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Review

Current Status of Antibiotic Resistance in the Six Major Foodborne Bacteria

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ABSTRACT: Bacterial pathogens still represent a serious public health issue. Special attention should be paid to bacteria that are usually transmitted through food. More relevantly, several isolates found in food exhibit (usually high) antibiotic resistance, which, in the case of human or animal infection, will reduce treatment efficacy. Hence, this review seeks to summarize and make available to researchers on the subject the most recent findings regarding antibiotic resistance profiles of common pathogens that are transferred into food. The bacterial pathogens responsible for most poisonings and illnesses include *Salmonella* spp., *Listeria* spp., *Campylobacter* spp., *Staphylococcus* spp., *E. coli* pathotypes, and *Cronobacter* spp. Therefore, we will focus this review on these pathogens. In this way, this writing will not only provide valuable information regarding which matrices are more susceptible to bacterial contamination, but in the end, the reader will be able to identify which antibiotics have been tested on these isolates and where the gaps are in the phenotypic determination of resistance to antibiotics, while highlighting several genotypic traits specific to some of these bacteria.

Keywords: Pathogens; Bacteria; Foodstuffs; Antibiotic; Resistance

1. Introduction

1.1. Foodborne Bacterial Pathogens

Foodborne pathogens have gained notoriety because, despite sustained quality practices and regulations regarding bacterial load in food production, foods are still found to be contaminated with bacteria. Pathogens are usually poor competitors and do not survive in the presence of existing food microflora [1] or after food processing or unit operations for food preservation (e.g., vacuum, pasteurization, nano/microfiltration) [2]. However, this ecological defense is not a guarantee of safety; food extended, erroneous manipulation, or bacterial survival mechanisms favor pathogen persistence. FDA food recalls are targeted actions to remove or correct food products that violate U.S. food safety laws. They are primarily driven by microbiological contamination, undeclared major allergens (such as milk or peanuts in mislabeled packages), and foreign objects. For example, of the 233 total food and beverage recalls from 2023, 70 (30.0%) were associated with possible or confirmed foodborne illness/bacterial contamination.

Understanding the relevance of these recalls involves knowing how the FDA classifies and communicates the associated health risks. The most common contaminants were found to be 28 (41.2%), 32 (47.0%), 3 (4.4%), 4 (5.9%), and 1 (1.5%) for *Salmonella* spp., *Listeria monocytogenes*, *E. coli*, *Cronobacter sakazakii*, and *Clostridium botulinum*, respectively (Table 1). *C. sakazakii* has been the subject of contamination and product recalls of powdered and dairy formulas in Chile as well [3]. More recently, the most serious food recalls have involved *Salmonella* contamination in foods such as ice cream [4], cereals [5], peanuts [6], soft cheese [7], shelled walnuts [8], crispy fried onions [9], and hummus (Table 1) [10]. Recent French data indicate that, with some yearly decline in the number of cases, meats, dairy, and fishery products are among the most recalled products [11].

Table 1. List of Governmental food recalls requested within a two-year window [1].

Product Description [2]			**Recall Reason and Description**		
Year 01–12/2023					
Salmonella	*Listeria monocytogenes*	*Escherichia coli*	*Cronobacter* spp.	*Clostridium botulinum*	Summary
28 (41.2%)	32 (47.0%)	3 (4.4%)	4 (5.9%)	1 (1.5%)	68
Alfalfa Sprouts			Contamination with Shiga toxin-producing *E. coli*		
All Purpose Flour, bleached and unbleached			Potential to be contaminated with *Salmonella*		
Bagged Collard Greens			Possible *Listeria monocytogenes* contamination		
Bean Sprouts			*Listeria monocytogenes*		
Biltmore Smoked Wild Sockeye Salmon			Potential Foodborne Illness/*Listeria*		
Black Fungus (Nam Meo)			*Salmonella*		
Breeders Choice Raw Pet Food 2 lb			*Salmonella* contamination		
Cantaloupe Chunks and Cubes and Fruit Mixes and Medleys Containing Cantaloupes (×5)			Potential *Salmonella* Contamination		
Cheese products			Potential *Listeria monocytogenes* contamination		
Cocktail Shrimp			*Listeria monocytogenes*		
Dairy and Non-Dairy ice cream (parve), sorbet, cakes, and novelty items			Potential to be contaminated with *Listeria monocytogenes*		
Diced onions			*Salmonella*		
Diced Organic Butternut Squash			Potential *Escherichia coli* O45 contamination		
Dog and Cat food			Potential to be contaminated with *Salmonella*		
Dog food, Select Beef Meal & Brown Rice Formula			Potential *Salmonella* contamination		
Dry Dog, Dry Cat, and Catfish Food			Potential *Salmonella* contamination		
Enfamil Prosbee Simply Plant-Based Infant Formula in 12.9 oz containers			Potential *Cronobacter sakazakii* contamination		
Enoki Mushrooms (×4)			*Listeria monocytogenes*		
Fresh Cantaloupe (×2)			Potential to be contaminated with *Salmonella*		
Frozen Fruit			Potential for *Listeria monocytogenes* contamination		
Fruit cups and trays containing cantaloupe (×4)			Potential to be contaminated with *Salmonella*		
GEISHA Medium Shrimp, 4 oz can (×2)			Potential contamination with *Clostridium botulinum*		
Gift Baskets with Quaker Chewy Granola Bars			Potential *Salmonella* contamination		
Granola Bars and Granola Cereals			Potential for *Salmonella* contamination		
Ground Cumin			*Salmonella*		
Ice Cream, Yogurt, Ice Cream Bars, and Gelato in a Variety of Flavors			Potential to be contaminated with *Listeria monocytogenes*		
Kale, Spinach, Collard Green products (×2)			Potential for *Listeria monocytogenes*		
Lettuce & Salad Kits (×2)			*Listeria monocytogenes*		
Mini Chunk Chicken Recipe Dry Dog Food			Potential *Salmonella* contamination		
Multiple frozen fruits with mango products			Potential *Listeria monocytogenes* contamination		
Mung Bean Sprouts (×2)			*Listeria monocytogenes*		

Numerous human foods, animal (pet) food, medical devices, and drug products	Potential *Salmonella* contamination and presence of rodent activity at the distribution center & temperature abuse
Nutramigen Powder infant formula in 12.6 and 19.8 oz cans	Potential *Cronobacter sakazakii* contamination
Organic frozen Pineapple and Frozen Fruit Blend Containing Organic Frozen Pineapple	Potential to be contaminated with *Listeria monocytogenes*
Organic green kiwifruit	Possible *Listeria monocytogenes* contamination
Organic Tahini	Potential Foodborne Illness/*Salmonella*
Pepper Jack Raw Milk Cheese	Presence of *Listeria monocytogenes*
Powdered Infant Formula (×2)	Potential *Cronobacter sakazakii* contamination
Premade Salads	Potential *Listeria monocytogenes* contamination
Ready-to-Eat (RTE) Sandwiches, Salads, Yogurt, Wraps, and related products	Potential *Listeria monocytogenes* contamination
Refrigerated and Frozen Cooked Lobster	Possible *Listeria monocytogenes* contamination
Salad Greens	Due to potential *Escherichia coli* O157:H7 contamination
Salads Kits	*Listeria monocytogenes*
Sambhar Masala and Garam Masala Spices	Potential Foodborne Illness-*Salmonella*
Soft Serve ice cream and sorbet cups	Possible *Listeria monocytogenes* contamination
Sophelise, Tobasi, and Berkshire Bloom Cheeses (×2)	Potential contamination with *Listeria monocytogenes*
Soybean Sprouts in 1 lb bags	Potential contamination of *Listeria monocytogenes*
Spinach	*Listeria monocytogenes*
Strawberry Granola & Greek Yogurt Parfait Bar	*Listeria monocytogenes*
Various Deli Salads	The product may be contaminated with *Listeria monocytogenes*
Whole Cantaloupe	Potential to be contaminated with *Salmonella*
Whole Peaches, Plums, and Nectarines	Potential to be contaminated with *Listeria monocytogenes*

Year 01–12/2024					
Salmonella	*Listeria monocytogenes*	*Escherichia coli*	*Cronobacter* spp.	*Clostridium botulinum*	Summary
43 (38.7%)	57 (51.3%)	7 (6.3%)	1 (0.9%)	3 (2.7%)	111

Falafel Bites	Potential Shiga toxin-producing *Escherichia coli* O121:H19 contamination
Crab meat	Potential foodborne illness—*Listeria monocytogenes*
Cashews	Potential to be contaminated with *Salmonella*
Aged Cojita Mexican Cheese	Potential to be contaminated with *Listeria monocytogenes*
Alfalfa and Onion Sprouts	*Listeria monocytogenes*
Atovaquone oral suspension, USP, 750 mg/5 mL	Potential *Bacillus cereus* contamination
Turkey Sandwiches	Potential foodborne illness—*Listeria monocytogenes*
Baby Arugula	Potential to be contaminated with *Salmonella*
Bacon Ranch Crunch Chopped Salad Kit (×2)	Potential to be contaminated with *Listeria monocytogenes*
Beef and Chicken Dog Foods	Due to Potential *Salmonella* and *Listeria*
Black bean six-layer dip	Potential to be contaminated with *Listeria monocytogenes*
Southwest Chipotle Crunch Salad Kit	Potential to be contaminated with *Listeria monocytogenes*
California Shelled Walnuts, Organic Light Halves and Pieces	Due to potential *Escherichia coli* O157:H7 contamination
Chicken Chips Dog Treats (×2)	Potential to be contaminated with *Salmonella*
Cereal, Bars, and Snacks	Potential to be contaminated with *Salmonella*

Cheese, Yogurt, and Sour Cream	Expanded recall for potential *Listeria monocytogenes* contamination
Chicken Enchiladas Verde, Cilantro Salad Dressing, Elote Chopped Salad Kit, and Southwest Salad	Potential to be contaminated with *Listeria monocytogenes*
Chicken Street Taco Kit (×6)	Potential to be contaminated with *Listeria monocytogenes*
Chillimami Sauce	Potential foodborne illness—*Clostridium botulinum*
Chocolate Caramel Corn and Candy Tray	Possible *Salmonella* contamination
Cilantro Line Crema, Everything Sauce Fiesta, Cilantro Cotija Dressing, Poblano Caesar Dressing, Cilantro Dressing, Street Taco Express Meal Kit	Potential to be contaminated with *Listeria monocytogenes*
Coffee Products	Potential to be contaminated with *Clostridium botulinum*
Cold Smoked Capelin	Potential to be contaminated with *Clostridium botulinum*
Cucumbers and Salads with Kit	Potential Foodborne Illness—*Salmonella*
Curly Mustards Greens	Potential foodborne illness—*Listeria monocytogenes*
Cucumber Slices	Potential Foodborne Illness—*Salmonella*
Eggs (×2)	Potential to be contaminated with *Salmonella*
Enchiladas	Potential to be contaminated with *Listeria monocytogenes*
Enoki Mushroom (×3)	Potential to be contaminated with *Listeria monocytogenes*
Fresh Express Salsa Ensalada Kit, Southwest Chopped Salada Kit (×2)	Potential to be contaminated with *Listeria monocytogenes*
Fresh Guacamole Products	Potential to be contaminated with *Listeria monocytogenes*
Fresh Organic Basil (×2)	Potential to be contaminated with *Salmonella*
Frozen Waffle Products (×2)	Potential foodborne illness—*Listeria monocytogenes*
Chicken Caesar Salad Bowl	Potential foodborne illness—*Listeria monocytogenes*
Green Onions	*Salmonella*
Ground black pepper	Potential Contamination with *Salmonella*
Gyro Family Kit	Potential Foodborne Illness—*Salmonella*
Ham & Cotija Torta Sandwich on Telera Roll	Potential to be contaminated with *Listeria monocytogenes*
Hedgehog food (×2)	Potential Contamination with *Salmonella*
Honey Roasted Peanuts and Deluxe Lightly Salted Mixed Nuts	Potential to be contaminated with *Listeria monocytogenes*
Ice Cream Products	*Listeria monocytogenes*
Individually Wrapped Sandwiches	Potential to be contaminated with *Listeria monocytogenes*
Jalapeños, Green Peppers, Green Beans	Potential foodborne illness—*Listeria monocytogenes*
Smoked Salmon	Potential foodborne illness—*Listeria monocytogenes*
Kitten Grind, Kitten Mix, Puppy Mix	Potential Contamination with *Salmonella* and *Listeria monocytogenes*
Macadamia in the Raw	Potential Contamination with *Salmonella*
Mango bars in the Variety Pack	Potential Contamination with *Salmonella*
Meal Kits Containing Chicken	Potential to be contaminated with *Listeria monocytogenes*
Mediterranean Inspired Party Tray	
Mexican Style Street Corn Bites	Potential to be contaminated with *Listeria monocytogenes*
Moong Dal, Crunchy Green Gram	Potential Contamination with *Salmonella*
Multiple Cucumber Products (×3)	Potential Foodborne Illness—*Salmonella*
Thyroid Formula	Potential to be contaminated with *Salmonella*

Organic Carrots and Celery	Potential Foodborne Illness—Shiga toxin-producing *Escherichia coli* O121:H19
Organic Chia Seeds	Potential Presence of *Salmonella*
Organic Whole Carrots and Baby Carrots	Potential Foodborne Illness—Shiga toxin-producing *Escherichia coli* O121:H19
Parrot Food	Due to Potential *Salmonella* contamination
Pepperjack Cheeseburger, Bacon Cheeseburger	Potential foodborne illness—*Listeria monocytogenes*
Plain Whipped Cream Cheese, Plain Cream Cheese, and Cookies & Cream Mix	Potential to be contaminated with *Salmonella*
Powdered Goat Milk Infant Formula	*Cronobacter* spp. contamination
Puppy Mix	Potential Foodborne Illness—*Salmonella*
Queso de Mano PAISA	Potential to be contaminated with *Listeria monocytogenes*
Raw Cheddar Cheese	Possible Contamination *E. coli* O157:H7
Raw Dog and Cat Food	*Listeria monocytogenes*
RTE Fruit and Vegetables	Potential foodborne illness—*Listeria monocytogenes*
Shelled Walnuts	Potential foodborne illness—*Listeria monocytogenes*
Smoked Norwegian Salmon Slices—Toast	Potential to be contaminated with *Listeria monocytogenes*
Soft Ripened Cheese (×2)	Potential to be contaminated with *Listeria monocytogenes*
Soybean Sprouts	Potential to be contaminated with *Listeria monocytogenes*
Spinach and Salad Kits (×3)	Potential to be contaminated with *Listeria monocytogenes*
Saint Jerome Cheese	Potential foodborne illness—*Listeria monocytogenes*
Tahini (×2)	Potential to be contaminated with *Salmonella*
Beef & Lamb Gyro Sandwich Express Meal Kits	May be Contaminated with *Salmonella*
Torta Sandwiches	Potential to be contaminated with *Listeria monocytogenes*
Various Confectionery Products (×2)	Potential Contamination with *Salmonella*
Vegetable Medleys and Whole Organic Carrots	Potential Foodborne Illness—Shiga toxin-producing *Escherichia coli* O121:H19
Vegetable products (×4)	Potential foodborne illness—*Listeria monocytogenes*
Whole Cucumbers (×5)	*Salmonella*
Yogurt-covered pretzels	Potential to be contaminated with *Salmonella*

[1] Adapted from the United States Food and Drug Administration (US FDA) [12]. [2] Counters expressed as ×*n* represent the number of times a specific food item has been subjected to a safety callback.

1.2. Official Guidelines: Regulatory Documents, Methods, and Institutes

The presence of pathogens, especially in RTE foods, and the evidence of antibiotic resistance among these strains have evolved into a worldwide public health challenge [13,14]. Hence, detection and constant surveillance programs of these pathogens in foods are paramount. A primer on novel approaches to analyzing these bacteria in food can be found in recent work [15,16]. From the regulatory standpoint, the European Commission decision 2020/1729 includes the surveillance and antibiotic resistance report of the specific pathogens *Salmonella* spp., *E. coli* (especially those strains with extended spectrum β-lactamases (ESBL), AmpC β-lactamases, or carbapenemases), *C. coli*, *C. jenuni*, *Enterobacter faecium*, *E. faecalis* in foods such as broilers, laying hens, fattening turkeys and pigs, bovine animals under a year of age, fresh meat from broilers, turkeys, pigs, and bovine animals. Analogously, it has regulations regarding microbiological criteria for foodstuffs, specifically, 2073/2005/EC.

Official methods for detection of pathogens include ISO 6579-1:2017, ISO 11290-1:2017, ISO 10272-1:2017/Amd 1:2023, ISO 6888-1:2021, ISO 22964:2017 [17], ISO 16649-1:2018, DIS 13136-1, for *Salmonella* spp., and for *Listeria* spp., *Campylobacter* spp., *Staphylococcus* spp., *Cronobacter* spp., and *E. coli*, respectively. Relevant methods for food analysis also comprise ISO 20976-1:2019, 23418:2022, and 20976-2:2022. These methods have also evolved with the advent of new technologies for detecting and controlling foodborne pathogens [18–24]. Rapid, reliable, and cost-effective methods for bacteria detection are of paramount importance in food safety monitoring [25].

In the case of regulations for antimicrobial susceptibility testing, the European Committee on Antimicrobial Susceptibility Testing (EUCAST) sets epidemiological cut-off values (ECOFFs) and tentative ECOFFs (TECOFFs). For the USA, the Clinical & Laboratory Standards Institute CLSI sets these guidelines, and a workbook is available [26]. Additional guidelines for monitoring and reporting in zoonotic and commensal bacteria include 2013/652/EU (repealed by 2020/1729/EU) and 2003/99 [27]. Finally, ISO 20776-1/-2:2022 sets standards for micro broth dilution methods and other *in vitro* diagnostic tools for testing minimal inhibitory concentration (MIC).

Official methods for detecting pathogens and performing Antimicrobial Susceptibility Testing (AST) combine traditional phenotypic cultures with rapid molecular diagnostics. Standardized by global authorities, these tools are vital for guiding life-saving therapies, managing antimicrobial resistance (surveillance, policy, and stewardship), and ensuring optimal patient outcomes [28].

Only phenotypic results from recognized, standardized *in vitro* antimicrobial susceptibility testing of isolates, along with interpretive criteria, can successfully help classify multiple, extended, pan, and resistant bacteria [29].

