrent non-infective disease, and exposure to antibiotics and anthelmintics, may result in gut microflora disturbance and disbiosis which leads to pathogenic bacteria gut colonization and faecal excretion (Daniels et al., 1993). Some bacterial infections result in composition changes in commensal microbiota through depopulation of beneficial or competing bacteria which enable successful colonization of the gut by pathogenic organisms (Argüello et al., 2018). The detection of pathogenic bacteria in faeces of asymptomatic animals is referred to as shedding and is an indication of whole or partial gastrointestinal tract bacterial colonization (Ishola, 2009). Short duration faecal bacteria shedding, especially observed with bacteria which do not infect the gut is not considered as gut colonization (Barrow et al., 1988).

6. *Campylobacter* colonization and shedding in ruminants and suids

Campylobacter is frequently isolated in clinically healthy animals and, therefore, is considered as normal flora in domestic and non-domestic animals (Cummings et al., 2018;

Dong et al., 2014; Mdegela et al., 2011; Sproston et al., 2011). Host factors including species, age and physiological status determine the level of *Campylobacter* prevalence and shedding in animals. Higher *Campylobacter* faecal shedding was observed in cattle than in sheep exposed to the same environmental conditions (Sproston et al., 2011). A study conducted in beef herds reported nearly 100 times higher *Campylobacter* count in faecal samples from calves born free from infection at 60 days of age compared to adult animals (Stanley et al., 1998). However, no significant difference in shedding was observed between calves and adult dairy herds kept under high hygienic conditions (Merialdi et al., 2015). Stresses associated with lambing in ewes, calving and lactation in cattle and large herd sizes also increase *Campylobacter* prevalence and shedding (Grove-White et al., 2010; Stanley et al., 1998;). Feed type may alter the gastrointestinal microbiota which in turn impact the rate of colonization and faecal shedding of *Campylobacter*. Feeding pigs with a diet containing medium-chain fatty acids, lactic acid and oregano oil was reported to reduce the recovery rate from faecal and intestinal contents (Rasschaert et al., 2016).

Temporal variation in *Campylobacter* prevalence and shedding occurs in various animal species and under different management systems. The highest peak in cattle and sheep in temperate countries has been reported during the summer months (Grove-White et al., 2010). During summer, *Campylobacter* faecal prevalence is higher in grazing than in housed dairy cattle, the variations were accounted for by the different types of feed eaten by the two herd categories which contribute to change in the gut microbial ecosystem (Grove-White et al., 2010). However, a study conducted in Italy revealed double peaks of *Campylobacter* faecal shedding in dairy cattle kept in-house throughout the year without a change in diet and water supply, suggesting a weak association between change in diets and seasonal variation in bacterial shedding (Merialdi et al., 2015). In Hungary, seasonal variation presented a different picture whereby higher *Campylobacter* prevalence in cattle, poultry and pigs has been observed in colder autumn and winter months than in summer (Schweitzer et al., 2011).

7. *Campylobacter* colonization and shedding in birds

Birds are considered to be the primary reservoirs of *Campylobacter* spp. *Campylobacter* in chickens have been isolated from the gastrointestinal tract (Gomes et al., 2006; Jacob et al., 2011), mature and immature ovarian follicles (Cox et al., 2005); liver, spleen, gallbladder and thymus (Cox et al., 2006; Schmid et al., 2005; Simaluiza et al., 2015). *Campylobacter* spp. are also recorded in non-domestic birds including blackbirds, house sparrows, tree sparrows and crows which continue to maintain the bacteria in the ecosystem (Hald et al., 2016; Mdegela et al., 2006; Taff & Townsend, 2017). However, most of the strains found in non-domestic birds are host specific, hence, of less public health importance (Griekspoor et al., 2013).

