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Antimicrobial resistance in selected bacteria from poultry

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Abstract

This paper reviews the present state of antimicrobial resistance (AMR) in the zoonotic bacteria *Salmonella*, *Campylobacter jejuni* and *Campylobacter coli*, and in *Escherichia coli* from chickens and turkeys. For *Salmonella*, the frequencies and patterns of AMR vary depending on time, region, serovar, the particular farm, layers versus broilers, and the antimicrobial agent. There is usually a higher frequency of AMR in *Salmonella* from turkeys compared with *Salmonella* from chickens. Clonal and horizontal transmission of AMR occur and there is concern about the spread of transmissible plasmids that encode extended spectrum cephalosporinases. Resistance to fluoroquinolones is generally low. For *Campylobacter*, resistance to tetracycline is usually at moderate to high frequency, resistance to quinolones/fluoroquinolones varies from low to high, and resistance to macrolides is usually low. There are high levels of fluoroquinolone resistance in some countries. Avian pathogenic *E. coli* are often highly resistant, especially to tetracycline, streptomycin, and sulfonamides. Plasmid-mediated resistance is common. High levels of resistance to ciprofloxacin have been reported from China. Commensal *E. coli* from poultry have similar patterns of resistance but at lower frequencies. Integron associated resistance occurs commonly in *Salmonella* and *E. coli* but has not been detected in *Campylobacter*.

Keywords: *Salmonella*, *Campylobacter*, *Escherichia coli*, plasmids, integrons

Introduction

Antimicrobial agents are used extensively in poultry production and are usually administered in the feed or drinking water. Use of antimicrobials has been suggested to be a contributor to the transformation of the poultry industry from large numbers of small-scale farmers to a smaller number of large-scale producers who operate at high efficiency (Bywater, 2005). The antimicrobials are used for growth promotion, disease prophylaxis, metaphylaxis, and treatment. The permitted uses vary among countries and regions. For example, use of antibiotics for growth promotion is banned in the European Union (EU) but permitted in the USA and Canada and much of the rest of the world.

The antimicrobial agents that are available for use as growth promoting agents in the USA and Canada include zinc bacitracin, procaine penicillin, tetracyclines, tylosin, virginiamycin and monensin. Antimicrobials that are used for prophylaxis and therapy include amoxicillin, sulfonamides, tylosin, fluoroquinolones, lincosamides, aminoglycosides, tetracyclines, colistin and pleuromutilins.

Accurate data on antimicrobial use are available for Denmark, where a requirement for prescription for all antimicrobials (except coccidiostats in poultry) permits collection of precise data. The 2007 report from DANMAP (The Danish Integrated Antimicrobial Resistance Monitoring and Research Program) (http://www.danmap.org/pdfFiles/Danmap_2007.pdf) identified a number of shifts that have taken place. In broilers, total consumption of antimicrobials (Animal Daily Doses kg^{-1}) had declined by 26% between 2006 and 2007, and use of fluoroquinolones had decreased by 75% over the same time frame. In turkeys, use of amoxicillin for treatments fell to 47% in 2007 compared with 92% of treatments in the previous year, whereas use of fluoroquinolones increased from 7% of treatments to 16%. These swings in antibiotic use are

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Table 1. Percentages of United States *Salmonella* isolates from poultry that were resistant to selected antimicrobials

	Percent of isolates resistant					
Data source	Lee *et al.* (1993)	Parveen *et al.* (2007)	Zhao *et al.* (2007)		Santos *et al.* (2007)	Nde and Logue (2008)
Samples	Chicken	Chicken	Chicken[a] and turkey[a]		Turkey	Turkey
Year(s) of isolation	NR	2004–2005	2002–2003		2002–2003	2004
Number of isolates	105	425	22	32	42	80
Resistance to 1 or >	57	80	68	91	95	76
Resistance to 3 or >	NR	53	NR	NR	71	NR
Tetracycline	45	73	36	66	86	76
Streptomycin	41	35	46	75	64	40
Ampicillin	ND	53	27	47	36	1
Amoxicillin/ clavulanic acid	ND	52	9	22	0	1
Ceftiofur	ND	52	9	13	2	0
Gentamicin	10	0	9	53	41	5
TMP/SU	8	0	0	9	7	0
Sulfonamides	ND	22	23	53	71	6
Ciprofloxacillin	ND	0	0	0	0	0
Nalidixic acid	ND	0	9	6	5	0
Chloramphenicol	ND	0	9	13	0	ND

[a]Diseased; ND=not done; NR=not reported; TMP/SU=trimethoprim and sulfonamide.

related primarily to variations in outbreaks of disease from year to year and to shifts from one agent to another because of resistance.

