REVIEW

Salmonellosis: the role of poultry meat

P. Antunes[1,2], J. Mourão[2], J. Campos[2] and L. Peixe[2]

1) *Faculdade de Ciências da Nutrição e Alimentação, Universidade do Porto and* 2) *UCIBIO/REQUIMTE. Laboratório de Microbiologia, Faculdade de Farmácia, Universidade do Porto, Porto, Portugal*

Abstract

Salmonellosis remains one of the most frequent food-borne zoonoses, constituting a worldwide major public health concern. Currently, at a global level, the main sources of infection for humans include meat products, including the consumption of contaminated poultry meat, in spite of the success of *Salmonella* control measures implemented in food-animal production of industrialized countries. In recent years, a shift in *Salmonella* serotypes related to poultry and poultry production has been reported in diverse geographical regions, being particularly associated with the spread of certain well-adapted clones. Moreover, antimicrobial resistance in non-typhoidal *Salmonella* is considered one of the major public health threats related with food-animal production, including the poultry production chain and poultry meat, which is an additional concern in the management of salmonellosis. The circulation of the same multidrug-resistant *Salmonella* clones and/or identical mobile genetic elements encoding antibiotic resistance genes from poultry to humans highlights this scenario. The purpose of this review was to provide an overview of the role of poultry meat on salmonellosis at a global scale and the main problems that could hinder the success of *Salmonella* control measures at animal production level. With the increasing globalization of foodstuffs like poultry meat, new problems and challenges might arise regarding salmonellosis control, making new integrated intervention strategies necessary along the food chain.

Keywords: AmpC, extended-spectrum β-lactamases, multidrug-resistance, plasmid-mediated quinolone resistance, *Salmonella*, Enteritidis, Infantis, Kentucky, Heidelberg, Typhimurium, Virchow
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Corresponding author: L. Peixe, Laboratório de Microbiologia, Faculdade de Farmácia, Universidade do Porto, Rua Jorge Viterbo Ferreira n° 228, 4050-313 Porto, Portugal
E-mail: lpeixe@ff.up.pt

Introduction

Salmonella infections are a worldwide major public health concern; Salmonellosis is caused by non-typhoidal *Salmonella enterica* serotypes (serotypes other than S. Typhi and S. Paratyphi) and is typically characterized by a self-limiting gastroenteritis syndrome (manifested as diarrhoea, fever and abdominal pain), with an incubation period between 4 and 72 h and mortality being rare [1–3]. In healthy humans, the infectious dose is generally 10^6 to 10^8, but lower bacterial counts can cause disease in certain conditions, as well as in infants and the elderly [2]. Although uncommon, life-threatening invasive infections with bacteraemia (5%–10% of infected persons) and/or other extra-intestinal infections may occur, affecting especially the risk groups (infants, young children, older people and immunocompromised patients) [1–3]. In severe cases, effective antimicrobial agents are essential, so the emergence of *Salmonella* that are resistant to critical antibiotics is of concern [1,2].

In industrialized countries, the main reservoir of non-typhoidal *Salmonella* is the intestinal tract of food-producing animals, which readily leads to contamination of diverse foodstuffs [3–5]. Therefore, despite other sources (e.g. contact with animals/reptiles, environment or person-to-person), food-borne salmonellosis is the most relevant source with a high

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global impact in human health. It was estimated that non-typhoidal *Salmonella* causes around 93.8 million illnesses and 155 000 deaths each year worldwide [6]. In the USA, more than 1 million annual cases of food-borne salmonellosis were estimated by the CDC; they were associated with the largest number of hospitalizations and deaths compared with other food-borne microbial agents [7]. In Europe, salmonellosis has been the second most common zoonosis (82 694 confirmed cases and 20.4 cases per 100 000 population in 2013) and the most frequent cause of food-borne outbreaks, in spite the reported decreasing trend that has resulted from *Salmonella* control programmes [8].

Although different serotypes have been associated with salmonellosis, a limited number are responsible for most human infections; *S. enterica* Enteritidis being the most frequent one in the EU (39.5% in 2013) and USA (14.5% in 2012) followed by *S. enterica* Typhimurium (including its monophasic variant) (28.8% in EU, 2013; 11.6% in USA) [8,9]. *Salmonella* Enteritidis is commonly associated with poultry and products thereof, whereas *S.* Typhimurium has a wider species range, including pigs and cattle as well as poultry [10]. Therefore, foods of animal origin, in particular contaminated poultry products (eggs and poultry meat) have been considered the main vehicles of *Salmonella* infection and clearly associated with the worldwide epidemic of *S.* Enteritidis [4,5,11,12]. Moreover, diverse epidemiological studies have supported the great contribution of poultry foodstuffs to the salmonellosis burden [4,5,12,13].

In recent years, with the implementation of *Salmonella* control programmes mainly in poultry production (e.g. in the EU and USA), changing trends in food-borne salmonellosis and associated serotypes were observed, with the expansion of previously less common serotypes, frequently resistant to antibiotics. With the increasing globalization of foodstuffs like poultry meat, which is one of the most consumed and increasingly globally traded meat products, new problems might arise regarding salmonellosis control. An overview of the role of poultry meat in salmonellosis at a global scale is provided in this review.