Phenotypic testing is the recognized gold standard; it works by exposing isolated bacteria to specific antimicrobial concentrations and observing their actual growth response. While molecular/genotypic tests (such as PCR or sequencing) are excellent for identifying specific resistance genes, they cannot determine the cumulative effect of multiple resistance mechanisms. Because of this, standardizing definitions of drug resistance relies exclusively on phenotypic measurements [28].

1.3. Foodborne Bacterial Pathogens and Antibiotic Resistance

The long-term, overuse and misuse of antibiotics in food animals and humans create ideal conditions for the rising threat of antibiotic resistance. Resistant bacteria in animals may reach humans directly or indirectly through food, water, mud, and manure used as fertilizer [30]. Some types of bacteria (high-burden resistant pathogens such as *Salmonella*, *Shigella*, *Neisseria gonorrhoeae*, *Pseudomonas aeruginosa*, and *Staphylococcus aureus*) [31,32] that cause serious infections in humans have already developed resistance to most or all the available treatments, and there are very few promising options in the research pipeline [33,34].

Interventions that restrict antibiotic use in food-producing animals, such as biosecurity, improved animal management, vaccination, improved hygiene, and changes in animal housing and husbandry practices, have reduced antibiotic-resistant bacteria in these animals [35]. Hygiene practice alone can attenuate the effect of antibiotic selection pressure [36]. These practices, in conjunction with One Health approaches, should be implemented to counter antibiotic resistance [37,38]. In this regard, the One Health approach is a collaborative strategy recognizing that human, animal, plant, and environmental health are deeply interconnected. Because antibiotic resistance easily spreads across these domains, containing it requires integrated monitoring, responsible prescribing, and environmental stewardship across all sectors [39].

The overall reduction in the use of antibiotics in food-producing animals, including the complete restriction of these substances for growth promotion and disease prevention, without proper diagnosis. Malaise animals should be assessed to determine the most effective and prudent antibiotic to treat their specific infection. Meanwhile, healthy individuals should only receive antibiotics to prevent disease if, within a particular population, an animal has already been diagnosed [40].

Antibiotic use is further exemplified by the application of streptomycin (STR), oxytetracycline (OXY), copper-based products, and certain fungicides (e.g., triazoles) in plant agriculture. Their use is correlated with increased resistance among plant pathogens [41–43]. Horizontal gene transfer is responsible for genes being exchanged among a variety of bacteria in the plant production setting, including phytopathogens, soil bacteria, and zoonotic bacteria that are occasionally present in that environment and the food chain [30,42]. Through gene transfer, co-resistance, cross-resistance, and gene up-regulation, resistance to one compound may confer resistance and multi-drug resistance to other similar, or even very dissimilar, compounds [42].

Genetic information encoding bacterial resistance mechanisms can be chromosomal or carried by mobile elements called plasmids. Some bacteria are also inherently resistant to a particular antibiotic if they lack the structure on which the antibiotic acts. Several mechanisms of resistance have continuously evolved, including target modification or mutation, permeability reduction, expression of efflux pump genes, production of hydrolases or inactivating enzymes, metabolic enhancement or auxotrophy, synthesis of target-protective proteins, self-repair systems, changes in cell morphology, and biofilm protection (Figure 1) [44,45]. For a thorough primer on specific mechanisms of resistance by antibiotic class, the work by van Hoeck et al. [46] is suggested.

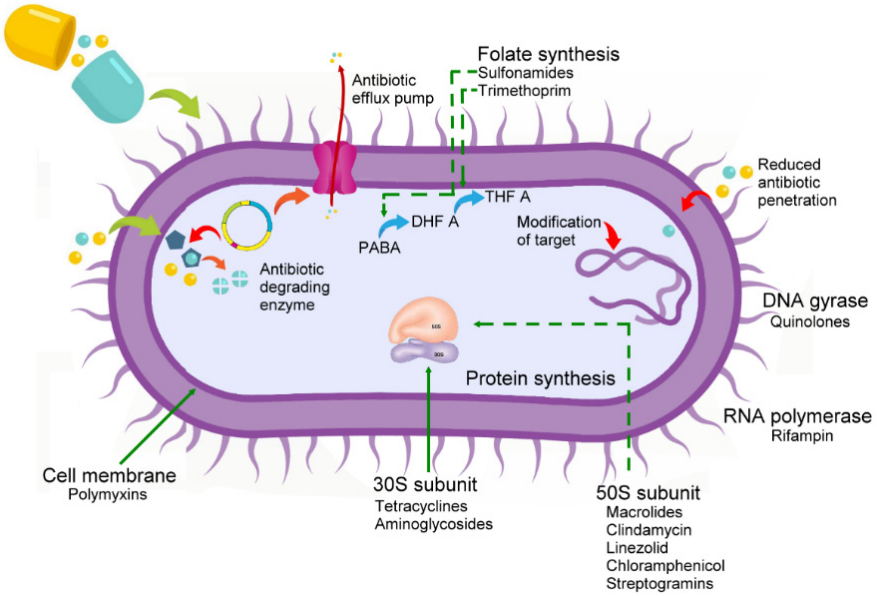

Figure 1. Schematic representation of common mechanisms of antibiotic resistance exhibited by bacteria. Yellow/Light blue spheres: Antimicrobial/active ingredient. Green arrows: antimicrobial introduction routes or target cell structures. Red arrows: antimicrobial export or target inhibition (e.g., outward export from the cell). Figure prepared using CorelDRAW® Graphics Suite 2026 (Corel Corporation, Ottawa, ON, Canada).

Plasmids are major vectors of bacterial antibiotic resistance [47]. Recent evidence demonstrates that antibiotic resistance-related plasmids are differentially dispersed among humans and livestock, reflecting known antibiotic prescribing practices [48]. For example, using a large-scale multivariate approach, the authors found that only 0.42% of livestock plasmids carried carbapenem resistance (compared with 12% of human plasmids); conversely, tetracycline resistance was enriched in livestock *vs*. human plasmids [48]. However, they also found that the prevalence of carbapenem and colistin plasmid-related resistant genes is on the rise.

Despite the long list of antibiotics commercially and clinically available (Table 2), resistance has made some of these drugs therapeutically useless against multidrug-resistant bacteria. Hence, the discussion of alternatives to antibiotics has resulted in natural product-led research [49–51]. Several primers regarding natural products with antimicrobial capabilities are advised [52–57]. Interestingly, recent research suggests

that constant bacterial exposure to even these alternatives can affect their resistance profile (that is, decreased sensitivity). Exposure to biocides, pesticides, common home cleaners, heavy metals, food preservatives, and even natural products can lead to a cross-adaptation to antibiotics induced by exposure to non-antibiotic antimicrobials [58–60]. This co-resistance occurs when bacterial exposure to sub-lethal concentrations of non-antibiotic agents, used within the clinical, agricultural, and domestic settings, inadvertently selects strains that are resistant to therapeutic antibiotics (*i.e.*, the physiological changes often double as defense mechanisms against antibiotics) [61]. More worrisomely, evidence of this behavior in pathogenic foodborne bacteria such as *S. aureus*, *E. coli*, *S. typhimurium*, *P. aeruginosa*, *K. pneumoniae*, *L. monocytogenes*, *A. baumanii*, *C. sakazakii*, and other species is clear [59].

Table 2. The ninety-three antimicrobials mentioned during this survey, their mechanisms of action, and their abbreviations.

Drug Class		
Action Mechanism [1]	**Antibiotics**	**Abbreviations**
Aminoglycosides		
Inhibition of protein synthesis.	Amikacin	AMK
	Apramycin	APM
	Gentamycin	GEN
	Kanamycin	KAN
	Neomycin	NEO
	Netilmicin	NTM
	Spectinomycin	SPC
	Streptomycin	STR
	Tobramycin	TMP
Ansamycins/Rifamycins		
Inhibits bacterial DNA-dependent RNA synthesis (RNA polymerase).	Rifampicin	RIF
β-lactam/β-lactamase inhibitor		
Bind to plasmid-mediated β-lactamases and inactivate them.	Amoxicillin-clavulanic acid	AMC
	Ampicillin-sulbactam	SAM
	Cefotaxime-clavulanic acid	CTC
	Ceftazidime-avibactam	CVI
	Ceftazidime-clavulanic acid	FOX
	Piperacillin-tazobactam	TZP
Carbapenems/β-lactams		
Fix to PBPs [2], inhibiting bacterial cell wall synthesis.	Ertapenem	ETP
	Imipenem	IMP
	Meropenem	MEM
Carboxypenicillins/β-lactams		
Inhibit cell-wall synthesis.	Carbenicillin	CAB
	Ticarcillin	TIC
Carboxylic acids		
Pseudomonic acid inhibits isoleucine—tRNA ligase in bacteria, leading to depletion of isoleucyl-tRNA & accumulation of the corresponding uncharged tRNA. Depletion of isoleucyl-tRNA results in inhibition of protein synthesis.	Mupirocin (Bactroban)	MCP
Cephalosporins/β-lactams		
Inhibit cell-wall synthesis.	Cefalexin (1st class)	CPX
	Cefazolin (1st class)	CEZ
	Cefepime (4th class)	CFP
	Cefixime (3rd class)	CFM
	Cefotaxime (3rd class)	CFX
	Cefotetan (2nd class)	CTT
	Ceftiofur (3rd class)	CFT

	Cefovecin	CFO
	Cefoxitin (2nd class)	CEX
	Ceftachlor (2nd class)	CFC
	Ceftazidime (3rd class)	CZA
	Cefpodoxime (3rd class)	CPD
	Cefoperazone (3rd class)	CPZ
	Cefquinome (4th class)	CFQ
	Ceftaroline (5th Class)	CRN
	Ceftriaxone (3rd class)	CTX
	Cefuroxime (2nd class)	CXM
	Cephalothin (1st class)	CEP
Diaminopyrimidines/Sulfonamides		
Dihydrofolate reductase inhibitor & Competitive inhibitors of the enzyme dihydropteroate (folate) synthase.	Trimethoprim/sulfamethoxazole (Bactrim® or Septra®)	STX
	Sulfadiazine	SDZ
	Sulfamethaxole	SMZ
	Sulfafurazole/Sulfisoxazole	INN
	Trimethoprim	TMP
(Fluoro)quinolones		
Interferes with DNA replication by preventing bacterial DNA from unwinding and duplicating. Specifically, they inhibit the ligase activity of the type II topoisomerases, DNA gyrase, and topoisomerase IV, which cut DNA to introduce supercoiling, while leaving nuclease activity unaffected.	Ciprofloxacin	CIP
	Enrofloxacin	ENR
	Flumenique	FMQ
	Gamifloxacin (4th generation)	GMX
	Gatifloxacin (4th generation)	GTX
	Levofloxacin	LFX
	Nalidixic acid	NAL
	Marbofloxacin	MBF
	Moxifloxacin	MFX
	Norfloxacin	NOR
	Ofloxacin	OFX
	Oxolinic acid	OXO
	Pefloxacin	PFX
Phosphonic acid derivatives		
Bactericidal inhibits bacterial cell wall biogenesis by inactivating the enzyme UDP-*N*-acetylglucosamine-3-enolpyruvyltransferase (MurA)	Fosfomycin (Monurol)	FOS
Glycopeptides		
Bind to acyl-D-alanyl-D-alanine in lipid II, preventing the addition of new units to the peptidoglycan.	Vancomycin (1st gen)	VAN
	Teicoplanin (Targocid)	TEI
Macrolides/Polyketide/Ketolide		
Bacteriostatic, protein synthesis inhibitors. Prevent peptidyltransferase from adding the growing peptide attached to *t*RNA to the next amino acid. Inhibit bacterial ribosomal (bind reversibly to the P site on the 50S) translation. Dissociate the peptidyl-tRNA from the ribosome prematurely.	Azitromycin	AZM
	Erythromycin	ERY
	Clarithromycin	CAM
	Midecamycin	MDY
	Telithromycin	TYM
	Tylosin	TYL
Nitrofurans		
Rapid reduction inside the bacterial cell by flavoproteins to multiple reactive intermediates that attack ribosomal proteins, DNA, respiration, pyruvate metabolism, and other macromolecules within the cell.	Furazolidone	FZD
	Nitrofurantoin	NFT
Lincosamides		
Bacteriostatic, interferes with the synthesis of proteins. Bind close to the peptidyl transferase center on the 23S portion of the 50S subunit of bacterial ribosomes.	Lincomycin	LIN
	Clindamycin	CDA

Oxazolidinones		
Blocks the initiation of protein production	Linezolid	LZD
Penicillins/β-lactams		
Inhibit the completion of the synthesis of peptidoglycans, the structural component of the bacterial cell wall. Inhibits the activity of enzymes that are needed for the cross-linking of peptidoglycans during the final step in cell wall biosynthesis.	Amoxicillin	AMO
	Ampicillin	AMP
	Aztreonam (monobactam)	ATM
	Cloxacillin	CLX
	Methicillin	MET
	Oxacillin	OXA
	Penicillin G	PEN
	Temocillin	TMC
Phenicols		
Bacteriostatic, inhibits protein synthesis. Prevents protein chain elongation by inhibiting the peptidyl transferase activity of the bacterial ribosome. It specifically binds to A2451 and A2452 residues in the 23S rRNA of the 50S ribosomal subunit, preventing peptide bond formation.	Chloramphenicol	CHL
	Florfenicol	FLO
Polymyxins		
Bind to lipopolysaccharide in the outer membrane of Gram-negative bacteria, polymyxins disrupt both the outer and inner membranes. The hydrophobic tail is important in causing membrane damage, suggesting a detergent-like mode of action (increase membrane permeability/disorganization).	Colistin (Polymyxin E)	COL
	Polymyxin B	PMB
Steroids		
Binds to EF-G after translocation and GTP (guanosine-5′-triphosphate) hydrolysis.	Fusidic acid (Fucidin)	FAS
Streptogramins		
Bacteriostatic, binds to the bacterial 50S ribosomal subunit and inhibits the elongation process of protein synthesis.	Pristinamycin	PRI
Tetracyclines		
Protein synthesis inhibitors. Prevent the initiation of translation in various ways by binding to the 30S ribosomal subunit. Hinder the binding of aminoacyl-*t*RNA to the *m*RNA translation complex.	Doxycycline (Semi-synthetic)	DOX
	Minocycline (Semi-synthetic)	MIN
	Oxytetracycline (Naturally occurring)	OXY
	Tetracycline (Naturally occurring)	TET
	Tigecycline (Glycecyclines)	TIG
Ureidopenicillins/β-lactams		
Inhibit cell-wall synthesis	Mezlocillin	MEZ
	Piperacillin	PIP

[1] Mechanisms of action for antimicrobials adapted from Singh et al. [62]. [2] PBPs, Penicillin-binding proteins.

2. *Salmonella* spp.

2.1. Foods for Human Consumption

Salmonella is a genus of rod-shaped (bacillus), motile, non-spore-forming, chemotrophic, facultative anaerobe, and Gram-negative bacteria of the family Enterobacteriaceae. It is known for its two species, *S. enterica* and *S. bongori*. *S. enterica* is further divided into six subspecies that include over 2600 serotypes [63,64].

Nontyphoidal *Salmonella* serotypes are zoonotic and can be transferred from animals to humans. Infection by this pathogen is usually due to ingestion of contaminated, undercooked food. *Salmonella* is one of the most common causative agents of foodborne illness in humans, causing approximately 1.35 million infections, 26,500 hospitalizations, and 420 deaths in the United States alone every year [65].

Treatment of salmonellosis is further complicated by the fact that isolates may also carry resistance genes conferring resistance to antimicrobials. For example, *Salmonella* species carrying antimicrobial resistance genes have been isolated from animal- and plant-derived foods, including poultry, eggs, fish,

pork, beef, vegetables, fruits, nuts, and flour [56]. Outbreak studies have recognized food commodities, including fresh produce, vegetables, cantaloupes, cereals, alfalfa sprouts, fruit/fruit pulp, pistachios, poultry meat, turkeys, tuna, ground beef, pork, dried/shredded coconut, tomatoes, and mangos, as sources of foodborne *Salmonella*-related outbreaks in the past decade [66–69].

Soubeiga et al. [70] found *Salmonella*-related virulence genes associated with vegetable/fruit sources. Multidrug resistance profiles were consistent determinants in the 148 isolates, as genes *bla*$_{\text{TEM}}$, *tem*AB (β-lactams), *Str*A, *aad*A (aminoglycosides), *sul*1, *sul*2 (sulfonamides), and *tet*AB (tetracyclines) were consistently present (Figure 2).

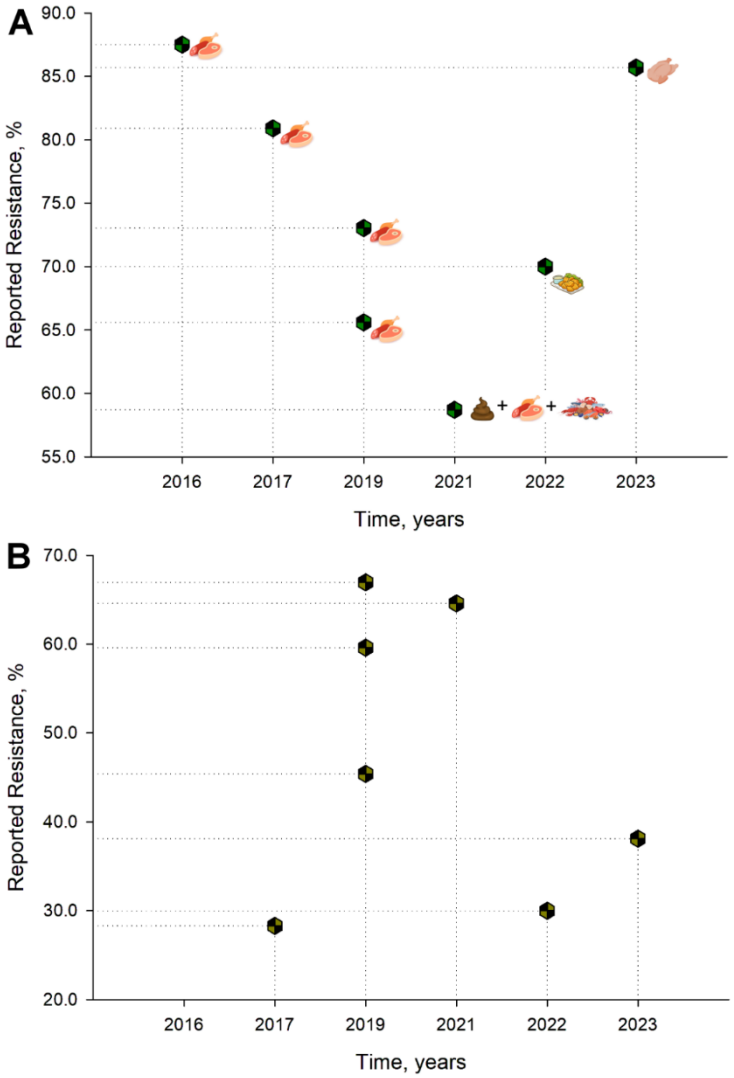

Figure 2. Reported resistance profiles for (**A**) Tetracycline and (**B**) Ampicillin for foodstuffs and related matrices (assorted meats, RTE, feces, aquatic products, and poultry) from China from 2016–2024. China was selected as it is the country with the most entries (nine) as *per* Table 3. Figure elaborated using Sigma Plot 16 (Grafiti LLC, Palo Alto, CA, USA).