Antimicrobial resistance (AMR) data are published primarily for zoonotic pathogens and for indicator organisms that may reflect the pool of AMR genes in the intestine. The major zoonotic pathogens associated with poultry are *Salmonella, Campylobacter jejuni*, and to a lesser extent, *Campylobacter coli*. The usual indicator bacteria are *Escherichia coli* and enterococci. There are variations in results associated with the method of testing for antimicrobial susceptibility. In one study, Nayak *et al.* (2007) tested 105 *S.* Heidelberg isolates for antimicrobial susceptibility by agar disk diffusion, broth microdilution using a Sensititre panel, a broth microdilution done manually, and a Vitek machine with GNS-207 cards. They reported agreements among the four methods of 100% for ciprofloxacin and amikacin; 94–97% for ampicillin, amoxicillin/clavulanic acid, trimethoprim/sulfonamide and chloramphenicol; and 80% for tetracycline and gentamicin. The state of AMR in isolates of these four bacterial species that originate with poultry will be discussed below. The breakpoints that are used also have a profound effect on the results.

AMR in *Salmonella* from poultry

Most *Salmonella* serovars, except *S.* pullorum and *S.* gallinarum and sometimes *S.* Enteritidis, are carried by chickens and turkeys without ill effects. However, chickens and turkeys are major sources of *Salmonella* that cause disease in humans and Salmonella are recovered more frequently from poultry than from red meats. Frequencies of 33% for chicken and 24% for turkey have been compared with 18% for pork and 6% for beef (White *et al.*, 2004).

Certain serovars of *Salmonella* are commonly associated with poultry. These include *Salmonella enterica* serovars Enteritidis, Typhimurium, Kentucky, Heidelberg, Agona, Senftenberg, Montevideo, Mbandaka, Hadar and Thompson. *S.* Enteritidis is found primarily in poultry worldwide and is recovered from humans but uncommonly from other animal species. *S.* Heidelberg is frequently recovered from chickens and eggs in the USA and Canada and has been examined extensively for occurrence of AMR.

There is remarkable variation in resistance of *Salmonella* from chickens and turkeys to a wide range of antimicrobial agents (Tables 1–3). As will be discussed later, possession of conjugative or co-transmissible plasmids encoding resistance is often a major factor in dissemination of resistance. Variation in resistance is also associated with turkeys versus chickens, the country, the year, the serovar of *Salmonella*, broilers versus layers, one farm versus another, and the particular antimicrobial agent. In many studies it is not possible to separate out the influence of these individual factors, but certain trends can be observed. Frequency of resistance tends to be higher in isolates from turkeys compared with isolates from chickens (Tables 1 and 2; Poppe *et al.*, 2001). Overall frequencies and patterns of resistance can vary remarkably from one country to another. Note, for example, the contrast between the high frequencies of resistance to tetracycline and ampicillin in *S.* Enteritidis from Kuwait (Table 2) with the low frequencies of

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Table 2. Percentages of isolates of selected serovars of *Salmonella* from poultry that were resistant to selected antimicrobials

	Percent of isolates resistant							
Authors	1		2	3	4		5	6
Serovar	*S.* Typhimurium		*S.* Infantis	*S.* Enteritidis	*S.* Agona		*S.* Heidelberg	*S.* Heidelberg
Year(s) of isolation	1999		1998–2003	2004–2005	1997–2003		1992–2003	2002–2006
Country	USA		Japan	Kuwait	USA		USA	USA
Samples	Chickens	Turkeys	Chickens and turkeys	Chicken	Chickens	Turkeys	Turkeys	Chickens and turkeys
N	131	38	135	173	53	148	180	288
Tetracycline	34	82	96	97	47	58	29	40
Streptomycin	40	87	97	1	21	30	31	38
Ampicillin	46	79	1	97	6	10	ND	20
Amoxicillin/ clavulanic, acid	29	61	ND	1	2	7	ND	10
Ceftiofur	30	58	ND	0	0	1	3	9
Gentamicin	13	34	ND	4	13	14	25	26
TMP/SU	2	0	ND	4	0	10	21	ND
Sulfonamides	29	79	96	2	34	57	ND	ND
Ciprofloxacillin	ND	ND	36	1	ND	ND	ND	0
Nalidixic acid	1	58	ND	100	0	3	ND	ND
Chloramphenicol	11	63	ND	1	0	6	ND	ND

1, Zhao *et al.* (2005a); 2, Shahada *et al.* (2006); 3, Al-Zenki *et al.* (2007); 4, Douris *et al.* (2008); 5, Kaldhone *et al.* (2008); 6, Zhao *et al.* (2008).
ND=not done; TMP/SU=trimethoprim and sulfonamide.