Non-typhoidal *Salmonella* and poultry meat

Poultry populations, in particular chicken and turkey, are frequently colonized with *Salmonella* without detectable symptoms (sub-clinical infections/healthy carriers) by horizontal and vertical transmission at primary production level [4,5]. The presence of *Salmonella* in healthy poultry animals is suggested as the main risk factor, by allowing bacteria to easily transmit in table eggs and poultry meat to humans [10]. In fact, in Europe it is assumed that the observed reduction in salmonellosis cases (32% between 2008 and 2012) is mainly due to successful *Salmonella* control measures (involving surveillance, biosecurity and vaccination) implemented in poultry/egg production and focused on particular serotypes (e.g. *S.* Enteritidis and *S.* Typhimurium) that are considered of public health significance [4,8,10,12]. These measures led to the achievement of reduction targets for poultry populations in most EU countries and lower non-compliance regarding *Salmonella* in poultry products [4,8]. Moreover, decreasing contamination rates in raw poultry products are in agreement with those recently observed in industrialized countries from other geographical regions with pathogen reduction programmes, such as the USA [12,14,15]. It should be noted that by the 2000s a high incidence of *Salmonella* in poultry products was reported in the EU, with rates >50% for several countries [16]. In the 2013 zoonosis EFSA/ECDC report involving data from European countries, as in previous years, *Salmonella* was most frequently reported, although at low levels, in fresh turkey (5.4%) and fresh broiler meat (3.5%), in comparison with eggs (0.1%) or fresh pig meat (0.7%) [8]. Despite the highest incidence being detected in poultry meat, eggs still remain the most important source of food-borne *Salmonella* outbreaks [8]. In fact, using quantitative source attribution models the higher number of human salmonellosis cases in Europe was attributable to eggs (65% in 2011 and 17% in 2012) and pigs (28% in 2011 and 56.8% in 2012) compared with broilers (2.4% in 2011 and 10.6% in 2012) and turkey meat (2.6% in 2011 and 4.5% in 2012) [17,18]. However, diverse surveys targeted to detect *Salmonella* in poultry products in developing countries, some with expansion of the poultry industry, still detected high percentages of positive samples, ranging from ~13% to 39% in South America [19,20], ~35% in Africa [21,22] and ~35% to 50% in Asia [23–25]. Those differences possibly reflect diverse poultry production husbandry practices and absence of control measures along the food chain, highlighting the importance for *Salmonella* spread of the extensive international trade in animals and their products [4].

Worldwide data about *Salmonella* serotype prevalence in humans and in the diverse range of foodstuffs have contributed to establish an epidemiological link between salmonellosis and poultry products, with diverse serotypes overlapping between humans and poultry meat (chicken and turkey) (Fig. 1). In the EU, recent changes in the frequency of *Salmonella* serotypes causing human infections were reported, which in some cases were in line with those occurring in poultry (Fig. 1). Nevertheless, interpretation of these data should be cautious, owing to limitations in the number of poultry isolates serotyped each year. Of particular relevance is the decrease in *S.* Enteritidis human cases (19% reduction between 2011 and 2013 in the EU), a serotype typically associated with poultry meat and egg

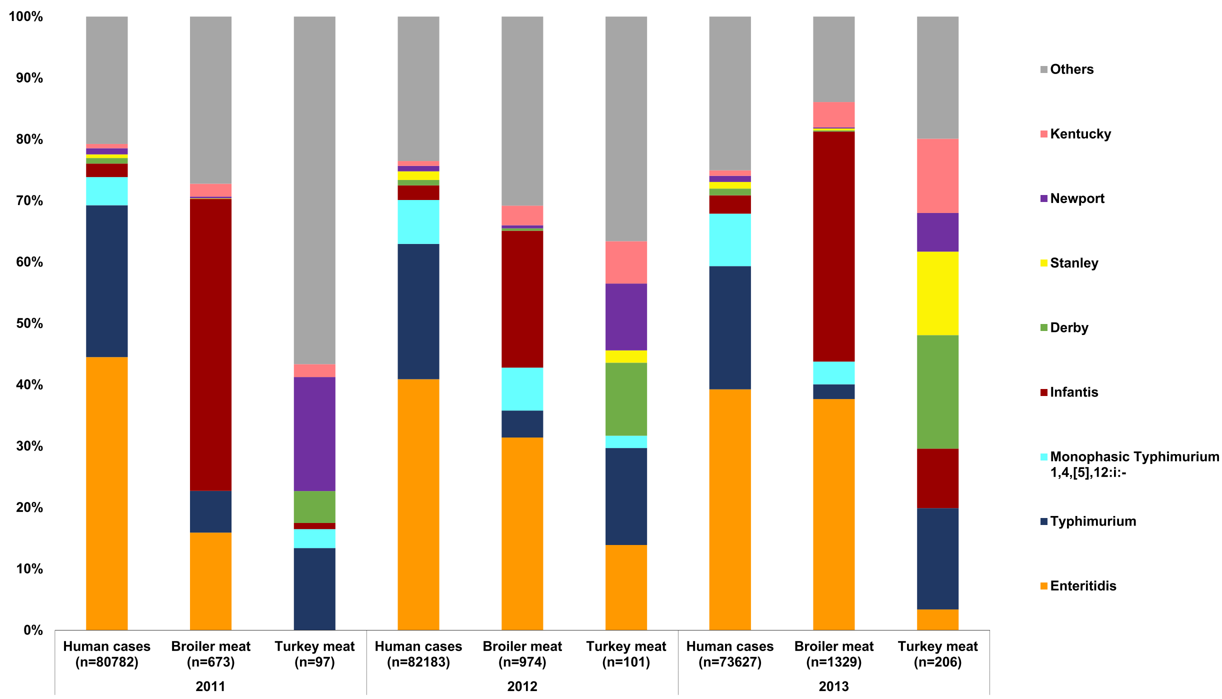

FIG. 1. Distribution of the major serotypes of non-typhoidal *Salmonella* associated with human cases (salmonellosis) and poultry meat in EU, 2011 to 2013. Data were obtained from EFSA reports: humans (2011–2013) and turkey/broiler meat (2013) [8]; turkey/broiler meat (2011–2012) (http://www.efsa.europa.eu/en/efsajournal/pub/3129 and http://www.efsa.europa.eu/en/efsajournal/pub/3547) (last accessed 1 September 2015). The percentages were calculated based on the total number of serotyped isolates per type of meat or human salmonellosis cases.

consumption, in line with a decreasing trend in poultry and poultry products pointed by different studies [8,12,26–29]. Increasing occurrences of other serotypes implicated in human infections (e.g. *S.* Infantis, *S.* Stanley, *S.* Kentucky) related with poultry meat (chicken and turkey) have been reported in the EU (Fig. 1). However, one major difference in the serotype pattern between humans and poultry is related to *S.* Typhimurium and its monophasic variant, both frequently associated with human salmonellosis, but less common in poultry meat, pigs and pig meat being the main source [8]. In USA and Canada, other serotypes, like *S.* Heidelberg and *S.* Kentucky, have emerged as predominant serotypes in poultry and have also been implicated in human salmonellosis, beyond *S.* Enteritidis [9,12,14,15,28,30–32].