Similar gene profiles [e.g., *aadA*, *aac*, *aph*, *bla*$_{\text{CARB}}$, *bla*$_{\text{PSE}}$, *bla*$_{\text{TEM}}$, *bla*$_{\text{CTX-M}}$, *bla*$_{\text{CMY}}$, *floR* (phenicols), folate pathway inhibitors *sul* and *dfrA* (folate pathway inhibitors), *qnrAB*, *oqxAB* (fluoroquinolones), *tetABM*, and *mph*(*A*) and *lnu*(*F*) (macrolides)] were found recently, but in retail American poultry [71], Mexican ground beef samples [72], and Chilean poultry production line samples [45]. Analogous gene profiles were also found in food chain links in Poland [73]. On the other hand, recent Italian isolates from swine mostly exhibited resistance determinants *parC*, *gyrA*, *catA*, *nfsAB*, *bla*$_{\text{TEM}}$, and *tetAB*. For a detailed

primer regarding mechanisms of resistance for *Salmonella*, the work by Monte et al. [74] and Wang et al. [75] is recommended.

Furthermore, as global trends indicate that more people are basing their diets on fresh produce and vegetables [76], Salmonella contamination is relevant, as an increase in produce-related outbreaks has been documented [77]. Additionally, multidrug-resistant bacteria can disseminate more quickly due to an ever-expanding regional and international food trade [77]. More problematic still, it is easy to forget that foods, in general, and especially fruit and vegetables [78], can carry more than one pathogen, and these pathogens can carry resistance genes and even share them amongst themselves and other bacteria. In a very thorough Cuban study, 14 different food groups were analyzed for the presence of *Salmonella* spp., *E. coli*, *Staphylococcus* spp., and *V. cholerae* [79]. Meat and dairy products and RTE foods showed not only multiple pathogen contamination but also multiple drug resistance profiles [79]. A recent study saw lettuce, cabbage, spinach, carrot, tomato, and green peppers contaminated with other antibiotic-resistant species alongside *Salmonella* (e.g., *E. coli*, *S. aureus*, *S. epidermis*) [78].

On the other hand, Cao et al. [80] found a high prevalence of *Salmonella* (isolating the bacteria at a rate of 29.4% per sample tested) contamination in cow's milk. A similar account was reported by Ejo et al. [81], who found both a higher prevalence of contamination and a drug resistance profile in raw meat, eggs, and milk.

Quesada et al. [82] reviewed *Salmonella* reports from 2003–2014 from Latin America, as well as the antibiotic-resistant profiles of these isolates (especially recovered from the Brazilian and Mexican poultry industry). Among their findings, *S.* Enteritidis, *S.* Typhimurium, *S.* Paratyphi, and *S.* Heidelberg were the most commonly encountered serovars. Similar to other reports [83,84] most strains were multidrug-resistant and showed a high tolerance to STR, NAL, AMP, TET, CHL, and STX (Table 3). Relatedly, a 22-year historical analysis of antibiotic-resistant *Salmonella* from Bangladesh found 81% tetracycline resistance [85], rendering this antibiotic effectively without any therapeutic or clinical use. However, the continued use of tetracyclines in other agricultural settings (e.g., crop production, apiculture, and aquaculture) still provides a selective pressure on bacteria [40].

As macrolides (the first-choice drugs) for *Salmonella* infections in humans have failed, cephalosporins are now the paramount therapeutics. However, ESBL enzymes encoded by *bla*$_{\text{CMY2}}$, *bla*$_{\text{SHV}}$, and *bla*$_{\text{TEM}}$ emerged, thus reducing the efficacy of cephalosporins. Also, generalized *mcr* genes have been described in *Salmonella* and encode colistin resistance, an antibiotic regarded as critical. In both cases, resistance genes were carried by conjugative plasmids (e.g., IncI2, IncHI2, IncX3, IncX4) [86].

Interestingly, Siddique et al. [87] not only found *Salmonella* strains carrying β-lactam, cephalosporins, and carbapenems resistance genes (e.g., *bla*$_{\text{CMY-2}}$, *bla*$_{\text{OXA-1}}$, *bla*$_{\text{PSE-1}}$, *bla*$_{\text{TEM-1}}$, *bla*$_{\text{NDM-1}}$, and *ampC*), and the zoonotic potential virulence gene *sopE*, but also noted that the strains recovered had moderate-to-high abilities to aggregate into biofilms at 30 and 37 °C. Other virulence factors (e.g., *fimA*, *invA*, *spvC*) co-occurring with similar resistance gene patterns have been recently reported in Poland [73], Italy [88] and China [89–92].

For Brazilian poultry farms, Rau et al. [93] found, in two different sampling moments (*i.e.*, 3 years apart), that traditional *Salmonella* serovars Typhimurium and Enteritidis have been supplanted by other serovars like Heidelberg or Kentucky. In the same period, Brazil saw an increase in the number of isolates exhibiting antimicrobial resistance by almost double. Similar phenomena seem to be occurring of late in countries like the USA and Costa Rica [94,95].

As the debate about rendering animals without antibiotics rages on, evidence suggests that alternative meat production practices reduce the frequency of bacteria exhibiting antibiotic resistance, which favors "organic" practices [71]

2.2. The Relation Between the Poultry Industry and the Emerging Salmonella Infantis (pESI)-Plasmid

Salmonella enterica serovar Infantis (or *S*. Infantis) is an emergent serotype worldwide (Table 3) [96]. This serotype has been reported as one of the most prevalent non-typhoidal *Salmonella* (NTS) in humans in Europe and the USA [97–99]. Several studies describe *S*. Infantis as the most prevalent serotype in poultry [98,99]. Recent data from over 10,000 isolates demonstrated that *S*. Infantis and *S*. Seftenberg with pESI plasmid carrying a *bla*$_{\text{CTX-M-65}}$ gene constitute one of the biggest clusters of *Salmonella* along the United States, both originating from turkeys [100].

Moreover, multidrug-resistant phenotypes of this serotype are of public health concern [101]. For example, Mattock et al. [102] recently related the presence of pESI megaplasmid with 73% of the poultry isolates from 74 different countries showing multidrug resistance. Hence, the presence of *Salmonella* in poultry production has attracted serious attention, and several studies have found in poultry a vector for several species of this bacterium. Whole genome sequencing from broiler integrations determined that the most prevalent non-typhoid *Salmonella* serotype was *S*. Infantis [103]. Not only do most isolates show potential for resistance against medically important antibiotics [especially aminoglycosides (mutations in genes *aac*, *ant*, *aph*) and quinolones (*parC*, *gyrA*)] and disinfectants, but also almost all isolates harbored the pESI-like megaplasmid, which plays an important role in the global dissemination of antimicrobial resistance. Among analogous Latin American studies, the *bla*$_{\text{CTX-M-65}}$ ESBL antibiotic resistance gene is also prevalent in isolates. This was more recently confirmed by Costa Rican-led research, in which ampicillin resistance in the more prevalent *S.* Infantis reached 81.6% [95]. In terms of plasmid prevalence, a similar trait has been observed in *S.* Muenchen, *S.* Schwarzengrund, *S.* Agona, and *S.* Senftenberg in a large-scale broiler and chicken isolate study [104]. Previous studies, again in the Andean Region (mostly Ecuador, Chile, and Peru), seem to support similar findings [105–109]. A more recent Chilean study [47] has reported mobile elements carrying multiple drug resistance determinants in the poultry production line, predominantly related to *S.* Infantis and *S*. Heidelberg (IncFIB and Incl1-Iα plasmids, respectively).

Furthermore, the ESI clone carrying an extended spectrum β-lactamase *bla*$_{\text{CTX-M-65}}$ on a pESI-like plasmid and a mutation in the gyrA gene has also been found in poultry meat in regions such as Russia, USA, Italy, Germany, Hungary, Poland, and Slovenia [110–114]. All these data suggest that pESI is not only widespread but is acquired by *Salmonella* spp. with relative ease. Finally, recent evidence has described pESI-like megaplasmids as carriers of additional antimicrobial resistance genes, such as tet, dfr, and sul, and has demonstrated that these structures are genetically plastic and can also harbor virulence and fitness genes, as well as toxin/antitoxin systems that enhance their persistence in the S. Infantis host [97].

2.3. Animal Feeds and Related Matrices

Salmonella monitoring and surveillance in animal feed are not only related to production costs and animal welfare but are also instrumental in understanding the behavior of foodborne pathogens at the start of the food chain and how this relates (if any) to prevalence, drug-resistant profiles, and specific species found downstream in human or clinical isolates.

Relatively few studies have tackled feed contamination despite being considered a main source of contamination on farm grounds (Table 3) [65]. In Thailand, the prevalence of *Salmonella* contamination in compound feeds (a specially formulated, balanced mixture of feed components designed for feeding livestock and poultry) was registered at 12.5% [115]. Similar data have been recovered from isolates from American and Australian feeds [71,116–118]. The authors found more prevalence in the compound feed than in any of its respective ingredients. However, Parker et al. [118] recently related contamination hotspots with the milling equipment during feed manufacturing. Hsieh et al. [117] found an 84% contamination in fish meals and 48% in animal products. From these samples, the acquisition of the *bla*$_{\text{CMY-2}}$ gene, which confers resistance to cephalosporins, was most commonly observed. Interestingly, multidrug-resistant isolates were

recovered from monensin (an ionophore/Rumensin®)-medicated dry beef cattle feeds. A possible association between the use of ionophores in livestock and antibiotic resistance has recently been raised [119].

Of all the bacterial pathogens discussed, *Salmonella* seems to have received the most attention in the feed sector (both in surveillance and research). Antibiotic resistance in *Salmonella* often stems from agricultural practices, where antimicrobial usage in animals selects resistant strains that spread into the human food supply. This poses a major public health issue, as these pathogens can trigger severe infections that are difficult to treat with standard medications. The cycle of how antibiotic resistance moves from animal feed to human consumers operates as follows: i. Contaminated Feed, ii. Livestock Exposure, iii. Indirect Transmission to Humans [120].

As stated, however, there is a very close link between livestock and human pathogen contamination. For instance, the main source of *Salmonella* infections in humans is contaminated animal-derived foodstuffs, with pork products being among the most important contributors [65].

Table 3. Summary of bacterial isolates from foodstuffs and other food-related matrices for *Salmonella*.

Country	Isolates	Source	Antibiotics Tested	Resistance to [1]	Testing Method	References
			Feeds			
USA	*S.* Senftenberg, *S.* Montevideo, *S.* Mbandaka	Animal feeds (finished feeds), feed ingredients, pet foods, treats, & supplements (*n* = 2058)	AMC, AMP, CEX, CHL, CIP, GEN, KAN, NAL, NOR, STX, INN, STR, TET	TET, INN, AMP, NAL	Sensititre system (micro version of the broth dilution method)	[116]
Costa Rica	*S.* Give, *S.* Rissen, *S.* Havana, *S.* Soerenga, *S.* Schwarzengrund	Feed & ingredients (*n* = 1725; meat and bone meal, poultry feed, pet foods)	TET	TET (7.4%)	E-test	[121]
USA	*S.* Newport, *S.* Typhimurium var. O 5-(Copenhagen), & *S.* Lexington var. 15+ (Manila)	Dry beef (*n* = 3) & dry cattle feeds (*n* = 1), cabbage culls (*n* = 2), animal protein products (*n* = 2), & fish meal (*n* = 1)	AMC, AMP, CEX, CFT, CHL, KAN, STR, INN, TET, SXT	AMC, AMP, CEX, CFT, CHL, STR, INN, TET	Sensititre automated antimicrobial susceptibility system	[117]
Tanzania	*Salmonella* spp.	Commercial chicken feed samples (*n* = 384; Broiler starter mash (*n* = 121), Broiler grower mash (*n* = 47), Broiler finisher mash (*n* = 102) & Layers mash (*n* = 114)	STR, AMO, AMK, CIP, TET, KAN, GEN, STX	TET, AMK, KAN, GEN, STX	Kirby-Bauer disk-diffusion	[122]
Kenya	*Salmonella* spp.	Poultry feed (*n* = 150)	AMP, CTX, STX, TET, CHL, CIP	AMP (41%), STX, CTX	Kirby-Bauer disk-diffusion	[123]
Colombia	*Salmonella* spp.	Feed for swine, poultry, canine, feline, leporine, & equine species (*n* = 1758)	AMP, SAM, CEZ, CFP, CEX, CTX, CIP, IMP, MEM, TZP	AMP (44.5%), SAM, CEZ	Becton Dickinson Phoenix™ Automated Dilution System	[124]
Costa Rica	*S.* Typhimurium, *S.* Braenderup, *S.* Newport, *S.* Anatum, *S.* Westhampton	Non-human primate feces (*n* = 180) & feed (*n* = 43)	AMP, AMC, TPZ, CFX, CZA, CFP, IMP, MEM, AMK, GEN, NAL, CIP, NFT, COL, STX	CIP (9.8%)	VITEK®2 AST-N279 cards	[125]
Thailand	*S.* Rissen, *S.* Mbandaka, & *S.* Livingstone	Compound feed (*n* = 60), Soybean (*n* = 10), pork (*n* = 5), fish (*n* = 3) & poultry meal (*n* = 2)	AMP, AMC, PIP, CPX, CFP, CFT, CFO, AMK, GEN, TMP, IPM, STX, CHL, ENR, MBF, TET, DOX, MIN, NFT	TMP (100%), CPX, AMK, GEN	VITEK®2 Card type AST-GN65	[115]
			Foods and related matrices			
Thailand	*S.* Rissen, *S.* Weltevreden & *S.* Bredeney for pork; *S.* Albany & Typhimurium for chicken; *S.* Typhimurium & *S.* Hvittingfoss for vegetables	Pork (*n* = 41) & chicken meat (*n* = 40) & fresh vegetables (*n* = 80)	TET, CIP, CHL, AMP, NOR, NAL, STR, STX, CEP, GEN	STR (92%), TET, NAL, CHL, AMP, CEP	Kirby-Bauer disk-diffusion	[126]

Türkiye	*Salmonella* spp.	RTE salads & vegetables (*n* = 81)	KAN, NEO, NAL, TET, SPC, STX, AMP, AMC, CHL, FLO, GEN, CIP, STR, CFT	NEO, NAL	Micro dilution method	[127]
Nigeria	*Salmonella* spp.	Fecal samples of cattle, pig, sheep, goat, & chicken (*n* = 200 each)	AMP, AMO, AMC, CHL, STR, TET, CEP, GEN, CIP, SMZ, NAL	Cattle [TET (85%), AMP, CIP, NAL], Sheep [AMP (25%), STR, CHL, TET] Goat [TET (44%), AMP, CHL, STR, CEP, SMZ, NAL], Chicken [TET (90%), NAL, SMZ, AMP, CHL, STR, CEP], Pig [TET (75%), AMP, CHL, CEP, SMZ, NAL]	Kirby-Bauer disk-diffusion	[128]
Nigeria	*S.* Typhi, *S.* Paratyphi & *S.* Typhimurium	Cabbage, lettuce, cucumber, tomatoes, green pepper & spinach	AMC, STX, CIP, CTX, GEN, TET, KAN, CEP	CEP, STX, TET, KAN, multidrug-resistant profile	Kirby-Bauer disk-diffusion	[129]
Poland	*S.* Enteritidis	Foods other than meat: confectionery products, eggs, fruits, vegetables, spices	ATM, AMC, AMP, CFP, CFX, CEX, CZA, CTX, CHL, CIP, ETP, GEN, IMP, NAL, STR, TMP, TET, STX	NAL (35.2%)	Kirby-Bauer disk-diffusion	[130]
Malaysia	*Salmonella* spp., *S.* Enteritidis & *S.* Typhimurium	Ulam (salad, fresh leaves, vegetables, or fruits; *n* = 96)	CHL, CIP, AMP, ERY, CEP, STR, AMC, NAL, GEN, STX, TET	AMP (100%), ERY (100%), AMC, CEP, STR, CIP	Kirby-Bauer disk-diffusion	[131]
Ghana	*S.* Kentucky, *S.* Nima, *S.* Muenster, *S.* Enteritidis	Laying hens & broilers (feces *n* = 75, dust *n* = 75, feed *n* = 10 & drinking water *n* = 10)	AMP, CFX, CEX, GEN, CZA, TET, CHL, TMP, SMZ, NAL	NAL, TET, CIP	Kirby-Bauer disk-diffusion	[132]
Ethiopia	*Salmonella* spp.	Animal-origin food samples (*n* = 384: egg sandwich, minced & raw meat, burger patties, cottage cheese, cream cake, beef pizza, raw egg & pasteurized & raw milk from restaurants, hotels, cafeterias, & retail shops)	AMO, AMP, CEP, CTX, GEN, NAL, NFT, STX, TET	TET (42.6%), STX, AMP	Kirby-Bauer disk-diffusion	[81]
Nigeria	*Salmonella* spp.	Raw chicken (retail table) eggs (*n* = 340)	NEO, DOX, STX, AMO, VAN, NFT, PEN, CIP, ERY, GEN, STR, TET, OXA, AMC	STR (85%), AMC, GEN, VAN, DOX	Kirby-Bauer disk-diffusion	[133]
China	*S.* Typhi, *S.* Enteritidis, *S.* Typhimurium	Pork (*n* = 85) & chicken (*n* = 200) at retail stores	CFX, GEN, LFX, TET, DOX	TET	Kirby-Bauer disk-diffusion	[89]
South Africa and Brazil	*Salmonella* spp.	Broiler chicken caecum samples (*n* = 200)	GEN, AMO, ERY, CHL, TET, TMP, AMP, STR, STX	TET (93%), STX, TMP, KAN, GEN, AMP	Kirby-Bauer disk-diffusion	[134]
China	*Salmonella* spp.	Pork (*n* = 137), chicken (*n* = 91), & beef (*n* = 99) from supermarkets	AMO, AMC, AMP, CFT, CIP, OXY, LFX, TMP, GEN	OXY (80.9%), TMP, AMP, LFX	Agar dilution method	[58]