Table 3. Percentages of *Salmonella* isolates that are resistant vary with time, serovar, and phage type[a]

	Percent of isolates resistant							
Serovar	*S.* Enteritidis			*S.* Typhimurium			*S.* Typhimurium DT104	
Years of isolation	1984–1989	1990–1995	1996–2001	1984–1989	1990–1995	1996–2001	1990–1995	1996–2001
Number of isolates	1071	1466	430	5147	1613	119	22	37
Tetracycline	2.1	1.6	1.6	3.5	5.0	28.6	72.7	67.6
Ampicillin	3.6	2.7	2.8	1.8	4.9	36.1	ND	99.9
TMP/SU	1.2	0.7	0.2	1.3	9.4	4.2	4.5	2.7
Chloramphenicol	0.3	0.2	0.2	1.0	1.9	22.7	72.7	67.6
Kanamycin	0.3	0.2	0.2	0.8	1.4	0.0	0.0	0.0
Furazolidone	0.7	1.2	7.9	0.9	1.7	1.7	0.0	0.0
Flumequine	ND	ND	0.9	ND	ND	1.7	ND	0.0
Susceptible to all	94.3	94.5	87.5	94.5	83.1	57.5	27.3	16.2
Resistant to >1	2.0	1.1	1.4	1.8	3.6	25.2	72.7	67.6

[a]Data from van Duijkeren *et al.* (2003); isolates from the Netherlands.
ND=not done; TMP/SU=trimethoprim and sulfonamide.

resistance to these agents in isolates of the same serovar from the Netherlands (Table 3). Variations over time may be due to differences in serovars. See for example, the increase in tetracycline resistance in *S.* Typhimurium in the Netherlands between 1990–1995 and 1996–2001 and the absence of an increase for *S.* Enteritidis and *S.* Typhimurium DT104 in the same time interval (Table 3).

A dominant clone that carries resistance genes may be the major determinant of resistance patterns. For example, occurrence of the multi-resistant *S.* Typhimurium DT104 may be responsible for a specific pattern of resistance (Table 3). The high frequency of resistance in *S.* Infantis from poultry in Japan (Table 2) probably represents another example of dissemination of a highly resistant clone. Interestingly, Nógrády *et al.* (2007) also identified a dominant clone of tetracycline-streptomycin-sulfonamide-resistant *S.* Infantis in broilers (and humans) in Hungary. On the other hand, some isolates of *S.* infantis are highly susceptible to antimicrobials

The prevalence of AMR is usually lower among layers than among broilers, likely due in part to limitation of antimicrobial use in layer flocks to prevent the occurrence of antimicrobial residues in eggs. A study on 177 *Salmonella* isolates from laying farms in the UK between 2004 and 2005 showed that 77% of the isolates were susceptible to 16 antimicrobials that were tested (Snow *et al.*, 2007). The highest frequencies of resistance were to ampicillin (15%), tetracycline (14%), sulfonamides (11%),

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streptomycin (11%) and chloramphenicol (7%). Most of the resistance was found in *S.* Enteritidis and *S.* Typhimurium. Asai *et al.* (2006) found that the percentages of Japanese *Salmonella* isolates that were resistant to streptomycin, tetracycline, kanamycin and trimethoprim/sulfonamide were 87, 84, 59, and 44%, respectively, for isolates from broilers compared with 32, 14, 0 and 4% for isolates from layers. This pattern of lower frequency of resistance for isolates from layers has been reported by others (e.g. Li *et al.*, 2007a).

The percentage of resistant isolates from eggs (and other sources) varies markedly with the serotype of *Salmonella* and the antimicrobial agent. Low frequencies of resistance to ceftiofur were reported by Frye and Fedorka-Cray (2007), who compared the frequency of 3.6% (28/783) for isolates from eggs with 6.8% (213/3123) and 7.1% (543/7697) for isolates from turkeys and chickens, respectively. In contrast, Musgrove *et al.* (2006) found that 61% of *Salmonella* from shell eggs were resistant to ceftiofur, and 60% of the isolates were resistant to 11 or more antimicrobials. Much of the resistance was associated with *S.* Typhimurium, the most frequently isolated serovar. None of the isolates were resistant to ciprofloxacin, amikacin or trimethoprim/sulfonamide, but 63% were resistant to nalidixic acid. However, some would argue that the breakpoint (4 μg ml^{-1}) set for ciprofloxacin by The National Committee for Clinical Laboratory Standards (NCCLS) is too high (see Poppe *et al.*, 2001).