The shift in *Salmonella* serotypes related to poultry and poultry production has been associated with the spread of certain clones. For instance, the *S.* Infantis increase (26.5% in human cases between 2011 and 2013 accounting for the fourth most common serotype and the most reported in broilers and broiler meat) [8], has been associated with the spread of several clones of broiler origin in diverse European countries, including the dominant Hungarian clone [33–35]. Also, *S.* Stanley showed an increase since 2011 with a peak in 2012, being the sixth most common human serotype and one of the three most common in turkey meat, together with *S.* Derby and *S.* Kentucky in 2013 [8]. A large *S.* Stanley outbreak caused by a new clone (novel Pulsed Field Gel Electrophoresis-type), was linked with the consumption of turkey meat, and is still circulating in the European food market (at least since 2011), with a considerable risk of becoming endemic in the poultry production chain in Europe [36–38]. In the USA, *S.* Heidelberg in particular has been identified as one of the top human and poultry serotypes, with several clones implicated in diverse large multistate outbreaks resulting from the consumption of contaminated chicken or turkey products [12,31]. The spread and the global persistence of serotype *S.* Kentucky reflect other particular situations related to the increased globalization of travel and the food/animal trade in different geographical regions. This serotype has been associated with a worldwide (Europe, Africa and Asia) spread of a particular epidemic clone (*S.* Kentucky ST198-X1), recovered from several livestock reservoirs, particularly poultry farms, with chicken and turkey implicated as the potential major human infection vehicles [39–43]. These and other examples of multi-country/multi-state outbreaks or clonal expansion of *Salmonella* infections linked to poultry meat (Table 1) serve as a reminder of the importance of acting upon any *Salmonella* contamination in the food chain and monitoring to detect the emergence of any serotype or new clone. This

TABLE 1. *Salmonella* outbreaks and emerging clones linked with poultry meat products (2002–ongoing)

Serotype (outbreak/clone designation)[a]	Source	Year(s)[b]	Geographical region	No. of cases[c]	Reference
Enteritidis (outbreak)	Chicken	2015–	USA	3	CDC, 2015[d]
Enteritidis (outbreak)	Chicken	2015–	USA	9	CDC, 2015[d]
Hadar (outbreak)	Turkey	2010–2011	USA	12	CDC, 2015[d]
Heidelberg (outbreak)	Chicken	2013–2014	USA, Puerto Rico	634	CDC, 2015[d]
Heidelberg (outbreak)	Chicken	2013	USA	9	CDC, 2015[d]
Heidelberg (outbreak)	Chicken	2012–2013	USA	134	CDC, 2015[d]
Heidelberg (outbreak)	Chicken	2011	USA	190	CDC, 2015[d]
Heidelberg (outbreak)	Turkey	2011	USA	136	CDC, 2015[d]
Infantis (Israel clone)	Broiler chickens	2007–2009	Israel	NA	[26]
Infantis (Hungarian clone)	Broilers and chicken	2004–2009	Europe	NA	[33–35]
Kentucky (ST198-X1)	Chicken and turkey	2002–2013	Europe, Africa, Asia	NA	[39,40,42]
Stanley (outbreak)	Turkey	2011–2013	Europe	710	[36,37]

[a]ST, sequence type.
[b]'year-' include ongoing reported outbreaks.
[c]Estimated number of cases only when outbreaks were reported. NA, not applicable in emerging clones.
[d]CDC, 2015. *Salmonella*. Reports of selected *Salmonella* Outbreak Investigations. Available at: http://www.cdc.gov/salmonella/outbreaks.html [accessed September 2015].

scenario also remains alert for the need for inclusion of those serotypes, or particular clones, considered to be of public health significance, in control and surveillance programmes [10,12,38].

Salmonella serotypes and clones associated with human infections and with an enhanced ability to colonize several food animals, able to persist along the food chain (e.g. primary production on-farm, slaughter operations, equipment and meat handlers, retail meat) with efficient transmission and rapid spread are of public health relevance [11,34,43–45]. Although understanding the exact mechanisms of their persistence and spread in poultry production are still largely unknown, recent studies focusing on emergent poultry-associated *Salmonella* strains unveiled specific features that could provide a significant advantage both in the environment and in the host (poultry/human) [12]. For example, in Israel, an *S.* Infantis emergent clone possessed a megaplasmid, which increased its tolerance to stress factors (e.g. mercury and oxidative stress) and its virulence/pathogenicity (e.g. enhanced biofilm formation, adhesion and invasion into avian and mammalian host cells) [46]. Also, a genomic study of several predominant *Salmonella* serotypes from Canadian broiler chickens showed the presence of multiple features related with pathogenicity (e.g. genes encoding adhesins, flagellar proteins, iron acquisition systems, type III secretion system) and stress tolerance (e.g. metal and antiseptic tolerance genes; better acid-stress response) [32]. *S.* Heidelberg, including ground turkey outbreak isolates, carried phages and plasmids with diverse virulence factors (e.g. P2-like phage-*sopE1* gene, IncX-type IV secretion system), which could play a role in their virulence (a serotype highly related to invasive infections), colonization and persistence (a poultry-associated serotype) [12,31]. In *S.* Kentucky, the acquisition of an *E. coli* ColV virulence plasmid was also associated with enhanced colonization ability in chicken, particularly in a dominant avian clonal type [12]. These features can play a role in the successful spread of emergent and virulent serotypes/clones that could contribute in a short time to replacing other *Salmonella*. Moreover, those emergent *Salmonella* serotypes are usually enriched with antimicrobial resistance determinants conferring multidrug-resistance [12,31,32,46], which is currently one of the major public health concerns (discussed in the next section).

Antimicrobial-resistant non-typhoidal *Salmonella* and the poultry linkage

The emergence and spread of *Salmonella* isolates presenting resistance to several antibiotics is of concern because these medicines are crucial to the successful treatment of invasive infections [1,11]. Since resistance to older antibiotics (e.g. ampicillin, chloramphenicol and trimethoprim-sulfamethoxazole) has been increasing for many years, recommended treatment options for salmonellosis included fluoroquinolones (ciprofloxacin) and extended-spectrum cephalosporins [1,2]. However, resistance to those 'critically important antibiotics for human health' is emerging, leading to increased severity, morbidity and mortality of diseases and the need for the use of last-line antimicrobials (e.g. carbapenems) in therapy [47].