Malaysia	*S.* Corvallis, *S.* Typhimurium, *S.* Braenderup, *S.* Albany	Spent hens (*n* = 470)	AMP, CTX, CHL, CIP, ERY, GEN, KAN, NAL, STR, STX, TET	ERY (97%), TET, STR, STX, AMP, NAL	Kirby-Bauer disk-diffusion	[135]
Latvia	*S.* Typhimurium, *S.* Derby, *S.* Enteritidis	Meat and meat products (*n* = 3152)	AMP, ATM, CFX, CZA, CHL, MEM, CIP, TET, TIG, NAL, COL, GEN, TMP, SMX.	SMX (38%), NAL, CIP, AMP, TET	Broth microdilution (Sensititre® EUVSEC3® & EUVSEC2® plates)	[136]
Ghana	*Salmonella* spp.	Cabbage and lettuce samples	AMP, PEN, CHL, CIP, CTX, GEN, ERY, OFX, STX, TET	AMP (72.2%), ERY, OFX	Kirby-Bauer disk-diffusion	[137]
Vietnam	*Salmonella* spp.	Fecal samples (*n* = 240) & Environmental samples (feed, water, barn floor & wastewater; *n* = 640) from household and pig farms	AMC, CZA, CXM, COL, GEN, AMK, STR, TET, DOX, CHL, STX, AMP, OFX, LFX	STX (64.5%), CHL, AMP	Kirby-Bauer disk-diffusion	[138]
Bangladesh	*Salmonella* spp.	Fuska (*n* = 55), sugarcane juice (*n* = 58), Borhani (*n* = 30)	AMP, AMO, CIP, ENR, COL, OXY, TET, AZM, ERY, PFX, CTX	High level of resistance to all antibiotics tested, especially TET, AZM, ERY, AMP, AMO	Kirby-Bauer disk-diffusion	[139]
Ethiopia	*S.* Dublin, *S.* Virchow	Fecal samples of slaughtered cattle (*n* = 720)	AMP, AMC, CHL, CTX, CEP, CIP, CEX, GEN, KAN, STX, TMP, TET, SMZ, STR, NFT, NAL	STR (89.3%), CEP, AMP, AMC	Kirby-Bauer disk-diffusion (BD BBL™ Sensi-Disc™)	[140]
USA	*S.* Newport	Humans (*n* = 2763), animals (*n* = 901), & retail-meats (*n* = 64)	AMK, APM, GEN, KAN, STR, AMC, TZP, CEP, CEX, CTX, CFT, CZA, CFX, CFQ, CFP, INN, STX, AZM, ATM, IMP, AMP, CHL, CIP, NAL, TET	Multidrug resistance-AMP & single drug resistance-TET	Agar dilution Method	[141]
South Africa	*S. bongori*, *S.* Pullorum, *S.* Typhimurium, *S.* Weltevreden	Fecal samples (poultry pens of broilers, layers & indigenous chickens, *n* = 20 each)	AMP, OXY, CIP, STR, GEN, STX, CHL, ERY, NOR, CEP, NAL	ERY (100%), STR, STX, OXY, AMP	Kirby-Bauer disk-diffusion	[142]
Nigeria	*S.* Enteritidis, *S.* Typhimurium	Ready to eat shrimp (*n* = 1440)	KAN, GEN, STR, ERY, TOB, AMP, AMO, IMP, SAM, MEM, CEP, TMP, AMC, COL, CHL, CHL, PEN, PMB, OXY, DOX, TET, OFX, CIP	ERY, PEN (100%), AMO (92.9%), AMC, AMP (85.7%)	Kirby-Bauer disk-diffusion	[143]
China	*S.* Enteritidis, *S.* Typhimurium, *S.* Kentucky	Feces, cecum, & milk (*n* = 1578) from chicken, pig, duck, & cows	AMC, AMP, CFT, CZA, GEN, ENR, OFX, MEME, STX, SPC, APM, FLO, INN, TET, COL	AMP (59.6%)	Not indicated	[80]

China	*S.* Derby, *S.* London, *S.* Rissen	Pork, chicken & the Environment (*n* = 1112)	AMP, TET, PIP, CZA, DOX, CTX, MIN, NOR, CHL, SMX, OFX, CIP	TET (73.04%), AMP, DOX	Kirby-Bauer disk-diffusion	[144]
Thailand	*S.* Brunel & *S.* Hvittingfoss for vegetable, *S.* Stanley for fermented pork, *S.* Tennessee for fermented fish	Vegetables (*n* = 100) & 72 Thai fermented foods (*n* = 72, pla-som & nham)	GEN, TET, CIP, STX, NAL, SMZ, CEP, NEO, NFT	SMZ (20%), TET, STX, NAL, GEN	Kirby-Bauer disk-diffusion	[145]
USA	*S.* Typhimurium	Humans (*n* = 6381), animals (*n* = 2940), & retail meats (*n* = 2126)	AMK, APM, GEN, KAN, STR, AMC, TZP, CEP, CEX, CTX, CFT, CZA, CFX, CFQ, CFP, INN, STX, AZM, ATM, IMP, AMP, CHL, CIP, NAL, TET	AMP, CHL, STR, STX, TET, AMC, CTX, CFT	Agar dilution Method	[146]
China	*S.* Derby, *S.* Typhimurium, *S.* London, *S.* Rissen	Pork (*n* = 287), beef (*n* = 161), mutton (*n* = 92), dumplings (*n* = 212), & smoked pork (*n* = 55).	AMP, AMC, CEZ, CEX, CTX, CZA, CFX, CFT, CFP, ATM, IMP, GEN, KAN, AMK, STR, TET, CIP, ENR, NAL, STX, CHL, FLO	TET (65.6%), AMP, STX, STR, NAL	Kirby-Bauer disk-diffusion	[147]
Brazil	*S.* Mbandaka, *S.* Braenderup	Layer hens' fecal samples (*n* = 2008)	NAL, ENR, NOR, CIP, CHL, KAN, STR, GEN, AMK, STX, CFX, CFP, CFT, AMP, AMO, AMC, IMP, ATM, TET, OXY, PMB	STX, STR, CIP	Kirby-Bauer disk-diffusion & dilution method for PMB	[148]
Zambia	*Salmonella* spp.	Raw retail table eggs (*n* = 1080)	AMC, AMP, CTX, IMP, CHL, NAL, CIP, COL, TET	TET, COL (83.3%)	Kirby-Bauer disk-diffusion	[149]
Ecuador	*S.* Infantis, *S.* Gallinarum	Retail fresh meats (*n* = 1095, chicken, pork, veal, lamb, beef, and turkey)	STR, SXT, CTX, AMC, CIP, NAL, TET, CHL, GEN, AMP, AZM, KAN	TET (97.1%), NAL, STR, CIP, AMP, CTX (all > 90% resistance)	Kirby-Bauer disk-diffusion	[150]
Cuba	*Salmonella* spp.	Meat, dairy, eggs & seafood, RTE foods	NAL, AMK, AMP, AZM, CAB, CFX, CZA, CTX, CIP, CHL, DOX, ERY, STR, GEN, KAN, OXA, PEN, STX, TET	TET (59.3%), NAL, AMP, CAB	Kirby-Bauer disk-diffusion	[79]

China	*Salmonella* spp.	Fecal samples patients with diarrhea (*n* = 14,579), chicken meat (*n* = 1237), pork (*n* = 1354), aquatic products (*n* = 814)	AMP, SAM, CZA, CFX, IMP, MEM, STX, GEN, TET, CIP, NAL, CHL	Human: AMP (68%), TET (68%), NAL (56%); Aquatic food products: TET (56%), CHL (48%), AMP (42%); Chicken meat: NAL (82%), AMP (53%); Pork: TET (85%), AMP (68%), NAL (68%), STX (53%)	Broth dilution method and Biofosun Gram-negative bacterial panels	[90]
Rwanda	*Salmonella* spp.	Pig fecal samples (*n* = 180)	AMC, AMP, AZM, CEX, CTX, CHL, CIP, COL, MEM, NAL, STR, TET	All pan-susceptible	Kirby-Bauer disk-diffusion	[151]
Vietnam	*Salmonella* spp.	Chicken feces (*n* = 417), Environmental samples [bedding (*n* = 170), feed (*n* = 219), & drinking water (*n* = 142)], & Pest animals [rats (*n* = 32), geckos (*n* = 808), flies (*n* = 450), ants (*n* = 530), & cockroaches (*n* = 287)	AMP, AMK, AMC, CZA, CHL, COL, CXM, DOX, GEN, OFX, LFX, STR, STX	CHL (63.0%), TET, AMP, STX	Kirby-Bauer disk-diffusion	[152]
Brazil	*S.* Heidelberg, *S.* Minnesota *&* *S.* Saintpaul	Poultry meat	AMP, AZM, CZA, CHL, CIP, COL, CFX, GEN, MEM, NAL, STX, TET, TIG	CIP (91.3%), NAL, AMP, CZA, CFX, TET	Broth microdilution	[93]
Pakistan	*S.* Typhimurium, *S.* Enteritidis	Poultry feces (*n* = 180), organs (*n* = 70), meat (*n* = 60), & eggs (*n* = 60)	AMK, CHL, TET, AMC, CIP, GEN, NAL, STX, AMP, IMP, MEM, STR, ERY, MIN, KAN, CFM, CFP, VAN, LZD, RIF, ENR, OXA, CDA	All isolates are resistant to OXA, CDA, ERY, NAL, LZD, RIF, TET, MIN & VAN. ENR (95%), GEN (93%), KAN (91%), STX (91%), AMP & AMC (81%), CFP (76%)	Kirby-Bauer disk-diffusion	[87]
USA	*Salmonella* spp.	Poultry (Chicken, breasts with bone-in & skin on, legs, wings, & thighs, *n* = 27,591 & ground turkey products, *n* = 19,346). Conventional & "organic"	GEN, STR, AMP, AMC, CEX, CFT, CTX, AZM, CHL, NAL, CIP, INN, STX, TET	TET (57.6–75.0%), GEN/STR (27.0–52.9%), AMP (17.7–44.3%)	Broth microdilution	[71]
Italy	*S.* Infantis, Monophasic Variant of *S.* Typhimurium 4 [5], 12:I (MVST), *S.* Typhimurium, *S.* Kentucky	Meat (broiler, swine & cattle), mixed meat, mussels, sheep milk & cheese & feed. Carcasses, feces, swabs from poultry (broiler and laying hens), cattle, sheep & pigs.	AMP, AZM, AMK, GEN, TIG, CZA, CFX, COL, NAL, TET, TMP, SMZ, CHL, MEM, CIP, IMP, CFP,	NAL (63.6%), CIP, TET, TMP, AMP, CFX, CZA	Broth microdilution (Sensititre® EUVSEC3® & EUVSEC2® plates)	[153]
Italy	*S.* Typhimurium, *S.* Enteritidis, *S.* Rissen	Pig slaughterhouses (*n* = 150) carcasses, cecal samples (*n* = 30), environmental samples (*n* = 180) & traditional pork dry sausages (*n* = 75).	AMP, AMC, CPD, CFT, TMP, MBF, PIP, GEN, AMK, ENR, CHL, TET, NTF, STX	AMK, TMP, GEN (86.1%), TET, STX	VITEK® 2 AST GN-65	[154]

Iran	*Salmonella* spp.	Chicken meat samples (*i.e.*, breast muscle, *n* = 150)	PEN, TYL, TET, ERY, TIA, FOS, SXT, DFX, LIN/SPC, FLM, FLO	TET, PEN, TYL, ERY, TIA (100%)	Kirby-Bauer disk-diffusion	[155]
Russia	*S.* Infantis, *S.* Enteritidis, *S.* Typhimurium	Poultry (*n* = 112), pork (*n* = 91), beef (*n* = 103), & minced meat (*n* = 168)	AMP, IMP, AMK, STR, TOB, CFX, CEZ, STX, CHL, ATM, AMC, NFT, TET	STR (75%), STX, TET, ATM, CEZ	Kirby-Bauer disk-diffusion	[156]
Chile	*S.* Typhimurium, *S.* Infantis, *S.* Enteritidis, *S.* Derby	Stool samples from pigs (*n* = 500), from chickens (*n* = 300)	AMP, AMC, CZA, CFT, CTX, CIP, GEN, NAL, STX, TET, STR, ENR, ATM, TMP, SMZ, CHL	Chickens: NAL (94.7%), Pigs: TET (53.3%)	Kirby-Bauer disk-diffusion	[157]
Italy	*S.* Derby, *S.* Typhimurium, MVST, & *S.* Infantis	Pigs (*n* = 5), broiler (*n* = 8), pigeon, turkey, and laying hen (*n* = 1 each). Pork (*n* = 20), bovine (*n* = 4), & chicken meat (*n* = 7), mollusks (*n* = 4). Food processing (*n* = 2) & slaughter rooms (*n* = 4) & poultry farms (*n* = 3)	AMP, CFX, CZA, AMC, CEX, MEM, TET, CHL, CIP, NAL, PFX, GEN, STR, STX, SMZ, TMP	INN (86%), TET, AMP, STR, NAL	Kirby-Bauer disk-diffusion	[158]
Burkina Faso	*Salmonella* spp.	Sesames (*n* = 480), mango juices (*n* = 156), lettuces (*n* = 92), salads (*n* = 324)	AMC, AMP, CHL, STX, NAL, TET, IMP, MEM, GEN, AMK, CIP, CFP, CZA, CFX, ATM	GEN (26.8%), AMP, CEX, NAL	Kirby-Bauer disk-diffusion	[70]
Bangladesh	*S.* Enteritidis, *S.* Typhimurium	Carcass dressing water, chopping board, & knife swabs (*n* = 290)	AMK, GEN, STR, MEM, CTX, CFX, CZA, ATM, AMC, AMP, AZM, CIP, NAL, STX, TET, CHL	CIP (68.9%), NAL, TET, AMP, STR	Kirby-Bauer disk-diffusion	[159]
Poland	*Salmonella* spp.	Food chain llinks	AMP, SAM, AMC, PIP, TZP, CTX, CFP, CZA, IMP, MEM, ATM, CIP, PFX, LFX, OFX, NOR, AMK, GEN, TOB, CHL, STX	AMK (58.5%), GEN, TOB	Kirby-Bauer disk-diffusion	[73]
China	*S.* Derby, *S.* Meleagridis, *S.* Enteritidis, *S.* Senftenberg	RTE food samples (*n* = 74 cooked meat, *n* = 175 cooked poultry, *n* = 30 cold vegetable dishes, *n* = 21 fried rice/noodles)	AMC, AMP, CEZ, CEX, CZA, CTX, CFX, CFT, CFP, IMP, ATM, SRT, GEN, AMK, KAN, TET, NAL, CIP, ENR, STX, FLO, CHL	TET (70%), AMP, STR, STX	Kirby-Bauer disk-diffusion	[91]

Ethiopia	*Salmonella* spp.	Lettuce, cabbage, spinach, carrots, tomatoes, & green peppers (*n* = 30 each).	AMC, AMP, PEN, STX, CIP, CHL, GEN, ERY, TET, DOX, CEX, CTX, IMP, MEM, CFX, CZA	AMC & AMP (87.5%), STX, GEN, ERY, TET, DOX, CEX	Kirby-Bauer disk-diffusion	[78]
Mexico	*S.* Montevideo, *S.* Meleagridis	Calves, periparturient cow feces, & maternity beds (*n* = 377)	AMP, CIP, FLX, AMK, GEN	AMP, GEN (10%)	Kirby-Bauer disk-diffusion	[160]
Mexico	*S.* Aantum, *S.* Adelaide, *S.* Newport, *S.* Infantis	Retail ground beef (*n* = 115)	AMP, AMC, CTX, CFP, MEM, AMK, STR, CIP, AZM, TET, CHL, STX	TET (39.7%), CHL, STR, STX, AMP	Kirby-Bauer disk-diffusion	[72]
India	*Salmonella* spp.	Fresh eggs (backyard & commercial chicken & duck eggs, *n* = 60 each)	AMP, CFX, CIP, GEN, OXY	CFX (50%), AMP (39.3%)	Kirby-Bauer disk-diffusion	[161]
Italy	*S.* Infantis, *S.* Typhimurium	Poultry (*n* = 145) & pig meat (*n* = 106), beef (*n* = 54), bivalve molluscs (*n* = 109), eggs (*n* = 43) & sprouted seeds (*n* = 36).	KAN, GEN, STR, TOB, AMP, AMC, CFX, IMP, NAL, CIP, ENR, CTX, CZA, LFX, STX, TET, CHL	TET (50.7%), NAL, STX, KAN	Kirby-Bauer disk-diffusion	[88]
Vietnam	*Salmonella* spp.	Poultry fecal samples (*n* = 200), house floors (*n* = 150), drinking water (*n* = 45), feed (*n* = 45), sewages (*n* = 45) & tools (*n* = 30)	AMP, CIP, CZA, GEN, NAL, NFT, NOR, STR, TMP, TET	STR (89.2%), TET, AMP, NAL	Kirby-Bauer disk-diffusion	[162]
Chile	*S.* Infantis & *S.* Heidelberg	Poultry meat from the production line	AMP, CFP, CZA, CTX, CIP, GEN, AMK, IMP, MEM, ETP, TET, CVI, TZP, STX, SAM, NFT, CHL, ATM	GEN, KAN, STR, AMP, CEX, CTX, CHL, TET, STX	Kirby-Bauer disk-diffusion	[47]
Costa Rica	*S.* Infantis, *S.* Anatum, & *S.* Kentucky	Poultry meat (*n* = 38), Broiler caecum (*n* = 63)	AMK, GEN, AMP, CEX, CFX, CFP, ATM, AMP, AMC, TZP, CHL, AZM, NAL, CIP	NAL (92.1%), CHL, AMP, CFX	Kirby-Bauer disk-diffusion	[95]
Kenya	*Salmonella* spp.	Fresh Nile tilapia (*Oreochromis niloticus*) fish	PEN, VAN, RIF, AMP, CFP, CPD, CHL, NFT, CTX, MEM, STR	PEN (22.2%)	Kirby-Bauer disk-diffusion	[163]
Bhutan	*S.* Typhimurium, *S.* Paratyphi	Healthy broiler carcasses (*n* = 180) from commercial farms	AMP, AMO, STR, STX, GEN	TET (95.7), STX, AMO, AMP	Kirby-Bauer disk-diffusion	[164]
China	*S.* Enteritidis & *S.* Typhimurium	Pork (*n* = 140), chicken (*n* = 128), vegetables (*n* = 232)	CIP, GEN, STR, ERY, CFX, AMP, AMO, ENR, KAN, SMZ, CEP, TET	TET (85.7%), CIP (71.4%)	Kirby-Bauer disk-diffusion	[92]

Morocco	*S.* Kentucky, *S.* Muenster, *S.* Typhimurium, *S.* Menston	Miscellaneous foods	AMP, CFX, CEX, CZA, CTX, CHL, CIP, GEN, ERT, NAL, TET, TMP, STX	TET (46.7%)	Kirby-Bauer disk-diffusion	[165]
Spain	*S.* Derby	Human clinical samples (*n* = 20), pig carcasses, pork- or pork & beef-derived products, or wild boar (*n* = 16)	AMP, AMC, CFP, CFX, CEX, ERT, AMK, GEN, STR, NAL, CIP, KAN, ATM, NFT, TET, TOB, CHL, TMP	TET (66.7%), STR, NAL, AMP	Kirby-Bauer disk-diffusion	[166]
China	*S.* Enteritidis, *S.* Corvallis, *S.* Indiana, *S.* Typhimurium, & *S.* Kentucky	Poultry meat	TET, CHL, SMZ, AMP, CTX, CZA, IMP, GEN, NAL, CIP, ATM, COL, CEX, CEZ	TET (59.2%), NAL, CHL	Broth microdilution	[167]

[1] Numbers in round brackets next to the first antibiotic represent the percentage of resistance reported for the antibiotic for which the strains analyzed showed the most tolerance. If no number is indicated, please assume 100% resistance.