Certain general trends have been observed with respect to resistance of *Salmonella* to individual antimicrobial agents. Resistance to tetracyline and streptomycin tends to occur at relatively high frequency (Tables 1–3). Resistance to gentamicin is usually low among isolates from chickens and often moderate to high among turkey isolates, and resistance to ciprofloxacin is usually absent or very low (Tables 1 and 2).

Multi-drug resistance has been reported in many serovars of *Salmonella* associated with poultry. Among 38 *S.* Typhimurium isolates from turkeys in the US, Zhao *et al.* (2005a) found that 12 were resistant to 10 antimicrobials and 10 were resistant to 11 agents. Ten of 131 chicken isolates and 2 of 38 turkey isolates had a typical ACSSuT DT104 penta-resistance phenotype. One chicken isolate and two turkey isolates with this pattern that were tested were phage type DT104. A recent study by Andrysiak *et al.* (2008) investigated the genetics of multi-drug resistance among *S.* Heidelberg from humans and poultry agri-food sources. All eight multi-drug resistant (MDR) chicken isolates and one MDR turkey isolate that had an extended spectrum cephalosporin (ESC) resistance carried the $bla_{cmy\text{-}2}$ gene on a plasmid. One isolate also had resistance to tetracycline mediated by *tetB*; one carried *tetB* and *strA*; and one had *tetA, strA, floR* and *sulI*. The association of ESC resistance with large conjugative $bla_{cmy\text{-}2}$ plasmids has been reported by others for this serovar (Kaldhone *et al.*, 2008; Zhao *et al.*, 2008), *Salmonella* Newport (Lynne *et al.*, 2008) and other serotypes (Frye and Fedorka-Cray, 2007).

The $bla_{cmy\text{-}2}$ gene has been detected in *Salmonella* isolates all over the world. One study in Mexico identified ceftriaxone resistance in 77% of *S.* Typhimurium from chickens (Zaidi *et al.*, 2008). However, the strains were considered resistant at 16 μg ml^{-1}, rather than the 64 μg ml^{-1} prescribed by the NCCLS. This lower level may be more appropriate but renders comparisons with other data difficult. In Canada, Poppe *et al.* (2006a) noted that 3 of 35 *S.* Newport strains resistant to the ESCs, the cephamycins and other antimicrobials contained not only the $bla_{CMY\text{-}2}$ gene but several other drug-resistance genes including the flo_{st}, *sulII, tetA, aadA, aadB, dhfr1, qacEΔI-sulI* associated with or inserted into the integron *intI* gene. There is concern about the emergence and spread of ESC resistance because ESCs are important for the treatment of severe salmonellosis, especially in children.

Genes that encode extended spectrum beta-lactamases have also been reported on transposons on transmissible plasmids in Salmonella from poultry (see for example Cloeckaert *et al.*, 2007). These researchers showed that ESC-resistant *Salmonella* from poultry in Belgium carried $bla_{TEM\text{-}52}$ on a Tn*3* transposon on an IncI1 plasmid. The antibiotic resistance profile of these strains included resistance to ampicillin, ceftazidime, cephalothin, ceftriaxone and ceftiofur. The researchers provided evidence that the dissemination of the $bla_{TEM\text{-}52}$ gene in many countries in Europe was due to horizontal transmission. A number of strains examined by Cloeckaert *et al.* (2007) also carried additional drug resistance genes on *Salmonella* genomic island 1 (SGI1), a complex class 1 integron.

Class I integrons appear to be important in the acquisition and spread of genes that encode AMR in many serovars of *Salmonella* from poultry. In one study (Riaño *et al.*, 2006), three *Salmonella* isolates from poultry were shown to possess class 1 integrons that carried $bla_{TEM\text{-}1b}$ and $bla_{CTX\text{-}M\text{-}9}$ genes as well as *dfrA16*, *aadA2*, *sul1* and *sul2*. One of the isolates also had *tet*(*A*) in the integron. In another study, 28% of *S.* Typhimurium isolates from chicken and 24% of isolates from turkeys carried a 1-kb integron with *aad*A2, encoding resistance to streptomycin/spectinomycin, or a combination of the 1-kb integron and a 1.2-kb integron that carried $bla_{pse\text{-}1}$ that encoded resistance to ampicillin (Zhao *et al.*, 2005a). Class 1 integrons that carry other *bla* genes and resistances to other antimicrobial agents have been reported in *Salmonella* (see for example, Cloeckaert *et al.*, 2007).