For several decades, the contribution of the food-animal as a reservoir of antimicrobial resistance with impacts on human health has been controversial, but accumulating evidence linking particularly poultry production with human disease have been reported, namely involving non-typhoidal *Salmonella* [48–50]. The first evidence is the close association between the use of antimicrobial agents and the occurrence of resistance. In fact, regular use of antibiotics (mainly for animal health and in some countries as growth promoters), a practice associated with modern intensive food-animal/poultry production, has been considered the main driver for the development of antibiotic resistance in zoonotic bacteria, such as *Salmonella* [48,50,51]. For example, licensing of the fluoroquinolone enrofloxacin for animal use, especially in poultry, in the 1990s led to increased rates of decreased susceptibility to ciprofloxacin in *S.* Typhimurium DT104 recovered from animal/food (particularly poultry) and humans [5]. Other findings points to a link between resistance to nitrofurans in human *Salmonella* and the food chain, suggesting that its illegal use in the poultry industry might have contributed to the selection and persistence of *S.* Enteritidis in poultry, and consequently to human salmonellosis in Portugal [52]. More recently, a voluntary withdrawal of ceftiofur by the poultry producers in Canada was correlated with a decreasing occurrence of ceftiofur-resistant *S.* Heidelberg (one of the most common serotypes associated with salmonellosis in this country) from both human infections and retail poultry, with an increase of the resistance levels after reintroduction of use [30].

Further evidence for the impact of poultry production on human health problems associated with antimicrobial resistance in *Salmonella* is the correlation between different reservoirs (humans and food-animals) obtained from systematic surveillance data. In the last EU report, *Salmonella* resistant (R) or multidrug-resistant (MDR) to commonly used antimicrobials was frequently detected in humans (R = 50%; MDR = 31.8%) and animals, especially broilers (MDR = 56%) and turkeys (MDR = 73%), but also in derived meat products [43]. Also, in the USA, high levels of resistance and MDR in chicken (R = 60%; MDR = 26%) and turkey (R = 77%; MDR = 39.6%) seems to greatly contribute to levels in humans (R = 19%; MDR = 10%) [53]. Those data about MDR are extremely worrying because of the possible role of diverse antibiotics in the co-selection of *Salmonella* strains resistant to clinically relevant antibiotics, such as fluoroquinolones and extended-spectrum cephalosporins. In the EU, relatively low levels of *Salmonella* non-susceptible ('clinically' resistant and 'intermediate' resistant categories combined) to ciprofloxacin (3.8%) and 'microbiological' resistant (non-wild type by epidemiological cut-off values) to cefotaxime (1.4%) were observed in humans. Moreover, the highest levels of 'microbiological' resistance to these critically important antimicrobials were detected in broiler meat (68% ciprofloxacin and 10.1% cefotaxime) and turkey meat (73.4% ciprofloxacin and 4.7% cefotaxime), suggesting an important contribution of the poultry production chain to the human burden [43]. In addition, it was reported that the highest levels of resistance to ciprofloxacin were more common in *S.* Enteritidis, *S.* Infantis and *S.* Kentuchy, three serotypes commonly associated with poultry meat [43]. Also, in the USA, in spite of a decreasing trend since 2009, cephalosporin's resistance levels are low in humans (2.5% ceftriaxone), but still high in turkey (9%) and retail chicken (20%), especially in *S.* Heidelberg a poultry-associated serotype [53].

In middle-income countries such as in the Asiatic continent, resistance to ciprofloxacin and extended-spectrum cephalosporins is currently a growing problem, with poultry products playing a potential role in its emergence [2,3]. High levels of *Salmonella* non-susceptible to ciprofloxacin (15%–48%) and cephalosporins (38% ceftriaxone) were observed in humans in Asian countries [54,55]. These data are in agreement with several studies that documented a high prevalence of resistance to fluoroquinolones (>22.5% ciprofloxacin) and cephalosporins (12.5% to >23.4% ceftriaxone and 26.6% ceftazidime) in poultry meat from South Korea and China [24,25]. In these countries the high rates of antimicrobial resistance detected reflect the levels of antimicrobial consumption in livestock, including for growth promotion, an area that remains largely unregulated [25,55,56]. Recent global estimates indicate that consumption of antibiotics in livestock (especially in poultry), which outranks the consumption by humans, will rise especially in middle-income countries. In these countries extensive farming systems will be replaced by large-scale intensive husbandry systems that routinely use antibiotics, to respond to the increasing demand for animal protein [56]. Therefore, international trade of contaminated breeding animals (poultry production depends on a pyramid-like breeding system), feed and poultry products with antibiotic-resistant *Salmonella* may contribute to the rapid worldwide spread of these bacteria, with impacts on human health.

A third indication of the significant impact on human health of antibiotic-resistant *Salmonella* contaminating these foodstuffs, is provided by diverse reports demonstrating their association with plasmid-mediated resistance determinants to cephalosporins and fluoroquinolones [49,51,57]. Moreover, several studies provide further evidence of transmission from poultry to humans of those clinically relevant MDR *Salmonella* clones [11,49,51,57]. A wide range of *Salmonella* serotypes (e.g. Enteritidis, Heidelberg, Infantis, Kentucky, Typhimurium, Virchow) frequently recovered from poultry (animal and food) have been associated with the worldwide dissemination of extended-spectrum β-lactamases, plasmid-encoded AmpC β-lactamases (AmpC), or plasmid-mediated quinolone resistance genes (Tables 2 and 3). By far the most common genes, found in poultry and/or poultry meat samples, associated with resistance to extended-spectrum cephalosporins, were those coding for extended-spectrum β-lactamases, CTX-M (e.g. CTX-M-1, -2, -9 and -15) and TEM-52 enzymes followed by AmpC-type CMY-2 (Table 2). For example, in several European countries, spread of *S.* Virchow producing CTX-M-2 or CTX-M-9 and *S.* Infantis producing TEM-52 has been found among poultry and humans [58–66]. Instead, *S.* Heidelberg, one of the

TABLE 2. ***Salmonella* serotypes/clones carrying extended-spectrum and AmpC β-lactamases recovered from poultry and poultry products**