Colonization of the gastrointestinal tract by *Campylobacter* in chickens is rapid and followed by abrupt faecal excretion of bacteria (Van Gerwe et al., 2005). Seventy percent of one-day-old chicks flock started shedding bacteria 48 hours post-exposure with the proportion of shedders dropping progressively, while 12.5% remained chronic shedders in the absence of repeated exposure (Achen et al., 1998). Carrier, non-shedding birds may become shedders under a range of circumstances including stress and changes in diet. The age at exposure in chickens determines the post exposure commencement of *Campylobacter* faecal shedding. Post-exposure faecal shedding occurs after 2-3 days in chickens exposed at an older age (≥21 days) compared to exposure at a young age (0-14 days) which may delay shedding up to 49 days (Yano et al., 2014). The proportion of birds shedding *Campylobacter* in faeces depends on the age and specie of the bird. A study conducted in broilers under semi-intensive systems reported an increase in *Campylobacter* prevalence from 20% in week 5 to 88% in week 11 of age, after that the prevalence averaged 40% until week 63 (Colles et al., 2011). In free-range ducks, the opposite was observed whereby faecal shedding was reported to be significantly higher in adult ducks than in ducklings (Nonga & Muhairwa, 2010).

The interaction and alteration of the mechanical and immunological line of defence by chemical and other microorganisms affects the extent of *Campylobacter* colonization in birds. The penetration of the gastrointestinal mucus layer by *Campylobacter* is facilitated by mucin which is a component of mucus and has *Campylobacter* chemoattractant properties. The coliform bacteria, including *Lactobacilli,* frequently isolated during the entire period of chick growth as observed by Achen et al. (1998), inhibit *Campylobacter* gut colonization by competitive utilization of mucin as a growth substrate (Mead, 2002). Feeding chickens with a diet containing xylanases decreases mucus viscosity and hence, inhibits *C. jejuni* gastrointestinal translocation and colonization (Fernandez et al., 2000). Also, concurrent infection of chickens with the infectious bursal disease virus and *Campylobacter* results in increased colonization, faecal shedding and reduce clearance of the later in chickens through host immunosuppression which is a normal outcome of infections cause by the former (Li et al., 2018; Subler et al., 2006). The systemic immune response in chickens towards *Campylobacter* infection in resistant genetic lines is characterized by apoptosis and cytochrome c release from mitochondria which is lacking in susceptible genetic lines (Li et al., 2012). The presence of immune responses indicates the ability of some chicken genetic cell lines to tolerate *Campylobacter* infection which can be exploited through breeding to produce *Campylobacter*-resistant chicken genetic lines.

Biosecurity practices on poultry farms have an impact on *Campylobacter* prevalence in the flock. Poultry farms with a higher biosecurity score are found to have low *Campylobacter* infection prevalence compared to farms with a low biosecurity score (Smith et al., 2016). Nevertheless, in practical terms, it is difficult to attain a level which is considered appropriate to overcome the problem. Other factors including partial depopulation, slaughtering the birds in summer and autumn period and recent bird mortality in the flock are key factors for *Campylobacter* colonization at slaughter age (Lawes et al., 2012).

8. *Salmonella* colonization and shedding in ruminants and suids

Salmonella serovars are often isolated in asymptomatic cattle, sheep, pigs, and non-domestic ruminants and suids (Afema et al., 2016; Cummings et al., 2016; Eguale et al., 2016; Love et al., 2017; Zishiri et al., 2016). The magnitude and duration of colonization and shedding of *Salmonella* in animals varies along the different stages of infection or carriage and not all infected animals shed *Salmonella* in faeces continuously (Donoghue et al., 2006). The age of the animal is the important factor in prediction of shedding duration in cattle whereby adult can shed bacteria for up to 391 days post infection compared to 30 days observed in calves (Cummings et al., 2009). Pigs infected with *S.* Derby or detected as *Salmonella* positive at 10 weeks of age shed bacteria in faeces for a longer duration compared to pigs infected with other serovars or detected as *Salmonella* positive at 12 weeks of age (Pires et al., 2014).

The physiological status of an animal determines the rate of *Salmonella* faecal shedding in pigs. The rate of *Salmonella* shedding through faeces is relatively low in sows during gestation, around farrowing and during lactation but increases significantly in the first seven days post weaning (Nollet et al., 2005). The increase in faecal shedding rate is associated with stresses resulting from reproductive hormonal changes after lactation ceases. Increase in catecholamine production mostly observed during stress conditions results in inhibition of gastric acid production which favours *Salmonella* colonization with subsequent faecal shedding (Schwartz, 1999). Also, cortisol, a glucocorticoid hormone produced during stress has immunosuppressive effects which favour the intracellular proliferation of *Salmonella* in macrophages with subsequent colonization in carrier animals (Verbrugghe et al., 2011).