3. *Listeria* spp.

Listeria is a genus of Gram-positive, rod-shaped, facultatively anaerobic, and non-endospore-producing bacteria that acts as an intracellular parasite in mammals. Although in food analysis *L. monocytogenes* is the most targeted species, early reports have focused on other strains, such as *L. innocua*, *L. seeligeri*, and *L. welshimeri*. Though no resistance was found in the latter, 19.3% of the *L. innocua* isolates, mostly from frozen food items, were resistant to one or more antibiotics [168]. A more recent study showed that 29% of samples from butcher shops were positive for *Listeria* spp. (48, 28, and 7% for *L. innocua*, *L. seelligeri*, and *L. monocytogenes*, respectively) [169].

L. monocytogenes resistance has been attributed to conjugation (e.g., plasmid horizontal transfer from other Gram-positive bacteria such as *Enterococcus*, *Streptococcus*, and *Staphylococcus*), efflux pumps [170,171] genetic alteration, and biofilm formation (especially contamination during food packaging) [172]. An excellent primer on *Listeria*-specific mechanisms of resistance can be found in the work of Luque-Sastre and collaborators [173].

Listeria isolates are differentiated by probing for immunoreactivity to two cell-surface structures, *i.e.*, the somatic O and flagellar H antigens. For *L. monocytogenes*, four O-serogroups (1/2, 3, 4, 7) have been recognized, which are further differentiated into serotypes 1/2a, 1/2b, 1/2c, 3a, 3b, 3c, 4a, 4b, 4c, 4d, 4e, and 7. Three of these (1/2a, 1/2b, and 4b) cause most of the human illness cases. Specifically, serotype 4b is most associated with outbreaks [174,175]. For example, in Mexico, from 300 food samples, 5.6% of recovered strains were identified as *L. monocytogenes*, of which 68.4% belonged to serogroups 4b, 4d, and 4e, and 92.1% exhibited at least four virulence genes (*i.e.*, *actA*, *hly*, and *plcB*) [176]. A similar case was found in Romania, where *L. monocytogenes* isolates from RTE, meat, and dairy foods included 47.1 and 29.4% of the 1/2a-3a and 4b-4d-4c serotypes, respectively [177]. An additional study in this country found that 75% of *L. monocytogenes* strains recovered from RTE foods were serotype 1/2a (with regulatory factor *prfA* present in all isolates). Analysis of antimicrobial resistant genes identified tetracycline-resistant genes, particularly *tet*(*C*), *tet*(*M*), and *tet*(*K*). The presence of *ampC* and *dfrD* was also noticeable [178].

From a total of 50 *Listeria* strains isolated from meat and dairy products, consisting of seven *L. monocytogenes* and 43 *L. innocua* strains, which showed the presence of antimicrobial resistance genes: *tet M*, *tet L*, *mef A*, *msr A*, *erm A*, *erm B*, *lnu A*, and *lnu B*. Multidrug resistance was identified in 27 *Listeria* strains, four belonging to *L. monocytogenes*. Resistance to CDA (a lincosamide) was the most common resistance phenotype, identified in 45 *Listeria* strains. Hence, the preferred first-line therapy remains AMP or PEN, often combined with GEN or RIF for synergistic effects [170]. Worryingly, recent data suggest *L. monocytogenes* strains recovered from foods exhibited 87.3% of multidrug resistance and 92.4% to β-lactams [179]. Similarly, South African isolates exhibit resistance determinants for sulfonamides (*sul1* and *sul2*, 64.4%), aminoglycosides [*strA*, *aadA*, *aph* (*3*)-*IIA*, 47.9%], and β-lactams (*bla*$_{\text{TEM}}$, and *blaz*, 44.3%). For patients allergic to β-lactams, STX is the standard alternative, as *Listeria* remains broadly susceptible to it (Table 4) [170]. Additionally, in some cases, high resistance to FOS has been documented as a natural feature of the pathogen (together with NAL, FMQ, and cephalosporins) (Table 4) [179–181].

Interestingly, a longitudinal study found that significant resistance genes in *L. monocytogenes* included *fosX*, *lin*, *abc-f* (macrolide), and *tet*(*M*). No increase in antimicrobial resistance determinants was observed over 11 years [182]. There is additional evidence suggesting co-selection of resistance traits in food production systems and bacterial responses to stress and disinfectants (e.g., *bcrABC*) [181]. Over eight years, acquired antimicrobial phenotypes were shown to confer resistance to tetracyclines (*tetM*), trimethoprim (*dfrD*), lincosamides (*lnuG*), macrolides (*ermB* and *mphB*), and phenicols (*fexA*). A similar trend was recently described in isolates recovered from Chile, in which 100% of the *L. monocytogenes* strains carried the *fosX*, *lin*, *norB* (fluoroquinolones), *mprF* (lipopeptides), *tetA*, and *tetC* resistance genes. In addition, the *arsBC*, *bcrBC*, and *clpL* genes were detected, which conferred resistance to stress and

disinfectants [183]. Recent research also supports these findings, with next-generation sequencing of *L. monocytogenes* showing that *fosX* determinants are ubiquitous across 58 studies and, in up to 60.38% of reports, the presence of the *lin* and *norB* genes [184].

Since *L. monocytogenes* is ubiquitous in agricultural environments, the cultivation of fresh produce predisposes it to contamination. Cold-stored dairy, meat products, fresh produce, and novel foods made thereof (e.g., hummus or guacamole) are considered high-risk foods [185].

In this scenario, the contamination of RTE foods originates either from raw ingredients (of both plant and animal origin) or, more commonly, from cross-contamination within food-processing facilities [163]. Interestingly, recent research has also demonstrated that stressors in food-processing environments (e.g., heat, acidic and alkaline pH, UV irradiation, and high osmolarity) can induce tolerance that may contribute to the predominance of *Listeria* and the development of antimicrobial resistance, even without antibiotic selection pressure [186]. Said stressors induce bacterial tolerance by triggering global stress responses that alter cellular physiology. When bacteria encounter stressors such as sublethal antimicrobials, temperature shifts, or nutrient starvation, they temporarily slow their metabolism, deploy protective chaperones, and alter membrane permeability, thereby effectively blocking antibiotics from reaching their targets [187].

For example, in carcasses obtained from poultry slaughterhouses in Northern Greece, an 80 and 99% of samples were positive for *Listeria* spp. and *L. monocytogenes*, respectively [166]. All isolates were resistant to NAL (a naphthyridone) and OXO (both used to treat Gram-negative bacteria), most were resistant to CDA, and only a few were resistant to OXY and TET [188].

Finally, although relatively recent attention has been drawn to the resistance of *Listeria* species in food, some countries, possibly compelled by listeriosis outbreaks, have already amassed considerable research on the matter [189,190]. Notably, some other African countries have also identified human breast milk as a reservoir for *Listeria* [191].

Table 4. Summary of bacterial isolates from foodstuffs and other food-related matrices for *Listeria* species.

Country	Isolates	Source	Antibiotics Tested	Resistance to [1]	Testing Method	References
United Kingdom	*L. monocytogenes*	Foods	AMP, CHL, COL, ERY, GEN, KAN, STR, SPC, SMZ, TET, TMP, VAN, FZD, NAL, CIP	TET (2–5%), CIP (2.2%), *Listeria* spp. are constitutively resistant to NAL, COL & cephalosporins	Agar dilution Breakpoint	[192]
Ireland	*L. monocytogenes*, *L. innocua*, *L. seeligeri*, *L. welshimeri.*	*n* = 67 retail food samples	AMP, CHL, ERY, GEN, PEN, STR, TET, VAN	TET (6.3%), PEN (3.7%), AMP (2.0%)	Kirby-Bauer disk-diffusion	[168]
Greece	*L. monocytogenes*	Poultry slaughterhouses (*n* = 4 establishments; 100 samples)	AMO, AMP, CFX, CEP, CHL, CIP, CDA, ENR, ERY, GEN, KAN, NAL, NEO, OXO, OXY, PEN	OXO & NAL (100%), CDA (83.6%), OXY (12.7%)	Kirby-Bauer disk diffusion	[188]
Türkiye	*L. monocytogenes*	Raw or cooked foods, including sausage, raw minced beef, chicken breast, chicken gizzard, raw meat, raw milk, cooked turkey döner, anchovy, and mussel	PEN, VAN, TET, CHL, RIF, ERY, GEN, TMP, FOS, STR	FOS (92.9%), STR (7.1%)	Kirby-Bauer disk diffusion	[180]

Spain	*L. monocytogenes*, *L. innocua*	RTE products of animal origin (meat and dairy products)	AMP, CIP, CDA, ERY, GEN, PEN, RIF, TET, VAN	CDA (100%), CIP (52%), AMP (32%)	Kirby-Bauer disk-diffusion	[193]
South Africa	*L. monocytogenes*	Environmental, raw seafood, raw meats, & RTE foods (e.g, fresh produce, dairy, deli meats), *n* = 177 isolates	AMP, CHL, ERY, GEN, TET	RTE foods 25% at least to *n* = 2 (CHL, ERY, TET) antibiotics, raw meats 50% at least to *n* = 4 antibiotics	Kirby-Bauer disk-diffusion	[189]
South Africa	*L. monocytogenes*	RTE foods (*n* = 194 isolates)	FOS, CHL, OXY, CIP, VAN, STR, AMK, GEN, STX, TRP, CAM, CTT, CTX, SMX, ERT, MEM, ERY, IMP, AMO, SAM, AMP, PEN	CTX (53.1%), TMP (56.2%), SMZ & CTT (61.9%), VAN & OXY (62.9%)	Kirby-Bauer disk diffusion	[194]
Chile	*L. monocytogenes*	RTE foods (*n* = 436). Cheeses (*n* = 161), cooked meats (artisanal ham, pâté, sausages, & blood sausage) (*n* = 186), pre-processed fruit & vegetables (chopped fruit, fruit salads with strawberries, melon, & peaches, & leafy vegetable salads) (*n* = 22), & meals and mixed dishes with raw & cooked ingredients (*n* = 67)	AMP, PEN, STX, ERY, VAN, TET, CIP, CHL	AMP (78% sensitivity)	Kirby-Bauer disk diffusion	[183]
Romania	*L. monocytogenes*	*n* = 130 RTE products (ham sausages, smoked specialties), *n* = 47 raw meat samples (minced pork & pork organs, snails), *n* = 44 dairy samples (assorted cheese)	PEN, IMP, GEN, CIP, MFX, FOS, TEI, TIG, VAN, LIN, CDA, ERY, LZD, FAS, RIF, STX, TET	PEN & FAS (100%), MFX (88.2%), FOS (82.4%), CDA (76.5%), IMP (52.9%)	Vitek 2 Compact automated system	[177]
France	*L. monocytogenes*	Food isolates (*n* = 2424)	AMO, AMP, CTX, CIP, CDA, CHL, ERY, FOS, FAS, GEN, IMP, TET, LVX, MXF, NAL, KAN, PEN, RIF, STR, TMP, VAN	NAL (100%), CTX (99%), FOS (96%)	E-test	[181]
South Africa	*Listeria* spp. (*L. monocytogenes*, *L. innocua*, & *L. welshimeri*)	AMC, PEN, AMP, CFX, STR, GEN, KAN, TET, DOX, NAL, CIP, ENR, AZM, CDA, STX	NAL 100%, CFX & CDA 66.7%, TET 33.3%, AMC 22.2%	NAL (100%), CFX (80.4%)	Kirby-Bauer disk-diffusion	[195]
Mexico	*L. monocytogenes*	Raw poultry (*n* = 60), ground beef (*n* = 60), seafood (*n* = 20 fish, *n* = 20 shrimp, & *n* = 20 crabs), cheese (*n* = 30 fresh cheese & *n* = 30 mature cheese), & milk (*n* = 30 pasteurized milk and *n* = 30 raw milk)	AMP, CHL, CIP, ERY, GEN, LFX, MEM, STR, STX/TMP, TET, VAN	STX (88.4%), STR & MEM (30.7%)	Kirby-Bauer disk-diffusion	[176]

Ethiopia	*L. monocytogenes*	Bovine milk from dairy farms (*n* = 166), shops (*n* = 120), & cafeterias (*n* = 98). Bovine meat from abattoirs (*n* = 240), butcher shops (*n* = 84), & restaurants (*n* = 60)	PEN, AMO, AMP, VAN, CIP, STR, NAL, GEN, ERY, CDA, CLX, TET	NAL (96.1%), TET (53.8%), STR (15.4%), PEN (11.5%)	Kirby-Bauer disk-diffusion	[196]
Romania	*L. monocytogenes*	RTE foods (*n* = 8151)	AMP, CIP, CDA, CHL, GEN, OXA, CEP, LVX, MXF, PEN, RIF, STM, TET, VAN	STM (26.9%), OXA (23.1%)	Kirby-Bauer disk diffusion	[178]
Spain	*L. monocytogenes*	*n* = 104, *n* = 52 carcasses & *n* = 52 chicken cuts	AMP, OXA, CEX, CFX, CFP, GEN, ERY, VAN, SXT, RIF, TET, CHL, CIP, ENR, NFT	OXA + CEX, CTX + CEP (48.7%)	Kirby-Bauer disk diffusion	[197]
Italy	*L. monocytogenes*	Meat products (*n* = 173), seafood (*n* = 54), dairy products (*n* = 19), sauces (*n* = 2), confectionery products (*n* = 1), RTE rice dishes (*n* = 1), & food-processing environments (*n* = 19).	AMP, LIN, OXA, FMQ, FOS, GEN, MER, ERY, STX, TET	OXA (88.48%), FOS (85.87%) & FMQ (78.44%).	Kirby-Bauer disk diffusion	[179]
Ethiopia	*L. monocytogene*, *L. innocua*, & *L. seeligeri*	Raw meat from abattoirs & butcher shops	AMO, CHL, CLX, PEN, TET, VAN, SMZ, GEN, NAL, AMP	CLX & NAL (100%), PEN (76%), TET (59%), CHL (24%)	Kirby-Bauer disk diffusion	[169]
South Africa	*L. monocytegenes* (*n* = 24) & *Listeria* spp. (*n* = 122)	Beef and beef products	TET, STX, STR, PEN, NAL, KAN, ERN, DOX, CDA, CEX, GEN, CIP, AZM, AMP, AMC	NAL (100%), STR (45.8%), ENR (41.7%), DOX (37.5%), AMP & ATM (33.3%)	Kirby-Bauer disk diffusion	[198]
India	*L. monocytogenes*	Local ethnic foods (*n* = 2829). Raw meats, cooked foods, fermented products, dairy, street foods, & beverages	AMP, PEN, SXT, MEM, CHL, CIP, GEN, TET, ERY, CDA, VAN	CDA (48%), ERY (45%), AMP (42%), PEN (38%)	Microbroth dilution technique	[171]
Romania	*L. monocytogenes*	*n* = 10,306 samples (*i.e.*, milk, milk-based beverages, cheese, cream, butter, yogurt, ice cream, dairy desserts, milk, and whey powders	AMP, PEN, OXA, MET, CIP, LFX, MFX, CDA, TET, GEN, CHL, RIF, SMZ	OXA & SMZ (13.95%), AMP, TET (11.62%)	Kirby-Bauer disk diffusion	[199]
Poland	*Listeria* spp.	*n* = 750 raw fish samples (Crucian carp, Sturgeon, Trout, Herring)	OXA, PEN, MER, ERY, RIF, VAN, TET, SMZ, CHL, CIP, ENR, NIT, CDA	OXA, CEF, MER, RIF, SMZ (100%), CIP (91.7%), TET (75.0%)	Kirby-Bauer disk diffusion	[200]

[1] Numbers in round brackets next to the first antibiotic represent the percentage of resistance reported for the antibiotic for which the strains analyzed showed the most tolerance. If no number is indicated, please assume 100% resistance.

4. *Campylobacter* spp.