Salmonella serotype	ESBL or AmpC[a] enzymes (no. of isolates)	Source	Concomitant presence in humans[b]	Country(ies)/ year(s)	Non-β-lactam resistance phenotype[c]	Genetic element PL – Inc group	Reference(s)
Agona	CTX-M-1 (n=1)	Poultry (caecum)		The Netherlands/2006	SUL-TET	PL – I1	[65,66]
	CTX-M-2 (n=2)	Poultry		Brazil/2011	NR	PL – NR	[71]
		Turkey carcass		Brazil/2008	CIP-NAL-STR-SXT-TET	PL – P	[72]
	CTX-M-8 (n=3)	Poultry		Brazil/2008, 2010	NR	PL – NR	[71]
	TEM-52 (n=3)	Poultry		Belgium/2001, 2004	(−)	PL– I1	[62]
	CMY-2 (n=5)	Turkey		Germany/2005	(−) or NAL	PL – I1	[73]
Bareilly	ACC-1 (n=6)	Poultry	Yes	The Netherlands/ 2001–02	(−)	PL – NR	[74]
Blockley	TEM-52 (n=6)	Poultry, poultry meat	Yes	The Netherlands/ 2001–02	(−) or SPT-SUL-TMP	PL – NR	[74]
Brackenridge	CTX-M-14 (n=1)	Poultry		Brazil/2011	NR	PL – NR	[71]
Braenderup	ACC-1 (n=2)	Broilers		The Netherlands/2006	(−)	PL– NT	[65]
		Broiler		The Netherlands/2001	(−)	PL – NR	[74]
	SHV-12 (n=1)	Poultry		Italy/2006	(−)	PL – NR	[75]
Bredeney	CTX-M-1 (n=1)	Turkey		USA/2010	NR	PL – N	[76]
	CMY-2 (n=1)	Turkey		Canada/1999	SUL-TET	PL – A/C	[77]
Derby	TEM-52 (n=1)	Poultry		Belgium/2001	(−)	PL – I1	[62]
Enteritidis	CTX-M-2 (n=1)	Poultry		Brazil/2004	NR	NR	[71]
	CTX-M-9 (n=1)	Broiler		Spain/2000–04	STR-SUL-SXT-NAL-TET	NR	[60]
	CTX-M-14 (n=5)	Imported chicken meat		China/2004	NAL	PL – NR	[78]
		Poultry		China/2012–13	CHL-CIP-ENR-FFC-NAL-OLA- SXT-(AMK-GEN-LVX-TET)	PL – HI2, F, N or B/O	[70]
	CTX-M-15 (n=34)	Chicken meat, faeces or disease	Yes	Korea/2009	STR-SUL-TET-(GEN-NEO)	PL – FII	[79]
		Chicken		South Korea/2009–10	NR or GEN-STR-SUL-TET	PL – FII	[80]
	SHV-12 (n=2)	Broiler		Portugal/2012–13	CHL-CIP-SUL-NAL-TET	NR	[81]
		Poultry		Italy/2006	TET	NR	[75]
Emek	CMY-2 (n=1)	Poultry		Brazil/2011	NR	NR	[71]
Essen	CTX-M-15 (n=1)	Diseased chicken		Korea/2009	GEN-STR-SUL-TET	PL – FII	[79]
Gaminara	CTX-M-14 (n=1)	Poultry		Brazil/2009	NR	NR	[71]
Give	CTX-M-2 (n=1)	Poultry		Brazil/2009	NR	NR	[71]
Hadar	CTX-M-14 (n=1)	Poultry		Brazil/2005	NR	NR	[71]
Havana	CTX-M-1 (n=1)	Broiler		Portugal/2012–13	SUL-TET	NR	[81]
	CMY-2 (n=2)	Broiler		Portugal/2012–13	(−)	NR	[81]
Heidelberg	CTX-M-1 (n=1)	Broiler carcass		Portugal/2012–13	SUL-TMP	NR	[81]
	CTX-M-2 (n=14)	Poultry		Brazil/2009, 2011	NR	NR	[71]
		Chicken		Venezuela/2005–07, 2008	CIP-GEN	PL – NR	[82]
	CTX-M-14 (n=1)	Poultry		Brazil/2011	NR	NR	[71]
	SHV-2 (n=1)	Retail chicken meat		Canada/2007	GEN-STR-SUL	PL – I1	[83]
	CMY-2 (n=25)	Chicken or chicken retail	Yes	Canada/2001–04	CHL-GEN-KAN-STR-SUL- SXT-TET	PL – A/C, I1	[67]
		Chicken food		USA/2002, 2004, 2010	(CHL-GEN-KAN-STR- SUL-TET)	PL – A/C, I1	[31]
		Poultry		Brazil/2011	NR	NR	[71]
Indiana	CTX-M-14 (n=21)	Poultry		China/2012–13	ENR-NAL-SXT-(AMK- CHL-CIP-FFC-GEN- LVX-OLA-TET)	PL – HI2, A/C, F, N, P-1α, B/O	[70]
	CTX-M-24 (n=29)	Chicken		China/2008–09	AMK-CHL-FFC-GEN- NAL-OLA-RIF-STR- SXT-(TET)	PL – HI2	[84]
	CTX-M-65 (n=3)	Poultry		China/2012–13	CHL-NAL-OLA-SXT-(CIP- ENR-FFC-GEN-LVX- TET)	PL – HI2, F, N	[70]
	TEM-52 (n=1)	Broilers		The Netherlands/2006	(−)	PL – NT	[65]
	DHA-1 (n=3)	Chicken faeces		South Korea/2006–07	SUL-TMP-(APM-NAL- NEO-STR-TET)	PL – NR	[85]
Infantis	CTX-M-1 (n=2)	Poultry (caecum or unknown)		The Netherlands/2006	SUL-TMP	PL – I1	[65,66]
	CTX-M-2 (n=3)	Poultry		Brazil/2005	NR	NR	[71]
		Retail Chicken Products		Japan/2002-03	(−)	NR	[86]
	TEM-20 (n=2)	Retail Chicken Products		Japan/1997, 2003	(−)	NR	[86]
	TEM-52 (n=14)	Poultry	Yes	Belgium/2001–05	(−)	PL – I1	[62]
		Poultry (caecum or unknown)		The Netherlands/2006	(−)	PL – I1	[65,66]
		Broiler		Belgium/2004	(−)	PL – I1	[63]
		Chicken		Japan/2004–06	(−)	PL – NR	[87]
		Retail Chicken Products		Japan/2000, 2003	(−)	NR	[86]
	CMY-2 (n=48)	Retail Chicken Products		Japan/1997, 1999–2003	(−)	PL – NR	[86]
Kentucky	CTX-M-25/OXA-21 (n=1)	Turkey		Poland/2009	CIP-NAL	PL – A/C	[42]
	SHV-12 (n=3)	Whole chicken and chicken neck skin		Ireland/2008–09	CHL-SUL-TET	PL – NR	[88]
	CMY-2 (n=3)	Whole chicken		Ireland/2009	(−)	PL – NR	[88]
		Chicken meat		Germany/2005	STR	PL – I1	[73]
Kiambu	SHV-2 (n=1)	Abattoir chicken cecum		Canada/2006	STR-SUL-SXT	PL – I1	[83]
Livingstone	SHV-12 (n=9)	Poultry or turkey carcasse, poultry faeces, broiler faeces		Italy/2005-06	GEN-NAL-(STR-SUL)	NR	[75]
Llandoff	CTX-M-1 (n=1)	Poultry		France/2006	SUL-TET	PL – I1	[89]