Nalidixic acid resistant strains show reduced susceptibility to ciprofloxacin (Poppe *et al.*, 2001) and are more readily converted to high-level fluoroquinolone resistance than are nalidixic acid susceptible strains. Interestingly, a very high frequency of resistance of *Salmonella* to nalidixic acid has been reported for isolates from Kuwait (100%; Al-Zenki *et al.*, 2007) and Venezuela (95%; Boscán-Duque *et al.*, 2007). Nalidixic acid resistance is

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Table 4. AMR in *C. jejuni* isolated from poultry

	Percent of isolates resistant								
Data source	1	2	3	4	5	6	7	8	9
Country	USA	USA	Canada	Canada	France	Estonia	Thailand	Australia	Iceland
Number of isolates	426	188	228	332	263	131	69	125	349
Tetracycline	47	99	63	50	57	ND	26	19	0.3
Erythromycin	1	0	5	2	0.3	ND	17	0	0
Enrofloxacin	ND	ND	ND	ND	17	ND	ND	ND	1
Ciprofloxacin	17	30	0	4	ND	73	77	0	ND
Nalidixic acid	17	30	0	4	25	ND	77	20	1
Ampicillin	ND	ND	ND	11	23	76	22	19	0

1, NARMS (2006); 2, Son *et al.* (2007); 3, CIPARS (2005); 4, Larkin *et al.* (2006); 5, Avrain *et al.* (2003); 6, Roasto *et al.* (2007); 7, Boonmar *et al.* (2007); 8, Miflin *et al.* (2007); 9, Thorsteinsdottir *et al.* (2008).

associated with mutations in the quinolone resistance-determining region (QRDR) of genes that encode gyrase or topoisomerase IV. Increased efflux of the drug through the AcrAB-TolC efflux system may also mediate resistance to quinolones. Plasmid-borne *qnr* genes are rarely implicated in fluoroquinolone resistance.

C. jejuni and *C. coli*

Although there is a lack of internationally standardized methods for antimicrobial susceptibility tests for *Campylobacter*, there is little variation in the results obtained with the commonly used protocols for disc diffusion, agar dilution, or the Epsilometer-test (E-test) (reviewed by Moore *et al.*, 2006). AMR to human isolates of *Campylobacter* is highly variable within and among countries. Padungton and Kaneene (2003) noted a generally high prevalence of resistance to tetracycline and fluoroquinolones and moderate to low levels for other agents. A similar pattern has been reported for isolates from poultry, which are a major source of campylobacteriosis in humans.

Tetracyclines are used extensively for therapy for infections in poultry in some countries such as the United Kingdom (Piddock *et al.*, 2008). There is therefore concern about tetracycline resistance in *C. jejuni* as resistance is usually carried on a conjugative plasmid with the *tet*(*O*) gene. Resistance to tetracycline in *C. jejuni* has been reported to be as high as 99.5% in one US study (Son *et al.*, 2007) and as low as 0.3% in Iceland (Table 4). Several studies on AMR in poultry isolates have been conducted in Iceland, a country in which antimicrobial agents are not used in chicken production. Interestingly, the levels of resistance to all the antimicrobials tested are either 0 or no more than 1% in *C. jejuni* from chickens in Iceland (Thorsteinsdottir *et al.*, 2008; Table 4). Differences in extent of AMR by country are also shown in Table 5, in a single study involving the same procedures and the same time frame for four countries. Although the number of isolates from Swedish poultry was low, it is clear that the general level of resistance was much lower than for the other European countries.

Table 5. Variations in AMR in *C. jejuni* isolated from chickens in four European countries[a]

	Percentage of isolates resistant			
Country	Netherlands	France	UK	Sweden
Number of isolates	116	213	200	16
Tetracycline	30	58	35	0
Erythromycin	3	8	2	0
Ciprofloxacin	34	32	6	0
Nalidixic acid	34	32	6	0
Gentamicin	0	0	0	0

[a]From Bywater *et al.* (2004).

Fluoroquinolones are an important part of the antimicrobial arsenal used to treat campylobacteriosis in adults. Quinolone resistance has therefore been monitored in many countries. Important aspects of *C. jejuni* and *C. coli* resistance to fluoroquinolones have been reviewed by Zhang *et al.* (2003): resistance is most commonly due to mutations in the QRDR regions of *gyrA*, with high levels of resistance to ciprofloxacin associated with the Thre-86-Ile mutation and intermediate levels associated with the Asp-90-Asn or the Thr-86-Lys mutation; a functional efflux pump is required for the *gyrA* mutations to confer resistance; over-expression of the efflux pump is not required for high-level resistance. The fact that a single mutation in *gyrA* can confer high-level resistance to fluorquinolones indicates that such resistance may occur readily. Furthermore, resistance is not accompanied by increased fitness costs and colonizing ability appears to be enhanced. Selection pressure associated with oral administration of fluoroquinolones in humans or animals results in emergence of fluoroquinolone resistant *C. jejuni* (Moore *et al.*, 2006; van Boven *et al.*, 2003; reviewed in Zhang *et al.*, 2003).