Campylobacter spp. are Gram-negative spiral, non-spore-forming, chemoorganotrophic, rod-shaped, or curved bacteria. These bacteria are a leading cause of foodborne gastroenteritis [201,202]. The advent of molecular detection of genes responsible for antibiotic resistance (e.g., *gyr* for fluoroquinolones, *erm* for macrolides, *tet* for tetracyclines, or *aph* for aminoglycosides) has facilitated clinical therapy and surveillance of the emergence and dissemination of antibiotic-resistant bacteria [203]. For an excellent

primer regarding *Campylobacter* resistance mechanisms (including fluoroquinolones, macrolides, FLO, β-lactams, aminoglycosides, and tetracyclines, the work by Iovine, Shen et al., Tang et al., and, more recently, Aleksic et al., are proposed [204–207].

In a very thorough work regarding contamination in a slaughterhouse, Schreyer et al. [208] found not only *Campylobacter* spp. in chicken cecum but also evisceration knives and workers' hands, and samples before and after the chiller. Interestingly, *C. coli* contamination was significantly higher than that of *C. jenuni*. This trait has been observed in analogous (poultry-related) studies in other latitudes [209,210]. Not only was the contamination within the meat chain relatively high, but the strains also exhibited several genes responsible for resistance, such as *cmeA/B*, *tet*(*O*), and *bla*$_{OXA-6}$.

Efflux pump CmeABC expels substances such as antimicrobials, toxic heavy metals, dyes, and detergents from the interior of the bacterial cell [211]. Interestingly, it has been correlated with surface polysaccharides, which serve as a resistance mechanism against phenolic compounds [212]. It is also largely responsible for macrolide [213] and multidrug resistance in Gram-negative bacteria [211,214], and its role in the clinical context is well defined, as it contributes significantly to high-level resistance to CIP and TET in *C. jejuni* and *C. coli* [215].

Additionally, the *tet*(*O*) determinant is a common trait and has been described in similar studies [216,217]. Such evidence adds to the previous body of research, which heavily linked fluoroquinolone-resistant *Campylobacter* spread from poultry (since *Campylobacter* is a normal enteric flora in many avian species) to humans [209,218,219]. However, as a zoonotic infection, it can be present in domestic and wild birds and other animals [220]. Hence, campylobacteriosis warrants a One Health approach to tackling this problem [221].

Alike results have also been obtained from pig slaughterhouses. *Campylobacter* spp. have been isolated from pig guts (200 samples, 47.6% contaminated), feces, and surfaces. 90.8% of strains exhibited multidrug resistance [222]. A general increase in *Campylobacter* resistance toward fluoroquinolones (e.g., NAL/CIP) and TET has been reported worldwide [220,223–225]. EFSA reported that rates of resistance to CIP were very high in *C. jejuni* and *C. coli* isolates from humans and very high to extremely high in *C. jejuni* and *C. coli* isolates from poultry, pigs, and calves [224]. A recent review that reported South American *Campylobacter* isolates indicated that although the bacteria showed an overall low resistance to ERY (a drug of choice to treat campylobacteriosis), it was widespread [225], a trait that persists in Europe [224]. On the other hand, in general, cattle and chickens seem to be important hosts in the Sub-Saharan African region, and may play an important role in transmitting to humans. Most *Campylobacter* isolates were resistant to ERY (44%), AMP (39%), TET (33%), NAL (31%), and CIP (30%) [226].

A recent study [227] found multidrug resistance in almost all isolates from cattle, chicken, and water samples, and also determined that the most resistance determinant within the strains was the *tet*(*O*) gene. Despite several restrictions in some countries, tetracyclines are still among the most systematically used as growth promoters in animal feed, which maintains selective pressure over gut microbiota [228–231]. A recent Canadian study [232] found that, even in 2021, the most used antibiotic in turkey farming includes bacitracin (at 472.7 mg·kg^{-1} per biomass), followed by β-lactams, orthomycin (a combination of isoniazid and a streptomycin derivative) [233], and tetracyclines (at 58.8 mg·kg^{-1} per biomass). Other genes coding for resistance were those for β-lactams (*bla*$_{OXA-61}$), aminoglycosides (*aph-3-1*), (fluoro)quinolones (*gyrA*), and multidrug efflux pump (*cmeB*). Tunisian laying hens and eggs have been recently found to harbor similar resistance determinants [234]. The authors also found the *erm*(*B*) gene in almost all the isolates from these samples. Byambajav et al. also found the *erm*(*B*) gene or a nucleotide substitution at nt 2075 of 23S rDNA in all *C. coli* isolates from Mongolia [235].

An interesting finding that supports the (over)use of antibiotics in livestock as a major driver of the selection of resistant bacteria is reported by Paintsil et al. [210]. The authors found that fecal samples from

animals on smallholder farms exhibited not only significantly lower *Campylobacter* contamination but also reduced antibiotic resistance.

Notably, a Belgian study [236] showed that human isolates (from diarrheal cases) had resistance profiles similar to those found in animals, with a tendency toward increased resistance to NAL, CIP, and TET. Whole genome sequencing of human isolates from the USA [237] found antimicrobial resistance genes encoding mostly resistance to the β-lactam (*bla*$_{OXA-193}$, *bla*$_{OXA-460}$), tetracyclines [*tet*(O), *tet*(O/32/O)], fluoroquinolones (*gyrA*), and aminoglycosides (*aph*(3′)-III). Another African study reports similar results in pediatric cases with clinical diarrhea, supporting the transfer of genetic determinants of antibiotic resistance from animals to humans [238].

In conclusion, evidence indicates that the relatively high rates of fluoroquinolone resistance (Table 5) have limited their usefulness in treating *Campylobacter* infections. Macrolides like azithromycin are the current drugs of choice when antibiotic treatment is indicated. Resistance to macrolides in *Campylobacter* has remained stable. The increased prevalence of antibiotic-resistant *Campylobacter* cannot be solely attributed to antibiotic overuse. Interspecies transmission and subsequent clonal expansion also contribute to the dissemination [221].

There seems to be a certain plasticity in *Campylobacter* species, and genetic material from *C. jejuni* to *C. coli* is a possibility, which then increases virulence [234]. The result is a higher number of antibiotic-resistant infections, which could become a health burden. Furthermore, genetic exchange between *Campylobacter* and Gram-positive bacteria occurs in the natural environment and is more frequent than previously realized. These antibiotic-resistance genes present in *Campylobacter* species can further disseminate by clonal expansion or horizontal gene transfer [221].

Table 5. Summary of *Campylobacter* bacterial isolates from foodstuffs and other food-related matrices.

Country	Isolates	Source	Antibiotics Tested	Resistance to [1]	Testing Method	References
Poland	*C. jejuni* & *C. coli*	Chicken meat and giblets (*n* = 218)	CIP, ERY, TET, GEN	CIP (97.9%)	Kirby-Bauer disk-diffusion	[209]
Poland	*C. jejuni* (*n* = 132) & *C. coli* (*n* = 189)	Retail raw meat beef (*n* = 105), pork (*n* = 85), poultry (*n* = 368)	CIP, NAL, STR, TET, ERY	CIP (91% *C. jenuni*; 86.1% *C. coli*) & NAL (89.3% *C. jenuni*; % *C. coli*)	Kirby-Bauer disk-diffusion	[239]
France	*C. jejuni* (*n* = 175)	Chicken meat products: carcasses (*n* = 120), legs (*n* = 121) & fillets (*n* = 120)	GEN, STR, CIP, NAL, TET, ERY, CHL		Broth microdilution	[240]
Nigeria	*C. jejuni* (*n* = 242)	Retail chicken (*n* = 252)	NAL, GEN, ERY, ENR, CHL, STR, TET	NAL (100%), GEN, ERY, ENR, CHL, STR, TET	Kirby-Bauer disk-diffusion	[241]
Canada	*C. jejuni* (*n* = 53) & *C. coli* (*n* = 3); (23.5 & 14.2% from chicken and turkey simples)	Retail chicken (*n* = 204), turkey (*n* = 110), ground beef (*n* = 145) & pork (*n* = 147)	TMY, AZM, CDA, ERY, GEN, NAL, FLO, TET	TET (48.1%)	Broth microdilution	[216]
United Kingdom	*C. jejuni* & *C. coli* (*n* = 393)	Chilled chickens at retail (skin samples)	CIP, ERY, TET, GEN, STR	CIP (52% *C. jenuni*; 48% *C. coli*) & TET (52% *C. jenuni*; 60% *C. coli*)	Broth microdilution	[242]

Egypt	*Campylobacter* spp. (*n* = 98)/*C. jejuni* (*n* = 65)	Chicken (*n* = 315), Animal Products (*n* = 122) & Human Stool Swabs (*n* = 128)	AMP, CEP, ERY, GEN, NAL, OXY	CEP (94.7%), TET, ERY, NAL	Kirby-Bauer disk-diffusion	[243]
Canada	*C. jejuni* & *C. coli* (*n* = 178)	Chicken, Turkey, Duck, Game Birds	GEN, TMY, CDA, AZM, ERY, FLO, CIP, NAL, TET	TET (56.25%)	Broth microdilution	[244]
Mongolia	*C. jejuni* (*n* = 25) & *C. coli* (*n* = 6)	Cloacal Swabs of Chickens (Broiler/Laying, *n* = 71)	CIP, ERY, NAL, NOR, TET	NAL (51.6%)	E-Tests	[235]
Russia	*C. jenuni* (*n* = 40)	Raw milk, poultry products, and washings from processing equipment	ERY, AZM, CDA, CAM	ERY (27.5%)	Kirby-Bauer disk-diffusion	[213]
Brazil	*C. jejuni* (*n* = 54)	Broiler carcass/Poultry slaughterhouses	CHL, CIP, ERY, GEN, NAL, TET	TET (51.8%), ERY	Broth microdilution	[217]
Japan	*C. jejuni* (*n* = 13) & *C. coli* (*n* = 3)	Pork (*n* = 14) & chicken (*n* = 53)	AMP, CEZ, STX, IPM, MIN, GEN, KAN, ERY, AZM, NAL, CIP, LFX	CEZ, STX, NAL, CIP, LFX	Kirby-Bauer disk-diffusion	[245]
Benin	*C. jejuni* & *C. coli*	Cutting Tables at Swine Slaughterhouse and Taverns	AMP, GEN, ERY, CIP, TET, AMC	CIP (44%), AMP, ERY, GEN, AMC	Kirby-Bauer disk-diffusion	[222]
Italy	*C. jejuni* (*n* = 2734)	Domestic/wild animals & humans	NAL, CIP, CHL, ERY, GEN, STR, TET	NAL (67.39%), CIP, TET	Broth microdilution	[246]
Tunisia	*C. jejuni* & *C. coli* (*n* = 177)	Layer hens and eggs	AMP, AMC, GEN, TET, ERY, NAL, CIP, CHL	ERY (98.87%) & TET	Kirby-Bauer disk-diffusion	[234]
Malaysia	*C. jejuni* & *E. coli*	Wild birds (*n* = 38), chickens (*n* = 71), humans (*n* = 47), & environment (*n* = 153).	CIP, ENR, SAM, TET, GEN, STR, ERY, NAL, SXT, CPD	CPD & TET	Kirby-Bauer disk-diffusion	[247]
Ghana	*C. jejuni* & *C. coli*	Livestock fecal samples from commercial & smallholder farms	CIP, TET, STR, AMP, KAN, ERY, CHL	CIP (41.3% *C. jenuni*; 58.7% *C. coli*) & TET (52.9% *C. jenuni*; 43.6% *C. coli*)	Kirby-Bauer disk-diffusion	[236]
Argentina	*C. jejuni* & *C. coli*	Poultry slaughterhouse (*n* = 333)	CIP, ERY, TET, ENR, GEN, AMP, CHL, STR	*C. jenuni*: CIP, TET, ENR. *C. coli*: CIP, ERY, TET, ENR, AMP	Kirby-Bauer disk-diffusion	[208]
Estonia/Latvia/Lithuania	*C. jejuni* (*n* = 46) & *C. coli* (*n* = 15)	Fresh broiler chicken meat and human patients	ERY, CIP, STR, NAL, GEN	NAL (100–86.7%), CIP, TET, STR (68.8–26.7%)	Broth microdilution	[248]
Pakistan	*Campylobacter* spp. (*n* = 38/6)	Chicken, beef & mutton (*n* = 300)	NAL, CFX, CDA, TYL, ENR, STR, DOX, TET	TET (100%), CFX, TYL, ENR, CDA, NAL	Kirby-Bauer disk-diffusion	[249]

Canada	*C. jejuni* (*n* = 871) & *C. coli* (*n* = 383)	Turkeys (fecal samples, *n* = 293 flocks)	CIP, AZM, ERY, GEN, NAL, TET,CIP, NAL, TET TYM, CDA, FLO		Broth microdilution	[232]
Kenya	*C. jejuni* (*n* = 74) & *C. coli* (*n* = 29)	Chicken, cattle, and cattle-trough water samples	AMP, TET, GEN, ERY, CIP, NAL	AMP (100%), TET, ERY, CIP	Kirby-Bauer disk-diffusion	[227]

[1] Numbers in round brackets next to the first antibiotic represent the percentage of resistance reported for the antibiotic for which the strains analyzed showed the most tolerance. If no number is indicated, please assume 100% resistance.

5. *Staphylococcus* spp.

Staphylococci are clump-forming Gram-positive cocci of 1 μm in diameter. They are salt-tolerant and often hemolytic. *S. aureus* and *S. intermedius* are coagulase-positive. All other staphylococci are coagulase negative. Staphylococcal food poisoning is a rapid-onset illness caused by eating foods contaminated with *S. aureus*, often transmitted by food handlers or through dairy/meat products.

An early report on whey and cheese showed that staphylococci coagulase-negative (CoNS, 54% of the isolates) included species such as *S. lentus*. Coagulase-positive staphylococci identified were divided into 3 groups: *S. aureus* (40%), *S. intermedius* (2%), and *S. hyicus* (4%), indicating a high incidence of PEN resistance. *S. lentus* isolates exhibited resistance to OXA, ERY, and LIN [250].

More recently, Osman et al. [251] found *S. hyicus*, *S. aureus*, *S. schleiferi* subsp. *coagulans*, *S. intermedius*, and *S. lentus* in beef meat. These strains were characterized by possessing genes *gyrA*, *gyrB*, and *grlA* (encoding essential type II/IV topoisomerases in bacteria that regulate DNA supercoiling during replication and transcription). Though phenotypically already resistant to OXA, only 40.7 and 7.4% carried the *mec*A and *cfr* genes, respectively. The chloramphenicol-florfenicol resistance gene is a mobile genetic element that encodes a 23S rRNA methyltransferase, conferring broad-spectrum, multidrug resistance to Phenicols, Lincosamides, Oxazolidinones, Pleuromutilins, and Streptogramin A [251].

Although *S. aureus* is mostly considered a clinically relevant pathogen [252], several reports have contributed to establishing its incidence in food samples, food handlers, food-producing animals, and food processing environments worldwide (e.g., Brazil [253,254], Portugal [255], China [256], Italy[257]). Of special interest are reports that include the presence of Methicillin-Resistant *Staphylococcus aureus* (or MRSA) in foods. MRSA (resistance primarily driven by the *mecA* gene, which encodes a low-affinity penicillin-binding protein [PBP2a]) is one of the leading causes of infections and a major threat to human health worldwide due to its numerous toxins [252,258].

One particularity among food *Staphylococcal* contamination is the specific attention given to direct handling (Table 6) [259]. *S. aureus* is known to easily colonize the hands and nose. In fact, among health professionals, carriage of *S. aureus* on hands and nose was found to be 8.9 and 39.6% (4.7 and 17.2% for MRSA), respectively. In addition to β-lactams, the majority of nasal MRSA were also resistant to ERY, and CIP [260].

Mekhloufi et al. [261] found that the *S. aureus* strains recovered from foods belonged to seven different staphylococcal enterotoxin gene (SEg)-types harboring the following combination of *se* and *sel* genes: (1) *sel*W, *sel*X; (2) *egc* (*se*G, *se*I, *se*M, *se*N, *se*O), *sel*W, *sel*X; (3) *se*A, *se*H, *se*K, *se*Q, *sel*W, *sel*X; (4) *se*B, *sel*W, *sel*X; (5) *se*D, *sel*J, *se*R, *sel*W, *sel*X; (6) *se*H, *sel*W, *sel*X, *sel*Y; and (7) *se*A, *egc* (*se*G, *se*I, *se*M, *se*N, *se*O), *sel*W, *sel*X. Meanwhile, 2.1% and 4.2% tested positive for the *tst*- (toxic shock syndrome toxin-1) and *mecA*- (staphylococcal chromosomal cassette *mec*-type IV) genes, respectively.

Interestingly, Elsalkh et al. [262] found that 48.6 and 8.6% of isolates recovered from pizza were identified as methicillin- and vancomycin-resistant *S. aureus* through detection of *mec*A and *van*A genes, respectively.

In yet another report [263], the *hla* (encoding an α-hemolysin) gene was detected in 87.1% of the isolated strains. Antimicrobial treatments heavily influence the *hla* gene; while some antibiotics (like β-

lactams) can inadvertently trigger its expression, others (like CDA) actively suppress toxin production to help limit tissue damage [263].

Analogously, do Nascimento Pereira et al. [264] evaluated *S. aureus* strains isolated from food handlers of pilot kitchens. In this case, 83.8 and 18.9% of isolates exhibited *seA* and *tst* genes, respectively. Also, *agr* (the accessory gene regulator locus is a critical quorum-sensing system in *S. aureus* that controls virulence factor expression based on cell density). Typing classified 58.3% of the strains as type I, and 18.9% were classified as MRSA. The SCC*mec* typing characterized strains as type II, III, IV, and V. For a thorough description of the staphylococcal cassette chromosome *mec* (SCC*mec*) typing, please refer to Uehara [265].

Achek et al. [266] found in both food and clinical isolates, the *tet*M/K, *blaZ*, *aac*A-*aph*D, *erm*C, and *mec*A genes. More recently, Anas et al. [267] found that the prevalence of *Staphylococcus* was very high (75 and 50%) in street kebab and raw buffalo meat, respectively. These isolates (82%) showed not only multidrug resistance (MDR) patterns but also produced β-lactamases or extended-spectrum β-lactamases, at rates of 48% and 24%, respectively. The most detected resistance genes were *mecA*, *sul1*, and *qnrS*/*qnrB* (29.2, 25, 20.8%, respectively). Similarly, Urimi et al. [268] found that 75% of *S. aureus* isolates from fast food restaurants were MDR, but their indices of multiple antibiotic resistance (MAR) ranged from 0.2 to 0.6. For a comprehensive list of resistance genes found in *Staphylococcus*, food, and food-related environments, the work by Chieffi et al. [257] is suggested.