Continued

TABLE 2. Continued

Salmonella serotype	ESBL or AmpC[a] enzymes (no. of isolates)	Source	Concomitant presence in humans[b]	Country(ies)/ year(s)	Non-β-lactam resistance phenotype[c]	Genetic element PL – Inc group	Reference(s)
Manhattan	CTX-M-2 (n=2)	Retail Chicken Products		Japan/2000, 2003	(–)	NR	[86]
	CTX-M-15 (n=4)	Retail Chicken Products		Japan/2002, 2003	(–)	NR	[86]
	TEM-52 (n=4)	Retail Chicken Products		Japan/2000, 2002–03	(–)	NR	[86]
	SHV-12 (n=2)	Retail Chicken Products		Japan/2002, 2003	(–)	NR	[86]
	CMY-2 (n=2)	Retail Chicken Products		Japan/2002	(–)	PL – NR	[86]
Minnesota	CTX-M-2 (n=1)	Poultry		Brazil/2009	NR	NR	[71]
	CTX-M-8 (n=1)	Poultry		Brazil/2008	NR	NR	[71]
	CTX-M-14 (n=1)	Poultry		Brazil/2010	NR	NR	[71]
	CMY-2 (n=2)	Poultry		Brazil/2011	NR	NR	[71]
Newport	CTX-M-2 (n=1)	Poultry		Brazil/2008	NR	NR	[71]
Ouakam	CTX-M-1 (n=6)	Turkey		USA/2011	NR	PL – N	[76]
Panama	CTX-M-1 (n=1)	Poultry		Brazil/2009	NR	NR	[71]
Poona	CTX-M-2 (n=1)	Poultry		Brazil/2009	NR	NR	[71]
	CTX-M-8+CTX-M-14 (n=1)	Poultry		Brazil/2005	NR	NR	[71]
Rissen	CMY-2 (n=1)	Poultry		Brazil/2005	NR	NR	[71]
Saintpaul	CMY-2 (n=1)	Poultry		Brazil/2011	NR	NR	[71]
Schwarzengrund	CTX-M-2 (n=10)	Turkey, chicken, chicken carcass		Brazil/2008	CIP-NAL-STR-TET	PL – P	[72]
Senftenberg	CTX-M-15 (n=1)	Chicken		South Korea/2009	NR	PL – FII	[80]
Typhimurium	CTX-M-1 (n=1)	Poultry meat		Germany/2006	KAN-NEO-STR-SUL-SXT-TET-TMP	PL – I1	[73]
	CTX-M-2 (n=10)	Poultry		Brazil/2004–05, 2007	NR	NR	[71]
		Poultry	Yes	Brazil/2003–04	SUL-SXT-TET	PL – NR	[90]
	CTX-M-8 (n=1)	Poultry		Brazil/2011	NR	NR	[71]
	CTX-M-14 (n=1)	Poultry		Brazil/2005	NR	NR	[71]
	CTX-M-15 (n=1)	Broiler		Belgium/2007	(–)	PL – I1	[63]
	TEM-52 (n=4)	Poultry	Yes	Belgium/2002, France/2004	(–)	PL – I1	[62]
		Poultry		The Netherlands/2001–02	SPT-SUL-TMP-(NEO-TET)	NR	[74]
	TEM-52+SHV-12 (n=1)	Poultry meat		The Netherlands/2002	(–)	NR	[74]
Virchow	CTX-M-2 (n=12)	Poultry or poultry product		Belgium/2000–01, 2003	NAL-SUL-TET-TMP-(STR)	PL – HI2	[61]
		Poultry		Ireland/UN	SUL-TET-TMP	PL – P	[77]
		Broiler		Belgium/2001, 2004	STR-SUL-TET-TMP	PL – HI2	[63]
		Poultry	Yes	Belgium-France/2000–03	NAL-SUL-TMP-(STR-TET)	PL – NR	[59]
	CTX-M-2+SHV-2+TEM-1 (n=1)	Broiler		The Netherlands/2002	NAL-SPT-SUL-TET- TMP	NR	[74]
	CTX-M-9 (n=8)	Chicken faeces		France/2002–03	KAN-NAL-SPT-STR-SUL-TET-TMP	PL – NR	[58]
		Chicken faeces and retail chicken meat	Yes	France/2002–03, Spain/2000	NAL-SPT-STR-SUL-TET-TMP-(KAN)	PL – HI2	[61]
		Broiler	Yes	Spain/2000–04	STR-SUL-SXT-NAL-(TET)	NR	[60,64]
	CTX-M-32 (n=2)	Poultry		Greece/2001	CHL-KAN-STR-SUL-TET-TMP	PL – NR	[91]
	TEM-52 (n=1)	Poultry		The Netherlands/2002	SPT-STR-SUL-TMP	NR	[74]
Weslaco	CTX-M-8 (n=1)	Poultry		Brazil/2009	NR	NR	[71]
35:c:1,2	SHV-12 (n=5)	Poultry	Yes	Senegal/2000	CHL-GEN-TET-TOB	NR	[92]