A 2001 report from Japan showed that 32% of 68 *Campylobacter* isolates from broilers were resistant to fluoroquinolones (Chuma *et al.*, 2001). Resistance was associated with a mutation in *gyrA* (T(86)→I(86)). In Korea, resistance to ciprofloxacin was detected in 88%

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Table 6. AMR in *C. coli* isolated from broilers

	Percent of isolates resistant				
Data source	1	2	3	4	5
Country	USA	Canada	France	Australia	Iceland
Year of isolation	2006	NR	2004	NR	2001–2005
Number of isolates	145	101	74	27	13
Tetracycline	47	59	72	15	0
Erythromycin	6	20	18	11	0
Enrofloxacin	ND	ND	ND	ND	54
Ciprofloxacin	22	43	32	0	ND
Nalidixic acid	21	44	54	0	31
Ampicillin	ND	19	24	7	0

1, NARMS (2006); 2, Larkin *et al.* (2006); 3, Gallay *et al.* (2007); 4, Miflin *et al.* (2007); 5, Thorsteinsdottir *et al.* (2008).
ND = not done; NR = not reported.

of 594 *Campylobacter* isolates from broilers (Kang *et al.*, 2006). A pattern of moderately high levels of resistance to fluoroquinolones has been reported in several other countries (Tables 4 and 5). Interestingly the frequency is zero in Australia (Table 4) and in Sweden (Table 5). Miflin *et al.* (2007) have suggested that the absence of resistance to fluoroquinolones in *Campylobacter* originating from Australian poultry may be because fluoroquinolones have never been licensed for use in poultry in Australia. It is interesting that there were high levels of resistance to enrofloxacin and nalidixic acid in *C. coli* isolates from Iceland, although antimicrobials are not used in chicken production. The number of isolates examined was low and it is not known whether a similar percentage would be obtained with a larger isolate collection.

Because of a concern with an increase in fluoroquinolone-resistant *Campylobacter* infections in humans, the Food and Drug Administration in the United States proposed in 2000 that the fluoroquinolone enrofloxacin be withdrawn from use in poultry. This drug had been used for treatment of colibacillosis in chickens and turkeys. The withdrawal went into effect in 2005 after a long legal battle (Nelson *et al.*, 2007).

There is also concern about resistance to macrolides in *C. jejuni* and *C. coli* from poultry as erythromycin is one of the drugs of choice for treating campylobacteriosis in humans. In the USA and Canada, tylosin is frequently added to poultry feed at subtherapeutic levels as a growth-promoting agent. Resistance to tylosin results in cross-resistance to erythromycin, which belongs to the same chemical class (macrolide) as tylosin. In general, levels of resistance to erythromycin are higher in *C. coli* than in *C. jejuni* (Tables 4–6). A Japanese study identified a high level of erythromycin resistance in *C. coli* isolates but none in *C. jejuni* isolated from broilers during 1992–1999 (Chuma *et al.*, 2001). Interestingly, Ladely *et al.* (2007) showed a difference in erythromycin resistance in *C. jejuni* and *C. coli* when chickens were exposed to macrolide-susceptible *C. jejuni* or *C. coli* and subsequently fed diets with therapeutic or subtherapeutic levels of tylosin. Pooled results showed that erythromycin resistance was present in 71% of the *C. coli* isolates compared with 37% of the *C. jejuni* isolates that were recovered from the chickens. Also, 63% of the *Campylobacter* isolates recovered from chickens on tylosin at the subtherapeutic level were erythromycin resistant whereas only 11.4% of isolates from chickens fed the therapeutic dose were resistant.

Table 7. AMR in APEC.

	Percent of isolates resistant	
Data source	Zhao *et al.* (2005b)	Yang *et al.* (2004)
Country	USA	China
Number of isolates	95	71
Tetracycline	87	100
Streptomycin	86	80
Gentamicin	69	30
Sulfonamides	93	79
TMP/SU	16	63
Ampicillin	45	77
Amoxicillin/ clavulanic acid	36	0
Cephalothin	37	27
Ceftiofur	13	0
Ceftriaxone	3	0
Nalidixic acid	59	100
Enrofloxacin	16	90
Ciprofloxacin	3	73
Chloramphenicol	11	24

TMP/SU = trimethoprim and sulfonamide.