Some researchers have used specific antibiotics against Staphylococci species, such as MCP (effective against topical infections caused by MRSA and *S. pyogenes*) [268], PRI (to treat severe Gram-positive infections, including MRSA) [250,261], or CRN (used to treat acute MRSA skin and skin structure infections) to test sensitivity [267]. Notably, from these three antimicrobials, resistance has already been proven towards MCP [269–271].

Finally, several approaches have been suggested as alternatives to antimicrobials for controlling *S. aureus* disease (e.g., bacteriophages, plant-based antimicrobials, nanoparticle- or light-based therapeutics, and probiotics) [272].

Table 6. Summary of *Staphylococcus* bacterial isolates from foodstuffs and other food-related matrices.

Country	Isolates	Source	Antibiotics Tested	Resistance to [1]	Testing Method	References
Spain	*Staphylococcus aureus*	Foods (*n* = 50 isolates) & Food handlers (*n* = 14)	AMP, PEN, OXA, MET, GEN, AMK, KAN, MCP, TMP, TET, ERY, CDA, CHL, CIP, MFX, RIF, LZD, VAN, TIG, TMP, STX	AMP & PEN (61.3%), ERY (25.8%) MCP (19.4%), OXA & MET (6.5%)	Kirby-Bauer disk-diffusion	[269]
Egypt	*Staphylococcus* spp. & coagulase-negative staphylococci	*n* = 30 each, fresh normal cow milk, pasteurized milk, pasteurized yogurt, beef burger & minced beef meat	CIP, ERY, TET, MET, RIF, PEN, VAN	PEN, MET, & TET (33.3%)	Kirby-Bauer disk-diffusion	[273]
Egypt	*S. hyicus*, *S. aureus*, *S. schleiferi* subsp. *coagulans*, *S. intermedius*, & *S. lentus*	*n* = 100 retail whole beef	MET, PEN, SAM, OXA, CHL, CIP, CDA, GEN, ERY, STX, TET, VAN	ERY (48.1%), CIP (59.3%), MET (63%), TET (66.7%), VAN (74.1%), OXA (77.8%), PEN (92.6%), CDA (96.3%), GEN (96.3%), STX (100%)	Kirby-Bauer disk-diffusion	[251]

Algeria	*Staphylococcus aureus* & MRSA	Raw milk (*n* = 30), minced beef meat (*n* = 25), chicken meat (*n* = 18), creamy cake (*n* = 14), pizza (*n* = 10), beef meat (*n* = 10) & sausages (*n* = 5)	PEN, OXA, CEX, AMC, GEN, ERY, KAN, TET, VAN, CDA, RIF, STX	PEN (100%), TET (45%)	Kirby-Bauer disk-diffusion/E-test	[266]
Türkiye	*Staphylococcus aureus*	*n* = 387 Cheese samples	PEN, OXA, AMP, MET, LZD, KAN, STR, GEN, NTM, VAN, TEI, ERY, ATM, RIF, CDA, LIN, TET, DOX, CEX, CEZ, CFP, CHL, TMP, FZD, SMZ, CIP, ENR, NOR, OFX	PEN (84.7%), AMP (72.9%), OXA (63.5%), LIN (57.7%), CEX (51.8%), CDA (50.6%), GEN (31.8%), MET (30.6%)	Kirby-Bauer disk-diffusion	[274]
Morocco	*Staphylococcus* spp.	Hospital food, work surfaces & food handlers. *n* = 608 samples: 300 food, 238 food contact surfaces & 70 nasal & hand	PEN, CEX, OXA, GEN, TMP, CIP, NOR, OFX, STX, FAS	OXA & PEN (100%)	Kirby-Bauer disk-diffusion	[275]
Algeria	*Staphylococcus aureus* & MRSA	*n* = 207 RTE foods (e.g., pastries *n* = 43 & cereals *n* = 17)	PEN, OXA, CEX, GEN, KAN, TMP, OFX, ERY, LIN, CDA, PRI, LZD, TEI, VAN, TET, FOS, NTF, FAS, RIF, STX	PEN (83.3%), TET & KAN (16.7%), OFX, ERY & LIN (8.3%)	Vitek 2	[261]
Malasya	*Staphylococcus aureus*	Food handlers & cooked food	PEN, CEX, ERY, CDA, MCP	PEN (58%)	Kirby-Bauer disk-diffusion	[271]
Bangladesh	*Staphylococcus* spp.	*n* = 60 samples of fast foods sold in different restaurants	ATM, ERY, PEN, AMO, AMP, CIP, DOX, GEN, CHL, CFX, CFM	ERY & ATM (95%), CFM (75%), AMP (50%), AMO (37.5%)	Kirby-Bauer disk-diffusion	[268]
Brazil	*Staphylococcus aureus*	*n* = 41 food handlers	PEN, OXA, CAM, ERY, CEX, TET, LFX, AMO, CDA, LZD, VAN	CAM & ERY (67.6%), OXA (64.9%, PEN (59.5%)	Kirby-Bauer disk-diffusion	[264]
Ethiopia	*Staphylococcus aureus* & *E. coli*	*n* = 525 Street Foods & *n* = 175 water samples	AMC, CHL, CIP, ERY, STR, SXT	ERY (78.6%), AMC (36.4%), STR (36.4%)—ERY (67.9% for *E. coli* strains)	Kirby-Bauer disk-diffusion	[276]
Ethiopia	*Staphylococcus aureus*	Milk, beef, eggs, and cheese, *n* = 96 each	CIP, ERY, TET, PEN, KAN, CEX, TMP, GEN, IMP, CRN	KAN (39%), TET (36%)	Kirby-Bauer disk-diffusion	[270]
India	*Staphylococcus* spp.	Raw buffalo minced meat (*n* = 70) & street meat kebabs (*n* = 20)	MET, CFC, SDZ, GTX, GMX, CFP, CZA, CTC, ATM, VAN, NAL, ERT, MEM, IMP, CFP, CTX, TET, OXA, CHL, CIP, KAN, ERY	NAL (80%), MET (68%), OXA (54%), CFP (36%)	Kirby-Bauer disk-diffusion	[267]
Poland	*Staphylococcus epidermis*	RTE foods including cheese, sushi, salad, & juice (*n* = 26 isolates)	AMK, GEN, OXA, MXF, VAN, CDA, ATM, CAM, ERY, NFT, LZD, FAS, TMP, STZ, TET	ERY (80.8%), CDA (73.1%), AZM (65.4%), CAM (61.5%)	Broth microdilution	[277]

Egypt	*Staphylococcus aureus*	*n* = 100 each, meat, chicken, & canned tuna pizzas	RIF, LZD, CIP, GEN, ATM, TET, AMP, PEN, KAN, CTX, CDA, CXM, STX, NFT	AMP, OXA & PEN (100%), CXM (87%), CTX (77%), KAN (76%)	Kirby-Bauer disk-diffusion	[262]
South Africa	*Staphylococcus aureus*	*n* = 168 samples, *n* = 42 each, maize meal/pap, chicken, pork & salad	TET, PEN, CEX, ERY, GEN, CIP	PEN (52%), CEX (46%), CIP (44%), GEN (24%), TET (14%)	Kirby-Bauer disk-diffusion	[278]

[1] Numbers in round brackets next to the first antibiotic represent the percentage of resistance reported for the antibiotic for which the strains analyzed showed the most tolerance. If no number is indicated, please assume 100% resistance.

6. *Escherichia coli*

E. coli is a gram-negative, facultative anaerobic, rod-shaped, coliform bacterium. As a fecal indicator, it may suggest fecal contamination or poor, unhygienic food handling. As an indicator organism of contamination, *E. coli*'s resistance profile is very relevant and has been documented (see discussion below and Table 7).

Babines-Orozco et al. [279] concluded that in Latin America, most antibiotic resistance genes present in *E. coli* strains are carried through IncF-type plasmids or class 1 integrons, including *qnr* (fluoroquinolones), *dfrA1* (diaminopyrimidines), *bla*$_{SHV}$, *bla*$_{TEM-1}$, *bla*$_{CTX-M}$ (β-lactams), *tet*A, *tet*B (tetracyclines), *aac* (*6*)-*Ib*, *aadA1* (aminoglycosides), *sul* (sulfonamides), and *cat-1*, *cmlA* (phenicols), being the most commonly found in diarrheagenic strains, food, water, and some livestock animals [279–282]. Similar findings have been documented elsewhere, e.g., China, Italy, Korea, or Nigeria in foods (including rabbits, poultry, pigs, dairy/beef cattle) [280].

Pathogenic *E. coli* utilizes a combination of specific virulence factors (molecules that enable it to cause disease) and antimicrobial resistance mechanisms to evade host immune responses and survive antibiotic treatments. These traits allow the bacteria to colonize tissues and cause severe intestinal or extraintestinal infections [281]. In this regard, at least 11 distinct pathotypes have been described in regional research [279].

For example, a recent study found that *E. coli* was present in 100% of food samples, with higher contamination rates in vegetables and fruits. Enterotoxigenic (ETEC: *elt*) and Uropathogenic *E. coli* (UPEC: *vat*, *cnf1*, *hylA*) genes were also identified in all samples; meanwhile, Diffusely Adhering *E. coli* (DAEC: *afa*) was found in 27% of the assay objects. The most effective antibiotics against the recovered strains were TET, STX, polymyxins, and quinolones [282]. Other virulence factors of pathogenic *E coli*, tested elsewhere, include Enteropathogenic (EPEC: *eae*A, *bfp*A), Enterohemorrhagic (EHEC: *hyl*A), and Enteroinvasive *E. coli* (EIEC: *ial*) [283].

Li et al. [284] found a detection rate of *E. coli* isolated from foods as follows: pork (59.6%), mutton (52.6%), retail fresh milk (52.4%), duck (36.4%), beef (35.3%), chicken (33.3%), RTE food (12.9%), and fish and vegetables were <11%. The detection rate of resistance genes was as follows: *tet*A (38%), *tet*B (27%), *bla*$_{OXA}$ (40%), *bla*$_{TEM}$ (20%), *flo*R (20%), *sul*1 (16%), *sul*2 (27%), *aad*$_{Ala}$ (19%), *aad*B (11%), *str*A (28%), and *str*B (24%); *tet*C and *bla*$_{PSE}$ were not detected. Virulence genes *fim*C, *agg*, *stx*2, *fim*A, *fyu*A, *pap*A, *stx*1, and *eae*A were found. Finally, they also found an interesting association between *fimC* and resistance toward CIP, GEN, AMK, LFX, and STR.

Likewise, Ronald et al. [285] isolated 30 *E. coli* with multiple antibiotic resistance (MAR) index of greater than 0.2 from meat samples; 88.9% of the samples tested positive. Isolates showed that the *tet*A (for TET resistance) and *sul*1 (for STX resistance) genes were present in 100.0% of isolates, while the *bla*$_{TEM}$ (for AMP resistance) and *str*A (for STR) genes were present in 2 isolates. O157 lipopolysaccharide O-antigen synthesis gene *rfbE-O157* was absent in all strains. Similar findings (*i.e.*, high resistance to TET and STX and high homology in genes *bla*$_{TEM}$ and *gry*A) have been further corroborated in food/clinical *E. coli* isolates from China [286].

A recent review of 61 studies from 18 countries showed that most food samples (*i.e.*, chicken meat and eggs) had prevalence rates of 8.9% and 80.5% for Shiga toxin-producing *E. coli* (STEC) and serotype O157, respectively. Additionally, the isolates were resistant to the following antibiotics: AMC, CHL, TET, CIP, GEN, AMP, NEO, and AMO [287]. An independent study found similar trends in eggs and poultry sausage, with prevalence of 59.3% and 14.4% for *E. coli* and 2.2% and 5.6% for *Salmonella*, respectively [288].

Finally, some reports demonstrate a close link between agriculture [289] and aquaculture [290] based human activities and the dissemination of bacteria with antimicrobial resistance traits. For example, van Hamelsveld et al. [291] showed that polluted water (with normal contamination levels of *E. coli*) in continuous contact with shellfish magnifies their microbial contamination levels, rendering the food above the threshold apt for human consumption. The authors also demonstrated that the bacteria found within the shellfish show a regular and increased rate of plasmid horizontal transfer. Osman et al. [292] demonstrated that β-lactam resistance genes (*bla*$_{OXA}$, *bla*$_{MOX}$, *bla*$_{CIT}$-like, *bla*$_{SHV}$, *bla*$_{FOX}$) in *E. coli* were abundant both in poultry hatchlings and in the hatchery environment. Isolates were also able to form biofilms, thereby increasing their tolerance to antibiotics [293].

Furthermore, at least eight studies, published from 1940–2016, representing 18% of all revised literature, could directly link the transmission of antimicrobial resistance in *E. coli* from food animals to humans, 25 studies (56%) suggested transmission between animals and humans with no direction specified, and 12 studies (26%) did not support transmission [294].

Table 7. Summary of *Escherichia coli* bacterial isolates from foodstuffs and other food-related matrices.

Country	Isolates	Source	Antibiotics Tested	Resistance to [1]	Testing Method	References
China	*Escherichia coli*	RTE food samples (supermarkets & street markets, *n* = 150, from each)	AMP, AMC, CFX, CPZ, CTX, CHL, CIP, GTX, GEN, KAN, NAL, STR, AMK, TET, STX	AMC (80.9%), STX (79.0%), NAL (77.8%), AMP (75.6%), TET (73.1)	Agar diffusion	[295]
USA	*Escherichia coli*	all available brands of retail chicken (*n* = 1367, 88% prevalence) & turkey (*n* = 546, 91% prevalence)	AMK, AMP, SAM, CEZ, CEX, CTX, CIP, GEN, IMP, NAL, TET, STX	AMP (62%), SAM (51%), CEZ (52%), TET (76%). Prevalence is highest in isolates from turkey meat	Kirby-Bauer disk-diffusion	[296]
Qatar	*ESBL-Escherichia coli*	*n* = 456 fecal samples from food handlers	AMP, AMC, GEN, CIP, CHL, TET, TMP, SMZ, CFX	SMZ (33%), AMP (32%), TMP (31%), TET (26%)	E-test & Double Disk Sinergy (for ESBL)	[297]
Egypt	*Escherichia coli* & *hemolytic E. coli* Serotypes: O1, O2, O8, O78, O119, & O126	*n* = 450 hatchlings & *n* = 24 environmental samples per hatchery. Water, broken eggshells, infertile eggs, swabs from the workers' hands, air tunnels, floors, incubators, hatchery machines & egg refrigerators	COL, FOS, GEN, NEO, STR, CHL, ENR, CIP, NOR, FMQ, CDA, AMO, AMP, STX, ERY, SPC, RIF, OXY, DOX	CIP (62.9% environment & 30% hatchlings)	Kirby-Bauer disk-diffusion	[294]
China	*Escherichia coli*	*n* = 431 retail foods. Pork, mutton, fresh milk, duck, beef, chicken, RTE foods, fish & vegetables	AMP, CFX, CZA, GEN, IMP, CIP, LFX, TET, CHL, AMK, PIP, STX, ERY, STR, NAL, PMB	TET (52%), AMP (42%), STX (37%), AMO (33%), NAL (32%)	Kirby-Bauer disk-diffusion	[284]

Iran	*Escherichia coli*	*n* = 350 Pastry cream samples	GEN, STR, NAL, CFM, CHL, CIP, TET, OXA, VAN, PEN	TET, VAN, OXA (100%)	Kirby-Bauer disk-diffusion	[298]
Guadaloupe	ESBL-*Escherichia coli*	*n* = 216 fecal samples from food-producing animals. *n* = 124 pigs, *n* = 75 beef cattle, & *n* = 17 poultry litter.	AMP, AMC, TMC, CFX, CZA, CEX, ERT, GEN, AMK, STR, ENR, NAL, CIP, TET, STX, FOS	Usage in farm: Tetracyclines 100–33%, β-lactams ≤ 54.5, aminoglycosides: ≤45.5%. Resistance: TET (50–82%), AMP (61–100%), STR (46–73%)	Kirby-Bauer disk-diffusion	[289]
Poland	*Escherichia coli* & *Klebsiella* spp.	*n* = 4496 *E. coli* isolates from liver, spleen, heart, and lungs of chickens from commercial farms	AMO, AMC, COL, DOX, ENR, FLO, NEO, NOR, SPC, STX	AMC (73%), DOX (52%), ENR (49%), NOR (45%), FLO (38%)	Broth microdilution	[299]
Emirate of Abu Dhabi	*Escherichia coli*	Isolated from different animal species (camel *n* = 42, sheep *n* = 42, goat *n* = 54, & poultry *n* = 27)	TET, OXY, PEN, AMP, AMO, OXA, CEX, GEN, STX, ENR, CFT	AMP, TET, STX, GEN, ENR (95–83%)	Kirby-Bauer disk-diffusion	[300]
Ethiopia	*Escherichia coli* (54.7% prevalence) & *Escherichia coli* O157:H7 (6.5% prevalence)	*n* = 384 different samples of foods of bovine origin. Carcass swabs (*n* = 162), udder milk (*n* = 146) & milk tank (*n* = 6), yoghurt (*n* = 36) & cottage cheese (*n* = 9), & beef swabs (*n* = 25) from abattoirs, butcher shops & restaurants	AMO, AMP, PEN, OXA, CIP, NOR, ERY, AMK, GEN, KAN, NAL, TET, DOX, STX	PEN, OXA, & VAN (100%), ERY (92%), AMO (40%), TET & AMK (4%)	Kirby-Bauer disk-diffusion	[301]
Sierra Leone	*E. coli* & *Salmonella* spp.	*n* = 100 Samples Fresh Poultry Excreta Used for Vegetable Farming	AMP, CHL, ERY, CEX, PEN, STR, INN, TET	TET, ERY, CEX (100%), AMP (12%)	Kirby-Bauer disk-diffusion	[302]
Bangladesh	Pathogenic *Escherichia coli*	Potato smash & chicken curry, 25 samples each	AMP, ATM, CIP, COL, CHL, GEN, LFX, TET	AMP (91%), COL (52%)	Kirby-Bauer disk-diffusion	[283]
Kenya	*Escherichia coli*	*n* = 105 RTE meat products	AMK, AMP, TET, NFT, NAL, STX, CIP	STX (80%), TET (73%), STR & AMP (67%)	Kirby-Bauer disk-diffusion	[285]
New Zealand	*Escherichia coli*	Aquatic wild foods/"mahinga kai": water, watercress, *Austrovenus stutchburyi*, *Nasturtium officinale* & *Perna canaliculus*	CHL, TET, CIP, TMP, GEN, KAN, AMP, CFX, CZA	AMP, CIP, CHL	Combination disk method	[291]
Bangladesh	ESBL-producing *E. coli*	*n* = 400 meat samples (beef & sheep, 200 each)	STX, CIP, COL, ERY, STR, GEN	STR, ERY, AMP (100%) ESBL (21%) resistant to CFX & CTX	Kirby-Bauer disk-diffusion Double Disk Sinergy (for ESBL)	[303]
Burundi	*Escherichia coli*	*n* = 30 heat-treated fresh milk samples	TET, CIP, AMP, CHL, STX, GEN	Amp (100%), TET (75%), STX (33%)	Kirby-Bauer disk-diffusion	[304]

Mexico	ETEC/UEPC/DAEC	*n* = 189 street foods	TET, CPX, STX, AMP, AMK, PMB, LFX, AMC, GEN	AMC (100%), CPX (45%)	Kirby-Bauer disk-diffusion	[282]
Benin	*E. coli* & *Salmonella* spp.	*n* = 135 table egg pools, *n* = 90 poultry sausages *n* = 81 clinical isolates	CTX, CXM, GEN, STR, TET, NAL, CIP, AMC, CHL, NFT	TET (88%), STR (65%), AMC (55%)	Kirby-Bauer disk-diffusion	[288]
Ethiopia	*E. coli* O157:H7	Fish (*n* = 120) and fish handling equipment	KAN, TET, SMZ, AMP, ERY, STR	AMP, PEN	Kirby-Bauer disk-diffusion	[305]

[1] Numbers in round brackets next to the first antibiotic represent the percentage of resistance reported for the antibiotic for which the strains analyzed showed the most tolerance. If no number is indicated, please assume 100% resistance.