Antimicrobial abbreviations: AMK, amikacin; APM, apramycin; CHL, chloramphenicol; CIP, ciprofloxacin; ENR, enrofloxacin; FFC, florfenicol; GEN, gentamicin; KAN, kanamycin; LVX, levofloxacin; NAL, nalidixic acid; NEO, neomycin; OLA, olaquindox; RIF, rifampicin; SPT, spectinomycin; STR, streptomycin; SUL, sulphonamides compound; SXT, trimethoprim/sulfamethoxazole; TET, tetracycline; TMP, trimethoprim; TOB, tobramycin; NR, not reported; NT, plasmids that were not typable with the scheme used; PL, plasmid.
[a]Only references with full-characterized extended-spectrum β-lactamases /AmpC genes were considered.
[b]'Yes', clones or serotypes simultaneoulsy detected in poultry and humans in the same study.
[c](–), Non-β-lactam resistance phenotype was not detected using the tested antibiotics and according to the susceptibility criteria adopted. Variable phenotypes were present between curved brackets.

top MDR serotypes in both poultry and humans (frequently associated with invasive infections) in North America, presented increasing resistance to cephalosporins related with CMY-2 [31,67]. In fact, transmission of these most reported genes in both human and poultry has been associated with diverse plasmid families, such as IncI1 (e.g. $bla_{\text{CTX-M-1}}$, $bla_{\text{TEM-52}}$ and $bla_{\text{CMY-2}}$), IncA/C (e.g. $bla_{\text{CMY-2}}$) or IncHI2 (e.g. $bla_{\text{CTX-M-2}}$ and $bla_{\text{CTX-M-9}}$) (Table 2). Recently, plasmid-mediated carbapenem-resistant bacteria from food-animals have been reported, alerting us to a new public health problem with indefinable risks [51]. One of the first reports was on a poultry farm in Germany where a $bla_{\text{VIM-1}}$ gene was detected on *S.* Infantis [68]. Besides the worldwide resistance to clinically important β-lactams, plasmid-mediated quinolone resistance mechanisms, which typically confer decreased susceptibility to ciprofloxacin, have been widely reported in *Salmonella* [57]. Among them, Qnr proteins (e.g. QnrB2, QnrB19, QnrS1) have been commonly described in different serotypes and geographic locations, with the aminoglycoside acetyltransferase AAC(6′)-Ib-cr and the efflux pump OqxAB associated with *Salmonella* serotypes recovered from Asian poultry and poultry meat (Table 3). In fact, poultry seems to be an important vehicle of non-typhoidal *Salmonella* carrying plasmid-mediated quinolone resistance genes, highlighting the role of food-producing

TABLE 3. ***Salmonella*** **serotypes/clones carrying plasmid-mediated quinolone resistance genes recovered from poultry and poultry products**

Salmonella serotype	PMRQ[a] mechanism (no. of Isolates)	Source	Country(ies)/year(s)	Antibiotic resistance phenotype[b]	Genetic element PL – Inc group	Reference(s)
Agona	QnrB2 (n=1)	Turkeys	Germany/NR	NR	NR	[69]
Braenderup	QnrD (n=2)	Fowls	Spain/NR	NR	NR	[69]
Dabou	QnrD (n=1)	Fowls	Spain/NR	NR	NR	[69]
Derby	QnrB2 (n=56)	Fowls or turkeys	Spain/NR	NR	NR	[69]
Enteritidis	QnrB2 (n=1)	Fowls or turkeys	Spain/NR	NR	NR	[69]
	QnrB10/B19 (n=1)	Laying hen flock	Poland/2009	CIP-NAL	NR	[93]
	QnrD (n=3)	Fowls	Spain/NR	NR	NR	[69]
	QnrS1/S3 (n=2)	Broiler meat, broiler flock – faeces	Poland/2008–09	AMP-CIP-(STR-TET)	NR	[93]
	OqxAB (n=3)	Poultry	China/2012–13	AMP-CHL-CIF-CIP-ENR-FFC-NAL-OLA-SXT-(GEN-LVX-TET)	PL – HI2, F, N, B/O	[70]
	OqxAB + AAC(6′)-Ib-cr (n=1)	Poultry	China/2012–13	AMK-AMP-CHL-CIF-CIP-CTX-ENR-FFC-GEN-LVX-NAL-OLA-SXT-TET	PL – HI2	[70]
Give	QnrB19 (n=1)	Imported turkey meat from Brazil	Finland/NR	NR	NR	[69]
Hadar	QnrB2 (n=2)	Fowls or turkeys	Spain/NR	NR	NR	[69]
	QnrB5 (n=4)	Imported turkey meat	Germany/2007	STR-TET	NR	[94]
	QnrB19 (n=15)	Fowls, turkeys	Germany, Denmark/NR	NR	NR	[69]
Havana	QnrB2 (n=3)	Poultry	Portugal/2009–10	(–) or NAL	PL – L/M	[95]
	QnrB19 (n=1)	Poultry	Portugal/2009–10	(–)	PL – HI2	[95]
Heidelberg	QnrB19 (n=2)	Chicken	Venezuela/2005–07, 2008	CIP-GEN	PL – NR	[82]
Indiana	OqxAB (n=50)	Poultry	China/2012–13	AMP-CIF-NAL-SXT-(AMK-CAZ-CHL-CIP-CTX-ENR-FFC-GEN-LVX-OLA-TET)	PL – HI2, F, N, P-1α, B/O	[70]
		Chicken	China/2008–09	AMK-CHL-FFC-GEN-NAL-OLA-RIF-STR-SXT-(TET)	PL – HI2	[84]
	OqxAB + AAC(6′)-Ib-cr (n=3)	Poultry	China/2012–13	AMP-CHL-CIF-NAL-SXT-(CIP-CTX-ENR-FFC-GEN-LVX-OLA-TET)	PL – HI2, A/C, N	[70]
Infantis	QnrS1 (n=1)	Chicken	Germany/2004	AMP	NR	[96]
	QnrB19 (n=1)	Retail chicken	Colombia/2004	KAN-NAL-NEO-STR-TET	PL – ColE like	[97]
Kentucky	QnrS1 (n=1)	Chicken	The Netherlands/NR	NR	PL – N	[98]
London	QnrB2 (n=22)	Fowls or turkeys	Spain/NR	NR	NR	[69]
Mbandaka	QnrB19 (n=1)	Poultry	Portugal/2009–10	NAL	PL – HI2	[95]
Montevideo	QnrB2 (n=3)	Fowls or turkeys	Spain/NR	NR	NR	[69]
	QnrD (n=6)	Fowls, turkeys	Italy/NR	NR	NR	[69]
Newport	QnrB5 (n=3)	Imported turkey meat	Poland/2007	(–)	NR	[94]
	QnrS1/S3 (n=12)	Broiler (meat, flock), turkey meat, goose flock – faeces, duck flock – faeces	Poland/2008–11	CIP-(AMP-CHL-FFC-KAN-STR-SUL-TET-NAL)	NR	[93]
	QnrB19 (n=3)	Turkeys	Denmark/NR	NR	NR	[69]
Ohio	QnrD (n=5)	Fowls	Spain/NR	NR	NR	[69]
Saintpaul	QnrS1 (n=15)	Imported turkey meat	Germany/2007–08 Poland/2008	AMC-AMP-STR-TET-(CPD-CHL)	NR	[94]
		Turkeys	Germany, Denmark/NR	NR	NR	[69]
Typhimurium	QnrA1 (n=1)	Turkeys	Germany/NR	NR	NR	[69]
	QnrD (n=2)	Fowls	Spain/NR	NR	NR	[69]
	OqxAB (n=2)	Chicken	China/2007–09	OLA-FFC-SMX-(AMP-CHL-CIF-GEN-NAL-TET)	PL – HI2, F	[99]
	OqxAB + AAC(6′)-Ib-cr (n=8)	Chicken, duck	China/2009–10	NAL-OLA-SMX-(AMP-CHL-CIF-ENR-FFC-GEN-TET)	PL – HI2	[99]
	OqxAB + AAC(6′)-Ib-cr + QnrS1 (n=1)	Duck	China/2010	AMP-CHL-CIF-FFC-GEN-NAL-OLA-SMX-TET	PL – HI2	[99]
Virchow	QnrS1	Chicken carcass	Korea/2002	AMP-CEF-STR-SUL- TET-TMP	N	[100]
		Chicken	UK/2004-05	AMP-CIP	N	[101]
		Chicken	Turkey/2005	AMP-NAL	PL – NT	[102]