The types and particle size of feeds have synergistic effects on *Salmonella* shedding in animals. Pigs fed with diets consisting of small-particle pellets shed more *Salmonella* than their counterparts fed with larger-size pellet diets and mash types of diet singly or in combination (Lebel et al., 2017). Coarse feeds stimulate the release of gastric acid resulting in lowered stomach pH which creates an unfavourable environment for *Salmonella* survival (Mikkelsen et al., 2004). Also, the combination of medium-chain fatty acids, lactic acid and oregano oil or organic acids, phytochemicals and a permeabilizing complex in feeds significantly reduce *Salmonella* faecal shedding in pigs (Rasschaert et al., 2016; Ruggeri et al., 2018).

In most temperate countries, *Salmonella* faecal shedding in cattle is observed more frequently during the summer than other periods of the year (Edrington et al., 2004; Hanson, 2015). However, in studies conducted in United States, no significant seasonal variations were observed in samples collected in harvest-ready feedlots and poorly productive culled beef and dairy cattle (Brichta-Harhay et al., 2011, Kunze et al., 2008) . High bacterial shedding during summer is not only reported in domestic animals but also in wild pigs (Cummings et al., 2016), and correspond with an increase in *Salmonella* infections in humans (Cummings et al., 2012). Hot conditions as observed in summer in temperate areas favour pathogen survival and virulence and is associated with seasonal changes in human behaviour which increase the interactions between pathogens and humans (Ravel et al., 2010).

Studies conducted in pigs reported genetic control over *Salmonella* spp. colonization and faecal shedding. The expression, and single nucleotide polymorphisms, of some genes were found to have a direct association with *Salmonella* shedding and colonization in pigs (Ainslie-Garcia et al., 2018; Kommadath et al., 2014; Uthe et al., 20110. Exploitation of links between *Salmonella* faecal shedding and host genetic variation is a breakthrough towards production of animals resistant to *Salmonella* infection through marker-assisted breeding, hence improving food safety.

9. *Salmonella* colonization and shedding in birds

Salmonella colonization in birds is not restricted to the gastrointestinal tract but also includes extra-gastrointestinal organs including the liver, spleen, ovaries, oviducts and muscles (Ainslie-Garcia et al., 2018; Aragaw et al., 2010; Babu et al., 2018; Gast et al., 2016). Wild birds also become infected and high mortality may be encountered in infections caused by some genotypes (Hughes et al., 2010). Migratory birds believed to be the reservoir of *Salmonella* spp. infections to human, and a similar strain of *Salmonella bongori* 48:z_{35}:–, has been isolated from migratory birds and humans in Italy (Foti et al., 2009). The physiological condition of birds, including starvation, affects *Salmonella* invasion of intestinal tissues. Gastrointestinal tissue colonization and faecal shedding in chickens experimentally exposed to *S.* Enteritidis is higher in food-deprived than in well-fed chickens (Holt et al., 2006, Moore & Holt, 2006). The effect of feed withdrawal on *Salmonella* gastrointestinal colonization and faecal shedding has public health implications as most farms withdraw feed from chickens prior slaughtering which may result in increased in carcass contamination during slaughter. The physical form of the diet and additives significantly affects the rate of *Salmonella* colonization and shedding in chickens. *S.* Enteritidis-infected chickens fed on finely milled diets mixed with whole wheat grains cleared bacteria from caecal contents and liver at a higher rate and had lower cloacal swab recovery than chickens fed with fine or coarse ground feeds under experimental conditions (Ratert et al., 2014). Inclusion of various chemicals additives in poultry feeds reduce *Salmonella* in gastrointestinal tract and extra-gastrointestinal organs colonization and faecal shedding in chickens (Adhikari et al., 2017; Adhikari et al., 2018; Rattanawut et al., 2017). Also, *Lactobacillus plantarum* given as a probiotic to chicks has proven successful in reducing *Salmonella* colonization mediated by colon-induced intestinal barrier disruption through regulating expression of tight junction genes and inflammatory responses (Wang et al., 2018).

Salmonella colonization in chickens is complex and not much is known regarding the pathogen-related determinants of gut colonization. Chicken-isolated *S.* Typhimurium, Enteritidis, Heidelberg, Hadar and Kentucky possess genes encoding adhesins, flagellar proteins, Type III secretion systems (T3SS), iron acquisition systems, and antibiotic and metal resistance genes that may account for their colonization capability and persistence in chickens (Dhanani et al., 2015). However, haemagglutination, motility and virulence-associated plasmids have been tested and found nonessential in *Salmonella* gut colonization in chickens (Barrow et al., 1988). Also, the role played by the genes encoding fimbrial units in gut colonization have been examined in *S.* Enteritidis whereby only plasmid-encoded fimbriae (*faeA*) gene was found to have an association with *Salmonella* caecal colonization in chickens (Clayton et al., 2008).