7. *Cronobacter* spp.

The genus *Cronobacter* comprises seven species that are opportunistic pathogenic, Gram-negative, facultative anaerobic, non-spore-forming, bacillus-shaped bacteria. They can cause serious and even fatal infections, affecting infants, immunocompromised patients, and the elderly. In infants, the typical infection can cause meningitis, necrotizing enterocolitis, and bacteremia, and is usually foodborne, whereas in adults, bacteremia and urosepsis are typical and are normally nosocomial [306].

Foodwise *C. sakazakii* has been isolated from various plant- and animal-derived matrices, including confectionery, dried herbs and spices, teas, nuts, pasta, rice, oats, linseed, and cereal products, fresh/frozen produce [306,307], fruits, and powdered infant, follow-up formulas and milk, cheese, and meats (usually powdered foods with low moisture and water activity values). Table 8 provides a detailed account of the prevalence of the bacteria. The work of Sani and Odeyemi, and, more recently, that of Kumar et al., is recommended [308,309].

A pivotal study on *C. sakazakii* in households was conducted in 2012 and demonstrated that the bacterium is not only a relevant foodborne pathogen but is also present in food-related domestic environments. From this study, 76.1% of isolates were resistant to penicillin. Most of the research regarding *C. sakazakii* in foods and its antibiotic resistance profile has been focused on infant formulae. Overall, strains isolated from foods have shown special resistance to β-lactams. For example, Fei et al. [310] found resistance to AMC/AMP with MIC ≤ 8 $\mu g \cdot mL^{-1}$. Similar values were found for isolates from a milk processing facility in Serbia [311]. The EUCAST threshold for assessing AMC is 8 $\mu g \cdot mL^{-1}$. They also found that some strains were tolerant to dryness and osmotic pressure, which has a profound impact on food processing and storage [312,313]. More worrisomely, at least one study has positively identified *C. sakazakii* as an ESBL-producer (e.g., class C β-lactamases) [312,314]. On the other hand, a Brazilian study demonstrated that 94.4% of isolates from infant foods were tested resistant to cefazolin. Additionally, six antibiotic-resistance genes, particularly those encoding efflux pumps, were identified. Pakbin et al. [315] found that isolates from powdered infant formula milk were highly resistant to AMC, AMP, CEX, CFP, ERY, CTX, CIP, and CHL and susceptible to GEN, TET, NOR, and ATM antibiotics. Meanwhile, the $bla_{CTX\text{-}M\text{-}1}$ gene was detected in 96% of the isolates. Previously, the same research group [316] also found a higher prevalence of *C. sakazakii* in bulky imported domestically packaged powdered milk infant formula samples.

Although isolated strains do seem to possess relevant resistant phenotypes, the overall prevalence is relatively low. For example, in an Iranian study of 200 samples (100 infant formula and 100 baby foods), only eight (4%) samples tested positive [317]. However, the sole presence of a few bacteria and their multidrug resistance profile suggests that this pathogen can disseminate resistance genes with relative ease within these food samples [318]. Worrisomely, most reports of *C. sakazakii* have demonstrated multiple drug resistance profiles and biofilm formation in isolates from infant contaminated foods; both bacterial mechanisms result in therapy failure [319]. Biofilms and drug resistance profiles are the primary drivers of chronic, recurrent, and untreatable infections. Together, they cause therapy failure by creating physical, chemical, and genetic barriers that prevent antibiotics from either reaching or eliminating target pathogens [320].

Holý et al. [321] found in their *C. sakazakii* isolates a type IV secretion system-related gene (found on hybrid or cointegrate plasmids, incFIB/incH1 are central components of bacterial conjugation machineries), which plays a pivotal role in bacterial evolution by facilitating the horizontal transfer of genetic material—such as antimicrobial resistance and virulence factors—between bacteria [307,318]. These genes have also been described in *C. malonaticus*, *C. turicensis*, *C. muytjensii*, and *C. universalis* [322]. Several antibiotic target site modification and efflux-related genes have also been identified in *C. sakazakii* isolates (e.g., *mdf*(*A*), which encodes a multidrug efflux transporter, *emrR*, *emrB*, *rsmA*, *cRP*, *adeF*, and *marR* for fluoroquinolones or *fos* genes encoding resistance for fosfomycin) [323–325]. Recently, in a large Chinese study performed by Gan et al. [318], Strains isolated from powdered infant formula and supplementary food collected from 29 provinces exhibited at least 7 antimicrobial resistance genes, which corroborates other findings supporting multidrug resistance. Similarly, Fei et al. [325] also isolated *C. sakazakii* from goat milk-based infant formula from Shaanxi Province, China. From the serotypes found, O2 was the most abundant (n = 15/32, 46.88%) and showed, as well, mostly resistance to antimicrobials such as CEP (87.5%) and AMO (25%). Resistance phenotyping for other *Enterobacteriaceae* can be found in the work by Mardaneh et al. [326]. Recently, Song et al. [327] found, using a proteomics approach, that there is a certain relation between antibiotic tolerance and the production of enterotoxin and hemolysin.

Antibiotic resistance and the production of enterotoxins and hemolysins are critical virulence characteristics in pathogenic bacteria like *S. aureus*, *E. coli*, and *B. cereus*. Bacteria often acquire genes for drug resistance and virulence simultaneously and therefore are often located together on the same genetic elements (e.g., plasmids, transposons, or pathogenicity islands). When bacteria share genetic material, they can spread both traits to neighboring cells [328].

When antibiotics are used, bacteria with resistance genes survive. Because these genes are linked to toxin-producing genes, antibiotic use promotes the survival and proliferation of the most virulent strains. Hence, it appears to be a correlation between multidrug resistance and an increased presence of hemolysin and enterotoxin genes. Strains exhibiting this combination are associated with severe complications and a higher mortality rate in clinical settings [328].

On the other hand, Oloninefa et al. [329] demonstrated that strains with antibiotic sensitivity (to CIP and GEN) were eliminated in culture conditions after 240 min of exposure to the antimicrobials. Hence, those sensitive strains still seem to respond quickly to antibiosis. Interestingly, Capita et al. [330] described that *C. sakazakii* strains increased their resistance profile after treatment with several biocides (e.g., sodium hypochlorite, peracetic acid, benzalkonium chloride) commonly used in food processing equipment cleaning procedures [331,332]. There is also compelling evidence that suggests that antibiotic resistance increases virulence in *Cronobacter* spp. isolates from food [321,333].

Finally, resistance in isolates from clinical cases of neonatal hemorrhagic diarrhea and meningitis has been reported in countries like Mexico and China [322,324,334–336].

Table 8. Summary of *Cronobacter* bacterial isolates from foodstuffs and other food-related matrices.

Country	Isolates	Source	Antibiotics Tested	Resistance to [1]	Testing Method	References
China	*C. sakazakii* (n = 9)	Infant Formula Milk	AMP, TET, VAN, CHL, NOR, CEP, GEN, ERY	VAN (100%), CEP	Kirby-Bauer disk-diffusion	[337]
USA	*C. sakazakii*	Kitchens Surfaces (n = 234/78)	TET, GEN, STR, AMP, KAN, PEN, CHL, CIP, CEF, NAL	PEN (76.1%), TET, CIP, NAL	Kirby-Bauer disk-diffusion	[338]

Egypt	*C. sakazakii* (*n* = 11)	Powdered Infant Formula Milk (*n* = 173), Powdered Infant Foods (*n* = 61), Blood (*n* = 7) & Environmt (*n* = 3)	LFX, NOR, OFX, CIP, NAL, GEN, IMP, CAZ, SXT, ATM, STR, CTX, AMC, CPX, RIF, AMP	RIF (100%), AMP, CPX	Kirby-Bauer disk-diffusion	[339]
Bangladesh	*C. sakazakii* (*n* = 6)	Assorted foods (*n* = 54)	VAN, CIP, NFT, CHL, PEN, TET, AMP, IMP, DOX, NEO, AMK, GEN	PEN (100%), AMP, IMP, NEO	Kirby-Bauer disk-diffusion	[312]
Iran	*C. sakazakii*	Infant Formula & Baby Foods (*n* = 200)	TIG, TET, TIC, CHL, CZA, CIP, CFP, IMP, LFX, MIN, PIP, TZP, CAB, TMP, STX, MFX, GEN, COL, AMP, AMO, ATM, CFX, AMK, STR, MEM, MEZ, NAL	AMO, TIG, TIC, ATM, CZA	Kirby-Bauer disk-diffusion	[317]
China	*C. sakazakii* (*n* = 66) & *C. malonaticus* (*n* = 4)	Powered Infant Formula & Processing Environment	AMK, AMC, AMP, ATM, CFX, CZA, CFP, CHL, CIP, COL, GEN, IMP, LFX, MEM, MFX, PIP, TZP, TET, STX	AMC (100%), AMP, CEZ	BD Phoenix™ 100 Automated Microbiology System	[310]
Iran	*C. sakazakii* (*n* = 9)	Powdered Infant Formula Milk (*n* = 125)	AMO, AMP, ATM, CFX, CZA, IMP, MEM, MEZ, TIC, MFX, NAL, STR, GEN, AMK, TET, CHL, LFX, CIP, CFP, MIN, PIP, TZP, CAB, TMP, STX, TIG, COL	CFX (77.8%), MEZ, STR, MIN, TMP, TIG	Kirby-Bauer disk-diffusion	[326]
Brazil	*C. sakazakii* (*n* = 44)	Powdered Infant Cereals (*n* = 11)	AMO, COL, CIP, CHL, ENR, GEN, STR, MEM, STX, TET, CEZ, CPD	CEZ (6.81%), AMO, STX, CFP	Kirby-Bauer disk-diffusion	[340]
Brazil	*Cronobacter* spp. (*n* = 72)	Infant Formulas (*n* = 77) & Cereals (*n* = 75)	AMO, ENR, CIP, CHL, GEN, STR, MEM, STX, TET, CEZ, CPD	CEZ (94.4%), AMO, CED, STR, STX	Kirby-Bauer disk-diffusion	[323]
Nigeria	*C. sakazakii*	Powdered Infant Formula	AMO, AMC, ERY, TET, GEN, CLX, STX, CHL, CIP, STR	CHL, AMO, AMC, ERY, TET, CLX, STX	Kirby-Bauer disk-diffusion	[329]
Iran	*C. sakazakii* (*n* = 6)	Imported and Domestic Powdered Milk Infant Formula (*n* = 118)	TET, LFX, AMC, AMO, CHL, IMP, CIP, CFP	AMP & AMO (100%), CIP & TET (intermediate)	Kirby-Bauer disk-diffusion	[316]
Iraq	*C. sakazakii*, *C. malonaticus*, *C. Dublinensis*	Powdered Infant Formula (*n* = 130), Spices & Herbs (*n* = 55) & Bouillon Flavoured Powder (*n* = 50)	AMP, CHL, CEP, ERY, GEN, KAN, NAL, STR, TET, NOR	CEP (66%), KAN, STR, ERY, NOR	Kirby-Bauer disk-diffusion	[341]
Serbia	*C. sakazakii* (*n* = 15)	Milk Powder Processing Facility (*n* = 100)	TZP, AMC, SAM, MEM, CFX	AMC (7%)	Epsilometer test (Etest)	[311]
China	*C. sakazakii* (*n* = 1048 infant supplementary food & *n* = 7 powdered infant formula	Powdered infant formula and supplementary food (*n* = 12,105)	PEN, AMP, SAM, CTX, CAZ, IMP, GEN, KAN, TET, CIP, NAL, SXT, CHL		Biofosun Gram-negative panels by the broth dilution method	[318]

Iran	*C. sakazakii* (*n* = 25)	Powdered Infant Formula Milk (*n* = 364)	NAL, CEX, AZM, STR, AMC, IMP, KAN, AMO, NOR, AMP, TET, CFP, GEN, COL, CHL, ERY, CTX, CIP	AMC, AMO, AMP, CEX, CFP, ERY, CTX, CIP, CHL	Kirby–Bauer disk diffusion	[315]
Mexico	C. *sakazakii* (*n* = 7), *F. helveticus*	Powdered and dairy formulas	CAZ, CTX, AMO, AMC, CIP, CEP, NAL, GEN, TET, CHL, AMP	CEP (71.4%), NAL, AMP	Kirby–Bauer disk diffusion	[324]
Czech Republic	*C. sakazakii* (*n* = 15)	Food (*n* = 997), milk-producing environments (*n* = 855), & feces from live poultry (*n* = 148)	AMP, AMC, CZA, CIP, CHL, CFP, GEN, CEP, TET, NAL	CEP (93%), AMP, TET, CFP, AMC	Kirby–Bauer disk diffusion	[321]
China	*C. sakazakii* (*n* = 35)	Powdered Infant Formula and Processing Environment	AMP, PIP, CEZ, CMX, CZA, CTX, CPZ, AMK, GEN, KAN, NEO, TET, DOX, ERY, NOR, OFX, CIP, PMB, STX, CHL	ERY (100%), STX, NEO, CEZ, KAN, CTX, AMK, AMP, CZA, CXM, PMB, GEN, NOR, PIP	Kirby–Bauer disk diffusion	[342]
China	*C. sakazakii* (*n* = 96)	Infant Formula Powder & Processing Environment	AMP, PIP, CAB, CEZ, CXM, CZA, CTX, CPZ, AMK, GEN, KAN, NEO, TET, DOX, ERY, MDY, NOR, OFX, CIP, CHL, PMB, VAN, STX, LIN	ERY (100%), MDY, VAN, LIN	Kirby–Bauer disk diffusion	[327]
Iran	*C. sakazakii* (*n* = 2/14 suspected)	Raw milk and Instant Formula (*n* = 120 raw, 60 powdered milk samples)	ERY, GEN, CHL, AMP, NEO, AMO, TET, CIP, SMZ	ERY (100%), AMP, AMO, TET	Kirby–Bauer disk diffusion	[343]

[1] Numbers in round brackets next to the first antibiotic represent the percentage of resistance reported for the antibiotic for which the strains analyzed showed the most tolerance.

8. Conclusions

Continuous use of an antibiotic that has reached the end of therapeutic usefulness, due to propagated or widespread resistance among bacteria, will only conserve the selective pressure and favor further phenotypic resistance. Consequences of the overuse of antibiotics, even after years of regulatory restrictions and efforts to reduce their application, are still visible today (e.g., overall resistance toward tetracyclines in *Campylobacter*). Recent cumulative findings reinforce that, despite some efforts [344], antibiotic resistance within pathogen species is increasing. The data herein are in line with current predictions, which set *E. coli* and nontyphoidal *Salmonella* resistance for β-lactams (often producing Extended-Spectrum Beta-Lactamases, which are resistant to critical, last-resort antibiotics), sulfonamides, and tetracyclines above 50% in most African, Asian (e.g., China), and American (e.g., Brazil, Chile) territories [345]. Foodborne pathogen contamination *per se* is a worrisome health issue that requires constant surveillance programs and allocation of resources, but disseminated antibiotic resistance among these bacteria exacerbates the problem as therapeutic options to fight infections caused by these microorganisms become more limited. This is especially true since a significant percentage of isolates are resistant to three or more antibiotic classes. Some crucial food industries deserve a closer look in terms of pathogen monitoring and inspection (e.g., Infant powdered milk products for *Cronobacter*, minced or ground bovine beef for *Staphylococcus*, raw milk/dairy for *Listeria*, or the poultry industry for *Campylobacter* and *Salmonella*) as they seem to be hotspots for multidrug-resistant bacterial proliferation and transmission. Resistant strains often originate in animal gut microbiota (often due to farm antibiotic usage) and transfer to humans through contamination

of meat, vegetables, or water. These foodborne pathogens can cause severe, antibiotic-resistant infections, limiting therapeutic options in clinical settings. Nevertheless, despite its relevance, we see few surveillance efforts regarding bacterial contamination and drug resistance within animal feed, an issue that should be addressed, especially in pet foods, considering the proximity of pets to their owners. In this respect, the One Health approach should be the go-to tool for preventing bacterial food contamination throughout the food chain. Food safety-wise, transmission pathways of antimicrobial-resistant bacteria can be diminished by proper handling and cooking of raw meat (especially poultry) to prevent cross-contamination. Also, for some particular foods, ensuring a continuous cold chain and proper refrigeration is a must.

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Informed Consent Statement

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