Antimicrobial abbreviations: AMC, amoxicillin/clavulanate; AMK, amikacin; AMP, ampicillin; CAZ, ceftazidime; CEF, cefalotin; CHL, chloramphenicol; CIF, ceftiofur; CIP, ciprofloxacin; CPD, cefpodoxime; CTX, cefotaxime; ENR, enrofloxacin; FFC, florfenicol; GEN, gentamicin; KAN, kanamycin; LVX, levofloxacin; NAL, nalidixic acid; NEO, neomycin; OLA, olaquindox; RIF, rifampicin; STR, streptomycin; SUL, sulphonamides compound; SXT, trimethoprim/sulfamethoxazole; TET, tetracycline; TMP, trimethoprim; NR, not reported; NT, plasmids that were not typeable with the scheme used; PL, plasmid.
[a]Only references with full-characterized plasmid-mediated quinolone resistance genes were considered.
[b](–), Antibiotic resistance phenotype was not detected using the tested antibiotics and according to the susceptibility criteria adopted. Variable phenotypes were present between curved brackets.

animals, including the animal/food trade, in its dissemination [69,70].

In addition to the therapeutic consequences, antimicrobial resistance acquisition to agents commonly used in livestock production has been associated with the spread of particular *Salmonella* clones in the poultry production environment, which might contribute to their association with human diseases. Interestingly, the high-level resistance to ciprofloxacin (due to *gyrA*/*par*C mutations) and other antibiotics (amoxicillin, streptomycin, spectinomycin, gentamicin, sulfamethoxazole and tetracycline) [39–43] of the previously mentioned *S.* Kentucky ST198-X1-SGI1 strain might also have contributed to its clonal expansion. In the EU, several *S.* Stanley outbreaks linked with the consumption of turkey meat products have been reported, with the clone presenting resistance to nalidixic acid and decreased susceptibility to ciprofloxacin. Additionally, in the recent outbreak in Austria three strains also presented resistance to gentamicin and cephalosporins (CTX-M-15) [36,38]. Several successful *S.* Infantis clones of broiler origin are also characterized by multidrug resistance profiles, including nalidixic acid, tetracyclines, sulphonamides or nitrofurans [26,35,46], antibiotics frequently used in livestock production, which could contribute to their co-selection in the poultry industry.

Data compiled here, highlight the role of the poultry production chain (including poultry meat) as a reservoir of epidemic MDR clones or genes conferring resistance to critical antibiotics, which might spread to humans through the food chain. Globalization of food-animal production is currently posing a major challenge in antimicrobial resistance of zoonotic bacteria like non-typhoidal *Salmonella* with a consequent involvement of human health. In particular in the poultry production pyramid it is crucial to restrict the global use of antimicrobials to minimize the selection of resistant *Salmonella* (from the top of the poultry production pyramid and within flocks), and also to control the spread of MDR epidemic clones by improving biosecurity measures from the farm (e.g. hygiene high standards, vaccination) throughout the food chain (e.g. slaughtering and processing of poultry meat) and control of animal/food trade.

Conclusions

In the last decade, *Salmonella* control programmes, mainly targeting poultry production, have led to a significant reduction in salmonellosis in different countries, including in the EU. This positive effect has been associated with a shift in *Salmonella* serotypes of poultry and human disease, associated with a marked reduction on *S.* Enteritidis and the increase of less common serotypes, driven by the dissemination of particular clones carrying features favouring host (poultry/human) adaptability and frequently MDR.

Poultry has been reported as a source of non-typhoidal *Salmonella* resistant to clinically relevant antibiotics with a remarkable higher incidence reported for middle-income countries, which due to food trade globalization can dramatically challenge worldwide the treatment of severe salmonellosis cases.

Integrated surveillance (collaboration between human health, food safety and animal health—the ‘One Health’ approach) and containment strategies (including farms, retail, catering and consumers) to minimize contamination and reduce the transmission of *Salmonella* (including epidemic clones) along the food chain (from primary production to consumption) are mandatory on a global scale, in particular in the poultry production chain. In addition, continuous surveillance of *Salmonella* resistance levels globally is critical for clinicians to support the best salmonellosis treatment choices, avoid treatment failures, particularly for patients that would benefit from empirical antibiotic treatment.

Continuous monitoring to detect the emergence of any serotype or new clone along the food chain is of critical importance for public health, warning of the emergence of new *Salmonella* food safety risks, involving foodstuffs like poultry meat, which is one of the most consumed and increasing globally traded meat products.

Transparency Declaration

The authors declare no conflict of interest.

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