Poultry husbandry systems which allow expression of normal behaviours in chickens accompanied by low stocking density decrease the gut and extra-gastrointestinal organs *Salmonella* colonization. The gut and extra-gastrointestinal organs of the chicken kept at low stocking density in colony cages enriched with perches are less colonized by *Salmonella* as compared to those kept in conventional cages at high stocking density (Gast et al., 2016). This trend of colonization and shedding of chickens in relation to type of cages and stocking density may vary depending on the *Salmonella* serovar infecting the birds (Gast et al., 2017). Access of broilers to non-starch polysaccharide, as seen in litter-floored houses, stimulates the gizzard and proventriculus mechanically and acts as a vehicle for competitive exclusive microorganisms against *Salmonella* reducing bacterial colonization (Santos et al., 2008). However, no difference was observed in *Salmonella* colonization among chickens with high and low diversity of intestinal microbiota (Nordentoft et al., 2011).

10. Public health risks associated with animals colonised and shedding *Campylobacter* and *Salmonella*

Infected domestic and non-domestic animals are potential sources of human *Campylobacter* and *Salmonella* infections. Human campylobacteriosis and salmonellosis acquired from animals colonized and shedding *Campylobacter* and *Salmonella* can be categorized into three types: (i) infections acquired from the consumption of contaminated animal products such as meat or eggs (Bertasi et al., 2016; Marshall et al., 2018; Nielsen et al., 2006; Schildt et al., 2006) (ii) infections acquired from close contact with infected animals (Behravesh et al., 2014; Gaffga et al., 2012; Gras et al., 2013); and (iii) infections acquired from environments contaminated with faeces from infected animals shedding bacteria. Although the environment is the main source of *Campylobacter* and *Salmonella* contamination of animal foods due to unhygienic handling, the potential of accidental intestinal contents spillage and extra-gastrointestinal colonization as a source of contamination should not be underestimated (Humphrey & Williams, 2017). The extended interactions between human and animals mostly observed with pet animals and their owners, extensive animal husbandry, animal handlers and wildlife habitat encroachment predispose humans to animal-associated infections (Afema & Sischo, 2016; Behravesh et al., 2014; Holmberg et al., 2015). Animals shedding *Campylobacter* and *Salmonella* contaminate environments including soil, manure, aquatic environments and water sources which increase the risk of humans acquiring infection when hygiene practices are not well-observed (Whiley et al., 2013) (Table 1).

However, not all strains found in animals are of equal public health importance. *S.* Typhimurium Phage types DT2 and DT99 appear to be specific to pigeons, phage types DT8 and DT46 adapted to ducks and DT40 to wild birds (Helm et al., 2004; Rabsch et al., 2002; Rabsch, 2007). The analysis of diverse strains of *Campylobacter jejuni* from a wide range of domestic ruminants, pigs, birds, dogs, cats and wild birds by multi-locus sequence typing (MLST) demonstrated that clonal complex (CC) 179, sequence type (ST) 637 and 1341 were found only in pigeons and gulls (Ogden et al., 2009). In Gambia, clonal differences in *Salmonella* among children and animals were reported in households with extended human-animal interactions which suggests predominance of human-related source of infections as compared to animal source (Dione et al., 2011).

10.1. Sources of infections related to foods of animal origin

Animals infected with and shedding *Campylobacter* and *Salmonella* are major sources of meat, milk and egg contamination (Cox et al., 2012; Gast et al., 2013; Nollet et al., 2005;

Schildt et al., 2006). Isolation of *Campylobacter* and *Salmonella* is common in animal-source food products including poultry meat (Anihouvi et al., 2013; Bertasi et al., 2016; Inns et al., 2015; Suzuki & Yamamoto, 2009; Trongjit et al., 2017). As a result, eating raw or undercooked meat especially from poultry (Colette et al., 2018; Doorduyn et al., 2010; WHO, 2012) and drinking unpasteurized milk (Burakoff et al., 2018; EFSA; 2015; Studahl & Andersson, 2000; Taylor et al., 2013) are the most important risk factors for human *Campylobacter* and *Salmonella* infections of animal origin (Table 1). The potential sources of contaminated animal products include bacterial extra-gastrointestinal colonization, intestinal contents spillage during evisceration, environmental contamination during processing and transportation and cross contaminations among carcases during food processing (Anihouvi et al., 2013; WHO, 2012; Wilfred et al., 2012; Simaluiza et al., 2015).