E. coli

Avian pathogenic *E.* (APEC) cause primarily a respiratory/septicemic disease in chickens and turkeys and antibiotics are used to treat these infections. Resistance of these strains to antimicrobials is therefore important in the selection of agents for treatment. Typical data for AMR in APEC are shown in Table 7. Zhao *et al.* (2005b) tested 95 APEC isolates from northern Georgia, USA (Table 7), and

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Table 8. AMR in *E. coli* isolated from broilers

	Percentage of isolates resistant						
Country	Netherlands[a]	France[a]	UK[a]	Sweden[a]	Iran[b]	USA[c]	Canada[d]
Number of isolates	204	199	200	199	181	418	218
Tetracycline	61	85	54	7	71	51	57
Ciprofloxacin	3	4	0.5	0	42	0	0
Ampicillin	37	51	43	5	67	20	38
Cefepime	0	0	0	0	ND	ND	ND
Cefotaxime	0	0	0	0	ND	ND	ND
Gentamicin	4	5	3	0	7	37	11
Streptomycin	38	47	42	7	ND	48	44
TMP/SU	38	50	47	2	71	9	9
Chloramphenicol	4	17	2	0.5	64	3	7

[a]Data from Bywater *et al.* (2004); [b]Moniri and Dastehgoli (2005); [c]NARMS (2006); [d]CIPARS (2005).
ND = not done; TMP/SU = trimethoprim and sulfonamide.

reported that resistance to quinolones was associated with mutations in *gyrA*, *gyrB* and *parC*, and with up-regulation of the multi-drug resistance pump encoded by *acrAB*. Resistance to three or more antimicrobials was found in 92% of the isolates. Ribotyping of 56 nalidixic acid resistant isolates showed that quinolone resistance was present in multiple ribotypes and could therefore not be attributed to the presence of a few resistant clonal groups. Yang *et al.* (2004) noted that 80% of 71 *E. coli* isolated from the livers of chickens that had died on 10 poultry farms in China were resistant to eight or more antibiotics (Table 7). All the isolates were resistant to nalidixic acid and tetracycline, but there was no resistance to the third generation cephalosporins ceftiofur and ceftriaxone, or to amoxicillin/clavulanic acid. The high levels of resistance to fluoroquinolones are in marked contrast to the low levels in the US isolates (Zhao *et al.*, 2005b; Table 7). Fluoroquinolone resistance was associated with the expected mutations in *gyrA* and *parC*. Integrons that were 0.7, 1.0 or 1.5 kb were present in 42 of the 72 isolates and encoded resistance to aminoglycosides, trimethoprim and beta-lactams. The *qnr* gene was not detected in association with the integrons. Similarly high levels of AMR were observed by Li *et al.* (2007b) who examined 70 *E. coli* isolates recovered from diseased chickens in China between 2004 and 2005. The isolates showed frequencies of resistance of 100% to tetracycline and trimethoprim/sulfonamide and 79–83% to chloramphenicol, ampicillin, ciprofloxacin and enrofloxacin. Petersen *et al.* (2006) in Denmark described vertical transmission of a pathogenic O45 strain of *E. coli* that was resistant to fluoroquinolone. They showed that a single clone was responsible and the bacterium recovered from five broiler chicks could be traced back to the broiler parents. The spread of AMR is facilitated by the pyramidal structure of the poultry industry and other studies have traced the spread of *Salmonella* from primary breeder flocks through multiplier flocks to rearing flocks.

Large plasmids are commonly found in APEC strains. In 2005, the DNA sequence for a 101-kb transmissible IncF plasmid from an O2 APEC strain was published (Johnson *et al.*, 2005). The plasmid has a class 1 integron and encodes resistance to tetracycline, sulfonamides, aminoglycosides, trimethoprim, and beta-lactams as well as resistance to heavy metals. In 2006, the same group (Johnson *et al.*, 2006) reported the DNA sequence of a 241-kb transmissible IncHI2 plasmid which encodes resistance to tetracycline, streptomycin, gentamicin and sulfonamides.