Animal food products are implicated in human *Salmonella* infection outbreaks related to local and multinational food distribution networks (EFSA & ECDP, 2017; Dallman et al., 2016; Zenner et al., 2014), and international in-flight catering (Rebolledo et al., 2014). The isolation of *Campylobacter* strains from chicken carcases similar to those frequently isolated in humans is not uncommon and signifies the importance of animals in human infections (Devane et al., 2013; Nielsen et al., 2006; Stone et al., 2013). Offal are potential sources of affordable animal-source food which can contribute sinificantly to nutrition security in resource-poor settings (Williams, 2007). Despite its importance, preparation of offal should be accompanied by thorough cooking especially intestines as they may harbour a large number of gastrointestinal pathogens (Humphrey & Williams, 2017). Frequent exposure to raw meat, particularly observed in kitchen, butchery and slaughterhouse workers, predispose humans to *Campylobacter* and *Salmonella* infections originating from animals (Table 1). Therefore, consumption of contaminated animal products is not the only predisposing factor for acquiring infections of animal origin (Doorduyn et al., 2010). The complex surface attachment mechanism (Nguyen et al., 2012), and effective adaptation to environmental changes (Humphrey, 2004; Spector & Kenyon, 2012) demonstrated by *Campylobacter* and *Salmonella*, respectively, make these bacteria highly successful foodborne pathogens. Infection acquired from contaminated animal-source food can be prevented through discouraging eating raw or insufficiently cooked food and through adequate cooking and proper hygiene practices.

Table 1: Risk factors associated with live animals, animal products and environmental derived human *Salmonella* and *Campylobacter* infections

	Risk factor	Example	References
1	Unhygienic food handling	• Poor hand washing • Poor hygienic conditions at slaughterhouse and butcheries • Improper storage facilitating bacteria multiplication • Safety of water used for washing meat • Spillage of intestinal contents onto meat • Cross contaminations of carcasses	(Anihouvi et al., 2013; Fahrion et al., 2014; Wilfred et al., 2012)
2	Eating raw or under cooked food	• Lifestyle trends with increased consumption of raw and under cooked food • Inadequate food safety measures at farm level	(Colette et al., 2018; Najwa et al., 2015)
3	Animal production systems	• Improper slurry disposal and treatment which predispose environment to contamination. • Extensive animal keeping which increases human-animal interactions	(Afema et al., 2016; Clark et al., 2003; Dione et al., 2011; Najwa et al., 2015)
4	Use of animal slurry for crop	• Rain water run-off washes slurry into water sources	(Pornsukarom & Thakur, 2016; You et

	production	• *Salmonella* spp. can stay dormant in soil for long periods resulting in crop contamination especially vegetables	al., 2006)
5	Sharing water sources with animals	• Animal faecal contamination of water sources • Drinking untreated water from shared sources	(Kusiluka et al., 2005; Lyimo et al., 2016)
6	Animal husbandry practices	• Type, physical status of the feed and feeding system • Feed withdrawal before slaughter in poultry • Partial depopulation in poultry • High stocking density	(Gast et al., 2016; Holt et al., 2006; Lawes et al., 2012; Lebel et al., 2017; Ratert et al., 2014)
7	Contact with live animals	• Close contact between pet animals and humans • Animal farm workers and animal attendants (occupational hazard)	(Behravesh et al., 2014; Leahy et al., 2016)
8	Contact with raw animal food products	• Slaughterhouse workers (occupational hazard) • Chefs and butchery workers (occupational hazard)	(Ibrahim et al., 2013; Kantsø et al., 2014; Wright et al., 2005)
9	Season of the year	• Most infections occur in human and animals during hot weather in temperate countries • Increase in temperature which favours bacterial multiplication and increased outdoor meals may be driving force for this trend	(Cummings et al., 2012; Hanson, 2015; Ravel et al., 2010, Zhang et al., 2009)
10	Wild-domestic animals interactions	• Act as the source of infection to each other which predispose the environment to contamination	(Cummings et al., 2016; De Lucia et al., 2018; Glawischnig et al., 2017; Hald et al., 2016)
11	Faecal	• Use of untreated water from shared	(Bell et al., 2015; Lyimo

environmental contamination by domestic and wild animals	sources • Rain water run-off which washout the faeces from the range land towards the water sources • Presence of faeces in human house and children playgrounds	et al., 2016)

10.2. Sources of infections related to interactions between humans and live animals

Often in resource-poor settings animals are kept in close proximity with humans, including access to every part of the house during the day and sharing the same spaces during the night (Dione et al., 2011; Msami, 2008). Frequent contact with poultry, sheep and cattle increases the risk of contracting *Campylobacter* infections (Kapperud et al., 2003; Studahl & Andersson, 2000). A study conducted in backyard poultry in Egypt reported increases of more than three times in *Campylobacter* infections in children from households keeping *Campylobacter*-infected poultry as compared to children in households with *Campylobacter* free flocks (El-Tras et al., 2015). Nonetheless, chicken corralling in resource-poor settings was reported to increase the risks of *Campylobacter* infections in children as compared to free-range kept chickens in Peru (Oberhelman et al., 2006). Therefore, promoting the building of appropriate animal shelters in resource-poor settings may not reduce the risk of animal and environmentally-related gastrointestinal infections if the use of shelter is not accompanied by good hygiene practices in both animal shelters and human dwellings.

Kissing or snuggling with pet birds as mostly practiced by children has been associated with human *Salmonella* outbreaks (Basler et al., 2016; Behravesh et al., 2014; Gaffga et al., 2012). *Campylobacter* and *Salmonella* shedding in cats and dogs is more of a public health concern due to the companion nature of these animals to human (Andrzejewska et al., 2013;

Holmberg et al., 2015; Leahy et al., 2016; de Massis et al., 2018). Several studies report indistinguishable *Campylobacter* strains from dogs and their owners (Gras et al., 2013), *Salmonella* and *Campylobacter* strains from human and chickens (Anderson et al., 2012, Elgroud et al., 2015; Kagambega et al., 2013), indicating cross infections between these hosts. Guinea pigs and turtles kept as pets are asymptomatic carriers of *Salmonella* spp. and have been implicated in multistate outbreaks of *Salmonella* infections in humans in the United States (Gambino-Shirley et al., 2018; Koski et al., 2018; Robertson et al., 2018). Pests, including rodents, can also be infected by *Salmonella* and *Campylobacter* spp. and serve as a source of compound, food and kitchen bacterial contamination through faeces or mechanical movement of the bacteria (Meerburg & Kijlstra, 2007; Ribas et al., 2016).

Human *Campylobacter* and *Salmonella* infections associated with live animals are acknowledged as occupational hazards which predispose animal handlers on farms and in veterinary facilities to the risk of infection (Ibrahim et al., 2013; Kantsø et al., 2014; Wright et al., 2005). Also, dry pet foods have been implicated as a source of *Salmonella* infections in pet animal handlers, children in the household and animal themselves (Behravesh et al., 2010).

10.3. Source of infections related to environmental animal faecal contamination

Campylobacter and *Salmonella* are recurrently isolated from soil, water bodies, animal houses and effluents (Afema et al., 2016; Lyimo et al., 2016; Mhongole et al., 2017; O'Mahony et al., 2011). Free-range or extensive systems of animal husbandry mostly practised in rural resource-poor settings, poor slurry management on animal farms and in slaughterhouses results in environmental bacterial contamination (Figure 1) (Afema et al., 2016). Also, *Campylobacter* and *Salmonella* spp. have been isolated in non-domesticated mammals and birds making these species another potential source of environmental contamination through faecal shedding (Carbonero et al., 2014; Jurado-Tarifa et al., 2016). Under favourable temperature, humidity and pH, *Salmonella* can survive in the natural environment including soil and water for several weeks without significant multiplication which makes shedding animals and poor slurry disposal of public health concern (Chouhan, 2015; Jensen et al., 2006). High ruminant and poultry density and presence of large poultry slaughterhouses have a strong association with higher *Campylobacter* incidences in humans suggesting pathogen movement among humans, domestic animals and environments (Arsenault et al., 2012a; Arsenault et al., 2012b;).