Numerous studies on AMR have been done on commensal *E. coli* from poultry. European data show a remarkable difference in the low frequencies of resistance to all antimicrobial agents among *E. coli* from poultry in Sweden compared with high levels for some agents in the other countries (Table 8; Bywater *et al.*, 2004). In the Netherlands, France, and the UK, the pattern is one of moderately frequent resistance to tetracycline, streptomycin, ampicillin and trimethoprim/sulfonamide, low frequencies for ciprofloxacin, gentamicin and chloramphenicol, and no resistance to the cephalosporins. This pattern is not always seen in other countries. Moniri and Dastehgoli (2005) noted resistance to nalidixic acid in 100% of 181 *E. coli* from broilers; resistance to ciprofloxacin was detected in 42% of the isolates. They showed that the frequency of resistance to ciprofloxacin was 50% in flocks which had used flumequine and enrofloxacin and 34% in flocks which had not used these drugs.

Plasmid-mediated quinolone resistance has also been detected at low prevalence and involves Qnr proteins that interact with topoisomerase, a quinolone-acetylating enzyme, and a Qep pump. The Qnr proteins confer low-level resistance but may be important in enhancing selection of high-level fluoroquinolone resistance (Yue *et al.*, 2008).

In addition to fluoroquinolone resistance, there is considerable interest in resistance to beta-lactams, especially extended spectrum beta-lactams. In one study in Belgium, Smet *et al.* (2008) recovered 295 ceftiofur-resistant *E. coli* from cloacal swabs of 489 broiler chickens from five farms. This high frequency occurred although

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cephalosporins have not been licensed for use in poultry in Belgium since 2000. The authors suggest that co-selection based on resistance to other agents may be involved. A total of 45% of these isolates produced ESBL, 43% produced AmpC beta-lactamase, and 12% produced a combination of the two and a wide range of beta-lactamase genes was identified, including the plasmid-borne bla_{CMY-2}. The bla_{CMY-2} plasmid has been shown by Poppe *et al.* (2006b) to be readily transmissible in the intestine of turkey poults. A conjugative plasmid carrying the bla_{CMY-2} gene readily transferred from a commensal *E. coli* O168:H7 strain to *S.* Newport and to a commensal *E. coli* O101:H9 and the *E. coli* O101:H9 likely transferred the bla_{CMY-2} back again to susceptible *S.* Newport bacteria.

A study on 194 *E. coli* recovered from shell eggs in the US determined that 73% were susceptible to all seven antimicrobials that were tested (Musgrove *et al.*, 2006). Isolates that were resistant were mostly resistant to tetracycline (17%). A similarly moderate frequency of resistance was reported for *E. coli* from 122 laying hens in Switzerland (Lanz *et al.*, 2003). Highest resistance was to tetracycline and sulfonamides (26%) and streptomycin (17%).

Price and coworkers (2007) tested the hypothesis that workers exposed to live chickens in the broiler industry were at increased risk of being colonized with antimicrobial resistant *E. coli*. Working with gentamicin resistance, they showed that 50% of the individuals working with poultry were colonized with resistant *E. coli*, compared with 3% of individuals in the community and 6.3% of hospitalized persons. Johnson *et al.* (2007) noted that extra-intestinal infections caused by *E. coli* in humans contribute to illnesses, deaths and healthcare costs and argued that resistance to first-line antimicrobials such as trimethoprim/sulfonamide, quinolones/fluoroquinolones and ESCs in *E. coli* was therefore a concern. They compared *E. coli* that were resistant to these agents and *E. coli* that were susceptible to these antimicrobials, with resistant and susceptible organisms isolated from humans and poultry. They concluded that resistant human isolates were more closely similar to poultry isolates than to drug-susceptible human isolates, whereas drug-resistant poultry isolates were more similar to susceptible poultry isolates. They suggested that it was likely that the drug resistant human isolates were derived from poultry whereas the drug-resistant poultry isolates were derived from drug-susceptible poultry isolates.

Conclusions

Much of the interest in AMR of bacteria that reside in poultry and other food animals is sparked by a concern for human health that is threatened by zoonotic pathogens and by selection for AMR determinants. Increasing AMR also threatens agriculture, as bacterial diseases in animals become more difficult to treat. Prudent use of antimicrobials will be necessary to preserve these valuable drugs for use in both animals and humans. The development of increasing prevalence of resistance to nalidixic acid is of concern as it increases the risk for resistance to fluoroquinolones through a second mutation. The dynamics of transmission of antimicrobial drug resistance and the evolution of populations of bacteria that are increasingly resistant to antimicrobials are very complex (see the article by Boerlin and Reid-Smith). The transmission of drug resistance genes is facilitated by a number of factors (selection and co-selection through the use of antimicrobials in animals and humans; large-scale animal production, food processing and distribution; and absence of regulations and/or oversight in some countries) and is a major contributor to the trends towards bacterial populations with higher frequencies of resistance to antimicrobials.

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