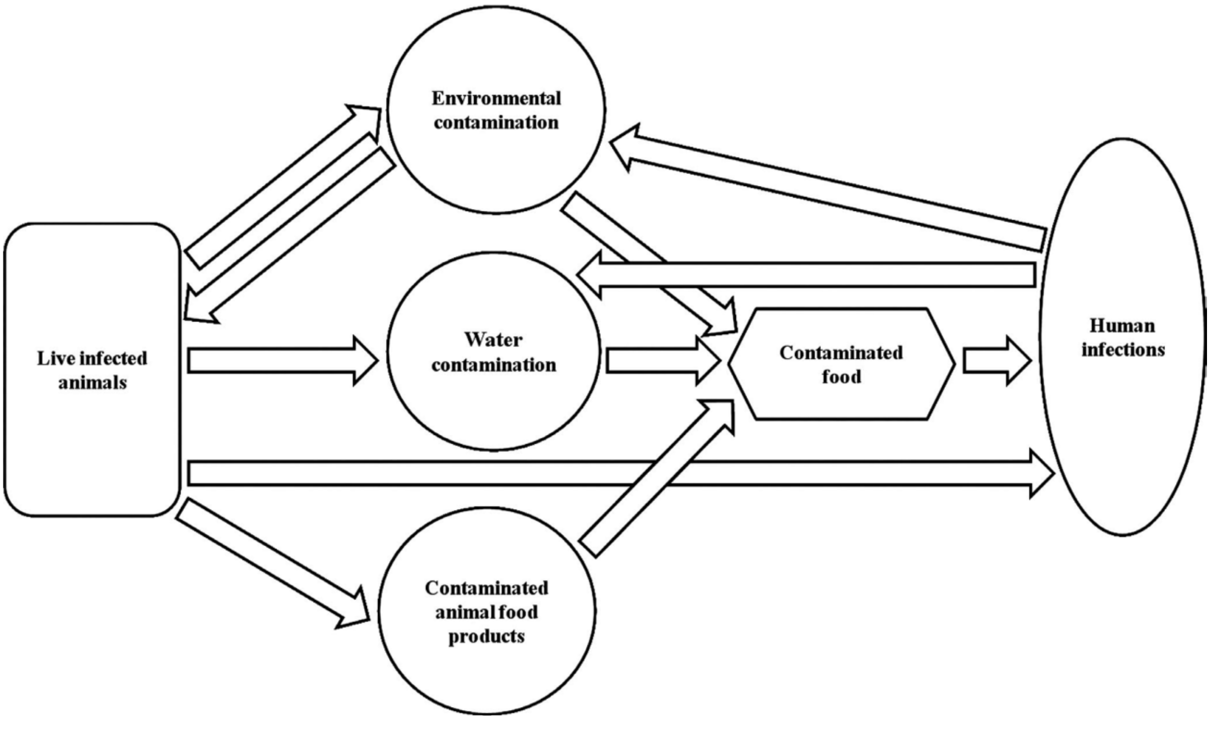

Figure 1: Schematic presentation of *Salmonella* and *Campylobacter* cycle among animals, human and environments

Isolates of *Salmonella* serovar 4,[5],12:i:- with similar phage type, pulse field gel electrophoresis (PFGE) and multilocus variable analysis (MLVA) profiles were reported from cattle, pigs and human faeces indicating a key role of animals in human *Salmonella* infection (Ido et al., 2015). The correlation of *Campylobacter* strains in humans and animals is not only restricted to the type of strain but also their temporal occurrences. The prevalence of sequence type (ST) 45 strain of *Campylobacter* is higher during the summer months in humans, cattle and broiler chicken faeces which suggests cross-infection between these hosts (Grove-White et al., 2011; Jorgensen et al., 2011; McCarthy et al., 2012). With increased encroachment and destruction of wildlife habitat by human activities, and keeping wild animals in captivity and as pets, the possibility of humans acquiring infection from wildlife is expected to increase. However, out of 50 *Salmonella* outbreaks reported in United States between 2006 - 2013, only five were related to non-domesticated animals (Gaydos, 2014).

Surface water bacterial contamination frequently occurs through rainwater run-off washing animal faeces in the environment towards water sources (Bell et al., 2015; Levantesi et al., 2012). Indistinguishable strains connected to *Campylobacter* waterborne outbreaks occurring during heavy rains were documented in humans, cattle and manure implying water source contamination by water run-off from animal farms (Clark et al., 2003). In resource-poor settings, water-sources sharing between humans and animals is not uncommon resulting in use of water contaminated by animal faeces (Kusiluka et al., 2005; Lyimo et al., 2016; Strauch & Almedom, 2011). The isolation of similar *Salmonella* strains in domestic and non-domestic animals in rural and urban surface water further confirms animals as reservoirs for environmental and water bacterial contamination (Thomas et al., 2013). Water treatment at public sources have been proven effective in preventing infections which may emerge from contaminated water (Maponga et al., 2013). Unfortunately, there is limited or often no reticulated or borehole water supply system in resource-poor settings, making water treatment difficult or impossible; hence, the promotion of drinking boiled or home chemical treated water become the only effective options (Diouf et al., 2014; Mengistie et al., 2013).

The use of water contaminated with animal faeces for irrigation and manure for soil fertilisation, poses risks to consumer health and environmental contamination (Pornsukarom & Thakur, 2016). *Salmonella* can survive in manure mixed with soil for 332 days which may result in crop and environmental contamination (You et al., 2006). Garden irrigation using water from sources receiving slaughterhouse slurry and rainwater run-off has been implicated in fresh vegetable *Salmonella* contamination (Bell et al., 2015; Najwa et al., 2015). Human *Salmonella* and *Campylobacter* infections of animal origin acquired from horticulture contaminated products are rising due increases in fresh vegetable consumption globally fuelled by urbaniation and globalisation (Evans et al., 2003; Hussain & Gooneratne, 2017). This necessitates promotion of the use of physical, chemical and biological treatment methods to reduce pathogen population in manure despite costs and environmental pollution challenges associated with use of these methods (Manyi-Loh et al., 2016).

Livestock shedding bacteria are also a source of infection to non-domestic animals which then may continue to sustain the bacteria in the ecosystem (Hald et al., 2016). Isolation of livestock-associated strains and unique strains of *C. jejuni* in non-domestic birds and absence of unique non-domestic bird strains in livestock suggest the direction of infection to be predominantly from livestock to non-domestic birds (Hughes et al., 2009), Also, cattle-derived *Salmonella* Dublin and pig-derived *S.* Typhimurium DT193 have been isolated in red foxes (*Vulpes vulpes*) and non-domestic birds, respectively; the former most probably acquired through ingestion of infected cattle materials such as abortion tissues (De Lucia et al., 2018; Glawischnig et al., 2017).

Conclusions

The consumption of food of animal origin, extended human-animal contacts, exposure of humans to animal faeces through faecal contaminated environment, water and food (through inappropriate horticultural practices) are the drivers for animal associated-human campylobacteriosis and salmonellosis. The risk of acquiring infection through consumption of food of animal origin especially poultry in low-income countries is lower as compared to high-income countries since food of animal origin are less frequently consumed in low-income countries (Ritchie & Roser, 2018). Keeping poultry of the same age and type/breed under intensive conditions as mostly practised in high-income countries favours bacterial multiplication and transmission with subsequent poultry product contamination. It is very difficult to achieve zero bacteria colonization at farm level, therefore, in addition to appropriate management, proper hygiene practices, adequate cooking of food from unsafe sources should be immediate strategies towards reducing magnitude of animal-origin human *Campylobacter* and *Salmonella* spp infections. Human-animal interaction including sharing the same house with animals does not always result in animal-related human sub-clinical and clinical *Campylobacter* and *Salmonella* spp. Frequent exposure to animals can enhance development of immune systems that are less allergic and more adaptive and responsive to common pathogens (Lambrecht & Hammad, 2017; Stein et al., 2016). Nonetheless, sharing living spaces with animals should be practised understanding that animals are potential sources of infections through bacterial faecal shedding and modifications made to mitigate these potential risks. However, the literature to date suggests that the risks of pathogen transfer from human–human contact are probably much greater than those from animals. Increases in environmental temperature over certain ranges, can increase bacterial colonization and shedding in animals, favour pathogen survival and multiplication in the environment and increases pathogen-human interaction due to increases in outdoor activities contributing to increases in infection in humans especially in temperate countries. As animal-source food remains an important component of human diets, achieving safe and sustainable production systems will require interdisciplinary research and development tailored to local conditions.

Conflict of Interest

The authors declare that there is no conflict of interest

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